Heritability and Gain for Early Height Growth and Foliage Retention in Eastern Cottonwood from the Southeast

Jonathan P. Jeffreys and Samuel B. Land, Jr.[1]

Abstract: Open-pollinated seeds were collected and kept identified by mother tree from 64 natural stands of eastern cottonwood (*Populus deltoides* Bartr. *ex* Marsh. *var*. deltoides) in the southeastern United States. Containerized rooted cuttings from the seedlings were planted in clonal trials at four sites: North Carolina, Florida, Alabama, and Missouri. Heights and late-season defoliation scores were measured at age one through three. Broad-sense heritabilities were 0.28 for third-year height and 0.38 for percent defoliation in October. The genetic covariance, total genetic correlation, and coefficient of genetic prediction were all negative, indicating that height increases as defoliation declines. Gains of 14-percent in height and 19-percent in foliage retention (reduced defoliation) were estimated from direct selection for clone performance over all locations. Ten-percent gains could be accomplished from indirect selection. Examination of ranked clone means indicated that selection should be based on both traits at the same time. Clone-by-test-location interactions were significant for both traits, indicating that increased gains might be accomplished by selection of site-specific clones. The same clones were seldom found in the top five clones at different test locations.

INTRODUCTION

Eastern cottonwood (*Populus deltoides* Bartr. *ex* Marsh. *var*. deltoides) is the fastest growing native commercial forest species in North America (Cooper and van Haverbeke 1990). Rapid growth of the genus has led to the establishment of poplar plantations worldwide. However, it is known that early or premature defoliation can drastically reduce the amount of annual growth and height growth of a tree. Early defoliation can also predispose the tree to disease and other environmental stresses (Land and Jeffreys 2005, Newcombe and others 1994).

Multiple factors can contribute to the defoliation of a tree. Kosola and others (2001) discovered that repeated insect defoliation in a stand of poplars decreased tree growth and increased the rate of top dieback. Ostry and others (1988) reported that defoliation due to *Melampsora* leaf-rust could reduce growth by 20 to 35 percent. In a study by Chen and others (2001) on Douglas fir, cumulative defoliation over a two-year period was discovered to be negatively correlated with height growth. Objectives of the present study were (1) to analyze early height growth and October leaf defoliation of eastern cottonwood clones from the population in the Southeastern United States, (2) to estimate genetic variation, broad-sense heritability, genetic correlations, and expected gains from direct and indirect selection for three-year height and late-season defoliation in that population, (3) to identify some clones for further testing, and (4) to determine if the same clones can be used at widely dispersed locations in the Southeast.

[1] Graduate Student and Professor respectively, Department of Forestry, Mississippi State University, P.O. Box 9681, Mississippi State, MS, USA

MATERIALS AND METHODS

Planting Material

The southeast was divided into six subregions in 1995 by Land and others (2001) for a clonal evaluation of eastern cottonwood from the Southern United States. The three eastern-most subregions, Southeast Atlantic (SA), East Gulf (EG), and East Central (EC), were used for the study reported here. Open-pollinated seeds were collected from mother trees in seventy-two natural stands on various rivers within these three subregions (Figure 1). Seeds collected from 64 of these stands were germinated, and 512 seedling clones were vegetatively multiplied as containerized rooted cuttings for use in four clonal trials (Warwell *et al.* 1999). These clonal trials were planted in Florida (30E 32.5' N, 84E 35' W), Alabama (32E 02' N, 88E 07' W), North Carolina (35E 58' N, 77E 09' W), and Missouri (32E 02' N, 89E 46' E).

