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Genetic Control of Growth Traits and Inheritance of Resistance to Bacterial Leaf Scorch in American Sycamore

By J. P. ADAMS[1),*)], R. J. ROUSSEAU[2)] and T. D. LEININGER[3)]

(Received 13th April 2012)

Abstract

Open-pollinated progeny tests of American sycamore (*Platanus occidentalis* L.), which included 55 open-pollinated families selected from several prior Westvāco progeny tests and seed orchards and six control-pollinated families were established in 2002 and 2003. The half-sibling families were planted at two sites in western Kentucky and southeastern Missouri. The six full-sibling families, generated from selections based on exhibition of parental disease resistance and susceptibility to a variety of diseases, were also planted near Stoneville, MS at the US Forest Service Center for Bottomland Hardwoods Research. All full-sibling families planted at the Stoneville site were inoculated in the fall 2002 with the leaf-scorch-causing bacterium, *Xylella fastidiosa*. Diameter and height data for trees of both half- and full-sibling families were recorded at ages three, five, seven, and nine at the various sites. Bacterial leaf scorch disease

1) University of Arkansas, School of Forest Resources, Arkansas Forest Resources Center, Monticello, AR, USA.
2) Mississippi State University, Department of Forestry, Starkville, Mississippi, USA.
3) USDA Forest Service, Center for Bottomland Hardwoods Research, Stoneville, Mississippi, USA.
*) Communicating Author: JOSHUA ADAMS. P.O. Box 3468, Monticello, AR 71656, Tel: (870)460-1348.
E-Mail: adamsj@uamont.edu

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

presence was also recorded as symptomatic or asymptomatic/mildly symptomatic. Average family heritability across ages was 0.58, 0.50, and 0.55 for height, diameter, and volume, respectively, indicating that increased growth traits can be gained from family selection. In conjunction with derived age-age correlations, selection based on age-five data results in the greatest gain per unit time for age nine gains for half-sibling families. Breeding for bacterial leaf scorch resistance can also be successfully undertaken if proper selection and breeding of two resistant parents are undertaken which can result in a 4.5 fold decrease in the probability in symptoms of offspring by age nine. Results indicate a large potential for increased growth and disease resistance in American sycamore through traditional breeding.

Key words: sycamore, selection, genetic gain, disease resistance, bacterial leaf scorch.

Introduction

American sycamore (*Platanus occidentalis* L.) is a species with broad geographic range that outperforms most fast-growth hardwood species except for various poplars (*Populus* spp.), and has been a target of tree breeding efforts since the 1960s (WITTMER and IMMEL, 1976). Several forest products companies began substantial efforts in breeding to increase specific gravity by increasing ray and fiber volumes and decreasing vessel volumes for use in the pulp and paper industry (JOURDAIN and OLSON, 1984; TAYLOR, 1969). Because of its excellent fiber production, growth rates, and coppice ability, sycamore also was studied for its suitability to produce biomass for bioenergy as a short-rotation alternative to poplar (STEINBECK, 1999; STEINBECK et al., 1972).

Sycamore has been and continues to be identified as one of the main species of interest in the Southeastern US for biomass/bioenergy needs (MERKLE and CUNNINGHAM, 2011; RANNEY et al., 1987; TUSKAN, 1998; WITTMER and IMMEL, 1976). While the species is endemic to the southern United States and should be better adapted to the climate than an introduced species such as a fast-growth hybrid poplar variety, one hindrance to large scale industrial deployment has been the species' susceptibility to a variety of diseases (BRITTON et al., 1998; FILER et al., 1975; LEININGER et al., 2001) including bacterial leaf scorch (BLS) caused by *Xylella fastidiosa* (WELLS et al., 1987). *Xylella fastidiosa* is a Gram-negative, xylem-limited bacterium that was first described as a disease of grapes in 1973 (HOPKINS, 1989; SIMPSON et al., 2000). BRITTON et al. (1998) conducted positive ELISA tests for *X. fastidiosa* from trees in 10 of 11 plantations surveyed in AL, GA, FL, IL, KY, NC, SC and VA, and observed plantations in southern AL to be most severely affected by dieback. Currently, the high probability of volume loss and mortality from this disease, aided by an efficient vector, the glassy-winged sharpshooter (*Homalodisca vitripennis* (Germar) (LEININGER et al., 2004), has limited sycamore as a potential high-yielding short-rotation biomass species.

