

ABSTRACT

SHERRILL, JOSHUA REID. Genetic and Cultural Effects on Stem Taper and Bark Thickness in Loblolly Pine (*Pinus taeda* L.). (Under the direction of Drs. Tim J. Mullin and Bronson P. Bullock.)

Total inside-bark volume is the most important selection criterion for productivity in tree breeding programs in the Southeastern U.S. Tree breeding programs typically estimate total inside-bark volume based on diameter at breast height (D) and total height (H) without accounting for stem taper or bark thickness. A genotype by cultural treatment study with weed control and fertilization treatments was measured in the 13th growing season. Twenty-five open-pollinated first- and second-generation loblolly pine (*Pinus taeda* L.) families were destructively sampled to measure diameters and bark thickness along the stem and to make a direct determination of total inside- and outside-bark volume.

Selection for volume using a combined-variable (D^2H) equation was found to be highly effective for making volume gains; although, overall estimates of total inside-bark volume using a combined-variable equation from Warner and Goebel (1963) were less accurate than those from destructive sampling. Precision could be improved by adding further terms to the prediction model, such as bark thickness and form quotients; however, these additional measurements could not explain all of the imprecision. Genetic components for both stem taper and bark thickness were estimated. These two factors had a small effect on volume estimates due to the high correlation between estimated and measured total inside-bark volumes. There was a positive genetic correlation between bark thickness and D that indicates that selection for larger D will produce individuals with thicker bark and may eventually affect total inside-bark volume estimates.

**GENETIC AND CULTURAL EFFECTS ON STEM TAPER AND BARK
THICKNESS IN LOBLOLLY PINE (*Pinus taeda* L.)**

By

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1. GENERAL INTRODUCTION

Loblolly pine (*Pinus taeda* L.) is the most planted timber species in the United States, due to its inherently fast growth, acceptable wood quality, and responsiveness to silvicultural treatments. Highly productive pine plantations can decrease harvest pressure in more ecologically important areas like hardwood forests, wetlands, and streamsides. There is a strong correlation between increasing pine plantation yields and conservation of natural forest types (Prestemon and Abt 2002).

Loblolly pine has been selected and bred since the 1950's by cooperative tree improvement programs, with emphasis on fast growth, superior form, and disease resistance. The North Carolina State University–Industry Cooperative Tree Improvement Program (TIP) is one of the cooperative programs working with industry and state agencies to make genetic gains. This program has completed two cycles of selecting, breeding, and testing. Seedlings from selected first- and second-generation parents are currently being grown by industry and state nurseries for planting on industrial, investment management, non-industrial private, and some public lands. The TIP has made third-cycle selections and has currently begun the next cycle of breeding and testing.

The objective of breeding, testing, and selecting is to make gains by narrowing the production population's genetic base to improve total value, while maintaining enough variation to mitigate risk. Total value is increased through accelerated growth, higher wood quality, and greater disease resistance. Tree improvement programs have generally estimated volume growth of genotypes based on diameter at breast height (D) and total stem height (H) without accounting for stem taper or bark thickness. If significant volume differences exist

due to variation in taper and bark thickness, then some favorable individuals or families may be passed over, while some less favorable individuals or families may be selected.

Stem taper is defined as the rate of narrowing of a tree bole up the stem (Larson 1963) and is important in determining total stem volume and product utilization. A tree of the same diameter and height but, with less taper than a counterpart, contains more total volume and produces longer lengths of wider, more valuable lumber. It is also advantageous for foresters to grow more cylindrical butt logs where more clear lumber can be produced. A higher percentage of wood going to lumber from a given log yields a higher return received from that log. Low stem taper may also be associated with increased veneer production.

Besides product values, stem taper differences associated with large altitude differences may indicate a survival mechanism. Callaham and Liddicoet (1961) found that as elevation increased, stem taper increased in ponderosa (*Pinus ponderosa* Laws.) and Jeffrey pines (*Pinus jeffreyi* Grev. & Balf.). Larson (1963) also found that as elevation increased the stems became more conical and tapered more. Therefore, there may be clinal genetic variation in taper between regions with large differences in altitude or wind forces.

Variation in stem taper among second-cycle improved loblolly pine families is unknown. There has not been adequate research to know if there are genetic taper differences among loblolly pine families planted operationally. Buford and Burkhart (1987) found that there was no difference in taper between unrogued and rogued first-generation open-pollinated (OP) families planted operationally.

In another study, Foster (1988), found that stem taper in loblolly pine is generally under additive genetic control. Additive genetic effects would benefit breeders desiring less taper if there is adequate variation in the natural population to make improvements. Foster (1988)

compared taper in loblolly pine rooted cuttings and seedlings and found that rooted cuttings have slightly less taper. However, the sample size from this study for seedlings was only ten trees total compared to 121 rooted cuttings. A later study looking at rooted cuttings found a family difference in taper but not between propagule types for ages 7 and 10 (Stelzer et al. 1998).

Chabreck (1977) compared taper in four geographic sources of loblolly pine planted on a site in Louisiana. Chabreck (1977) used analysis of variance and regression techniques to find that the four geographic sources were not statistically different in mean taper. The author noted that there was a significant taper difference in the crown region of the study trees and border trees, probably due to live-crown ratio.

There is a strong positive phenotypic correlation between stem taper and crown ratio for loblolly pine (Newberry and Burkhart 1986). Crown ratio is the proportion of the stem that has live crown compared to the total height (Burkhart and Walton 1985). Larson (1963) describes stem taper as an ultimate result of stocking and crown position, noting that open-grown trees tend to have longer crowns and more taper than suppressed or densely grown trees with shorter crowns. Newberry and Burkhart (1986) demonstrated that larger-crowned (high-quality site) trees spread diameter growth over the entire bole, creating a more conical shape. Conversely, smaller-crowned (low-quality site) trees focus diameter growth in the crown, creating a more cylindrical bole.

