Fast-growing short-rotation trees are a promising fuel source for developing bioenergy markets in the Southeast U.S. Species tested in Short Rotation Woody Crop (SRWC) systems are evaluated primarily on their sustainability and competitiveness of biomass production. The potential of *Populus* as a SRWC in the Southeast U.S. warrants the testing of genotype variation in performance and site adaptability. Furthermore, future improvements in productivity necessitate a better understanding of their physiological basis of yield.

Phenotypic variation, genotype by environment (GxE) interaction, heritability for growth, and disease incidence were examined in two-year-old trees of 52 *Populus* genotypes on a site in Raleigh, North Carolina and in Columbus, Mississippi. Diameters and heights were measured after the second growing season and stem volume and biomass were calculated. High genotypic variation in growth traits and disease incidence was observed among the 52 genotypes. The highest productivity rate observed among genotypes was 35.7 m$^3$ ha$^{-1}$ year$^{-1}$. The growth trait with the least amount of residual error was height, which ranged from 2.0-3.5 m yr$^{-1}$ in Raleigh and 1.5-3.9 m yr$^{-1}$ in Columbus. Heritability of genotype-means were relatively moderate in Columbus and Raleigh, and by site ranged from 0.56-0.81 for height, 0.41-0.61 for DBH, and 0.43-0.66 for volume, respectively. We observed significant GxE interactions for DBH and volume, but not for height. However, plasticity of individual genotypes was apparent for all growth traits due to the difference in rank between sites. Disease incidence of *S. musiva* was higher in NC than MS, affecting hybrid genotypes more severely than pure *P. deltoides* genotypes. Evaluating GxE
interactions and disease effects on genotype growth throughout plantation development is important for determining the long term sustainability of *Populus* genotypes in the Southeast U.S.

At the Raleigh, NC site, six *P. deltoides* clones and three hybrid poplar clones were selected to examine the contribution of leaf area and light interception dynamics on stem biomass accumulation. During the summer of the second year after establishment, stem growth was measured from June 24 to August 11 and examined in relation to light interception and light-use efficiency. Total tree leaf area was estimated allometrically using branch-level measurements. For both leaf area and mass, branch diameter was the best overall predictor, with additional improvements made by including branch height and clonal taxon to the equation. Overall, hybrids had higher leaf area due primarily to high branch leaf area, and a larger number of branches per tree. Together, intercepted photosynthetically active radiation (IPAR), and light-use efficiency (LUE) defined as the stem dry matter produced per MJ of IPAR, explained a large amount of the variation in stem growth ($R^2 = 0.99$); IPAR being the main determinant in stem growth, while LUE was more weakly related.
Growth and Leaf Area Dynamics of Short-Rotation Populus Genotypes

by
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A thesis submitted to the Graduate Faculty of
North Carolina State University
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DEDICATION

This thesis is dedicated to my parents, David and Wrenn Thomas. Your love and support is a constant encouragement. Thank you for inspiring me.
BIOGRAPHY

Nathan Thomas is the 2\textsuperscript{nd} child out of four children of Mr. David and Mrs. Wrenn Thomas. He grew up in several European countries before moving to attend NC State University where he received a Bachelor of Science degree in Forest Management in 2014. While pursuing his undergraduate he travelled abroad to gain research experience in forest plantation systems. In the fall of 2014, he pursued a Master of Science degree in Forestry with a focus on short-rotation \textit{Populus} growth and leaf area dynamics.
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INTRODUCTION

On the west coast of the U.S., the first commercial poplar plantation was established in Oregon in the late 1800s (Anonymous, 1952). A few decades later, eastern cottonwood was established in Ohio by Mead Corporation (Bearce 1918). Poplar would become known as the fastest growing temperate climate species, and as research in poplar genetics advanced, large gains in biomass yield were made through clonal hybrid crosses (Dickmann 2006; Heilman & Stettler 1990). Today, poplar plantations are distributed primarily in three areas: 17,000 ha of hybrid poplar in the Pacific Northwest, 10,000 ha of hybrid poplar in the Lake States, and 11,000 ha of eastern cottonwood in the Mississippi River Valley (Zalesny et al. 2011). Outside of the Mississippi River Valley, information about poplar in the Southeast has been relatively limited until recently. However, the evolving bioenergy market and its potential in the Southeast have created interest in poplar as a SRWC (Coyle et al. 2006; Luxmoore et al. 2008; Ghezehei et al. 2015). Known as the “wood basket” of the U.S., the Southeast has an established forest plantation economy and supporting infrastructure (Hinchee et al. 2009). The region has an experienced workforce, and private landowners and policy makers who are supportive of sustainable, highly-intensive forest operations. The Southeast region might also have the largest available land base for the production of SRWCs (Tuskan 1998).

The challenges of creating a renewable biomass industry warrant the deployment of clonal trials throughout the region, in order to supply an environmentally sustainable and economically competitive supply of biomass (Kells & Swinton 2014; Englund et al. 2012). Furthermore, future improvements in poplar productivity necessitate a better understanding of their physiological basis of yield (Cannell et al. 1988). The remainder of this thesis
contains two chapters. Chapter 1 investigates the phenotypic variation, GxE interactions and heritability for growth, and disease incidence, in two-year-old trees of 52 Populus clones on a site in the Piedmont of North Carolina and in mid-east Mississippi. Chapter 2 examines the contribution of leaf area and light interception dynamics on stem biomass accumulation in nine clones at the North Carolina site.
Chapter 1 - Genotypic Variation and Genotype by Environment (GxE) Interactions of 52 Populus Genotypes on two Sites in the Southeast US.

ABSTRACT
Genotypic Variation and Genotype by Environment (GxE) Interactions of 52 Populus Genotypes on two Sites in the Southeast US.

The demand for increased bioenergy production is a response to current dependence on non-renewable energy resources. Species tested in Short Rotation Woody Crop (SRWC) systems are evaluated primarily on their sustainability and competitiveness of biomass production. The potential of Populus as a SRWC in the Southeast U.S. warrants the testing of genotype variation in performance and site adaptability. This study investigates the phenotypic variation, genotype by environment (GxE) interaction, heritability for growth, and disease incidence, in two-year-old trees of 52 Populus genotypes on a site in Raleigh, North Carolina and in Columbus, Mississippi. Diameters and heights were measured after the second growing season and stem volume and biomass were calculated. High genotypic variation in growth traits and disease incidence was observed among the 52 genotypes. The highest productivity rate observed among genotypes in stem volume was 35.7 m$^3$ ha$^{-1}$ year$^{-1}$. The growth trait with the least amount of residual error was height, which ranged from 2.0-3.5 m yr$^{-1}$ in Raleigh and 1.5-3.9 m yr$^{-1}$ in Columbus. Heritability of genotype-means were relatively moderate in Columbus and Raleigh, and by site ranged from 0.56-0.81 for height, 0.41-0.61 for DBH, and 0.43-0.66 for volume, respectively. We observed significant GxE interactions for DBH and volume, but not for height. However, plasticity of individual genotypes was apparent for all growth traits due to the difference in rank between sites. Disease incidence of S. musiva was higher in Raleigh than Columbus, affecting hybrid genotypes more severely than pure P. deltoides genotypes. Evaluating GxE interactions and
disease effects on genotype growth throughout plantation development is important for determining the long term sustainability of *Populus* genotypes in the Southeast U.S.

**Introduction**

*Renewable Bioenergy*

International demand for bioenergy production is a response to policies that advocate reduced dependence on non-renewable energy resources (Cornelissen et al. 2012). Recent policy goals in the United States, driven by energy independence and security concerns, are aimed at transitioning from fossil fuels and corn-based ethanol to other energy sources (Dale et al. 2011). The Renewable Fuel Standard (RFS2) requires that the United States produce 136 billion liters of renewable biofuel by 2022, which was put into law by the Energy Independence and Security Act (EISA 2007). Furthermore, Congress has mandated that 79 billion liters must come from advanced biofuels (EISA 2007). Advanced biofuel has been defined as renewable biomass, other than ethanol derived from corn starch, which reduces baseline lifecycle greenhouse gas emissions by at least 50 percent. The production of an environmentally sustainable and economically competitive supply of biomass presents numerous challenges central to the development of a renewable biomass industry. (Kells & Swinton 2014; Englund et al. 2012).

*Poplar as a SRWC*

Trees grown under short rotation woody crop (SRWC) systems are promising feedstocks for bioenergy. There are many potential SRWC species being evaluated for their potential to supply the biomass needed for bioenergy production. Some have high potential across the
United States, while other species may be viable options only in certain regions. Varying environmental, economic, and climatic conditions interact to determine the feedstock species best suited for each region (Dale et al. 2011). *Populus* possesses several biological characteristics that make it a desirable option for SRWC systems. This genus has the fastest growth rates in the northern-temperate climate and is easily propagated by non-rooted cuttings (Dickmann 2006). The ability to coppice then exhibit vigorous growth after stem harvest is a key trait for successful short-rotation, coppice systems (Kauter et al. 2003). Worldwide, there are 29 species within the genus *Populus*, with 12 species occurring naturally in North America (Zalesny et al. 2011). These native species cover large distributional ranges and possess a substantial amount of genetic variation (Sannigrahi et al. 2010). Some native species will spontaneously hybridize with each other (Miermans et al. 2010) and artificial hybridization can result in improved site adaptability, pest resistance, and biomass qualities (Anderson et al. 1983). Interspecific hybrids have shown the potential for hybrid vigor and a substantial increase in stem volume (Ceulemans et al. 1992).