Disease symptoms on susceptible American sycamore trees begin as yellow zones of leaf blade tissue proximal to leaf vasculature. Leaf tissue mortality progresses to the point where leaves necrotize, turn brown and cup upwards, a condition often called bronzing; whereas petioles remain green or yellow and persistent giving a tree the appearance of having been scorched by fire. Within a few years, symptoms can progress from one or more branches exhibiting dieback initially to many dead branches, to the death of larger limbs, part of the main stem in the crown, and eventually tree death (COOPER et al., 1977). In one study in Mississippi, nine-year old BLS-diseased trees were reduced 26% in height and 27% in diameter growth compared to healthy trees; volumes of diseased trees were 74% less than healthy trees (T. LEININGER, unpublished data). Geneticially-derived mitigation strategies to allow widespread cultivation of American sycamore for pulpwood and biomass for bioenergy likely will be aided by knowledge of the genome of *X. fastidiosa*, which was sequenced using an isolate from a diseased Valencia sweet orange (SIMPSON et al., 2000).

The overall objective of this study was to determine the breeding value of a number of selected sycamore parents and optimal selection techniques for achieving greater disease resistance and volume yield at age nine for inclusion into a potential breeding program. One component of this objective was to evaluate parents for growth traits and BLS symptoms. From these assessments, the second goal was to calculate genetic parameters such as heritability and genetic correlation across ages. Finally, a recommendation for a breeding strategy to mitigate bacterial leaf scorch disease and promote growth was developed.

Material and Methods

Plant Material and Experimental Design

Four test plantings were included in a Sycamore Progeny Test Series established by Westvāco on alluvial and fertigated sites. In 2002, test locations included an alluvial site on Wolf Island, Hickman Co., KY and a fertigated site in Scott Co., MO. In 2003 test locations included an alluvial site on Wolf Island in Mississippi, Co., MO and a fertigated site in Scott, Co., MO. The plantings on in Hickman Co., KY and Mississippi Co., MO sites were on opposing sides of Wolf Island and, for conciseness, are collectively termed the Wolf Island sites and treated as blocks within one site. Seedlings for all test locations were derived from open-pollinated seed collected from 23 parents in the Westvāco High Wood Density Sycamore Seed Orchard, eight parental selections of the Westvāco First-Generation Sycamore Seed Orchard, and 24 individual selections from the 1983–1984 Limited-Range Sycamore Provenance/Progeny Test. In addition, seedlings from six control-pollinated families were established in the 2002 and 2003 plantings. Though plantings spanned different years, both plantings were measured so that they represented the same age of development. Thus, the field layout of trees was considered a randomized block design in which each site was divided into random blocks and individuals from each family were planted in four-tree plots.

The six control-pollinated families were generated from initial parental selections exhibiting disease resistance or susceptibility to a variety of pathogens in which

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

symptoms included leaf bronzing and crown dieback, both symptoms of BLS. Two other common diseases for which test American sycamores were initially screened were canker stain disease caused by the fungus *Ceratocytis fimbriata f. platani* (Ellis and Halst.) JM Walter and Botryosphaeria canker caused by the fungus *Botryosphaeria rhodina* (Cooke) Arx. An assortative mating design using these resistant and susceptible parents resulted in two families representing each combination of resistant by resistant parents (RxR), resistant by susceptible parents (RxS), and susceptible by susceptible parents (SxS), for a total of six families. Parents were selected based on visual symptoms observed in a seed orchard as well as the level of disease severity of the family in a progeny test. These six full-sibling families were incorporated with the half-sibling plantings at the Wolf Island sites and were given to the US Forest Service Center for Bottomland Hardwoods Research for testing near Stoneville, MS. All trees tested (i.e., only full-sibling families planted) in Stoneville were planted in May 2002 as one-year-old bare-root seedlings and the site was inoculated in September 2002 with the leaf-scorch-causing bacterium, *Xylella fastidiosa*. Every other test seedling was inoculated by injecting a slurry of *Xylella fastidiosa* cells grown on an artificial medium into xylem elements using a hypodermic needle.