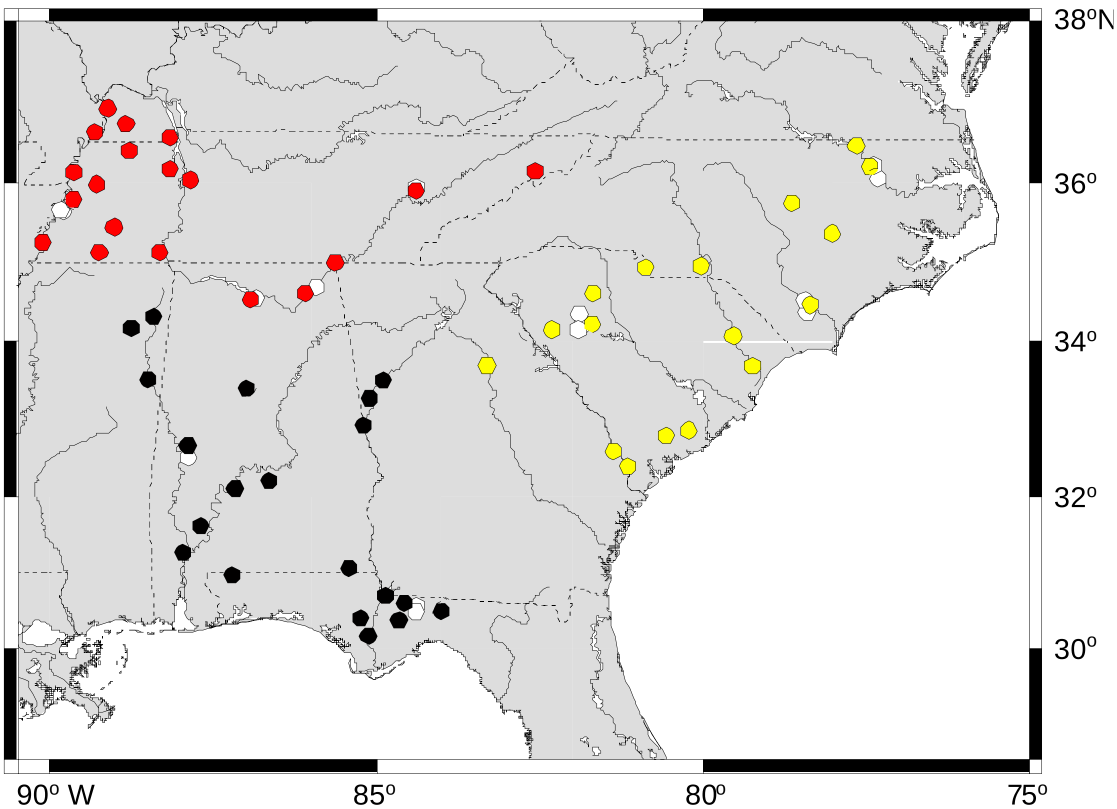

Figure 1. Map of 72 natural *Populus deltoides* stands from which seeds were collected for production of seedling cuttings to use in the southwide clonal trial. Stands in North Carolina, South Carolina, and eastern Georgia represent the Southeast Atlantic subregion. Stands in western Georgia, southern 80% of Alabama, and eastern Mississippi indicate the East Gulf subregion. Stands in Tennessee, western Kentucky, and the northern 20% of Alabama represent the East Central subregion. Non-filled circles represent two stands.

The rooted cuttings were planted at the four locations between June 1999 and March 2000. The field design at each location was a randomized complete block with three replications. Clones were arranged by origin in subregion split plots. Each clone was planted in a single-tree clone plot. The trees were measured for height and scored for leaf defoliation in October of each of the three years 2000-2002. Height was measured to the nearest tenth of a meter by a vertex laser hypsometer. Leaf defoliation was based on a scoring system. A tree was given a score for the amount of foliage lost. A defoliation score of "5" indicated that 100 percent of the leaves were gone, "4" indicated 80 percent defoliation, "3" indicated 60 percent, "2" was 40 percent, and "1" was 20 percent or less defoliated. These defoliation scores were converted to percent defoliation for analyses. Foliage "retention" was equated with 100 percent minus the defoliation percent.

Multivariate analyses of variance and covariance for height and defoliation over all test locations were performed according to the format in Table 1. PROC GLM and PROC MIXED (SAS 1999) were used to analyze the data. This was a mixed-effects model, with "Subregions" considered a fixed effect. Coefficients for the Expected Mean Squares were taken from the PROC MIXED printout, since there was unbalance in numbers of clones per subregion at each location. Variance components were computed by equating actual mean squares with the expected mean squares. Covariance components were computed in a similar manner from expected cross products that had the same composition of covariance components and coefficients as shown for the variance components and coefficients in Table 1.

