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Survival and growth of a range of *Populus* clones in central South Carolina USA through age ten: Do early assessments reflect longer-term survival and growth trends?

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ABSTRACT

Increased emphasis is being placed on developing bioenergy production capacity in the United States and *Populus* species or hybrids have been identified as strong candidates for the southeastern United States. Thirty-one *Populus* clones were planted in South Carolina and survival and growth assessments were completed after the 1st, 2nd, 3rd, and 10th growing seasons. Survival and growth differed significantly among clones. Age-to-age correlations for survival and growth traits were made and results suggest that for most clones, age 10 survival was strongly correlated with first-year survival. A small group of clones exhibited delayed mortality indicating poor longer-term adaptability. For growth, clonal selections based on age 3 volumes could be made and rank changes involve moderate to poorly performing clones. Clones with the greatest age 3 volumes, 184-411, WV416, and 52-225, ranked 1st, 2nd, and 3rd for age 10 volume. These clones represent both T × D hybrids and pure *Populus deltoides* clones suggesting growth is a function of specific clonal characteristics rather than overall species or hybrid traits. The growth obtained under these test conditions is generally less than the maximum growth rates of the same clones obtained in various tests. Potential reasons for this variation are discussed. To develop *Populus* as a commercially viable bioenergy crop for the southeastern United States, concurrent research to identify site requirements, adaptability, and appropriate management regimes is needed. Further breeding and clonal selection will be critically important, but it is unlikely that this alone will be sufficient to assure high productivity.

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1. Introduction

Increasing emphasis is being placed on developing greater bioenergy production capacity in the United States. Driving

forces behind this push include potential reductions in greenhouse gas emissions from use of nonrenewable carbon sources, increased carbon sequestration through establishment of bioenergy crops, decreased dependence upon foreign

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energy supplies, and the desire to increase economic diversity and potential economic developments of many depressed rural economies. Excellent reviews of the early technological developments and pathways forward have been provided by Tolbert and Wright [1] and Tuskan [2]. Later reviews highlighting developments and identifying outstanding challenges have also been developed [3–5]. In 2005, the Department of Energy (DOE) and Oak Ridge National Laboratory developed a report titled “Biomass as a feedstock for a bioenergy and bio-products industry: the technical feasibility of a billion-ton annual supply” [6]. This report was further updated in 2011 and provides the most up-to-date assessment of the capacity for bioenergy production in the United States [7]. This report models growth in potential bioenergy markets and biomass production scenarios through 2030. Available biomass at any given time period is a function of the rate of technological advancements made with potential bioenergy crops and the market prices consumers are willing to pay for the crops [7].

In order for these aggressive projections to occur, continued technology developments are needed. Fully capturing the potential advantages of dedicated energy crop production requires the selection of appropriate species and the development of effective and efficient cropping regimes. For the southeastern United States, potential candidate lists of dedicated energy crops were identified [8]. This list has been updated and includes switchgrass (*Panicum virgatum* L.), *Populus* species or hybrids, various tropical grasses, loblolly (*Pinus taeda* L.) or slash (*Pinus elliottii* Engelm) pine, sweetgum (*Liquidambar styraciflua* L.) and sorghum (*Sorghum bicolor* (L.) Moench) [5]. In milder winter climates, *Eucalyptus* species and hybrids are being investigated as a potential woody feedstock [9,10]. Kline and Coleman [11] summarized the potential advantages and disadvantages of the woody crop species based on previous experiences. The primary challenges to widespread *Populus* deployment were:

- Narrow site adaptabilities
- Variable productivity rates
- Intensive management and resource input requirements
- General lack of drought tolerance.

Potential advantages of *Populus* development and deployment included:

- High growth capacity under ideal conditions.
- Extensive genetic research ongoing including genomic mapping.
- The existence of commercial stands in parts of the South.
- The potential for further improvements in the medium term.

The history of *Populus* breeding and clonal selection in the United States dates to the 1920's [12]. Fast-growing clones can perform extremely well if proper silvicultural treatments are applied [13] and mean production rates of 7 Mg ha⁻¹ y⁻¹ in the Northeast [14], 9 Mg ha⁻¹ y⁻¹ in the Northcentral [15], and 25 Mg ha⁻¹ y⁻¹ in the northwestern US [16] have been attained. Deployment of *Populus* plantations on an operational-scale has been most common in the Pacific Northwest, Central and Upper Midwest, and the lower Mississippi River Valley

alluvial floodplains. Stanturf and Zhang [17] estimated that hybrid poplar plantations comprised approximately 50,000 ha in the Pacific Northwest and 7000 ha in the Upper Midwest. Alluvial eastern cottonwood (*Populus deltoides* Bartr.) plantations in the Mississippi River Valley were estimated to comprise approximately 15,000 ha.

In areas where *Populus* cultivation has been successful, several common features exist. The first step has been the determination of which *Populus* species or hybrids between species offer the best combination of survival, growth, site adaptability, and insect and disease resistance. Once these are identified, dedicated breeding programs are often developed to create a wide selection of clones for more advanced testing [14,18,19]. In the Southern United States, the USDA Forest Service began selecting and breeding eastern cottonwood clones for deployment on alluvial sites within the Mississippi River floodplain in the early 1960's. In these early testing efforts pure eastern cottonwood clones generally proved more productive than European hybrid poplar clones on alluvial test sites [20]. Following initial testing, fourteen cottonwood clonal selections were released [21]. When the Forest Service discontinued this program in the early 1980's, much of this work was carried forward by private forest industry [22] and university supported research programs [23]. These selections have been commercially deployed on alluvial test sites and additional breeding efforts have been initiated to develop widely-adapted clones for southeastern US conditions [23]. In these breeding programs, clonal selections are often made based on growth [24–27], but adequate survival assessments are also needed [28].