**G x E interaction of Poplar Genotypes**

Differential performance of genotypes across regions or sites is known as genotype by environment (GxE) interactions. Consequently, GxE interactions that result in genotypes that display high vigor and adaptability to a given site make potential candidates for SRWCs. Identifying and matching compatible genotypes and sites increases yield and is crucial to achieving maximum growth potential (Ceulemans & Deraedt 1999). These interactions can be the result of numerous environmental factors such as precipitation, temperature, and soil characteristics. In the Southeast U.S., poplar GxE interactions have mainly been tested in Mississippi, where eastern cottonwood is grown commercially (Robison et al. 2006). In
order to exploit GxE interactions in the Southeast, there is a need to better understand the amount of influence these interactions have on yield. This effort requires the establishment of genotypes across a wide range of sites to examine the various GxE interactions across a region (Hansen 1991). Certain genotypes are fairly site specific, only displaying vigor in their “niche” environment. Alternatively, many breeding efforts focus on selecting “general performers” that express good general adaptation across a range of sites (Matheson & Cotterill 1990). However, there can be a loss of potential gain on specific sites by breeding for general adaptation instead of specific adaptation (Matheson & Raymond 1984).

The potential of poplar as a SRWC in the Southeast U.S. led to the installment of numerous clonal trials throughout the region (Coyle et al. 2006; Luxmoore et al. 2008; Shifflett et al. 2014; Ghezehei et al. 2015; Helton et al. 2015). This study investigates the phenotypic variation, GxE interactions and heritability for growth, and disease incidence, in two-year-old trees of 52 Populus genotypes on a site in the Piedmont of North Carolina and in mid-east Mississippi.

**Materials and Methods**

*Site description*

The two sites were planted in March 2014. One site was located at the Horticultural Field Laboratory, North Carolina State University in Raleigh, North Carolina (35.79°N, 78.70°W). The other site was near Columbus, Mississippi (33.36°N, 88.31°W) on a former agriculture field. Raleigh is located on the eastern edge of the Piedmont of North Carolina, and Columbus is located in the Black Prairie region near the Mississippi-Alabama border. Both
sites are in a humid, subtropical climate characterized by hot summers and chilly, mild winters. Raleigh has an average annual temperature and precipitation of 16°C and 1183 mm, respectively; whereas, in Columbus, the annual averages are 17.5°C and 1448 mm, respectively. The plant hardiness zones are 7b (-15°C to -12.2°C) for Raleigh and 8a (-12.2°C to -9.4°C) for Columbus (USDA Plant Hardiness Zone Map 2012). The elevation is 143 m at the Raleigh site and 62 m at the Columbus site. The soil type at each site is listed as, Raleigh: Cecil gravelly sandy loam; and Columbus: Caledonia silt loam (Soil Survey Staff, Natural Resources Conservation Service, USDA).

Both sites were prepared during the first week of March, with shallow soil ripping to 20 cm deep and 18.3 mL per hectare of pre-emergent herbicide (Oust®). Triple superphosphate (TSP) (0-45-0) was applied at Raleigh in late April, 2015, but not in Columbus. Soil analyses of neighboring two-year old poplar stands at Columbus found high to very high phosphorus levels. Weeds were controlled at both sites using glyphosate, however with different outcomes. There was no observed herbicide damage in Raleigh, but substantial mortality was observed in Columbus after herbicide application in July. The presence of cottonwood leaf beetles (CLB) in Raleigh required insecticide (Sevin®) applications in May and July, but no insecticide applications were needed in Columbus.

Experimental design

The experiment was a randomized, complete-block design, with 8 blocks in Raleigh and 10 blocks in Columbus and one ramet of each clone in each block. The study consisted of clones from three species combinations: Populus deltoides (Bart. Ex Marsh), Populus trichocarpa (Torr. & Gray), and Populus maximowiczii (A. Henry). Of the 52 genotypes,
there were 43 that derived from crosses of *P. deltoides x P. deltoides* (DD), six from *P. trichocarpa x P. deltoides* (TD), and three from *P. deltoides x P. maximowiczii* (DM). All genotypes were provided by ArborGen Inc., Summerville, SC. Non-rooted, 33-38 cm cuttings were soaked in water overnight and planted at a spacing of 1.52 x 1.52 m (4328 TPH) in Raleigh and 2.92 x 0.91 m (3776 TPH) in Columbus. A single border row was installed around each site.

*Data collection and Analysis*

Stem height and diameter were measured after the first and second growing seasons. Diameter at breast height (DBH) was measured with a diameter tape to the nearest millimeter. Height was measured to the nearest centimeter using a telescopic height pole. Main stem outside-bark volume was estimated using a model developed through destructive harvesting of *P. deltoides* in the alluvial floodplain of the Lower Mississippi Valley (Shelton et al. 1982):

\[
Volume = 8.65 + (0.03 \times DBH^2 \times Height)
\]

where, volume is in dm³, DBH is in centimeters, and height is in meters.

At the end of the second growing season, all trees were rated for *Septoria musiva* (Peck) (Teleomorph=*Mycosphaerella populorum* (Thompson)) incidence on both sites. The trees were scored on a 0 – 2 scale to characterize canker severity where: 0 = no cankers, 1 = few and small cankers, and 2 = numerous or large cankers.

Statistical analysis of all traits was conducted on the two sites individually and then combined. In the individual site analysis, two similar variations of mixed linear models were used to test the effect of genotype on all responses. A mixed linear model (PROC MIXED) tested the genotype and taxon effect on the continuous variables of DBH, height, and
volume; whereas, a generalized linear mixed model (PROC GLMM) tested the genotype and taxon effect on the discrete variables of disease incidence and survival. The COVTEST option was used to generate Z statistics. Genotype and Block were both treated as random effects, whereas taxon was treated as fixed. A $\alpha=0.05$ significance level was used to test all hypotheses. All analyses were performed in SAS 9.4 (SAS Institute, Cary, NC, USA).

The two sites were analyzed jointly to obtain the total phenotypic variance and heritability values, and to strengthen the model by increasing the number of repetitions and environments. This model also included GxE interactions, which were tested by conducting the analysis of variance in PROC MIXED with the full model including the GxE interaction term, and then with a reduced model without the GxE interaction term. The likelihood ratio test (LRT) statistic was calculated to determine whether the GxE interaction term added significant value to the model. In order to control for the large difference in residual variation between the sites, the LRT statistic was also used to test whether partitioning the residual variance by site would improve the full model. The model treated the genotype, GxE, block, and residual variance (error) as random. The site and taxon effects were considered fixed. The six TD hybrids and three DM hybrids were analyzed together as one taxon and the 43 $P. \text{deltoides}$ were another taxon. The response traits tested were DBH, height and volume. The full model was written as:

$$Y_{ijklm} = \mu + G_i + S_j + T_k + GS_{ij} + B(S)_{l(j)} + e_{ijklm}$$

where $Y_{ijklm}$ is the $l^{th}$ observation of the $i^{th}$ genotype, $j^{th}$ site, $k^{th}$ taxon, and $l^{th}$ block; $\mu$ is the overall mean; $G_i$ is the random genotype effect; $S_j$ is the fixed site effect ($j=1,2$); $T_k$ is the fixed taxon ($k=1,2$); $GS_{ij}$ is the random $i^{th}$ genotype by $j^{th}$ site interaction; $B(S)_{l(j)}$ is the random $l^{th}$ block effect within the $j^{th}$ site; and $e_{ijklm}$ is the random residual term of the $l^{th}$
observation. The residual variance is heterogeneous (block diagonal), meaning that each site has a different residual variance for the traits.

The variance component estimates generated by the model were used to calculate the broad-sense heritabilities for height, DBH, and volume at each site. Heritability was calculated on a genotype-mean basis:

\[ H_G^2 = \frac{V_G}{V_P} = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_G^2 + \hat{\sigma}_{GE}^2 + \hat{\sigma}_e^2} \]

where \( V_G \) is the total genetic variation of the genotype effect, which is represented by the genotype variance component, and \( V_P \) is the total phenotypic variance, represented by the sum of the genotype, GxE, and error variance components. The number of environments is represented by \( e \) and the mean number of reps per genotype is represented by \( r \). To calculate the standard error of the \( H^2 \) estimate, the square root of the variance was taken using the delta method (Holland et al. 2002).

\[ SE_{H^2} = \frac{1}{(\hat{\sigma}_p^2)^2} \sqrt{\left( \frac{\hat{\sigma}_{GE}^2 + \hat{\sigma}_e^2}{\hat{\sigma}_p^2} \right)^2 \hat{V} (\hat{\sigma}_G^2) + \hat{V} (\hat{\sigma}_G^2) + \hat{V} (\hat{\sigma}_G^2) + 2\hat{C} (\hat{\sigma}_{GE}^2, \hat{\sigma}_e^2)} \]

-2\hat{\sigma}_G^2 (\hat{\sigma}_{GE}^2 + \hat{\sigma}_e^2) [\hat{C} (\hat{\sigma}_G^2, \hat{\sigma}_{GE}^2) + \hat{C} (\hat{\sigma}_G^2, \hat{\sigma}_e^2)]

The estimated Variance (\( V \)) and Covariance (\( C \)) of the estimates were generated by the SAS output in the Asymptotic Covariance Matrix of Estimates by adding the ASYCOV option to the PROC MIXED statement.