Diameter at breast height (dbh) and height data were recorded at various ages on each site including ages three, five, seven, and nine (*Table 1*). Volume (cubic meters) was calculated using the volume equation: volume = [0.0000785DBH (cm)^2] x height (m). At all sites, trees were visually inspected for environmental or pathological damage which were used to screen individuals from subsequent analyses of growth traits and only trees greater than 1.37 m. Bacterial leaf scorch disease symptoms on the full-sibling families were recorded as symptomatic, mildly symptomatic, or asymptomatic at age nine on the Stoneville and Wolf Island sites.

Analysis

Diameter and height data from all sites across ages were combined into one dataset. Then the percentage of trees that were asymptomatic or symptomatic was calculated per plot. Finally, the only trees deemed measureable (i.e., they did not have damage codes indicating mortality, crown break, severe dieback from disease, or severe lean) were retained in the final dataset for growth trait analysis. Data were analyzed using SAS PROC MIXED (SAS INSTITUTE, 1999) and the mixed model used was

Table 1. – Ages and sites for which diameter at breast height and stem heights were measured on American sycamore progeny tests.

Age at Measurement	Site[1]
3	Scott Co., MO; Wolf Island, KY[2]
5	Stoneville, MS; Wolf Island, KY
7	Stoneville, MS; Scott Co., MO
9	Stoneville, MS; Wolf Island, KY

[1] The Stoneville, MS site only contained full-sibling families.
[2] Wolf Island sites include separate plantings at Hickman Co., KY and Mississippi Co., MO sites.

$$y_{ijkl} = \mu + \alpha_i + \beta(\alpha)_{j(i)} + \lambda_k + \alpha\lambda_{ik} + e_{ijk} \quad [1]$$

where α was the fixed effect of the ith site, β was the fixed effect of the jth block effect within the ith site, λ was the random effect of the kth family, $\alpha\lambda_{ik}$ was the interaction effect between the ith site and kth family, and e_{ijk} was the within plot variance. BLUPs were used to estimate the solutions for the random effects. For any age with data from only one site (e.g., half-sibling families at ages 5, 7, 9), the model was condensed by removing the site effect, α.

Data for bacterial leaf scorch disease symptoms were analyzed differently. Since occurrence of leaf scorch was extremely rare at the Wolf Island sites, only data from the Stoneville site, which included only full-sibling families, was used in the analysis. Presence or absence of leaf scorch is inherently a binomial trait. Therefore, the data were analyzed with a generalized linear mixed model using SAS PROC GLIMMIX with a specified binomial distribution and logit link function.

$$\log[p/(1-p)]_{ijkl} = \mu + \beta_j + \lambda_k + e_{ijk} \quad [2]$$

In this function, log[p/(1-p)] is the logit function of the symptom's probability expressed by the of the ijklth tree, β was the fixed effect of the jth block effect on the Stoneville site, λ was the random effect of the kth family, and e was the within plot variance. BLUPs were used to estimate the solutions for the random effects and these estimates were then used with an inverse link function (equation 3) to predict the probability of a family to exhibit symptoms.

$$p = \exp[BLUP(\text{genotype})]/[1+\exp(BLUP(\text{genotype}))] \quad [3]$$

A second analysis was conducted by replacing the family component with a breeding-type component, which is a pedigree grouping that divides the families into their parental crosses of RxR, RxS, and SxS.

Narrow-sense individual tree heritability (h^2_i), family heritability (h^2_f), and within-family heritability (h^2_w) were calculated for each growth trait (i.e., height, dbh, and volume) at each measurement age (i.e., 3, 5, 7, and 9) with the estimated variance components from the mixed model (eq. 1) and equations from FALCONER and MACKAY (1996) and NAMKOONG et al. (1966)

$$h^2_i = \frac{4\sigma^2_f}{\sigma^2_p}, \quad [4]$$

$$h^2_f = \frac{\sigma^2_f}{\sigma^2_{p_f}}, \quad [5]$$

$$h^2_w = \frac{3\sigma^2_f}{\frac{\sigma^2_{plot}}{b} + \frac{\sigma^2_e}{bn}}, \quad [6]$$

where: σ^2_f was the variance between families, σ^2_p was the phenotypic variance, $\sigma^2_{p_f}$ was the variance of family means, σ^2_{plot} was the variance among plots, σ^2_e was the variance among individuals within plots, b was the number of blocks, and n was the number of trees per plot. For analysis of full-sibling families, heritability

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

was calculated separately and the constant correction for additive variance was changed to "2". Individual and family heritability standard errors were estimated using the Delta method (LYNCH and WALSH, 1996).