In an effort to begin to understand the growth performance of *Populus* species and hybrids under southeastern US test conditions, a research planting consisting of 31 clones was established in 2001 in the upper Coastal Plain of west-central South Carolina. Results through age three were reported earlier [29]. This paper summarizes survival and growth responses through age 10. These latest measurements will yield more definitive results on the growth and adaptability of these clones on upland sites in the Southeast. The objectives of this study were:

- To conduct initial performance screens of a wide variety of *Populus* genetic sources to begin to understand relative performance under southeastern US conditions.
- To determine if clear distinctions could be made among various species or broad hybrid groupings.
- To determine relative performance correlations between measurements made at various stages of plantation development to determine when reliable measures of survival and growth performance could be made under these test conditions.

2. Materials and methods

2.1. Study location

The experiment was conducted on an upland test site within the U.S. Department of Energy Savannah River Site, a National Environmental Research Park, located near Aiken, South

Carolina, USA (33°23'N, 81°38'W). The climate in this part of South Carolina is characterized by long, hot summers and short, relatively mild winters. The annual growing season averages 242 days (March 19 to November 16). Daily high and low summer temperatures (May through September) average 31.0 °C and 19.0 °C respectively. Winter (December through February) daily high and low temperatures average 14.7 °C and 2.6 °C respectively. Mean annual precipitation is 121.4 cm with rainfall fairly well-distributed throughout the year. Rainfall between March and October averages 84.4 cm [30].

The study site is flat (surface slopes less than 2%) with well-drained deep sandy surface horizons. The soil is a Blanton sand classified as a loamy, siliceous, thermic, Grossarenic Paleudult [30]. Upper soil surface horizons to a depth of approximately 100–120 cm are classified as sands. Deeper horizons have sandy loam to sandy clay loam textures. Previous vegetation was a longleaf pine (*Pinus palustris* Mill) plantation. Following harvest, site preparation consisted of debris removal and tillage. In the spring of 2000, 3.36 Mg per hectare of granular lime was applied to the soil with the goal of raising surface soil pH to 6.5. After application, additional soil sampling demonstrated soil pH increased in surface soil horizons to approximately 5.8. Additional information on site characteristics and site preparation treatments is outlined in Coleman et al. [31].

2.2. Plant material

A total 31 *Populus* clones (comprised of both pure species and hybrids) were planted at the study site (Table 1). Clones were obtained from commercial nurseries, government and industry research programs, and universities. Clones chosen represented a range of growing regions, genotypes, and hybrid crosses. Emphasis was placed on obtaining clones that were derived from southern genetic sources that could be well-adapted to these site conditions. Thirteen of the 31 clones tested were *P. deltoides* clones derived from Mississippi and an additional six *P. deltoides* clones were derived from Texas or Arkansas genetic sources. Two of the hybrid clones, 15-29 and 184-411 were *Populus trichocarpa* × *Populus deltoides* hybrids (abbreviated as T × D hybrids) with the *P. deltoides* parent originating in Mississippi and Oklahoma respectively. Hybrid origin designation follows the pattern; female parent clone (origin) × male parent clone (origin).

2.3. Study design and treatments

Dormant hardwood cuttings were obtained from each source and stored at 3 °C. Cuttings were transferred from cold storage and soaked in water for 48 h to promote optimum rooting [32]. The statistical design utilized in this study was a randomized complete block design with two replications. Within each

Table 1 – Clones included in the current test and their parentage if known. These clones were chosen to represent a range of regions and genotypes, with particular emphasis on clones reported or expected to do well in the southeastern United States. Table is adapted from Ref. [29].

Clone	Parentage	Origin or parentage (if known)
WV94	<i>P. deltoides</i>	Issaquena Co., MS × Issaquena Co., MS
WV99	<i>P. deltoides</i>	Issaquena Co., MS
WV316	<i>P. deltoides</i>	Issaquena Co., MS
WV415	<i>P. deltoides</i>	Washington Co., MS
WV416	<i>P. deltoides</i>	Washington Co., MS
ST66	<i>P. deltoides</i>	Issaquena Co., MS
ST70	<i>P. deltoides</i>	Issaquena Co., MS
ST71	<i>P. deltoides</i>	Issaquena Co., MS
ST109	<i>P. deltoides</i>	Bolivar Co., MS
110531	<i>P. deltoides</i>	Bolivar Co., MS
110804	<i>P. deltoides</i>	Bolivar Co., MS
112127	<i>P. deltoides</i>	Clairborne Co., MS
112830	<i>P. deltoides</i>	Wilkinson Co., MS
ST260	<i>P. deltoides</i>	Brazos County, TX
ST261	<i>P. deltoides</i>	Brazos County, TX
ST264	<i>P. deltoides</i>	Unknown eastern TX Co.
S7C1	<i>P. deltoides</i>	Brazos County, TX
S7C15	<i>P. deltoides</i>	Brazos County, TX
S13C20	<i>P. deltoides</i>	Miller County, AR
Kentucky 8	<i>P. deltoides</i>	Unknown Kentucky County
7300502	<i>P. deltoides</i>	Pulaski Co., IL
7302801	<i>P. deltoides</i>	Alexander Co., IL
D105	<i>P. deltoides</i>	Selection of C. Mohn, University of Minnesota
15-29	<i>P. trichocarpa</i> × <i>P. deltoides</i>	Chi 80-1 (Chilliwack, BC, Canada) × ST1 (Issaquena Co., MS)
52-225	<i>P. trichocarpa</i> × <i>P. deltoides</i>	GF93-968 (Snohomish Co., WA) × ILL 101 (Perry Co., IL)
184-411	<i>P. trichocarpa</i> × <i>P. deltoides</i>	Ran 91-568 (Cowlitz County, WA) × OK 17-10 (Morton Co., KS)
311-93	<i>P. trichocarpa</i> × <i>P. nigra</i>	NIS 8-1046 (Pierce Co., WA) × unknown (Loire Valley, France)
Eridano	<i>P. deltoides</i> × <i>P. maximowiczii</i>	Unknown parent France × unknown parent Japan
OP367	<i>P. deltoides</i> × <i>P. nigra</i>	Unknown parent clone origins, bred in Oxford Co., ME
I45/51	<i>P. deltoides</i> × <i>P. nigra</i>	Unknown parent clone origins, bred in Italy
NM6	<i>P. nigra</i> × <i>P. maximowiczii</i>	Unknown parent clone origins, bred in Germany