**Results**

**Survival**

High mortality at Columbus resulted in a large difference in survival between Raleigh (98%)
and Columbus (46%) (Table 1.1). In Columbus, the survival rate varied by genotype 
(p=0.0107) and the taxon (hybrid or P. deltoides) of the genotype (p=<.0001). The survival 
probability of a hybrid genotype was 80% compared to 39% for P. deltoides genotypes, using 
least-square means. Within the 43 P. deltoides genotypes, excluding the 9 hybrids, genotype 
did not significantly affect survival (p=0.2452). The survival rate among genotypes in 
Raleigh varied little (SE=3.20%); however, genotype still had a significant effect on survival 
(p=0.0121), whereas the taxon did not (p=0.6550) (Table 1.2).

*Growth and disease by site*

After two growing seasons, the mean diameters, heights, and volumes across all the 
genotypes were similar between the sites (Table 1.1). There was no significant difference 
between the overall genotype mean volume in Columbus (13.63 ± 3.62 dm³) and Raleigh 
(13.11 ± 1.24 dm³); however, the variation of volume among genotypes was almost three 
times higher in Columbus than in Raleigh. The same trend was also seen for DBH and 
height (Table 1.1). The best growing genotype in Columbus had 2.3 times more volume than 
the worst (20.49 dm³ and 8.88 dm³, respectively). There was less variation in growth among 
the best and worst genotypes in Raleigh (17.98 ± 3.98 dm³ to 10.02 ± 0.62 dm³, respectively). 
Consequently, the best growing genotypes in Columbus greater volume than the best 
genotypes in Raleigh, and the worst genotypes in Raleigh had greater volume than the worst 
genotypes in Columbus (Fig. 1.1).

At Raleigh, there was a significant genotype effect on the occurrence of *S. musiva* 
(p=0.0213), but no significant difference between taxon (p=0.5000) (Table 1.2). Genotype 
also significantly affected the growth traits of diameter, height, and volume (each p<0.0001).
For height, 17 of the genotype means were significantly different from the overall genotype mean. Eight of these genotypes were higher and nine were significantly lower (Fig 1.2). Twenty-one genotypes had diameters that were significantly different from the overall genotype mean (thirteen higher and eight lower) (Fig 1.3). Volumes of 20 genotypes were significantly different from the overall genotype mean (eight higher and twelve lower) (Fig 1.4). All of these growth traits had significant differences between taxa, with hybrids consistently outperforming *P. deltoides* genotypes.

The variation caused by genotype in Columbus yielded similar results for disease, but a somewhat different response on growth traits. Both genotype (p<.0001) and taxon (p<.0001) had significant effects on *S. musiva* severity. The mean canker severity was 0.02 for *P. deltoides* and 0.91 for hybrids. For growth traits, there was a significant genotype effect on height (p=0.0048), with five clones having heights significantly greater than the overall genotype mean (Fig 1.5). Unlike Raleigh, the tests found no significant genotype effect on diameter (p=0.0534), due to the large amount of within-genotype variation (Fig 1.6). However, there was high genotypic variation for volume (p=0.0112), (one higher and seven lower) (Fig 1.7). There was also a significant taxon effect on height (p=0.0109), but not on diameter (p=0.4166) or volume (p=0.7270).

*Joint site analysis on genotypic effects and broad-sense heritability of growth*

The sites were analyzed together to determine heritabilities and test the significance of the GxE effect. The heterogeneous residual variance resulted in significantly better goodness of fit for estimating DBH, height, and volume (p<.0001), so the model analyzed each site with a different residual variance for the traits. All traits had high genotypic variation and there
were significant differences between *P. deltoides* and hybrid genotypes, particularly in *S. musiva* incidence and survival rate (Table 1.4).

The genotypes in Raleigh exhibited relatively high broad-sense heritability values of 0.81, 0.61, and 0.66 for height, DBH, and volume, respectively (Table 1.5). The heritability of genotypes in Columbus yielded lower values of 0.56, 0.41, and 0.43 for height, DBH, and volume, respectively. Columbus exhibited a much lower percentage of phenotypic variation explained by genotype and a much higher percentage explained by the residual error. Height had the highest heritability of all traits and the smallest percentage of residual error variance for both sites.

*Genotype by Environment interactions*

To analyze the importance of GxE interaction effects between the two environments, the model was run with and without the GxE term for DBH, height, and volume. The log likelihood ratio test generated chi-square values of 6.8 for DBH (*p* = 0.0046), 2.4 for height (*p* = 0.0607), and 4.6 for volume (*p* = 0.0160). Thus, the addition of the GxE interaction term resulted in significantly better goodness-of-fit for modeling DBH and volume, but it did not explain variation in height. So, although the overall values of genotype-mean volume between Raleigh (13.11 dm³) and Columbus (13.63 dm³) were relatively similar (Table 1.1), there were large individual genotype differences in volume between the two sites (Fig 1.8). A small contrast can be seen between the high GxE effect on DBH (Fig 1.9) and the non-significant GxE effect on height (Fig 1.10) by observing the individual genotype deviations from the relationship. Table 1.3 summarizes the height response in terms of rank for the 10 most productive genotypes at each site. Among these top genotypes was a mixture of responses based on performance at the two sites. For example, genotype 8019 was
consistently productive on both sites, whereas genotype 114 was well adapted for Columbus but a poor fit for Raleigh. The GxE interaction variance components of growth traits ranged from 3-19% across sites (Table 1.5).

**Discussion**

**Survival**

Our results show a considerable difference in survival between sites. Raleigh is an example of the high potential of poplar establishment and survival, in contrast to the lower survival rate at Columbus. The main impact of high mortality at Columbus was a substantial decrease in sample size of specific genotypes and the effect of increased spacing on growth. Several studies have reported overall high clonal survival rates (Kaczmarek et al. 2014; Tharakan et al. 2001) however, clonal trials oftentimes have lower survival rates with high variability among clones (Abrahamson et al. 1990; Ghezehei et al. 2015; Paris et al. 2011). While significant genotypic variation in survival rate was observed at Columbus, it can be attributed mainly to genotype taxon. The nine hybrid genotypes exhibited a much higher survival rate and, within the *P. deltoides* taxon, there was no significant variation in survival among genotypes (p=0.2452). Other clonal studies have also found significantly higher survival rates of hybrids compared to pure *P. deltoides* clones in the Southeast U.S. (Coyle et al. 2006; Shifflett et al. 2014). Potential root-shoot ratios in *P. deltoides* can vary depending on the proportion of the cutting planted aboveground (Kaczmarek et al. 2014). Rooting in *P. deltoides* can also be low in some circumstances (Randall & Krinard 1977). Adaptability to the site is another possible cause of mortality and the difference in planting crews for each site may have led to differences in planting methods. However, the main cause of mortality
was apparently due to excessive weed competition at Columbus and the resulting damage from herbicide treatment.

**Growth and disease by site**

Reported yields of poplar vary greatly because of the different conditions that can influence growth in experimental trials. However, the majority of studies report values that fall into the range of 10-25 Mg ha\(^{-1}\) year\(^{-1}\) (Wang et al. 2013; Ceulemans et al. 1999). Using a dry wood poplar density of 416.7 kg m\(^{-3}\) (World Agroforestry Centre 2012), this is equivalent to 23 - 60 m\(^{3}\) ha\(^{-1}\) year\(^{-1}\). Based on survival and growth, the mean volume increment of genotypes over two growing seasons was 16.3 – 35.7 m\(^{3}\) ha\(^{-1}\) year\(^{-1}\) at Raleigh; comparable to the range of reported values. The effect of within-stand competition was likely increased due to the single tree design, resulting in the large range in yields between the best and worst clones. Our height results compared favorably to those reported by a poplar clonal study located in the upper North Carolina Piedmont and Blue Ridge Mountains (Ghezehei et al. 2015). These sites included 11 of the same genotypes that were tested in our study, but were purposefully planted on marginal lands at higher elevations. Also, these sites were not planted as single tree studies. As expected, the range of mean heights observed in Raleigh (2.0-3.5 m yr\(^{-1}\)) and Columbus (1.5-3.9 m yr\(^{-1}\)) were greater than those reported at the mountain (1.6-2.5 m yr\(^{-1}\)) and Piedmont (1.8-3.1 m yr\(^{-1}\)) sites.

A combination of environmental and site management conditions resulted in Columbus having the highest and lowest genotype yields, contrasting with a more uniform genotype yield across the Raleigh site (Fig 1.1). Although, genotype mean yields in Columbus had a greater range, genotypic variability for DBH was not significant. Aside from this, the results corroborate previous reports of high genotypic variation in yield.
(Verlinden et al. 2015; Ceulemans et al. 1992). The low genotypic variability in DBH in Columbus was largely due to the high within-genotype error explained by the lower number of surviving trees per genotype. However, this does not explain why Columbus showed high variation in genotype for height but not for DBH. Spatial variability in Columbus caused by mortality could explain this response. Spacing has been shown to have a much greater effect on diameter compared to its effect on height (Kirongo et al. 2012). This could explain why genotypic variability in height was significant, whereas the genotypic variability in diameter was obscured by the spatial variability. Therefore, height would be the best trait to determine genotype variation. Consequently, because volume is partially a function of height, the genotypic variation in volume was also significant.