Phenotypic and additive genetic correlation, were calculated. Because each site did not include all families at each age of measurement (e.g., Scott Co. site did not have age nine measurements), this analysis was limited to the Wolf Island sites at age three, five, and nine to accurately estimate age-age correlation. These calculations were based on equations from FALCONER and MACKAY (1996) and standard error estimates using the Delta method (LYNCH and WALSH, 1996). Specifically, Pearson's Product-moment Correlation Coefficients were calculated among trait and age across block using SAS PROC CORR. Additive genetic correlations were calculated by restructuring the data, creating dummy variables which combined the traits, and use of a multivariate model with SAS Proc Mixed using REML. Variance and covariance matrixes were fitted using an uncorrelated covariance structure and appropriate covariance and variance estimates were extracted. These estimates were then used in equation 7 to estimate the genetic age-age correlations; and standard errors of the correlations were estimated using the Delta method (LYNCH and WALSH, 1996).

$$r_{a_1a_2} = \frac{Cov_{a_1a_2}}{\sqrt{Var_{a_1} Var_{a_2}}} \qquad [7]$$

Correlations and heritabilities were used to calculate the correlated response for each juvenile age (i.e., age less than nine) using equations from FALCONER and MACKAY (1996). Intensities were set so that each selection technique retained approximately 70 trees.

Results

Variation among sites and families across ages

At each age, sites were overall very similar in regards to survival and exhibited no significant effect ($p = 0.35$) on the percentage of measureable stems at each age for either full-sibling or half-sibling families. Also, the random family parameter was not significant ($p = 0.06$), though close, to the *a priori* level of 0.05 on the percentage of measurable stems at each age. As expected, age had a negative effect (–4% decrease per year) on the percent stem retention in the plots.

Initially at age three across sites, full-sibling families were larger in regards to growth traits but by age nine, the half-sibling families had on average 60% greater volume then the full-sibling families (*Table 2*). When only measurable stems were included in the analysis, substantial individual and half-sibling family differences were apparent in regards to growth parameters (i.e., height, dbh, and volume). By age nine, individuals varied in range approximately 9.5 m, 19.3 cm, and 0.72 m^3 in height, dbh, and stem volume, respectively. The half-sibling family means varied much less in range at 2.3 m in height, 4.1 cm in dbh, and 0.21 m^3 in stem volume. Still, sufficient variation in growth traits among half-sibling families allows for gain to be achieved through proper genetic selections. Narrow-sense individual, family mean, and within-family heritability were calculated for each age and, as expected, family mean heritability was greater than individual heritability at each age for each growth trait except for age 3 DBH (*Table 3*).

Measurable stems of the six full-sibling families had much more complex variation in growth variables (i.e.,

Table 2. – Average height, dbh, and volume of full-sibling and half-sibling families at ages 3,5,7,and 9 across all sites.

Age	Height (m)		DBH (cm)		Volume (m^3)	
	Half-sib	Full-sib	Half-sib	Full-sib	Half-sib	Full-sib
3	7.82 (3.37)	5.13 (0.57)	5.46 (0.95)	5.60 (1.09)	0.02 (0.01)	0.14 (0.01)
5	10.47 (0.91)	8.70 (1.69)	12.03 (2.02)	9.67 (2.63)	0.12 (0.05)	0.07 (0.05)
7	11.69 (1.60)	9.21 (1.91)	12.77 (2.36)	11.15 (3.13)	0.16 (0.07)	0.10 (0.06)
9	16.47 (1.26)	12.05 (3.71)	16.03 (2.74)	13.49 (4.01)	0.35 (0.13)	0.21 (0.14)

Table 3. – Individual tree, family mean, and within-family heritability estimates for height, diameter, and volume across all measurement ages that included half-sib families planted at Wolf Island and Sloan Farm sites. Standard errors were estimated using the Delta method and are in parenthesis.