replication, each clone was represented by either 8 or 16 individual-tree block plots. Due to limited material availability, clones 110531, 112127, ST70, ST71, ST109, and ST260 were planted in eight-tree plots (2 rows of 4 trees); all others were planted in 16-tree plots. The test site was planted on 22 April 2001. Tree spacing was 2.5×2.5 m (1600 ha^{-1}). Two border rows of *P. deltoides* clone WV94 surrounded each block to minimize edge effects. Trees were irrigated up to 3.0 cm per week based on ambient rainfall, soil moisture holding capacity, and calculated evaporative demands. Environmental parameters were collected on-site with a fully automated weather station. All plots were fertilized once per week from April 1 through September 30 (2001 through 2008) with liquid fertilizer applied through the irrigation system. Trees were not irrigated or fertilized in 2009 or 2010 (plantation ages 9 and 10). Annual nitrogen application rates were 160 kg per hectare. All nutrients were applied in the form of 7–0–7 fertilizer in year 1 through 8. The fertilizer blend also contained potassium, calcium, magnesium, and a blend of micronutrients. We applied oxyflourfen (Goal 2XLs, Rohm and Haas, Philadelphia, PA) in the spring and glyphosate (Roundup PRO, Monsanto Corp., St. Louis, MO) as needed according to label directions for weed control. At least two directed spray applications of glyphosate were applied in the early years of this study (ages 1–3) with single applications occurring at ages 4 through 7. Following crown closure, less frequent applications were needed to reduce competition. No weed control was applied at ages 8 through 10, but cover of competing herbaceous vegetation was estimated to be less than 10% at ages 9 and 10 (D.J. Kaczmarek, personal observation).

2.4. Growth measurements

Total tree survival was recorded in fall following the 1st, 2nd, 3rd, and 10th growing seasons. For each of these measurements periods, tree heights were measured in meters. Following the 1st growing season, basal diameter (BD) at 10 cm was measured. Following the 2nd, 3rd, and 10th growing seasons, stem diameter at 1.37 m height (Referred to as diameter at breast height or DBH) was measured. Aboveground stem volume index (hereafter referred to as “volume”) was calculated as basal diameter squared \times height (cubic meters) for year 1 or DBH squared \times height for years 2, 3, and 10.

2.5. Pest and pathogen assessments

Susceptibility to insect pests and diseases was assessed at ages 2 and 3. Foliar damage caused by cottonwood leaf beetle (*Chrysomela scripta*) and poplar leaf rust (*Melampsora medusae*) was visually assessed and scored for all clones several times each growing season. *C. scripta* defoliation was rated on a 0 to 4 rating scale where 0 equals no *C. scripta* defoliation and 4 equals severe (greater than 75%) defoliation and/or terminal mortality. Leaf rust was assessed based on rust intensity and percent infestation. Full details of assessment protocols are described in Coyle et al. [33].

2.6. Statistical analyses

Standard ANOVA was utilized to determine if clonal differences in growth parameters existed at age 3 and 10. If clonal

differences were detected at the 5% level of significance, then mean separations were performed using Tukey's HSD test at the 5% level. To determine the relationships between survival measurements made at ages 1, 2, 3, and 10, Pearson Correlation Coefficients were calculated. The same procedure was used to determine the nature of the relationships for all growth parameters measured at ages 1, 2, 3, and 10. Simple linear regression models were developed to illustrate the relationship between age 3 and age 10 survival for each clone and for the relationship between age 3 and age 10 volume index for each clone. For each of these regressions, coefficients of determination were calculated. To understand potential impacts of insect and disease on growth in this study, the same approach described above was used to evaluate the consistency of insect and disease assessments at ages 2 and 3. When this relationship was defined, the impact of age 3 insect and disease assessments on age 10 volume was assessed. All statistical analyses were completed using the JMP statistical analysis software package (SAS Institute, Cary, NC).

3. Results

3.1. Survival

First-year survival varied widely among clones ranging from 100% for I45/51 to a low of 7% for clone ST70 (Table 2). Ten of the clones tested had survival rates less than 50% while eight of the clones tested had first-year survival rates exceeding 75%. Second and third-year survival were virtually unchanged from first-year survival rates (Table 2). Correlation coefficients for first and second-year and first and third-year survival were 0.998 and 0.995 (Table 3). Only four individuals died between the end of the first and end of the third growing seasons. Between the end of the 3rd and the end of the 10th growing seasons mortality increased for many of the clones. Age 10 survival ranged from 97% for clone Eridano to 0% for clone ST70. Clones Eridano, OP367, S7C15 and WV416 all had survival rates exceeding 75% at age 10. There were relatively strong positive relationships between survival after the 3rd and 10th growing seasons (correlation coefficients of 0.772, Table 3). The relationship between age 10 survival and age 3 survival remains relatively strong with coefficients of determination of 0.60 ($P < 0.0001$, Fig. 1). Clones I45/51, NM6, 311-93, ST109, and ST261 all exhibited survival decreases exceeding 40 percentage points between ages 3 and 10 (Fig. 1). Thirteen of the clones in the test exhibited survival decrease of less than 10 percentage points between ages 3 and 10. Survival assessments at age 1 were only slightly less related to age 10 survival compared to the relationship between age 3 and 10 survival. Correlation coefficients for first year and 10th year survival were 0.757 (Table 3).