Our study found that hybrids outperformed *P. deltoides* genotypes for all growth traits at year two after establishment. Other studies in the Southeast have reported superior hybrid (TD) growth (Shifflett et al. 2014) and no difference between *P. deltoides* and hybrid (TD) growth at year one (Ghezehei et al. 2015). At year three, Coyle et al. (2006) reported greater growth of *P. deltoides* genotypes compared to hybrid genotypes. In Missouri, Pallardy et al. (2003) and Dowell et al. (2009) found that growth of *P. deltoides* Bartr x *P. nigra* L. hybrid genotypes equaled or surpassed that of *P. deltoides* genotypes early in the rotation. However, by five years old, *P. deltoides* genotypes generally had greater growth.

Our results showed that *P. deltoides* genotypes were significantly less susceptible to *S. musiva* than the hybrid genotypes, confirming previous reports (Ostry & McNabb 1985). Significant genotypic variability in response to *S. musiva* also existed within the *P. deltoides* taxon. However, even though *S. musiva* may exist on *P. deltoides*, it is very rarely associated
with serious damage, whereas *P. trichocarpa* and TD hybrids are both more seriously affected (Ostry & McNabb 1985).

Joint-site analysis on genotype effects and broad-sense heritability of growth

The ANOVA of the joint-site data set showed high genotypic variation for growth traits and disease incidence indicating the potential of genetic gain through selection. In general, genetic control of growth traits in the literature has reported moderate to high broad-sense heritabilities, however these values can vary greatly, ranging from 0.18-0.91 (Yu et al. 2001; Pliura et al. 2007; Monclus et al. 2009; Zhang et al. 2012). Heritability of genotype-means were relatively moderate in Columbus and Raleigh, and by site ranged from 0.56-0.81 for height, 0.41-0.61 for DBH, and 0.43-0.66 for volume, respectively. Comparable heritabilities for height (0.65-0.80) and higher heritabilities for DBH (0.76-0.91) were reported in a study of 105 hybrid poplar clones in Lithuania (Pliura et al. 2014). A similar finding was reported in a study of 60 hybrid poplar clones in Sweden, with heritability for height and DBH ranging from 0.55-0.87 and 0.71-0.83, respectively (Yu et al. 2001). The comparatively lower heritability of DBH than height in this study could be due to the spatial variability effect that obscured the genetic control of DBH growth.

Genotype by Environment interactions

Significant GxE interactions for DBH and volume show the presence of variation in genetic adaptability to site. GxE interactions can influence yield and reduce the accuracy that breeding programs have in estimating breeding values and maximizing genetic gain. This is caused by environmental differences between test plots and deployment zones that result in unforeseen interactions that impact genetic control (Pliura et al. 2007). Testing for these
interactions is strategically important prior to clonal deployment. In addition, a clonal study in three North Central states reported genotype instability in rank throughout plantation development (Zalesny et al. 2009), warranting future testing of genotypes by age. The significant GxE interactions observed in this study for DBH and volume are similar to the findings reported in previous short-rotation poplar studies (Mohn & Randall 1973; Orlovic et al. 1998; Zhang et al. 2003). Although, the GxE interaction for height was non-significant, plasticity of individual genotypes was apparent from the difference in rank between sites. Some of the genotypes were generalists, exhibiting stable productivity across environments, while others were specialists, showing high suitability to specific environmental conditions. Our interaction variance components (3-19%) were much higher compared to those (2%) in a study of 36 poplar clones planted on two sites in Denmark (Nielsen et al. 2014). However, the interaction variance components were always smaller than the genotype variance components (Table 1.5), and never exceeded the 50% threshold that suggests significant problems for testing and selection (Shelbourne et al. 1972).

**Conclusion**

Large genetic variation was found in growth traits for two-year-old poplar, confirming the genus as a short rotation crop with the potential of considerable genetic gains through breeding and selection. With proper weed control, the observed yields meet estimated production levels for potential SRWCs (Kiser & Fox 2013). The genotype by site interactions and variation in site adaptability warrant testing of GxE interactions for clonal deployment throughout the region. Finally, after two growing seasons, hybrids exhibited higher yields, but the observed susceptibility of hybrids to S. musiva suggests that P.
*deltoides* genotypes may be better suited in the Southeast US region as plantation age increases.
References


Table 1.1 Means and 2 standard errors (SE) for growth traits and survival of 52 two-year-old poplar genotypes in Raleigh, NC and Columbus, MS.

<table>
<thead>
<tr>
<th>Site</th>
<th>Diameter cm</th>
<th>SE</th>
<th>Height M</th>
<th>SE</th>
<th>Volume dm³</th>
<th>SE</th>
<th>Survival %</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Raleigh</td>
<td>4.7</td>
<td>0.58</td>
<td>5.50</td>
<td>0.46</td>
<td>13.11</td>
<td>1.24</td>
<td>98.08</td>
<td>3.20</td>
</tr>
<tr>
<td>Columbus</td>
<td>4.4</td>
<td>1.66</td>
<td>5.66</td>
<td>1.24</td>
<td>13.63</td>
<td>3.62</td>
<td>46.13</td>
<td>46.82</td>
</tr>
</tbody>
</table>
Table 1.2 Results (p values) of the effect of genotype and taxon (*P. deltoides*, hybrid) on growth traits, *S. musiva* incidence, and survival for 52 two-year-old poplar genotypes in Raleigh, NC and Columbus, MS. Values in bold are <0.05.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Site</th>
<th>Diameter</th>
<th>Height</th>
<th>Volume</th>
<th><em>S. musiva</em></th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genotype</td>
<td>Raleigh</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
<td>0.0213</td>
<td>0.0121</td>
</tr>
<tr>
<td></td>
<td>Columbus</td>
<td>0.0534</td>
<td>0.0048</td>
<td>0.0112</td>
<td>&lt;.0001</td>
<td>0.0107</td>
</tr>
<tr>
<td>Taxon</td>
<td>Raleigh</td>
<td>0.0214</td>
<td>0.0043</td>
<td>0.0026</td>
<td>0.5000</td>
<td>0.6550</td>
</tr>
<tr>
<td></td>
<td>Columbus</td>
<td>0.4166</td>
<td>0.0191</td>
<td>0.7270</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>
Table 1.3 Ranking of the ten tallest (m) poplar genotypes at Raleigh, NC and Columbus, MS after two growing seasons, and the rank of each of these clones at the corresponding site.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>Site Raleigh</th>
<th>Site Columbus</th>
<th>Genotype</th>
<th>Site Columbus</th>
<th>Site Raleigh</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM8019</td>
<td>1</td>
<td>1</td>
<td>DM8019</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>DD140</td>
<td>2</td>
<td>35</td>
<td>DD114</td>
<td>2</td>
<td>37</td>
</tr>
<tr>
<td>DM7388</td>
<td>3</td>
<td>11</td>
<td>TD185</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>DM230</td>
<td>4</td>
<td>5</td>
<td>DD8994</td>
<td>4</td>
<td>28</td>
</tr>
<tr>
<td>TD185</td>
<td>5</td>
<td>3</td>
<td>DM230</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>DD434</td>
<td>6</td>
<td>8</td>
<td>DD116</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>TD339</td>
<td>7</td>
<td>24</td>
<td>DD7595</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>DD428</td>
<td>8</td>
<td>48</td>
<td>DD434</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>DD117</td>
<td>9</td>
<td>22</td>
<td>DD176</td>
<td>9</td>
<td>24</td>
</tr>
<tr>
<td>DD116</td>
<td>10</td>
<td>6</td>
<td>DD557</td>
<td>10</td>
<td>35</td>
</tr>
</tbody>
</table>
Table 1.4 Joint-site results (p values) of the effect of genotype, GxE, and taxon (*P. deltoides*, hybrid) on growth traits, *S. musiva* incidence, and survival for 52 two-year-old poplar genotypes in Raleigh, NC and Columbus, MS. Values in bold are <0.05.