Age	Individual Tree h^2			Family h^2			Within-Family h^2		
	Height	DBH	Volume	Height	DBH	Volume	Height	DBH	Volume
3	0.19 (0.02)	0.26 (0.02)	0.24 (0.00)	0.40 (0.01)	0.48 (0.01)	0.46 (<0.01)	0.15	0.21	0.19
5	0.50 (0.05)	0.30 (0.05)	0.39 (0.05)	0.66 (0.01)	0.52 (0.02)	0.59 (0.01)	0.43	0.24	0.32
7	0.45 (0.03)	0.25 (0.03)	0.30 (0.03)	0.63 (0.01)	0.47 (0.02)	0.52 (0.01)	0.18	0.20	0.24
9	0.45 (0.03)	0.33 (0.03)	0.41 (0.03)	0.63 (0.01)	0.54 (0.01)	0.61 (0.01)	0.38	0.27	0.35
Avg:	0.40	0.29	0.34	0.58	0.50	0.55	0.29	0.23	0.28

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

height, dbh, and volume) by age nine then the half-sibling families, recognizing that sample size was much smaller. The initial mixed model indicated that as early as age three, family effects were significant affecting growth traits with p-values of < 0.01 for height, dbh, and volume. These significant effects were reflected when narrow-sense individual, family, and within-family heritability were calculated for each age (*Table 4*). Overall, the heritabilities estimated for full-sibling families across ages and traits was greater than those estimated for half-sibling families. However, the heritability estimates were weaker as indicated by their standard error (s.e.) estimates which was probably due to the small sample size of families (n = 6).

In this study, site differences were extreme because the full-sibling families planted on the Stoneville site were inoculated with the leaf scorch bacterium. This may be a contributing factor to the interaction wherein much of the variation seen at the Stoneville site may be from negative growth effects caused by the bacterium not extensively exhibited at the Wolf Island sites. Because of the lack of BLS symptoms by age nine at the Wolf Island sites, the analysis of disease resistance was analyzed on the Stoneville site only. At age nine approximately 52% of the trees had disease symptoms. When the data were analyzed with the model including the family effect, the family effect was estimated to be significantly different from zero at 1.66 (s.e. = 1.04). The same data were analyzed using the breeding type in lieu of a family effect, which resulted in an estimated effect size of 1.40 (s.e. = 1.20) that was significantly different from zero. The large variation in leaf scorch occurrence between breeding types led to large individual and family heritability estimates of 0.67 and 1.00, respectively, from the family effect analysis. When the data were analyzed with the breeding type effect, the individual and family heritability estimates increased to 0.60 and 0.99, respectively. Both of these sets of heritability estimates indicate a large capacity for genetic improvement toward trees that do not exhibit leaf scorch. From these two analyses, the BLUP estimates were converted into probability estimates of the individual families or breeding types exhibiting signs of the leaf scorch (*Table 5*).

Gains in growth traits from selection of half-sibling families

Age-age correlations among growth traits and different ages were weak overall and sporadic for both phenotypic and genetic correlations (Table 6), but had a small average standard error of 0.024 (0.017–0.040). The genetic correlations were consistently higher then phenotypic correlations indicating the importance of the genetic component in the overall development of American sycamore. Even though overall correlations were

Table 4. – Individual tree, family mean, and within-family heritability estimates for height, diameter, and volume across all measurement ages that included full-sib families planted at Wolf Island and Stoneville sites. Standard errors were estimated using the Delta method and are in parenthesis.

Age	Individual Tree h^2			Family h^2			Within-Family h^2		
	Height	DBH	Volume	Height	DBH	Volume	Height	DBH	Volume
3	0.62	0.57	0.72	0.77	0.75	0.81	1.35	1.19	1.70
	(0.27)	(0.27)	(0.26)	(0.02)	(0.02)	(0.01)			
5	0.30	0.24	0.28	0.56	0.51	0.55	0.52	0.41	0.49
	(0.15)	(0.13)	(0.14)	(0.04)	(0.06)	(0.05)			
7	0.54	0.39	0.50	0.73	0.64	0.71	0.12	0.73	0.99
	(0.19)	(0.15)	(0.17)	(0.02)	(0.02)	(0.02)			
9	0.33	0.22	0.24	0.60	0.48	0.51	0.60	0.37	0.41
	(0.12)	(0.12)	(0.12)	(0.03)	(0.06)	(0.05)			
Avg:	0.45	0.36	0.44	0.67	0.60	0.65	0.46	0.36	0.46

Table 5. – The probability of a full-sibling family and breeding type exhibiting signs of leaf scorch by age nine on the Stoneville, MS site. The breeding type of each family is denoted in parenthesis, where RxR = resistant by resistant, RxS = resistant by susceptible, and SxS = susceptible by susceptible.