3.2. Growth

At both ages 3 and 10, height, diameter, and volume growth differed significantly by clone ($P < 0.0001$ for all traits). At age 3, mean clonal heights varied from approximately 2.3 m for clone D105 to 5.4 m for clone 184-411 (Table 4). Mean heights exceeded 4 m for clones 184-411, WV416, 52-225, and Kentucky

Table 2 – Clonal survival percentages and their relative rankings among all clones at ages 1, 2, 3, and 10. Clones are arranged in decreasing survival percentages based on age 10 survival.

Clone	Age 1 survival	Age 1 rank	Age 2 survival	Age 2 rank	Age 3 survival	Age 3 rank	Age 10 survival	Age 10 rank
Eridano	97	2	97	2	97	2	97	1
OP367	97	2	97	2	97	2	91	2
S7C15	91	6	91	6	91	6	78	3
WV416	81	7	81	7	81	7	78	3
184-411	72	9	72	9	72	9	72	5
ST260	81	7	81	7	75	8	69	6
52-225	72	9	69	10	69	10	69	6
NM6	97	2	97	2	97	2	50	8
WV99	56	15	56	14	56	14	50	8
7300502	69	11	69	10	69	10	47	10
15-29	66	12	63	12	63	12	47	10
112127	63	13	56	14	56	14	44	12
Kentucky 8	50	17	50	17	50	16	41	13
ST71	50	17	50	17	50	16	38	14
I45/51	100	1	100	1	100	1	34	15
WV415	41	22	41	22	41	22	34	15
311-93	97	2	97	2	97	2	31	17
WV94	63	13	63	12	63	12	31	17
7302801	50	17	50	17	50	16	25	19
S13C20	34	25	34	25	34	24	25	19
ST66	31	26	31	26	31	25	22	21
110531	50	17	50	17	50	16	19	22
ST264	38	23	38	23	38	23	19	22
D105	38	23	38	23	28	27	19	22
110804	31	26	31	26	31	25	16	25
ST109	50	17	44	17	44	21	13	26
WV316	16	30	16	30	16	30	13	26
S7C1	19	28	19	28	19	28	9	28
112830	19	28	19	28	19	28	9	28
ST261	53	16	53	16	47	20	3	30
ST70	7	31	7	31	7	31	0	31

8. Mean diameter growth followed similar trends to height growth with the tallest clones also having the greatest DBH growth. These two variables were highly correlated ($r = 0.89$, Table 5). Total seedling volume index followed similar trends with clones 184-411, WV416, and 52-225 exhibiting the largest age 3 volume indices.

Mean clonal heights at age 10 varied from approximately 4.3 m for clone 110804 to 12.2 m for clone 184-411. Mean heights of clones 184-411, WV416, and 52-225 all exceeded 10 m at age 10 (Table 6). Mean DBH at age 10 ranged from approximately 4.3 cm for clone I45/51 to 12.1 cm for clone 184-411. As with age 3 measures, age 10 heights and DBH's were highly correlated ($r = 0.93$). Age 10 plant volume indices were greatest for clones 184-411, WV416, and 52-225.

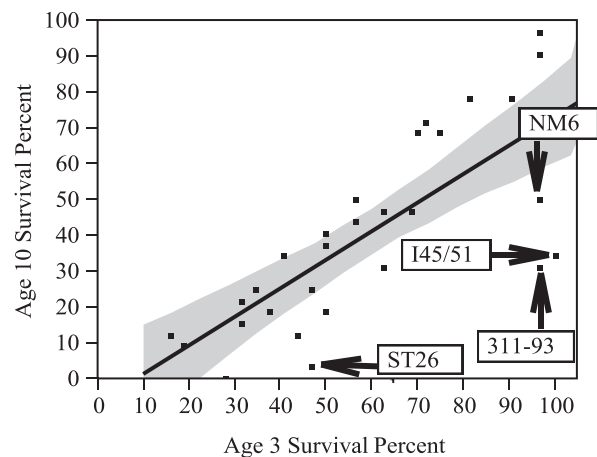


Fig. 1 – Linear regression equation developed for the relationship between survival at ages 3 and 10. Each point indicates mean survival percentage of each individual clone. The R^2 value is 0.60 and the regression equation is significant at the 1% level. The developed regression lines include all data points. Individual points are indicated for clones NM6, I45/51, 311-93, and ST26 since these clones represent large changes in survival between ages 3 and 10. The 95% confidence interval is shown shaded in gray surrounding the regression line.

Table 3 – Correlations matrix between survival percentages at ages 1, 2, 3, and 10. Correlations followed by a triple asterisk (*) are significant at the 0.1% level.**

	Survival age 1	Survival age 2	Survival age 3	Survival age 10
Survival age 1		0.998***	0.995***	0.757***
Survival age 2			0.996***	0.758***
Survival age 3				0.772***
Survival age 10				

Table 6 – Mean height (m), DBH (cm), and calculated volume index (m³) for all *Populus* clones at age 10. Relative rankings for each growth trait for each clone are listed to the right of the growth trait column. Clones are arranged from highest to lowest order based on age 10 volume index. For each growth parameter (columns) clones followed by the same letter do not differ significantly from one another at the 5% level.