Genetic parameters were determined from the estimates of variance and covariance components in the expected mean squares and expected mean cross products. Broad-sense heritability was calculated using the formula:

$$h_b^2 = \frac{\sigma^2_{C(S)}}{(\sigma^2_{C(S)} + \sigma^2_{C(S)L} + \sigma_{C(S)R(L)})}.$$

The total genetic correlation was calculated using the formula:

$$r_G = \frac{\sigma\sigma_{C(S)h\times d}}{\sqrt{\sigma^2_{C(S)h} \times \sigma^2_{C(S)d}}}$$

where h = height and d = defoliation.

Table 1. Composition of expected mean squares (EMS), genetic variance, and phenotypic variance for analyses of height and late-season leaf retention of cottonwood clones in three-year-old trials repeated over four locations in the southeastern United States.

Source of Variation	Expected Mean Square [a]
Location (L)	$\Phi^2_{C(S)R(L)} + k_{14}\Phi^2_{C(S)L} + k_{15}\Phi^2_{SR(L)} + k_{16}\Phi^2_{SL} + k_{17}\Phi^2_{R(L)} + k_{18}\Phi^2_{L}$
Reps in L (R/L)	$\Phi^2_{C(S)R(L)} + k_{12}\Phi^2_{SR(L)} + k_{13}\Phi^2_{R(L)}$
Subregions (S)	$\Phi^2_{C(S)R(L)} + k_{08}\Phi^2_{C(S)L} + k_{09}\Phi^2_{C(S)} + k_{10}\Phi^2_{SR(L)} + k_{11}\Phi^2_{SL} + Q_S$
S x L	$\Phi^2_{C(S)R(L)} + k_{05}\Phi^2_{C(S)L} + k_{06}\Phi^2_{SR(L)} + k_{07}\Phi^2_{SL}$
S x R/L	$\Phi^2_{C(S)R(L)} + k_{04}\Phi^2_{SR(L)}$
Clones in S (C/S)	$\Phi^2_{C(S)R(L)} + k_{02}\Phi^2_{C(S)L} + k_{03}\Phi^2_{C(S)}$
C/S x L	$\Phi^2_{C(S)R(L)} + k_{01}\Phi^2_{C(S)L}$
C/S x R/L	$\Phi^2_{C(S)R(L)}$

Total genetic variance = GV = $\Phi^2_{C(S)}$

Phenotypic variance (Individual-tree basis) = PV = $\Phi^2_{C(S)R(L)} + \Phi^2_{C(S)L} + \Phi^2_{C(S)}$

[a] These are Expected Mean Squares for a mixed-effects model, where the "Subregions" effect is considered a fixed effect (Q_S). There was unbalance in the number of clones per subregion and the number of clones per subregion planted at each location, so the k_{xx} coefficients were taken from Type III MANOVA analyses (PROC GLM in SAS). Those coefficients were as follows:

k_{01} = 1.6807	k_{06} = 28.9180	k_{11} = 76.8330	k_{16} = 82.7290
k_{02} = 1.5881	k_{07} = 86.7540	k_{12} = 40.4080	k_{17} = 82.7290
k_{03} = 4.3243	k_{08} = 0.7489	k_{13} = 121.2300	k_{18} = 248.1900
k_{04} = 42.0570	k_{09} = 1.8111	k_{14} = 0.8759	
k_{05} = 0.9111	k_{10} = 25.6110	k_{15} = 27.5760	

The coefficient of genetic prediction was calculated using the formula:

$$CGP = \frac{\sigma\sigma_{C(S)h \times d}}{\sqrt{PV_h \times PV_d}}$$

where PV is the phenotypic variance for height or defoliation and $\Phi\Phi_{C(S)hxd}$ is the covariance component. Predicted gain from direct selection (ΔG) was determined as:

$$\Delta G = i \times h_b^2 \times \sqrt{PV}$$

where i is the selection intensity (Namkoong and Snyder 1969). The correlated gain from indirect selection (ΔCG) was determined from the formula:

$$\Delta CG = i \times CGP \times \sqrt{PV}\ ,$$

where PV is the phenotypic variance of the trait being indirectly improved.