Family (Breeding type)	Probability of exhibiting disease
34 (RxR)	0.21
37 (RxR)	0.11
33 (RxS)	0.64
38 (RxS)	0.73
35 (SxS)	0.63
36 (SxS)	0.78

Breeding Type	Probability of exhibiting disease
RxR	0.16
RxS	0.69
SxS	0.70

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

Table 6. – Additive genetic correlations (above the diagonal), phenotypic correlations (below the diagonal), and family and individual (in parenthesis) heritabilities (along the diagonal) estimated from the 2002 and 2003 American sycamore half-sibling progeny test located on Wolf Island.

Traits and Age	Traits and Age								
	HT 3	HT 5	HT 9	DBH 3	DBH 5	DBH 9	VOL 3	VOL 5	VOL 9
HT 3	0.77 (0.62)	0.68	0.80	0.96	0.42	0.41	0.05	0.19	0.42
HT 5	0.16	0.56 (0.30)	0.76	0.87	0.98	0.51	0.02	0.18	0.14
HT 9	0.00	0.39	0.60 (0.33)	0.95	0.67	0.89	-0.01	0.07	0.22
DBH 3	0.70	0.14	0.05	0.75 (0.57)	0.86	0.88	0.01	0.16	0.40
DBH 5	0.10	0.58	0.54	0.17	0.51 (0.30)	0.69	0.02	0.12	0.85
DBH 9	-0.02	0.54	0.66	0.04	0.84	0.48 (0.22)	0.07	0.06	0.14
VOL3	0.77	0.16	0.05	0.96	0.20	0.05	0.81 (0.72)	0.52	0.09
VOL 5	0.14	0.70	0.52	0.20	0.97	0.83	0.24	0.55 (0.28)	0.99
VOL 9	-0.02	0.52	0.74	0.05	0.82	0.98	0.06	0.82	0.51 (0.24)

Table 7. – Correlated responses and genetic gains per unit time for age nine volume from indirect selection[a] from a 2002 and 2003 American sycamore half-sibling progeny tests located on Wolf Island.

Selected Traits	Correlated Response						Genetic Gain/Unit Time[b]		
	Mass Selection		Family Selection		Combined Selection		Mass	Family	Combined
	(m^3)	(%)[c]	(m^3)	(%)[c]	(m^3)	(%)[c]	(%)[d]	(%)[d]	(%)[d]
Age 3 Ht.	0.0005	0.15	0.0099	2.86	0.0074	2.14	0.03	0.57	0.43
Age 5 Ht.	0.0296	8.53	0.0297	8.54	0.0395	11.37	1.71	1.71	2.27
Age 3 DBH	0.0020	0.58	0.0188	5.42	0.0146	4.21	0.12	1.08	0.84
Age 5 DBH	0.0253	7.28	0.0288	8.29	0.0361	10.38	1.46	1.66	2.08
Age 3 Vol.	-0.0046	-1.34	0.0567	16.31	0.0402	11.56	-0.27	3.26	2.31
Age 5 Vol.	0.0322	9.27	0.0549	15.80	0.0599	17.24	1.85	3.16	3.45

[a] Selection intensity for (1) mass selection was 70/1376 individuals (i = 2.063), (2) family selection was 5/55 families (i = 1.8) and (3) combined selection was 10/55 families (i = 1.45) and 7/25 individuals within families (i = 1.655). These values were chosen so that a similar number of trees were selected by each method.
[b] Unit time is defined as selection age plus 5 years for selection types.
[c] Percent response- Correlated Response (m^3)/Average age nine volume (0.35 m^3).
[d] Percent Gain per Unit of Time-Percent Response/Unit time.

weak, age three dbh and height showed positively-strong correlations with age nine volume, +0.40 and +0.42 respectively. Interestingly, these genetic correlations are larger than age nine correlations with ages five dbh and height.