Clone	Height (m)	Height rank	DBH (cm)	DBH rank	Volume index (m ³)	Volume index rank
184-411	12.16	a	12.12	a	0.20207	1
WV416	10.47	ab	11.49	ab	0.15359	2
52-225	10.35	abc	11.16	abc	0.13998	3
112127	8.26	bcde	10.01	abcd	0.09190	4
Eridano	8.92	abcd	9.56	abcdef	0.08692	5
ST66	8.15	bcde	9.63	abcde	0.08020	6
ST264	7.95	bcdef	9.38	abcdef	0.07485	7
WV99	8.51	bcde	8.07	abcdefg	0.06293	8
S7C15	7.54	bcdefg	7.75	abcdefg	0.05749	9
7302801	7.73	bcdefg	7.69	abcdefg	0.05712	10
S13C20	6.35	defg	7.65	abcdefg	0.05140	11
S7C1	6.87	cdefg	7.93	abcdefg	0.04959	12
Kentucky 8	7.00	bcdefg	7.86	abcdefg	0.04878	13
ST260	6.87	cdefg	7.67	abcdefg	0.04529	14
WV316	6.33	defg	7.68	abcdefg	0.04109	15
7300502	6.63	defg	6.78	abcdefg	0.03920	16
WV415	6.53	defg	6.77	abcdefg	0.03449	17
WV94	5.73	defg	7.23	abcdefg	0.03259	18
ST261	5.93	defg	7.01	abcdefg	0.03002	19
110531	6.71	defg	5.98	cdefg	0.02847	20
15-29	6.17	defg	6.51	bcdefg	0.02807	21
ST71	6.38	defg	6.16	bcdefg	0.02723	22
112830	6.27	defg	5.46	defg	0.02043	23
NM6	5.11	efg	5.10	defg	0.01660	24
OP367	5.49	defg	4.44	efg	0.01607	25
110804	4.34	g	5.30	defg	0.01313	26
ST109	4.64	defg	4.59	cdefg	0.00838	27
311-93	4.40	fg	4.28	fg	0.00816	28
I45/51	4.47	fg	3.41	g	0.00643	29

improvement in correlations between age 3 growth parameters and age 10 volume indices. Correlation coefficients are 0.68, 0.67, and 0.80.

There are moderately strong correlations between age 10 volumes and age 3 volume indices (Fig. 2, $R^2 = 0.64$). This indicates that age 10 volumes can be reasonably predicted based on age 3 volume indices. Age 10 volumes were substantially lower than predicted for clones 311-93 and 15-29. These clones were among the largest clones at age 3, but age 10 volumes dropped to moderate (clone 15-29) to very low (Clone 311-93). Volume ranks for these clones dropped from #5 and #8 at age 3 to #21 and #31 at age 10 for clones 15-29 and 311-93 respectively (Tables 4 and 6). Clones ST66 and Eridano exhibited relatively large age 10 volume increases compared to their age 3 volume rankings. Age 10 volume ranks increased to #6 and #5 for clones ST66 and Eridano compared to age 3 volume ranks of #24 and #13. These results suggest that while overall clonal volume growth can be rather accurately estimated based on age 3 volume measures, there will be individual clones that exhibit either longer-term over or under performance based on their age 3 volumes. The most rapidly growing clones in this test, clone 184-411, had volume growth at age 3 that was substantially greater than the remainder of clones in the test. Clones 184-411, WV416, and 52-225 ranked #1, #2, and #3 for volume at age 3 (Table 2) and their volume rankings at age 10 remained unchanged (Table 6).

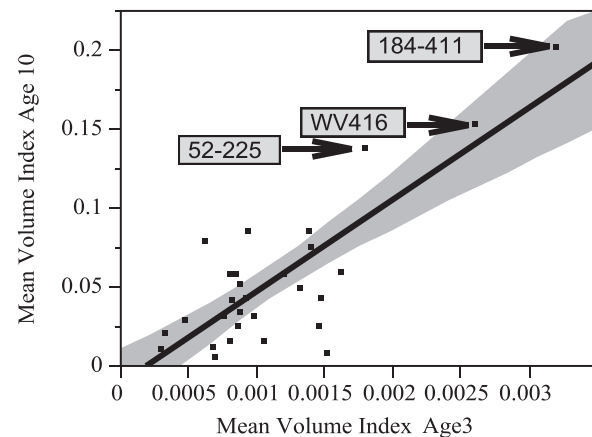


Fig. 2 – Linear regression equation developed for the relationship between volume index at ages 3 and 10. Each point indicates mean volume index of each of each individual clone. The R^2 value is 0.64 and the regression equation is significant at the 1% level. The developed regression line includes all data points. Individual points are indicated for clones 184-411, WV416, and 52-225, the highest ranking clones in this test based on age 10 volume indices. The 95% confidence interval is shown shaded in gray surrounding the regression line.

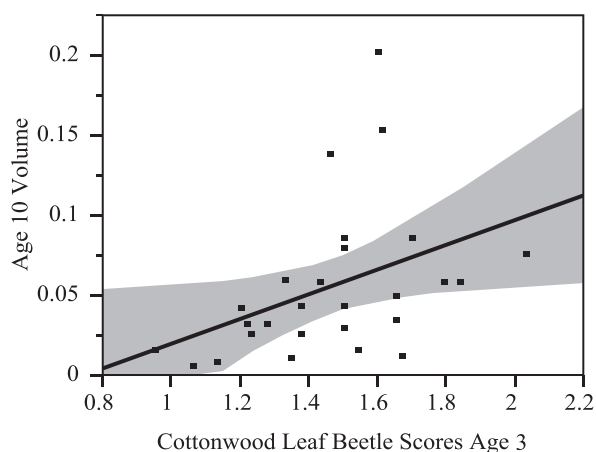


Fig. 3 – Linear regression equation developed for the relationship between cottonwood leaf beetle damage scores at age 3 and volume index at age 10. Each point indicates the mean damage score and mean volume index of each of each individual clone. The R^2 value is 0.17 and the regression equation is significant at the 5% level. The developed regression line includes all data points. The 95% confidence interval is shown shaded in gray surrounding the regression line.