<table>
<thead>
<tr>
<th>Effect</th>
<th>Diameter</th>
<th>Height</th>
<th>Volume</th>
<th>Septoria</th>
<th>Survival</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genotype</td>
<td>0.0227</td>
<td>0.0021</td>
<td>0.0084</td>
<td>0.0010</td>
<td>0.0140</td>
</tr>
<tr>
<td>GxE</td>
<td>0.0046</td>
<td>0.0607</td>
<td>0.0160</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td>Taxon</td>
<td>0.0307</td>
<td>0.0022</td>
<td>0.0072</td>
<td>&lt;.0001</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>
Table 1.5 Genotypic-mean height, DBH, and Volume of 52 two-year-old poplar genotypes in Raleigh, NC and Columbus, MS. Values of all variance components in the joint-site model with the percent of phenotypic variance explained by each component, including heritability and its standard error (SE).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Site</th>
<th>Trial mean (Genotype)</th>
<th>Variance components</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Genotype (%)</td>
<td>GxE (%)</td>
</tr>
<tr>
<td>Height (m)</td>
<td>Raleigh 5.50</td>
<td>0.23 (34)</td>
<td>0.06 (9)</td>
<td>0.12 (18)</td>
</tr>
<tr>
<td></td>
<td>Columbus 5.56</td>
<td></td>
<td>0.12 (18)</td>
<td>0.26 (39)</td>
</tr>
<tr>
<td>DBH (cm)</td>
<td>Raleigh 4.7</td>
<td>0.25 (22)</td>
<td>0.22 (19)</td>
<td>0.57 (50)</td>
</tr>
<tr>
<td></td>
<td>Columbus 4.4</td>
<td></td>
<td>0.22 (19)</td>
<td>0.57 (50)</td>
</tr>
<tr>
<td>Vol (dm³)</td>
<td>Raleigh 13.11</td>
<td>1.32 (24)</td>
<td>0.93 (17)</td>
<td>2.51 (46)</td>
</tr>
<tr>
<td></td>
<td>Columbus 13.63</td>
<td></td>
<td>0.93 (17)</td>
<td>2.51 (46)</td>
</tr>
</tbody>
</table>
Figure 1.1 Genotypic-mean volumes of 52 two-year-old poplars ordered from least to greatest at Raleigh, NC and independently ordered from least to greatest at Columbus, MS.
Figure 1.2 Genotype-mean height and confidence intervals of 52 two-year-old poplar genotypes in Raleigh, NC ranked from smallest to largest. Confidence intervals of genotypes that do not intersect the overall site mean (dotted line) are significantly different at the 0.05 level.
Figure 1.3. Genotype-mean DBH and confidence intervals of 52 two-year-old poplar genotypes in Raleigh, NC ranked from smallest to largest. Confidence intervals of genotypes that do not intersect the overall site mean (dotted line) are significantly different at the 0.05 level.
Figure 1.4 Genotype-mean volume and confidence intervals of 52 two-year-old poplar genotypes in Raleigh, NC ranked from smallest to largest. Confidence intervals of genotypes that do not intersect the overall site mean (dotted line) are significantly different at the 0.05 level.
Figure 1.5 Genotype-mean height and confidence intervals of 52 two-year-old poplar genotypes in Columbus, MS ranked from smallest to largest. Confidence intervals of genotypes that do not intersect the overall site mean (dotted line) are significantly different at the 0.05 level. Confidence intervals could not be calculated for genotypes with 3 or less observations.
Figure 1.6 Genotype-mean DBH and confidence intervals of 52 two-year-old poplar genotypes in Columbus, MS ranked from smallest to largest. Confidence intervals of genotypes that do not intersect the overall site mean (dotted line) are significantly different at the 0.05 level. Confidence intervals could not be calculated for genotypes with 3 or less observations.
Figure 1.7  Genotype-mean volume and confidence intervals of 52 two-year-old poplar genotypes in Columbus, MS ranked from smallest to largest. Confidence intervals of genotypes that do not intersect the overall site mean (dotted line) are significantly different at the 0.05 level. Confidence intervals could not be calculated for genotypes with 3 or less observations.
Figure 1.8  Linear correlation of 51 two-year-old poplar genotypes located in Raleigh, NC and Columbus, MS. Regression line is based on genotype-mean volume with the shaded area representing a 95% confidence interval.
Figure 1.9  Linear correlation of 51 two-year-old poplar genotypes located in Raleigh, NC and Columbus, MS. Regression line is based on genotype-mean DBH with the shaded area representing a 95% confidence interval.
Figure 1.10  Linear correlation of 51 two-year-old poplar genotypes located in Raleigh, NC and Columbus, MS. Regression line is based on genotype-mean height with the shaded area representing a 95% confidence interval.
Chapter 2 - Leaf Area, Light Interception, and Light-use Efficiency of Nine Poplar Genotypes

ABSTRACT

Leaf Area, Light Interception, and Light-use Efficiency of Nine Poplar Genotypes.

Fast-growing short-rotation trees are a promising fuel source for developing bioenergy markets in the Southeast U.S. However, future improvements in productivity necessitate a better understanding of their physiological basis of yield. The primary objective of this study was to determine the contribution of leaf area and light interception dynamics on stem biomass accumulation among six *Populus deltoides* and three hybrid *Populus* clones that varied in size. During the summer of the second year after establishment, stem growth was measured from June 24 to August 11 and examined in relation to light interception and light-use efficiency. Leaf area was estimated allometrically using branch-level measurements. For both leaf area and mass, branch diameter was the best overall predictor, with additional improvements made by including branch height and clonal taxon to the equation. Overall, hybrids had higher leaf area due primarily to high branch leaf area, and a larger number of branches per tree. Together, IPAR and LUE explained a large amount of the variation in stem growth ($R^2 = 0.99$); IPAR being the main determinant in stem growth, while LUE was more weakly related.
Introduction

Short Rotation Woody Crop Bioenergy

The concerns about fossil fuel dependence in the United States are well documented and encompass a broad spectrum of issues from energy security and economics to pollution and climate change (Lincoln 2005; Li et al. 2009; Liu et al. 2007). Fossil fuels are the main source of energy in the United States, accounting for 81 percent of the nation’s total energy consumption as of 2015 (Energy Information Administration 2016). This value has steadily decreased from 91 percent since 1975, because of the growth of renewable and nuclear energy (Energy Information Administration 2016). By 2015, renewable energy had increased to 10 percent of total US energy consumption, with bioenergy (energy from biomass) exceeding all other renewable sources of energy (Energy Information Administration 2016; DOE 2011). Studies estimate that bioenergy could potentially deliver 35 percent of the global energy demand (Guo et al. 2015; Haberl et al. 2013). The reason for the recent increase in bioenergy consumption is largely due to corn-based ethanol production of biofuels (DOE 2011). However, due to recent policy goals, the Renewable Fuel Standard (RFS2) now requires that 21 billion gallons must come from advanced biofuels by 2022. Advanced biofuels are defined as renewable biomass, other than ethanol derived from corn starch (EISA 2007). To meet this demand, short-rotation woody crops (SRWC) are considered a promising system for bioenergy production (Graham et al. 1992; Wright 2006; Keoleian & Volk 2005). Many potential SRWC feedstocks are being evaluated based on varying environmental, economic, and climatic conditions (Dale et al. 2011). This study researched Populus, a temperate climate species that possesses many characteristics of a desirable SRWC (Kauter et al. 2003; Dickmann 2006; Ceulemans et al. 1992).
**Physiological basis of poplar productivity**

Future improvements in biomass production are dependent on a better understanding of the physiological basis of yield (Cannell et al. 1988). Binkley et al. (2004) describe yield in terms of resources: resource supply, proportion of resources captured, and the efficiency at which these resources are used for carbon dioxide fixation. One critical resource is light and its effect on yield can be understood as total photosynthetically active radiation (PAR), the amount of PAR captured by leaves, and the efficiency at which it is then used to fix carbon dioxide. The linear relationship between biomass production and intercepted photosynthetically active radiation (IPAR) and light-use efficiency (LUE) is well established in forest plantations (Binkley et al. 2004; McCrady & Jokela 1998). Because these relationship dynamics directly affect biomass gain, they are important to assess in potential SWRC clones to better understand the physiological basis of short-rotation poplar growth.

Light interception is primarily a function of leaf area, which is quantified and expressed as leaf area index (LAI) (Cannell 1989). In intensive SRWC systems, poplar displays dynamic leaf and canopy properties to maximize leaf area and light interception (Ceulemans & Deraedt 1999). High LAI values can be achieved quickly even in young stands because of rapid early production of numerous leaves (Broeckx et al. 2012). This potential for high leaf area has been demonstrated in young poplar stands with LAI values as high as six (Ceulemans et al. 1993).

Light interception is often the main limiting factor in productivity because of its fixed availability (Loomis et al. 1971); however, the determinants of capturing and converting light to biomass vary among and within species (Ceulemans & Saugier 1991; Isebrands & Nelson 1982). These differences are caused by variation in canopy structure, leaf photosynthetic
rate, GxE factors, and respiration (Charles-Edwards 1982). Based on Monteith’s LUE model, the efficiency of crop production is calculated as the “ratio of energy output (carbohydrate) to energy input (solar radiation)” (Monteith & Moss 1977). Recognizing that several variations exist in defining these input and output terms, LUE was defined here as the stem dry matter produced per MJ of intercepted photosynthetically active radiation (IPAR), similar to other LUE models (Broeckx et al. 2012; Cannell 1988).

The primary objective of this study was to determine the contribution of leaf area and light interception dynamics on stem biomass accumulation among six *Populus deltoides* (Bart. Ex Marsh) and three hybrid *Populus* clones that varied in size in their second growing season in the field. To understand the contributors of clonal variation in growth, we examined: (i) what parameters were the best determinants of branch leaf area and leaf mass among clones (ii) what leaf, branch, and canopy traits were related to leaf area and light interception, and (iii) which of these parameters best explained stem growth.

**Materials and Methods**

*Site description*

The research site was planted in March 2014, at the North Carolina State University Horticultural Field Laboratory in Raleigh, North Carolina (35.79°N, 78.70°W). The humid, subtropical climate is characterized by hot summers and mild winters. The average annual temperature and precipitation are 16°C and 1183 mm, respectively. The plant hardiness zone is 7b (-15°C to -12.2°C) (USDA Plant Hardiness Zone Map 2012) and the soil type is classified as Cecil gravelly sandy loam (Soil Survey Staff, Natural Resources Conservation Service, USDA). The site was prepared during the first week of March, with shallow soil
ripping to 20 cm deep and 0.25 ounces per acre of pre-emergent herbicide (Oust®). Triple superphosphate (TSP) (0-45-0) was applied in late April, 2015. Weeds were controlled using glyphosate applications and the presence of cottonwood leaf beetles (CLB) required insecticide (Sevin®) applications in May and July.