Relatively strong age-age correlations allow for selection of superior individuals or families at early ages through indirect selection. When correlated responses and genetic gains were calculated from indirect selection on traits before age nine, several methods showed promising gains (*Table 7*). Family-selection yielded more gain per unit time than mass- or combined-selection on average over all the growth traits and ages. However, a combined-selection based on volume at age five yielded the single largest percent gain (17.24%) and gain per unit time (3.45%). Age three selections resulted in poor age nine yield overall except for family- and combined-selection based on age three volume. These selections resulted in by far the most genetic gain per unit time for the possible selections at age three but only surpassed age five selections based on height. Mass-selection would not be a profitable method, especially for example, with a selection based on age three volume actually resulting in a decrease in yield at age nine. Across the

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

three selection techniques, three growth traits, and two juvenile ages, results indicate that either family- or combined-selection based on age five volumes will result in the best gain in age nine volume.

Discussion

This study focused on growth and development of American sycamore to age nine. Plantation sycamore has primarily been grown for the production of pulpwood, as a result of its rapid growth, bright wood color, and the greater adaptability to sites when compared to Eastern cottonwood. Unfortunately, much of the plantation sycamore grown in the southeastern United States has succumbed to a number of diseases, with bacterial leaf scorch (caused by *Xylella fastidiosa*) being the most prevalent during surveys of plantations in eight southeastern states in 1996, 1997, 1998 (BRITTON et al., 1998). The result of this susceptibility has led to high mortality, with some evidence that mortality rates are greater in the more southern sites. BRITTON et al., (1998) isolated *X. fastidiosa* and *Brtryospaeria rhodina* from plantations in southern Alabama judged to be more severely affected by dieback then plantations surveyed in more northern states in their study. Today, greater interest has been seen in the production of short rotation woody crops for use as a biomass crop for energy production. Rotation lengths of 10 years or less is the goal of these dedicated woody biomass crops. Development of sycamore varieties resistant to BLS, as well as other pathogens, would allow sycamore to be evaluated as a potential biomass species. If breeding is successful, sycamore has the benefit of clonal reproduction in which good growth rates and disease resistance can be fixed and cuttings from progeny can be used directly for planting stock (LAND et al., 1995; SHOEMAKE et al., 2004).

Height, dbh, and volume variation among half-sibling families was significant at all ages and had moderate to high individual, family, and within-family heritability (*Table 3*). Except for dbh with an average individual tree heritability of 0.29, individual tree and family heritability across ages for each trait was consistently greater than 0.30. Overall, these values were considerably higher than those derived from studies by both WEBB (1973) and LAND (1981). These studies had ranges of 0.03 to 0.17 and 0.07 to 0.27 respectively for individual-tree heritability of both diameter and height. However, both of these studies were only conducted up to age four. The age-three heritability in the present study was generally weaker, except for dbh, than at later ages which is more in line with the previous sycamore heritability estimates (LAND, 1981; WEBB et al., 1973). By contrast, heritability in the present study was similar among traits after age five and has estimates more similar to a five-year study of American sycamore growth characteristics, which yielded estimates of 0.41–0.51 for height and dbh (Jourdain and Olson, 1983), and nine-year family heritabilities for height of 0.36–0.71 and volume of 0.51–0.46 (ROUSSEAU, 1989). These results may indicate that selections for sycamore material used for rotation ages less than five years can be done adequately through provenance selections because geographical seed-source differences have been observed before age five (LAND, 1981; WELLS and TOLIVER, 1987). However, material used for rotation ages greater than five years should be selected from among half-sibling families because the large amounts of variation may allow for significant genetic gains.

The results of the present study are comparable to those of other species. Results were similar to those reported previously in yellow poplar (*Liriodendron tulipifera* L.) ranging from 0.42–0.84 (KELLISON, 1970) and in six year-old hybrid poplar clones with dbh heritability ranging from 0.32–0.55 at each test site (RIEMENSCHNEIDER et al., 2001). Both Nuttall oak (*Quercus texana* Buckley) and cherrybark oak (*Quercus pagoda* Raf.) had large height heritabilities of 0.72–0.96 (GWAZE et al., 2003) and 0.50–0.70 (ADAMS et al., 2007), respectively. However, estimates were considerably greater than those reported for two to five year old Balsam poplar (*Populus balsamifera* L.) height heritabilities ranging from 0.04–0.19 (FARMER, 1993). Similarly, overall smaller heritabilities were reported for height and dbh in sweetgum (*Liquidambar styraciflua* L.). Sweetgum was also reported to have an inverse trend in heritability change across age in which age-two measurements resulted in greater heritability than age-11 with estimates of 0.25 and 0.08, respectively (FERGUSON and COOPER, 1977).