Performance levels were calculated by subtracting the clone's mean at a given location from the location's overall mean and then dividing by the standard deviation among clone means at that location. Each clone's average for its performance levels at the four locations was used in selecting the top–ranked ten clones across all locations for each of the two traits. Actual clone means for each trait, rather than performance levels, were used to pick the top five clones at each location for site-specific selections.

RESULTS AND DISCUSSION

Analyses of variance

Analyses of variance indicated significant effects of locations, subregions, and clones within subregions for height and defoliation (Table 2). Location means ranged from 7.3 to 11.0 meters for age-three height and 40.0 to 73.3 percent for average defoliation over three years (Table 3). Interactions between locations and clones within subregions were highly significant for both traits, but the interactions of locations with subregions were not always significant. This indicates that the GxE interaction of clones with locations may require that different clones be selected for different sites. Failure to include this GxE interaction in phenotypic variance of the two traits would cause overestimation of heritabilities, coefficients of genetic prediction, and estimates of genetic gains.

Table 2. Mean squares, mean cross products, F-tests of significance[a], and estimates of variance and covariance components from multivariate analyses of three-year height and late-season leaf defoliation of cottonwood clones in trials repeated over four locations in the southeastern United States.

Source of Variation	3-Yr Ht. M.S.	Ht.x Defol. M.C.P.	Lf. Defol M.S.	Var. Comp.	Var Comp or Cov Comp		
					Ht.	Ht.x Def	Defol.
Locations (L)	679.738**	3711.985	28876.9**				
Reps in L (R/L)	10.957**	0.574	157.9ns				
Subregions (S)	50.318*	- 442.620	4099.2*		<-----(fixed effect)----->		
S x L	6.073*	- 30.582	537.1ns				
S x R/L	2.709**	- 6.405	276.8**				
Clones in S (C/S)	3.883**	- 15.266	268.4**	$\Phi^2_{C(S)}$ =	0.538	- 2.855	42.337
C/S x L	1.587**	- 3.004	88.0**	$\Phi^2_{C(S)L}$ =	0.336	- 0.914	29.220
C/S x R/L	1.023	- 1.468	38.9	$\Phi^2_{C(S)R(L)}$ =	1.023	- 1.468	38.913

[a] Significance of F-tests are indicated as follows:
ns = not significant (probability level is greater than 0.05)
* = significant (probability level between 0.05 and 0.01)
** = highly significant (probability level less than or equal to 0.01)

Table 3. Site means for height and defoliation.

Site	Mean Height (meters)	Mean % Defoliation in October (average for first three years)
Missouri	11.0	73.3
Florida	10.4	73.3
Alabama	7.9	40.0
North Carolina	7.3	73.3

Genetic parameters and expected gains

Estimates of total genetic variance for three-year height and average percent leaf defoliation in October and for the genetic correlation between the two traits are given in Table 4. Phenotypic variances for the two traits are also given. Broad-sense heritabilities are moderate, ranging from 0.28 for height to 0.38 for late-season leaf defoliation. The genetic covariance, total genetic

Table 4. Estimates of genetic parameters and selection responses for height and leaf defoliation of cottonwood clones in trials over four locations in the southeastern United States.