**Experimental design**

The experiment was a randomized, complete-block design, with 8 blocks and one ramet of each clone in each block. The overall study (Chapter 1) consisted of 52 clones from three species combinations: *Populus deltoides* (Bart. Ex Marsh), *Populus trichocarpa* (Torr. & Gray), and *Populus maximowiczii* (A. Henry). Of the 52 clones, there were 43 that derived from crosses of *P. deltoides* x *P. deltoides* (DD), six from *P. trichocarpa* x *P. deltoides* (TD), and three from *P. deltoides* x *P. maximowiczii* (DM). All clones were provided by ArborGen Inc., Summerville, SC. Non-rooted, 33-38 cm cuttings were soaked in water overnight and planted at 4,444 trees ha$^{-1}$ at a spacing of 1.5 x 1.5 m. A single border row was installed around the site.

For the study of leaf area dynamics, nine clones were selected from the original 52, based on main stem biomass after the first growing season: three of the largest clones (DM8019, TD185, DD116), three intermediate (DD428, DD109, DD115), and three of the smallest (DD224, TD187, DD402). Selection was based on these three size categories so the effects of leaf area, light interception, and light-use efficiency could be examined across the range of productivity. Each clone had eight ramets except for genotype 8019, which had six.
Data Collection

Main stem measurements were taken every eight days from June 24 to August 11, 2015. Measurements of net gain in growth from this period are defined using the $\Delta$ symbol.

Diameter at breast height (DBH) was measured with a diameter tape to the nearest millimeter. Height was measured to the nearest centimeter using a telescopic height pole.

Main stem outside-bark volume was estimated using a model developed through destructive harvesting of $P$. deltoides in the alluvial floodplain of the Lower Mississippi Valley (Shelton et al. 1982). Main stem biomass was estimated using a dry wood poplar density of 416.7 kg m$^{-3}$ (World Agroforestry Centre 2012).

On July 22nd, canopy lengths and all branch heights, lengths, and diameters were measured and the number of leaves attached to the main stem were counted for each tree. Canopies were divided into thirds (lower, middle, upper) and a harvest branch was selected within each third using probability proportionate to size (PPS) sampling, in which the selection probability for each branch is set to be proportional to its size measure. Branch diameter was used to represent branch size. Therefore, three branches and a central main stem leaf were selected from each tree.

On August 11, the material was harvested and removed from the site to measure the dry weight and leaf area. A subsample of three randomly selected leaves was taken from each branch, scanned on a flatbed scanner, oven dried, and then weighed to calculate the specific leaf area (SLA) for each branch. Foliage and woody material were then separated and oven dried to obtain their individual weights. Each branch’s foliage weight was multiplied by its SLA ratio to calculate leaf area per branch. Finally, the area of each main
stem leaf was measured and multiplied by the number of main stem leaves for that tree to get an estimate of main stem leaf area.

*Branch-level leaf area and leaf mass*

The prediction equations for branch-level leaf area and leaf mass were obtained using a mixed linear model (PROC MIXED) in SAS 9.4 (SAS Institute, Cary, NC, USA). To decide the model of best fit, all branch-level and tree-level data were examined in the model including: branch diameter, branch length, branch height, relative branch depth into crown, branch direction, canopy position, tree height, tree diameter, clone, and taxon. Because multiple branches were selected per tree, a repeated measures statement was used to account for within-tree correlation among branches. The allometric relationships established for branch-level leaf area and leaf mass were used to estimate leaf area and leaf mass for all the branches on each tree. Leaf area of all branches were then summed together along with the main stem leaf area to get total leaf area per tree. Leaf area per tree (m) was divided by the spacing per tree (2.25 m) to calculate LAI. Also, the leaf masses of all branches were summed together along with the main stem leaf mass to get total leaf mass per tree. Leaf mass per area (LMA) was calculated by dividing total tree leaf mass by tree leaf area.

*IPAR and LUE*

Photosynthetically active radiation (PAR) values were retrieved from the Reedy Creek Field Laboratory as hourly averages, and summed to daily values from June 24 to August 11, 2015. Daily intercepted photosynthetically active radiation (IPAR) was calculated for each tree by using the Beer-Lambert equation:

\[
IPAR = PAR(1 - e^{(-k \times LAI )})
\]
where \( k \) is the light extinction coefficient (0.588) average for the study area, measured with an LAI-2200 (LiCor, Lincoln, NE, USA). The daily IPAR was then summed to get the total net gain in IPAR between June 24 and August 11, 2015. LUE (g/MJ) was calculated for each tree by dividing the net gain in stem biomass (g) by the net gain in IPAR (MJ).

\[
LUE = \frac{\Delta \text{Biomass}}{\text{IPAR}}
\]

Statistical Analysis

A general linear model was used to examine the effect of clone on all production and light related characteristics. Duncan’s multiple range test was used to find significant differences among clone means for all reported characteristics. A \( \alpha \)-value of 0.05 was used to test significance. Correlations among the characteristics were examined by regression, and the GLM procedure was used to find the best fit model for predicting \( \Delta \)stem and total stem biomass with LAI, LMA, IPAR, and LUE as predictors. The best fit approach was taken to account for the correlation of predictor traits. All analyses were performed in SAS 9.4 (SAS Institute, Cary, NC, USA).

Results

Branch-level leaf area and leaf mass

At the branch level, a square root transformation of branch leaf area significantly improved the linearity between branch leaf area and the model parameters, displaying normally distributed residuals. The form of the equation was:

\[
BLA = (-0.2562 + (0.043 \times BD) + (0.076 \times BH) + (T))^2
\]
where BLA was the branch leaf area (m$^2$), BD was branch diameter (mm) at 2.5 cm from the base of the branch, BH was height of branch from ground (m), and T was the taxon dummy variable. The parameters BD (p < .0001), BH (p < .0001), and T (p < .0001) resulted in the best-fit model and together accounted for the highest amount of variation (AIC = -392.0, $R^2 = 0.76$). BD was the single most important predictor, explaining 61% of the variation in BLA, and the addition of BH and T accounted for the remaining variation explained by the model. DD116 had the highest mean BD (11.22 ± 5.55 mm) and second highest mean BLA (0.17 ± 0.20 m$^2$). TD187 had the smallest mean BD (5.91 ± 2.20 mm) and BLA (0.04 ± 0.04 m$^2$) (Table 2.1). *P. deltoides* clones were not significantly different from one another (p = 0.2233); however, hybrid clones had significantly higher leaf area than *P. deltoides* clones for a given branch diameter. For example, the mean BD of TD185 (8.82 ± 3.68 mm) was similar to DD115 (8.82 ± 3.81), but the mean BLA of TD185 (0.12 ± 0.12 m$^2$) was significantly greater than DD115 (0.09 ± 0.09 m$^2$). Hybrid clones had nearly double the number of branches as *P. deltoides* clones, on average (55 and 29, respectively). The amount of leaf area from main stem leaves also varied among clones, contributing between 4 - 28% of total tree leaf area. The equation form for predicting leaf mass per branch used the same variables as the one for leaf area per branch.

$$BLM = (-3.472 + (0.420 \times BD) + (0.908 \times BH) + (T))^2$$

where BLM is leaf mass per branch (g), BD (p < .0001), BH (p < .0001), T (p < 0.0001) AIC = 548, and $R^2 = 0.76$. Table 2.1 shows the large differences between BLM within and among the three size categories of clones.

The specific leaf area (SLA) of harvest branches decreased as branch height increased (p < .0001) and did not vary among clones (p = 0.0795) (Table 2.2).
Net gain in stem biomass and total stem and leaf biomass

Clonal variation was significant for all yield related characteristics (Table 2.3). Clones varied more than threefold (374 – 1241 g) in Δstem (net gain in stem biomass between June 24 and August 11). While ΔDBH and Δheight varied from 0.7 - 1.2 cm and 0.68 - 1.12 m, respectively (Table 2.4). Aside from clone TD187 (0.7 ± 0.1 cm) and DD224 (1.2 ±0.2 cm), differences among ΔDBH means were relatively small (Table 2.4). The large clonal variation for Δheight (p = 0.0061) exhibited no significant differences among clone means, except for DD402, which was significantly smaller (Table 2.4). Although, clonal Δstem and total stem biomass means varied some in ranking (Table 2.4), they exhibited strong correlation (Adj. $R^2 = 0.86$), and differences among clone means only occurred within the three size categories.

Clones DM8019 and TD185 had significantly greater foliage biomass (895±302 g and 700±191 g, respectively) (Table 2.4) than the other clones and were also the only clones whose sample branches had the highest proportion of leaf area in the top third of the canopy. Sample branches from all other clones had the highest amount of leaf area in the middle third of the canopy and lower contributions of leaf area in the lower and top thirds, resulting in a curvilinear vertical distribution of leaf area. Overall, the relationship of total foliage and stem biomass was relatively high (Adj. $R^2 = 0.81$).

Leaf indices, light interception, and light-use efficiency

Clonal variation was significant among all four of the leaf and light related characteristics (LMA, LAI, IPAR, LUE) (Table 2.3). Table 2.5 was ordered from the largest clone (DM8019) to the smallest clone (DD402), to show the effect of each characteristic on clone size. LMA was moderately correlated with total stem biomass ($R^2 = 0.59$), and the two
largest clones (DM8019 and TD185) had the highest LMA values (Table 2.5). Clones varied in LAI by more than threefold (1.01 – 4.46 m²/m²), and LAI had a strong relationship with total stem biomass ($R^2 = 0.80$). Hybrids DM8019 and TD185 also had the highest LAI values, and hybrid TD187 had the highest LAI in its size category. LAI of DM8019 was significantly greater than all clones, had the highest mean BLA, and a large number of total branches compared to *P. deltoides* clones.