Genetic variation estimations for height, dbh, and volume were also conducted on six full-sibling families that showed large changes in estimated heritability across ages and the largest estimates at age three (*Table 4*). Unfortunately, all the estimates had large standard errors greatly reducing confidence in the results which is, in part, a function of the small sample size of families. Similarly, a study of maritime pine (*Pinus pinaster* Ait.) with only 15 families had extremely large standard errors on their relatively low dbh and height heritabilities (KUSNANDAR et al., 1998). Another reason for the large standard errors may be due to the close relationships among the full-sibling families, as they were derived from only six parents.

The full-sibling section of the study provided useful data in regards to implementing a breeding strategy based on BLS resistance. An analysis of the presence or absence of identifiable leaf scorch, even with a small sample size and relationships among families, revealed highly significant family and breeding type effects. This resulted in family heritability estimates for BLS susceptibility at approximately 1.00 at year-nine. While extremely high heritability may be expected for a trait such as this, the resulting probabilities for the families and breeding type were very interesting. Of the six full-sibling families, only two had a low probability (<25%) of expressing the disease while the other four all had probabilities greater than 60% (*Table 5*). Additionally when the families were segregated by breeding type, there was a clear difference in the crosses between two resistant parents and crosses with one or both parents susceptible. Based on these results, resistance to the BLS disease appears to be a recessive trait caused by a relatively few number of genes. Indeed, eastern cotton-

DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics

wood (*Populus deltoides* L.) exhibits a large array of resistance to the *Melampsora* leaf rust fungus and only has five identified genes controlling the degree of resistance (NEWCOMBE et al., 2001). The present results point to a relatively easy breeding strategy for developing bacterial leaf scorch resistance in American sycamore that involves the selection of two resistant parents. This natural resistance has been shown to be more prevalent when southern material was moved north than when northern material was moved south (COOPER et al., 1977). This may be due to co-adaption with the bacterium on warmer, humid sites more conducive to bacterial growth. Thus selection and testing should most certainly be done at southern sites.

The existing variation in growth traits and co-variation of growth traits at various ages allows for age nine volume gains to be made through indirect selection based on earlier age traits. Family and combined-selection techniques were both superior to mass-selection, and were similar to selection comparisons in cherrybark oak (ADAMS et al., 2007). The family- and combined-selection techniques were very similar in their genetic gain per unit time yield; however, family-selection had on average a greater yield then combined-selection. On the other hand, combined-selection had the single greatest genetic gain per unit time yield for year-five volume. This finding is similar to recommendations for cherrybark oak (ADAMS et al., 2007) and red pine [*Pinus resinosa* Ait. (DAVID et al., 2003)].

American sycamore has broad genetic variation that could be used to develop varieties with resistance to bacterial leaf scorch disease and good growth traits for use in plantations for pulp and paper or biomass for biofuels. Findings of genetic control of growth traits are similar to those previously found; however, a combined-selection, which includes family and within-family data, based on age five volume should be used for maximizing age-nine volume. Furthermore, selection of parents which both exhibit resistance to bacterial leaf scorch disease (caused by *Xylella fastidiosa*) must be made to yield progeny that are resistant to the disease.

Acknowledgements

The authors thank those individuals that worked at the Central Forest Research Center of MeadWestvaco located in Wickliffe, KY for recognizing the problem associated with sycamore diseases as well as establishment of the study and breeding of full-sibling families. We would like to acknowledge the Forest Land Group and Anderson-Tully Worldwide for allowing the test to remain intact and access and re-measurement of the sites. We also would like to acknowledge C.J. CHANG and RUTH DONALDSON University of Georgia, Griffin for assistance in preparing X.f. cultures for inoculations, technical support and helpful advice; AMY ABEL, BRYCE BURKE, KEVIN CORBIN, SHELLEY GRIFFIN, STEVEN HUGHES, CHRIS KIRK, CHARISSE OBERLE, CHUCK WALKER, USDA Forest Service, Center for Bottomland Hardwoods Research, Stoneville, MS for stand maintenance and technical support in the field and laboratory.

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DOI:10.1515/sg-2012-0025
edited by Thünen Institute of Forest Genetics