Genetic Parameter or Statistic	Trait		
	3-Yr Ht.	Lf. Defol.	Ht. x Defol.
(1) Total genetic variance [$\sigma^2_G = \sigma^2_{C(S)}$]	0.538	42.337	
(2) Genetic covariance [$\sigma\sigma_{Gh\times d} = \sigma\sigma_{C(S)h\times d}$]			- 2.855
(3) Phenotypic variance [$\sigma^2_P = \sigma^2_{C(S)R(L)} + \sigma^2_{C(S)L} + \sigma^2_{C(S)}$]	1.897	110.470	
(4) Broad-sense heritability: [h^2_b = (1)(3)]	0.284	0.383	
(5) Total genetic correlation [$r_{GhGd} = (2) \div \{\sqrt{(1_{Ht}) \times (1_{Df})}\}$]			- 0.598
(6) Coef. of genetic prediction [$CGP) = (2) \div \{\sqrt{(3_{Ht}) \times (3_{Df})}\}$]			- 0.199
(7) Test means (over all locations)	7.43 meters	54.7 %	
(8)Total number of clones tested (all locations)	512	512	
(9) Number of clones selected	5	5	
(10) Proportion selected	5/512 = 0.010	5/512 = 0.010	
(11) Selection intensity (i)	2.640	2.640	
(12) Predicted genetic gain (ΔG) from direct selection [$\Delta G = (11) \times (4) \times \sqrt{(3)}$]	1.03 meters	10.6 %	
(13) Predicted correlated gain (ΔCG) from indirect selection [$\Delta CG = (11) \times (6) \times \sqrt{(3)}$]	- 0.72 m. ht.	- 5.5% defol.	
(14) Percent gain over test mean (direct selection) {%G = [(12)/(7)] x 100%}	(+) 13.9 %	(+) 19.4 %	
(15) Percent gain over test mean (indirect selection) {%CG = [(13)/(7)] x 100%}	(-) 9.7 %	(-) 10.1 %	

correlation, and coefficient of genetic prediction (CGP) are all negative, indicating that height declines as late-season defoliation increases. Moderate gains of 14 percent in height and 19 percent in leaf retention in October can be achieved from direct selection of one clone in 100 from clonal tests repeated across test locations. Indirect selection of one clone in 100 for less leaf defoliation in October can result in a ten-percent increase in age-three height. Similarly, indirect selection of the tallest clone in 100 at age three can result in a ten percent reduction in late-season defoliation. Note that these direct and indirect gains are estimated for selection of clones that perform well over all four diverse test locations. Greater gains might be obtained from selection of site-specific clones for each location, since the large GxE interaction of locations with clones within subregions would not be included in the phenotypic variance. Thus, the broad-sense heritabilities and CGP would be larger and result in greater predicted gains for site-specific clones.

Clones to select for further testing over all test locations

Performance levels for three-year height and for average three-year October defoliation were used to rank clones for mean performance over all four test locations. The top ten clones by rank for each trait are given in Table 5. The only clone that occurred in the top ten for both traits was 3-1, which came from a mother tree in Hardin County, Tennessee, on the Tennessee River near the Mississippi-Alabama-Tennessee intersection of state lines. For the other clones in the top ten, there were patterns for river systems of origin. Top height-performing clones tended to come from the Tombigbee River and its associated rivers on the west-Alabama side of the EG subregion (four of the top ten) and from the southern half of the SA subregion (Catawba to Oconee Rivers in South Carolina and northeast Georgia)(four of the top ten). Clones with high late-season leaf retention came mainly from the EG subregion (four from the Chattahoochee/Apalachicola system on the border between Alabama and Georgia and three from the Tombigbee system in west Alabama). Only three of the 20 clones in Table 5 came from the EC subregion (includes clone 3-1 mentioned above and two clones from the Mississippi River along the western boundary of Tennessee). None of the 20 clones came from rivers in North Carolina or northeastern South Carolina.

When ranks for the alternative trait were examined, the alternative trait did not always rank very high. However, it appeared that height growth was more correlated with a high score for defoliation, than defoliation was with a high score for height growth. For example, when clones were ranked for height growth, clone 105-5 was ranked second and had a ranking of 105 for foliage retention. While clone 77-4 was ranked second for foliage retention and had a ranking of 18 for height growth. Therefore the negative genetic correlation between defoliation and height is not absolute, and some clones will have a high rank for one trait and a low rank for the other. It is recommended that the clones to select for further testing should be assessed for both traits at the same time. Those that are selected should have a high average for the combined ranks of the two traits. However, for early selection the foliage retention may provide a better measure for indirect selection of future yield than clone height, and it should be given more weight than height growth when combining performance levels. One solution is to use the five clones out of the top 10 for foliage retention that have the highest rank for height growth. The same procedure can be used in selecting the top ten for height growth. These procedures would identify the following 10 clones for further study: 3-1, 80-2, 96-2, 77-4, 80-3, 154C-4, 147-4, 120-6, 100-3, and 92-3.