3.3. Pest and pathogen assessments

Overall damage from cottonwood leaf beetle and cottonwood leaf rust would be considered low in this test but there were clonal differences in susceptibility to both damaging agents [33]. There was a strong positive relationship between clonal cottonwood leaf rust scores measured in years 2 and 3 ($P < 0.0001$, $R^2 = 0.96$). Similar consistency occurred for cottonwood leaf beetle damage measured in years 2 and 3, but this relationship was generally weaker than rust score consistency at ages 2 and 3 ($P < 0.0001$, $R^2 = 0.53$). There was no significant relationship between clonal rust scores measured at age 3 and age 10 volume growth ($P = 0.158$). There was a statistically significant, but very weak positive relationship between cottonwood leaf beetle damage measured at age 3 and age 10 volumes ($P = 0.034$, $R^2 = 0.17$, Fig. 3).

4. Discussion

4.1. Survival

Survival is important for intensively managed *Populus* production [28]. In this test, there was wide variation in first-year survival among clones ranging from 0% to 100% (Table 2). In the first three years of the study, virtually all mortality occurred in the first growing season and almost no mortality occurred in the second or third growing seasons. This resulted in strong correlations between first, second, and third year survival (Table 3). These results strongly suggest that mortality was caused by poor initial rooting of a significant percentage of these clones. Rooting ability can be one of the primary factors evaluated during clonal screening processes. Rooting ability can often vary among general species and

interspecific crosses, but general clonal variation among individual species or species groups can occur [15,34–36]. Clonal survival in this study could also have been affected by the upland site conditions since many *Populus* clones have been more widely tested on alluvial sites. An additional factor that may have contributed to variation in rooting may have been the original source of the cutting material. These potential nursery cultural effects can influence initial establishment success. Cutting size [32] and location source [37] have also been shown to impact tree survival and growth. Ideally, cuttings from all sources would be obtained and grown in a common cutting orchard and once this cutting orchard produced usable quantities of cuttings, new tests would be established using these cuttings. The disadvantage of this approach is the time delay associated with new cutting orchard establishment. A potential alternative that has been examined is the production of in-leaf cottonwood planting stock in containers using cottonwood whip-tip material. This procedure allows the propagation of a relatively large number of plants from limited, small diameter, branch tip material. This also eliminates the time delay associated with new cutting orchard establishment and production and reduces potential carry over effects from different cutting orchards since all plants are produced under common nursery conditions. This approach has been used for a number of cottonwood clones and plants propagated in this manner have survival and growth equal to or greater than tradition cutting propagation (Kaczmarek et al., unpublished data).

Between the end of the 3rd and the end of the 10th growing seasons, mortality increased for many of the clones. Four clones (Eridano, OP367, S7C15 and WV416) had survival rates exceeding 75% at age 10 (Table 2). Thirteen of the clones in the test exhibited relatively small survival changes of less than 10 percentage points between ages 3 and 10 (Table 2). There were four individual clones, I45/51, NM6, 311-93, and ST261, that exhibited survival decreases exceeding 40 percentage points between ages 3 and 10 (Fig. 1). These dramatic drops in survival suggest that longer-term adaptability of these clones on this site was impaired. These four clones represent three widely divergent hybrid crosses plus one additional native east Texas cottonwood clone. Clones I45/51, NM6, and 311-93 were all clones with very high initial survival (greater than 97%) while age 3 survival for clone ST261 was mediocre (47%), and decreased to 3% at age 10.

Septoria musiva is a significant disease threat to many *Populus* species and hybrids and is generally most prevalent in the northeastern and central United States. In these regions, clonal selections can be strongly influenced by *Septoria* susceptibility [34,38]. In the current study, it was not possible to identify the causes of the mortality and no visible stem cankers were observed. Mortality caused by *Septoria* is often most prevalent in *P. trichocarpa* and hybrids with *P. trichocarpa* appear to be especially susceptible [39,40]. When *P. trichocarpa* is crossed with *P. deltoides*, the *Septoria* susceptibility appears to be dominant to the resistance of *P. deltoides* and the resulting F_1 hybrids appear to be uniformly susceptible to *Septoria* [40]. Clones 52-225 and 184-411, both $T \times D$ hybrid clones, ranked 5th and 6th for age 10 survival and all trees surviving at the end of the first growing season survived through age 10. In previous testing, clone NM6 has been found

to be more resistant to *Septoria* [34] and has been included in many test series as a commercial check [38]. In the current test, it was one of the clones exhibiting the greatest decreases in survival between ages 3 and 10. The lack of visible *Septoria* symptoms, the low mortality of T × D hybrid clones, and the demonstrated disease resistance to *Septoria* of NM6 in other climates suggests that the decrease in survival is due to poor adaptation to southern test conditions rather than disease per se.

The relatively strong correlations between age 1 and age 10 survival suggest that for most clones, initial rooting will be the greatest limitation to survival in these plantations. The presence of clones such as I45/51, NM6, 311-93, and ST261 which all exhibit extensive mortality later in plantation development indicates that there are clones which will prove to be poorly adapted to these specific test conditions. These clones may exhibit delayed mortality after initial plantation establishment success. These mortality patterns may be difficult to predict unless the causes of the mortality can be identified. This may not be a significant problem for initial clonal screening efforts, but does suggest that more vigorous testing should be undertaken before commercial deployment decisions are made. For most clones in the current test, age 1 survival is as accurate as survival measures at ages 2 or 3. In this sense, age 1 survival is really a proxy for clonal rooting success. In order to select the most promising clones for further testing and potential commercial deployment, screening for rooting ability, growth, and longer-term adaptability would be needed. Rooting screens could be conducted to identify those clones which established at sufficient percentages that would make future commercial deployment possible. Alternately, a large number of potential clones could be screened for growth for three years in the field and only those possessing desirable traits could be further screened for rooting potential and longer-term adaptability.