IPAR varied more than twofold among clones (205.2 – 427.5 MJ), and high IPAR was related to $\Delta$stem production ($R^2 = 0.70$). By differentiating between *P. deltoides* and hybrid clones, this relationship slightly improved (Adj. $R^2 = 0.75$), mainly because the TD hybrids had less stem growth for a given amount of IPAR (Figure 2.1). LUE varied less among clones (Table 2.5) and accounted for a smaller amount of the variation in $\Delta$stem ($R^2 = 0.45$). However, by differentiating between *P. deltoides* and hybrid clones the relationship between LUE and $\Delta$stem was substantially improved (Adj. $R^2 = 0.65$) (Figure 2.2). Both TD clones had the lowest LUE in their size category, due to their high light interception and low $\Delta$stem production (Table 2.5).

**Discussion**

*Light interception and light-use efficiency*

To better understand the drivers of productivity, three sizes of clones were selected to analyze the influence of IPAR and LUE on stem biomass production. Overall, IPAR was the main determinant of $\Delta$stem production, and that larger clones did have significantly higher levels of light interception. The relationship between $\Delta$stem and IPAR was even higher when differentiating between hybrid and *P. deltoides* clones. Consistent with other findings, LUE was also an important determinant of $\Delta$stem production (Green et al. 2001; Broeckx et al.
2015). Our comparatively high range of LUE values indicates efficient clones, but could also be due to an overestimation of crown surface area resulting in underestimation of LAI. The variation in LUE values among *P. deltoides* clones was relatively small; however, TD values were significantly lower due to high LAI and low Δstem.

Although this study focused on leaf and canopy dynamics, several other physiological factors can also influence the relationship between LUE, IPAR, and stem biomass accumulation. Because LUE, in this study, is expressed in terms of stem biomass, variation in aboveground carbon allocation between stem, branch, and foliage biomass affects clonal LUE. Clonal differences in carbon allocation can also be caused by variation in allocation between roots and shoots among clones (Cannell et al. 1988). As observed, low LUE for Δstem in TD clones could be due to higher biomass allocation in the root system. Heilman et al. (1994) reported that the mean root/shoot ratios of 66 *P. deltoides*, *P. trichocarpa*, and TD clones were 0.10, 0.14, and 0.12, respectively. Total biomass growth is also negatively related to root respiration rates among poplar clones (e.g., Rewald et al. 2016).

The determination of the contribution of IPAR and LUE to stem growth was also potentially influenced by the period of time when these measurements were taken. Although, a good relationship between Δstem and total stem production existed (85%), the growth between June 24 and August 11 only represents the net gain in stem biomass for a relatively short period of time. We only measured leaf area characteristics during this one time period. Other time periods contributing to total stem biomass may have had differing leaf areas for the specific clones. In addition, clonal interactions with the specific environmental conditions might have resulted in lower or higher clonal productivity during that period, as
compared with the entire two years of growth. Consequently, IPAR and LUE were more accurate predictors of ∆stem than they were for total stem production.

Branch-level leaf area and LAI

In order to estimate clonal variation at the tree-level (e.g., LAI, IPAR, and LUE), the best predictors of branch-level leaf area and leaf mass were determined. The strong positive exponential relationship between BLA and BD corresponds with other branch-level leaf area studies of poplar and conifer species (Kershaw & Maguire 1995; Nelson et al. 2014; Weiskittel et al. 2009). However, unlike the allometric equations typically developed for branch-level leaf area, our analysis found that BH was a better predictor of leaf area than relative branch depth within the crown. This could be due to BH being a better measure of branch position relative to the stand and, thereby, competition for light from neighboring trees of other clones, while relative branch depth in the crown measured the exact location of a branch in its tree’s crown. The relationship of predictors to BLA and BLM differed significantly between hybrid and P. deltoides clones, indicating differences in branch and canopy structure. This relationship resulted in significantly higher LAI of hybrid clones.

IPAR was primarily a function of LAI, so the determinants of LAI largely explain the variation in IPAR. Consequently, a strong linear relationship also existed between LAI and biomass, with hybrid clones exhibiting the highest LAI. Overall, hybrids had higher leaf area, due primarily to the high BLA relative to branch size and a larger number of branches per tree. DM8019 had the lowest number of branches among hybrids, yet still had the highest LAI due to high BLA relative to branch size. Scarascia-Mugnozza et al. (1989) reported higher LAI for P. trichocarpa (1.2) and T x D crosses (2.9), compared to P. deltoides (1.0). The correlation between LAI and the large number of branches in hybrids,
especially TD clones, could be due to syllepsis. Syleptic branches form on the current year’s terminal stem and are positively related to maximum LAI in poplar clones (Rae et al. 2004; Marron et al. 2006; Dillen et al. 2009). In line with these observations, Ceulemans et al. (1990) reported a larger number of syleptic branches in some P. trichocarpa and TD clones than in P. deltoides. An additional hypothesis for the differences observed in LUE could be caused by the variation in vertical leaf area distribution. DM8019 and TD185 had the highest LAI, and were also the only clones whose sample branches had the highest proportion of leaf area in the top third of the canopy. While this might be a hybrid trait, it could also be caused by their dominant heights, which allowed the upper canopy to grow faster under less competitive conditions. A poplar coppice study (Proe et al. 2002) found net photosynthesis rates at the top of the canopy were three times higher than those at the canopy base, demonstrating the potential effects of vertical leaf area distribution. Finally, a higher proportion of main stem leaves could contribute to increased photosynthesis rates, because of their strategic location for light interception and minimum translocation (Larson & Gordon 1969; Isebrands & Nelson 1982).

Conclusion

The important conclusions of the study relate to leaf dynamics at the branch-level and the tree-level. Hybrid and P. deltoides branches differed in number, leaf area, and leaf mass, which contributed to greater leaf area in hybrid clones. Together IPAR and LUE explained a high amount of the variation in ∆stem production. IPAR was the main determinant in ∆stem production, while LUE had a weaker, but significant, relationship with ∆stem production due to the effect of TD clones. The importance of IPAR and LUE to stem biomass growth
supports the selection of genotypes with high light interception and efficiency, to increase yields in short-rotation poplar.
References


Table 2.1 Means and standard deviations of branch diameter (BD, mm), branch leaf area (BLA, m$^2$), branch leaf mass (BLM, g), and branch woody mass (BWM, g) of nine two-year-old poplar clones.

<table>
<thead>
<tr>
<th>Clones</th>
<th>n</th>
<th>BD</th>
<th>BLA</th>
<th>BLM</th>
<th>BWM</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM8019</td>
<td>44</td>
<td>10.50 (4.64)</td>
<td>0.20 (0.20)</td>
<td>18.0 (18.9)</td>
<td>36.4 (40.6)</td>
</tr>
<tr>
<td>TD185</td>
<td>62</td>
<td>8.82 (3.68)</td>
<td>0.12 (0.12)</td>
<td>10.1 (11.1)</td>
<td>20.8 (24.9)</td>
</tr>
<tr>
<td>DD116</td>
<td>27</td>
<td>11.22 (5.55)</td>
<td>0.17 (0.20)</td>
<td>14.6 (17.9)</td>
<td>45.7 (58.6)</td>
</tr>
<tr>
<td>DD428</td>
<td>19</td>
<td>10.34 (4.12)</td>
<td>0.14 (0.12)</td>
<td>11.7 (10.9)</td>
<td>33.2 (30.4)</td>
</tr>
<tr>
<td>DD109</td>
<td>30</td>
<td>9.21 (4.29)</td>
<td>0.10 (0.12)</td>
<td>8.3 (10.7)</td>
<td>26.1 (33.5)</td>
</tr>
<tr>
<td>DD115</td>
<td>32</td>
<td>8.82 (3.81)</td>
<td>0.09 (0.09)</td>
<td>7.1 (8.1)</td>
<td>21.9 (26.3)</td>
</tr>
<tr>
<td>DD224</td>
<td>36</td>
<td>9.83 (3.54)</td>
<td>0.07 (0.08)</td>
<td>5.5 (7.1)</td>
<td>25.2 (25.5)</td>
</tr>
<tr>
<td>TD187</td>
<td>57</td>
<td>5.91 (2.20)</td>
<td>0.04 (0.04)</td>
<td>3.6 (3.8)</td>
<td>5.2 (7.3)</td>
</tr>
<tr>
<td>DD402</td>
<td>29</td>
<td>9.00 (3.86)</td>
<td>0.08 (0.11)</td>
<td>6.2 (9.3)</td>
<td>22.4 (32.1)</td>
</tr>
</tbody>
</table>
Table 2.2 Specific leaf area means and standard deviations (SD) (m$^2$ kg$^{-1}$) for branches selected from the lower, middle, and upper portions of the canopies of nine two-year-old poplar clones.