Table 5. Best performing clones over all locations for mean height and percent defoliation.

Top Ten Ranked Clones	Performance Level Rank		Origin		Clone Average (4 loc's.)
	Height	Foliage Retention[a]	State	River System	
3-Year Height					(meters)
3-1	1	6	TN	Tennessee	10.5
105-5	2	105	AL	Tombigbee	10.7
92-3	3	80	AL	Tombigbee	8.2
141A-5	4	193	SC	Catawba to Oconee	7.8
47-1	5	176	MO	Mississippi (west Tennessee)	9.4
154C-4	6	41	SC	Catawba to Oconee	8.1
154B-3	7	216	SC	Catawba to Oconee	7.8
147-4	8	37	GA	Catawba to Oconee	9.2
120-6	9	95	AL	Tombigbee	9.5
100-3	10	57	MS	Tombigbee	9.6
3-Year October Foliage Retention					(%)
119-4	31	1	AL	Tombigbee	36.7
77-4	18	2	FL	Chattahoochee/Apalachicola	24.4
80-1	36	3	FL	Chattahoochee/Apalachicola	38.9
92-7	48	4	AL	Tombigbee	35.6
154A-1	75	5	SC	Catawba to Oconee	30.7
3-1	1	6	TN	Tennessee	38.9
80-2	16	7	FL	Chattahoochee/Apalachicola	34.4
96-2	17	8	MS	Tombigbee	26.7
80-3	23	9	FL	Chattahoochee/Apalachicola	40.0
68-1	108	10	TN	Mississippi (west Tennessee)	37.8

[a] Foliage retention rank equals inverse of defoliation rank, or 512 minus defoliation rank. Rank "1" for high foliage retention is rank "512" for low defoliation.

Site-non-specific vs. site-specific clones

The top five clones at each site for each trait are given in Table 6. There were few similarities among sites. Clone 147-4 was in the top five for height at the Alabama and Florida sites (both of which are in the southern half of the region), and clone 9-5 was in the top five for height at the North Carolina and Missouri locations. The only two clones that were in the top five for both height and foliage retention were 120-4 and 119-1, and this only occurred at the Missouri site. The general lack of repeatability of clones in the top five at different sites confirms the importance of the GxE interactions of locations with clones within subregions.

Table 6. Mean heights and foliage retention of the five best-performing clones for each trait at each site.

Location	Clone	Rank	Mean HT (meters)	Clone	Rank	Mean % defoliation
Alabama	112-3	1	9.1	111-1	1	20.0
	157-3	2	8.8	45-1	2	20.0
	154C-4	3	8.8	80-3	3	20.0
	92-3	4	8.5	92-7	4	20.0
	147-4	5	8.4	77-4	5	23.3
Florida	156A-3	1	13.4	120-4	1	20.0
	147-4	2	12.5	154A-1	2	20.0
	120-6	3	12.3	50B-3	3	23.3
	80-2	4	11.6	130G-1	4	26.7
	50B-5	5	11.5	3-2	5	26.7
Missouri	3-1	1	12.2	119-5	1	20.0
	119-1	2	12.1	80-2	2	26.7
	9-5	3	12.0	119-2	3	33.3
	120-4	4	12.0	120-4	4	33.3
	119-7	5	12.0	119-1	5	35.6
North Carolina	26B-3	1	8.2	158A-4	1	36.7
	3-1	2	8.1	92-5	2	37.8
	3-5	3	7.9	105-1	3	40.0
	141A-5	4	7.9	109-7	4	40.0
	9-5	5	7.8	111-4	5	40.0

Only eight of the 20 identified site-specific clones for height in Table 6 would have been used if the top ten clones over all locations for height (Table 5) had been selected, and only five of the 20 site-specific clones for foliage retention would have been chosen. This indicates that greater gains may be obtained from selection of site-specific clones (or at least half-region-specific clones for the northern and southern halves of the region) than from selection of non-specific clones for the whole region.