4.2. Growth

The wide variation in growth rates at early testing stages and at age 10 would be expected given the broad range of clones tested. Age three volumes exhibited an approximate 14-fold difference from the lowest ranked clone (D105) to the highest ranked clone (184-411). At age 10, these volume differences increased to approximately 32-fold when volume growth of the highest ranked clone (184-411) is compared to the lowest ranked clone (I45/51). These results suggest that a small percentage of the included clones (approximately 10%) exhibit growth rates that are far superior to the majority of clones in the test. The three top clones, 184-411, WV416, and 52-225, exhibit volumes approximately 4-fold, 3-fold, and 2½-fold greater than the mean volume indices of all 31 clones in the test at age 10. This range of variation among *Populus* clones is not unexpected considering the limited planting that has occurred with most of these clones in this region. In tests conducted in other regions, productivity differences ranging from approximately 35% greater to 2.3-fold greater occurred when the best identified clone in a test was compared to growth of the check clone [38]. Zalesny et al., [41], demonstrated productivity differences of approximately 3.4, 6.6, and 10-fold among the clones at each individual test site. In this

test series, genotype × environment interactions were significant factors affecting growth. It was also possible to identify generalist clones that performed well under all test conditions and a group of specialist clones that exhibited exceptional performance only under specific test conditions [41].

In the Pacific Northwest, extensive breeding work has taken place and this has led to the deployment of operational plantation programs [27,42]. In many *Populus* plantations in the region, hybrids between species, often T × D hybrids, possess superior traits to either parental species [43–45]. In two separate tests of 691 and 381 clones representing *P. trichocarpa* and various hybrids involving *P. trichocarpa* and *P. deltoides*, volume production at age 4 varied from approximately 200–300-fold when growth of the best clones was compared to the slowest growing clones [43]. At both test sites, F₁ hybrids were the most productive with volume production of the hybrids approximately 2–10 times greater than growth of pure *P. deltoides* or *P. trichocarpa* clones. In our test, it is not clear whether eastern cottonwood or T × D hybrids would be the most productive under these conditions. Commercial T × D hybrids including clones, 184-411, 15-29, and 52-225 exhibited variable performance at the South Carolina test site. While clones 184-411 and 52-225 ranked highly in this test, clone 15-29 ranked #21 for total volume index at age 10. Eastern cottonwood clone WV416 ranked second for volume at age 10 suggesting that selected clones of this species could be as productive under these test conditions as the top performing T × D hybrids tested. It is not possible to generalize performance potential among broad classes of *Populus* species or hybrids in the current test and performance appears to be a function of specific clonal characteristics rather than overall species or hybrid traits.

While *Populus* clonal selection influences productivity, there are also wide relative differences in productivity across regions and among various planting sites and management regimes within a given region. We attempted to include commercially available clones with known growth performance from other regions to help in interpreting growth responses in the current study. In Western Washington T × D hybrids including clone 15-29 were established on two test sites. Age six heights and diameters were approximately 20 m and 20 cm and 18 m and 13 cm [27]. In comparison, in our South Carolina test, clone 15-29 had heights and diameters of 6.2 m and 6.5 cm at age 10. In Oregon, tests including clones 184-411, 52-225, 15-29, and OP367 were established on two sites. Clonal differences in growth existed, but these differences were relatively small compared to the very large differences attributable to site and management. Heights and DBH's at age six were approximately 12.8 m and 15 cm at the low productivity site and 21 m–27 m and 17 cm–25 cm at the high productivity site [46]. In other tests in the Pacific Northwest, volume production on more productive sites was approximately 5 times greater than volume on the lower productivity site [43]. These wide variations in growth among the test sites suggest factors other than clonal selection alone must be identified and optimized to fully capture the high inherent productivity potential of *Populus*.

Eastern cottonwood productivity on Mississippi River floodplain sites can be high and offer attractive potential for wood fiber production [47,48]. Nelson et al., [48], reported age 8

heights and diameters of approximately 17.6 m and 19.4 cm for eastern cottonwood. These growth rates are much greater than the rates we were able to capture in the current study even though some of the clones deployed represent advanced breeding efforts and substantial growth advantages over unimproved wild selections [21,48]. At age 10 in the current study, the most rapidly growing eastern cottonwood clone, WV416, was 10.5 m tall with a DBH of 11.5 cm. These variable growth rates of eastern cottonwood are not uncommon when cottonwood is planted outside of its traditional site types even if resource availability is altered. Lockaby et al. [49] established a cottonwood factorial experiment with water and resource availability altered in the Upper Coastal Plain of Alabama. At age four, heights and DBH's ranged from approximately 3.6 m and 3.5 cm in the water and nutrient control treatments to 5.4 m and 6.0 cm in the fertilized and irrigated treatments. These are similar to the growth rates obtained in the current study but far lower than growth rates that can be obtained [47,48].