<table>
<thead>
<tr>
<th>Clone</th>
<th>Lower Third</th>
<th>Middle Third</th>
<th>Upper Third</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Mean</td>
</tr>
<tr>
<td>DD109</td>
<td>15.13</td>
<td>1.42</td>
<td>12.29</td>
</tr>
<tr>
<td>DD115</td>
<td>15.33</td>
<td>3.06</td>
<td>12.63</td>
</tr>
<tr>
<td>DD116</td>
<td>14.26</td>
<td>2.28</td>
<td>12.72</td>
</tr>
<tr>
<td>TD185</td>
<td>15.31</td>
<td>2.69</td>
<td>12.38</td>
</tr>
<tr>
<td>TD187</td>
<td>16.46</td>
<td>3.18</td>
<td>13.55</td>
</tr>
<tr>
<td>DD224</td>
<td>17.08</td>
<td>3.47</td>
<td>13.40</td>
</tr>
<tr>
<td>DD402</td>
<td>15.60</td>
<td>3.45</td>
<td>12.65</td>
</tr>
<tr>
<td>DD428</td>
<td>13.39</td>
<td>1.70</td>
<td>11.79</td>
</tr>
<tr>
<td>DD8019</td>
<td>14.74</td>
<td>3.57</td>
<td>12.29</td>
</tr>
</tbody>
</table>
Table 2.3 Results (P and F values) of clone and block effects on all yield (ΔDBH, ΔHeight, ΔStem, Stem Biomass, Foliage Biomass), leaf (leaf mass per area (LMA), leaf area index (LAI)), and light-related (intercepted photosynthetically active radiation (IPAR), light-use efficiency (LUE)) of nine two-year-old poplar clones in Raleigh, NC.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Clone p-value</th>
<th>Clone F value</th>
<th>Block p-value</th>
<th>Block F value</th>
</tr>
</thead>
<tbody>
<tr>
<td>ΔDBH</td>
<td>0.0003</td>
<td>4.59</td>
<td>0.0003</td>
<td>4.74</td>
</tr>
<tr>
<td>ΔHeight</td>
<td>0.0061</td>
<td>3.10</td>
<td>0.0006</td>
<td>4.40</td>
</tr>
<tr>
<td>ΔStem</td>
<td>&lt;.0001</td>
<td>9.15</td>
<td>0.0099</td>
<td>3.00</td>
</tr>
<tr>
<td>Stem Biomass</td>
<td>&lt;.0001</td>
<td>10.70</td>
<td>&lt;.0001</td>
<td>6.43</td>
</tr>
<tr>
<td>Foliage Biomass</td>
<td>&lt;.0001</td>
<td>16.24</td>
<td>0.0009</td>
<td>4.19</td>
</tr>
<tr>
<td>LMA</td>
<td>&lt;.0001</td>
<td>8.11</td>
<td>0.0001</td>
<td>5.36</td>
</tr>
<tr>
<td>LAI</td>
<td>&lt;.0001</td>
<td>15.76</td>
<td>0.0019</td>
<td>3.84</td>
</tr>
<tr>
<td>IPAR</td>
<td>&lt;.0001</td>
<td>10.96</td>
<td>0.0006</td>
<td>4.47</td>
</tr>
<tr>
<td>LUE</td>
<td>&lt;.0001</td>
<td>9.33</td>
<td>0.0080</td>
<td>3.11</td>
</tr>
</tbody>
</table>
Table 2.4 Means (2 standard errors) for net gain (Δ) of all growth related characteristics (DBH, height, and stem weight), measured between June 24 and August 11, 2015, and total stem and foliage biomass of nine two-year-old poplar clones. Clones that do not share a common letter are significantly different from one another at the alpha=0.05 significance level. Clones are separated into three size categories in descending order of stem biomass.

<table>
<thead>
<tr>
<th>Clone</th>
<th>Δ DBH (cm)</th>
<th>Δ Height (m)</th>
<th>Δ Stem (g)</th>
<th>Stem (g)</th>
<th>Foliage (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM8019</td>
<td>1.0ba (0.1)</td>
<td>1.12a (0.12)</td>
<td>1241a (353)</td>
<td>6771a (910)</td>
<td>895a (302)</td>
</tr>
<tr>
<td>TD185</td>
<td>1.0b (0.1)</td>
<td>1.01a (0.10)</td>
<td>891b (160)</td>
<td>5899b (540)</td>
<td>700b (191)</td>
</tr>
<tr>
<td>DD116</td>
<td>1.1ba (0.1)</td>
<td>0.99a (0.13)</td>
<td>955b (237)</td>
<td>5753b (642)</td>
<td>426c (146)</td>
</tr>
<tr>
<td>DD428</td>
<td>1.0b (0.2)</td>
<td>1.00a (0.14)</td>
<td>755cb (147)</td>
<td>5469b (379)</td>
<td>283dc (62)</td>
</tr>
<tr>
<td>DD109</td>
<td>0.9bc (0.1)</td>
<td>0.97a (0.18)</td>
<td>716cb (194)</td>
<td>5344b (430)</td>
<td>281dc (103)</td>
</tr>
<tr>
<td>DD115</td>
<td>1.0ba (0.2)</td>
<td>1.06a (0.18)</td>
<td>741cb (126)</td>
<td>5330b (400)</td>
<td>295dc (79)</td>
</tr>
<tr>
<td>DD224</td>
<td>1.2a (0.2)</td>
<td>0.90a (0.11)</td>
<td>608cd (107)</td>
<td>4776c (272)</td>
<td>226d (79)</td>
</tr>
<tr>
<td>TD187</td>
<td>0.7c (0.1)</td>
<td>0.96a (0.23)</td>
<td>373.5d (105)</td>
<td>4757c (294)</td>
<td>268dc (76)</td>
</tr>
<tr>
<td>DD402</td>
<td>0.9bc (0.2)</td>
<td>0.68b (0.20)</td>
<td>437d (122)</td>
<td>4723c (375)</td>
<td>185d (76)</td>
</tr>
</tbody>
</table>
Table 2.5 Means (2 standard errors) of total leaf mass per area (LMA), leaf area index (LAI), net gain in intercepted photosynthetically active radiation (IPAR) and light-use efficiency (LUE) of nine two-year-old poplar clones between June 24 and August 11, 2015. Clones that do not share a common letter are significantly different from one another at the alpha=0.05 significance level. Clones are separated into three size categories in descending order of stem biomass.

<table>
<thead>
<tr>
<th>Clone</th>
<th>LMA (g/m²)</th>
<th>LAI (m²/m²)</th>
<th>IPAR (MJ)</th>
<th>LUE (g/MJ)</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM8019</td>
<td>88.2a (3.1)</td>
<td>4.46a (1.42)</td>
<td>427.5a (46.7)</td>
<td>2.84a (0.58)</td>
</tr>
<tr>
<td>TD185</td>
<td>86.7ba (1.7)</td>
<td>3.57b (0.94)</td>
<td>405.4a (44.2)</td>
<td>2.17b (0.20)</td>
</tr>
<tr>
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Figure 2.1 Relationship between the net gain in stem biomass ($\Delta$Stem) and intercepted photosynthetically active radiation (IPAR) ($R^2 = 0.69$) of nine two-year-old poplar clones. The taxon effect increased the variance explained by a significant amount (Adj. $R^2 = 0.75$ with taxon effect).
Figure 2.2 Relationship between the net gain in stem biomass (ΔStem) and light-use efficiency (LUE) ($R^2 = 0.45$) of nine two-year-old poplar clones. The taxon effect increased the variance explained by a significant amount (Adj. $R^2 = 0.65$ with taxon effect).
CONCLUSION

This study tested 52 eastern cottonwood and hybrid poplar clones in NC and MS to determine their genetic variation in performance and site adaptability. We found large genetic variation in growth traits in the second year after establishment, confirming the genus as a short rotation crop with the potential of considerable genetic gains through breeding and selection. Differences in vegetation control showed that poor management can considerably reduce poplar survival and establishment. However, with proper weed control, the observed yields meet estimated production levels for potential SRWCs (Kiser & Fox, 2013). The genotype by site interactions and variation in site adaptability warrant testing of GxE interactions for clonal deployment throughout the region. Finally, after two growing seasons, hybrids exhibited higher yields, but the observed susceptibility of hybrids to *S. musiva* suggests that *P. deltoides* clones may be better suited in the Southeast US region as plantation age increases.

At the NC site, six *P. deltoides* and three hybrid clones were selected to examine the contribution of leaf area and light interception dynamics on stem biomass accumulation. Important taxon variation related to leaf dynamics at the branch-level and the tree-level were found. Hybrid and *P. deltoides* branches differed in number, leaf area, and leaf mass, which contributed to greater leaf area in hybrid clones. Together IPAR and LUE explained a high amount of the variation in ∆stem production. IPAR was the main determinant in ∆stem production, while LUE had a weaker relationship with ∆stem production due to the effect of TD clones. The importance of IPAR and LUE to stem biomass growth supports the selection of genotypes with high light interception and efficiency, to increase yields in short-rotation poplar.
BIBLIOGRAPHY


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APPENDIX
Appendix A

Table 1 Means and standard errors (SE) for volume of all 52 two-year-old poplar genotypes in Raleigh, NC and Columbus, MS.

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Appendix B

Figure 1 Relationship between the total stem biomass and intercepted photosynthetically active radiation (IPAR) \( (R^2 = 0.77) \) of nine two-year-old poplar clones.
Figure 2 Relationship between the total stem biomass (g) and light-use efficiency (LUE) ($R^2 = 0.22$) nine two-year-old poplar clones. The taxon effect increased the variance explained by a significant amount ($R^2 = 0.46$ with taxon effect).