SUMMARY AND CONCLUSIONS

Analyses of variance indicated significant effects for locations, subregions, and clones within subregions for height, and late-season defoliation. There was a significant and negative genetic correlation between height and defoliation, indicating that three-year height increases as defoliation declines (i.e., foliage retention increases). Interactions were detected for locations by clones within subregions. This GxE interaction indicates that increased gains may be obtained from selecting different clones for each location. Should this interaction be left out of the phenotypic variance, the heritabilities, coefficients of genetic prediction, and estimates of genetic gains would all be overestimated. Direct selection for traits can result in a 14-percent gain in height and a 19-percent gain in leaf retention. Indirect selection for either height growth or late-season foliage retention can result in a ten-percent increase for the other trait. However, the negative correlation between height and defoliation was not always reliable for individual clones. It is recommended that a clone should be assessed for both traits before selection is made. It is also recommended that clones be selected for no larger an area than the southern half and northern half of the region, rather than for the whole region. This may allow increased gains by reducing the location-by-clone interaction.

ACKNOWLEDGEMENTS

This manuscript is publication number FO-294 of the Forest and Wildlife Research Center, Mississippi State University.

LITERATURE CITED

Chen, Z., T.E. Kolb, K.M. Clancy. 2001. Mechanisms of Douglas-fir resistance to western spruce budworm defoliation: bud burst phenology, photosynthetic compensation and growth rate. Tree Physiology 21: 1159-1169

Cooper, D.T. and D. van Haverbeke. 1990. Populus deltoides Bartr. ex Marsh Eastern Cottonwood. P. 530-543 in Silvics of North America, Volume 2. Hardwoods. Burns, R. M. and B. H. Honkala (eds.). U.S. Department of Agriculture, Forest Service. Handbook 654. Washington, D.C.

Kosola, K.R., D.I. Dickmann, E.A. Paul, D. Parry. 2001. Repeated insect defoliation effects on growth, nitrogen acquisition, carbohydrates, and root demography of poplars. Oecologia 129 (1): 65-74.

Land, S.B. Jr., M. Stine, X. Ma, D.L. Rockwood, M.V. Warwell, and G.R. Alker. 2001. A tree improvement program for eastern cottonwood in the southeastern United States. *In* Jeffrey Dean (ed.). Proceedings of the 26th biennial southern forest tree improvement conference; 2001 June 26-29; Athens, GA: University of Georgia, Daniel B. Warnell School of Forest Resources. p 84-93. Sponsored publication no. 48; Southern Forest Tree Improvement Committee. Available from: NTIS, Springfield, VA.

Land, S.B. Jr., and J.P. Jeffreys. 2005. Geographic origin of cottonwood from the southeast affects *Melampsora* infection in three-year-old clonal trials. *In* Proceedings of the thirteenth biennial southern silvicultural research conference; 2005 Feb 28-March 3; Memphis, TN.

Namkoong, G, and E.B.Snyder. 1969. Accurate Values for Selection Intensities. Silvae Genetica 18: 172-173

Newcombe, G., G.A. Chastagner, W. Schuette, and others. 1994. Mortality among hybrid poplar clones in a stool bed following leaf rust caused by *Melampsora medusae* f.sp. *deltoidae*. Canadian Journal of Forest Research 24: 1984-1987.

Ostry, M.E., L.F.Wilson, H.S. McNabb Jr., and others. 1988. A guide to insect, disease, and animal pests of poplars. Agriculture Handbook 677. Washington, DC: U.S. Department of Agriculture, Forest Service. 118 p.

SAS Institute Inc. 1999. SAS/STAT User's Guide, Version 8. Carey, North Carolina: SAS Institute Inc. 3884 p.

Warwell, M.V., G.R. Alker, D.L. Rockwood, S.B. Land, Jr., and M. Stine. 1999. Culture and genetic influences on greenwood cutting propagation of a new collection of eastern cottonwood in the south. *In* Bowen, Mary, and Michael Stine, (comp.) Proceedings of the 25th biennial southern forest tree improvement conference; 1999 July 11-14; New Orleans, LA. Baton Rouge, LA: Louisiana State University, School of Forestry, Wildlife, and Fisheries. p 174-176. Sponsored publication no. 47; Southern Forest Tree Improvement Committee. Available from: NTIS, Springfield, VA; PB 2000-104560.