Climatic conditions across the lower Mississippi River Floodplain are similar to conditions across central South Carolina. It was assumed that eastern cottonwood clones developed from Mississippi or eastern Texas sources would be adapted to the climatic regimes in South Carolina. Direct comparisons of climatic variables in west-central Mississippi and those at the Savannah River Site suggest close matches of key environmental variables. As an example, Jackson, Mississippi is in close proximity to the point of origin of many of the eastern cottonwood clones tested in the current study. The climate in Jackson, MS closely matches the climate at the Savannah River Site previously described. At Jackson, MS the annual growing season averages 228 days (March 26 to November 9). Daily high and low summer temperatures (May through September) average 31.4 °C and 19.4 °C respectively. Winter (December through February) daily high and low temperatures average 14.9 °C and 2.5 °C respectively. Mean annual precipitation is 135.3 cm with rainfall fairly well-distributed throughout the year. Rainfall between March and October averages 86.3 cm [50]. These comparisons suggest, on average, the climate in west-central South Carolina closely corresponds to the climate in Mississippi that supports higher growth rates on the identical clones. This suggests that site conditions in the current test, not limiting climatic conditions, were responsible for lower growth rates of these elite eastern cottonwood clones. These potential site and cultural sensitivities of *Populus* have been identified by forest managers [11] and concerted breeding efforts are underway to develop genotypes more suitable for upland culture in the Southeastern United States. These efforts include traditional breeding approaches [51] and genetic modifications to increase growth, stress tolerance and site adaptability [52].

Examination of cottonwood leaf beetle and poplar leaf rust scores at ages 2 and 3 suggest that it is unlikely excessive insect or disease pressure limited overall productivity in this test [33]. Leaf rust scores were highly correlated in years 2 and 3, but neither individual score was correlated with age 10 volumes. Cottonwood leaf beetle scores were less highly correlated in years 2 and 3 than leaf rust scores, but the relationship was still significant. Age 10 growth was positively correlated with age 3 cottonwood leaf beetle damage assessments suggesting that,

on average, clones with higher cottonwood leaf beetle predation tended to be the more rapidly growing clones in the test. While significant, this relationship was still very weak ($R^2 = 0.17$) suggesting this factor does not explain a large amount of variation in growth rates measured in this test.

The more modest growth rates in the current study compared to higher growth rates measured in other regions are worth careful consideration. Identifying the causes for this reduced growth is more difficult. Limited experience with these clones under upland condition in the southeastern United States further complicates the issue. Climatic conditions in South Carolina closely correspond to weather conditions in central Mississippi near the point of origin for many of the eastern cottonwood clones tested so this seems an unlikely factor. While cottonwood leaf beetle and cottonwood leaf rust were present in the test, the general low damage rankings and poor to non-existent relationships to long-term growth at the site suggest that it is unlikely that this is the primary cause of reduced growth rates. We did not collect and analyze foliar samples in this study, but these measures would be warranted in future studies to begin compiling a database of foliar nutrient norms for clones of interest under Southeastern cultural conditions. Past concerns with *Populus* site adaptability [11] and concerted breeding [51] and transformation efforts [52] to increase adaptability and stress tolerances suggest this is the most probable cause of reduced growth in this study. This variation in growth when *Populus* clones are planted on a range of sites with varying cultural conditions suggests this will require sustained research emphasis.

The relatively strong consistency of growth measured at age three compared to age ten suggests that it is possible to make clonal selections based on volume growth at age three under these test conditions. While there are moderate changes in volume rankings between ages 3 and 10, most of these changes involve movement of moderate to poorly performing clones and this movement would not prevent the identification and selection of superior clones such as 184-411, WV416, and 52-225 at age three. These clones ranked number 1, 2, and 3 for volume at age three and their relative rankings were unchanged at age 10. Selections based on height, diameter, or volume at ages one or two would be less effective than selections based on age three volume index. Selections based on age two growth parameters are no better than selection based on age one growth parameters, but correlations between age three volumes and age 10 volumes increase to approximately 80%. These general patterns of age-to-age correlations have been found in other studies with *Populus*. Age five growth in *Populus* hybrids was not correlated with growth measured at the end of the first growing season, but relationships between growth after the second and fifth growing seasons did improve [53]. Hansen et al. [54] found similar trends with very weak relationships between first-year growth and age 12 growth. Much stronger relationships were found between age three and age 12 growth. In Argentina, eastern cottonwood and hybrid poplar growth after one year was poorly correlated with age 10 growth [55]. There was however a much stronger relationship between age three and age 10 growth. Approximately 30 percent of the clones in the trial had large rank changes between ages 3 and 10 while the remaining clones had very stable performance with increasing plantation

age [55]. This pattern is similar to what we measured in the current test. If the overall goal of any clonal screening program would be only to identify those clones with the greatest growth potential then selections at age three would be adequate. Selection of the just the top 10% of clones based on age three volumes would have correctly identified clones 184-411, WV416, and 52-225.

5. Conclusions

In the current study, as in many other studies utilizing *Populus* selections across the United States, selection of the appropriate clones can have large impacts on potential productivity. Under our testing conditions, age-to-age correlations suggest that for most clones, survival at age 10 was strongly correlated with first-year survival. For growth, it is possible to make clonal selections based on age three volumes and most rank changes that occur involve changes in moderate to poorly performing clones. Three clones with the greatest age three volumes, 184-411, WV416, and 52-225, also ranked 1st, 2nd, and 3rd for volume at age 10. These top performing clones are both T × D hybrids (184-411 and 52-225) and a pure *Populus deltoides* clone (WV416). Performance in the current test appears to be a function of specific clonal characteristics rather than overall species or hybrid traits.

Across large regions of the United States, wide variations in growth rates have been found and in many cases potential yields within a given region can be highly dependent upon site conditions and management regimes. Growth rates obtained in the current study are generally less than the maximum growth rates of the same *Populus* clones obtained in various tests. This suggests that site characteristics or the specific silvicultural regimes utilized in this test did not capture the full growth potential of the *Populus* clones tested. We believe individual site conditions posed the most likely explanation for these moderate growth rates. In order to develop *Populus* as a commercially viable bioenergy crop for the southeastern United States, concurrent research to identify site requirements, site adaptability, and appropriate management regimes is needed to capture the full potential of the species. While further breeding and clonal selection will be critically important, it is unlikely that this alone will be sufficient to provide the desired productivity unless key ecophysiological processes can be modified.

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