McCrary and Jokela (1996) found that loblolly growth performance was independent of crown ratio for five OP families. However, location of the highest foliage concentration in the crown was correlated with growth performance. McCrary and Jokela (1996) also found that there was a family effect for crown length and ratio before crown closure. However,

stand development might confound genotypic variation in crown length after crown closure. Crown ratio can be important in itself because trees with low crown ratios will have fewer tight knots on the bole.

In addition to stem taper, variation in bark thickness could contribute to volume estimation differences among loblolly pine families. Pederick (1970) did not detect any significant half-sib family differences in inside-bark taper measurements and felt that diameter inside-bark (d.i.b.) at breast height (BH) and H could adequately predict wood volume. The author's findings indicated bark thickness was more important than taper in progeny selection. It was noted that the estimated inside-bark volume calculated from D and H could be over- or under-estimated by 3.3% due to bark thickness. Pederick (1970) also found positive genetic correlation between bark thickness and d.i.b. growth ($r_g = 0.66$). Therefore, selection for larger diameter growth may result in trees with thicker bark. Pederick (1970) reported estimated individual-tree narrow-sense heritability for bark thickness as 0.60. The author reported that a great deal of phenotypic variation in bark thickness was due to d.i.b., age, deep bark fissures, and environmental effects.

Similar to Pederick's (1970) findings, Matziris (2000) found that bark thickness and D were correlated ($r = 0.85$) in Aleppo pine (*Pinus halepensis* Mill.). Matziris (2000) calculated narrow-sense heritability for bark thickness as 0.15 and 0.24 on two different sites in Greece. Persson and Downie (1992) found that D and relative height of BH to total height heavily influenced bark thickness in lodgepole pine (*Pinus contorta* Dougl. ex Loud.). However, locality and provenance variation were also significant after accounting for D and relative height. This indicates that D and H can account for some variation in bark thickness, but genetic and environmental effects can still exist. Persson and Downie (1992) illustrated

patterns of bark thickness in relative terms, where relative bark thickness is a ratio of double-bark thickness to D.

There may be some degree of genotype by cultural treatment interaction (GxC) for stem taper and bark thickness. GxC interactions arise when the relative performance of families change by the silvicultural treatments to which they are exposed. GxC interaction effects may be important because there are a variety of cultural treatments applied to forest lands in the Southeast. Snowdon and Waring (1985) found a significant genotype by fertilization interaction for diameter and H ratio in 4-year-old radiata pine (*Pinus radiata* D. Don). The ratio of diameter one inch above the ground line and H was considered an indication of taper. The diameter and H ratio differences among family-by-fertilization combinations shows that genotypes may possess different rates of taper in different environments and different genotypes have varying taper.

2. THE IMPORTANCE OF FAMILY AND CULTURAL EFFECTS THROUGH MIXED MODEL ANALYSIS

INTRODUCTION

The North Carolina State University–Industry Cooperative Tree Improvement Program (TIP) has used diameter at breast height (D) and total tree height (H) measurements in a combined-variable equation to estimate the volume of individuals in genetic trials. A simple linear regression with D^2H as the regressor, termed the combined-variable equation, has been shown to sufficiently predict total inside-bark volume when fit to datasets with 50 to 100 sampled stems (Spurr 1952). This type of equation applied to an entire tree improvement trial assumes every tree has the same rate of stem taper and the same rate of bark accumulation.

This chapter tests these assumptions of taper and bark-thickness consistency through the use of volume, height-diameter, stem-taper, stem-form, bark-thickness, crown-ratio, and form-quotient mixed models. The primary goal is to evaluate the impacts of family and cultural treatments on volume after accounting for D^2H . The other models are analyzed to supplement that foremost objective and give insight into related stem characteristics.

MATERIALS AND METHODS

Study Site

The study site was located on International Paper Co.'s Southland Forest, Bainbridge, GA (latitude 30.903N and longitude 84.575W) and was classified as an Orangeburg soil series. Orangeburg soils series are typically well-drained loamy soils on upland sites created from marine deposits (USDA 1986). Site preparation of the cutover site involved an application of 0.5 pint/acre imazapyr, an application of 1.0 pint/acre glyphosate, and a

prescribed burn. Six blocks were planted in December 1991 on an 8 x 10 foot spacing (one block was excluded in the present study). All treatments were then released with a herbicide application at age five (Table 1).

Table 1. Herbicide and fertilizer treatments in the GxC interaction study at Bainbridge, GA

Herbicide		Fertilizer	
Application	Age	Application	Age
0.75 oz./acre Metsulfuron methyl	Year 1	3 oz./tree 20-4-15	Feb. 1992 Year 1
Sulfometuron methyl and atrazine tank mix	Year 2	3 oz./tree 20-4-15	June 1992 Year 1
Hack and squirt with triclopyr and diesel	Periodic	1000 lbs/acre 20-5-15 with micro nutrients	Year 4
Directed spray – 2% glyphosate	Years 1-5	1000 lbs/acre 20-5-15 with micro nutrients	Year 5
Aerial release – imazapyr all treatments	Winter Year 5	1000 lbs/acre 20-5-15 with micro nutrients	Year 9

This study was a two-by-two factorial of herbicide and fertilizer treatments in a split-plot design. The main-plot factor was cultural treatment and the subplot factor was open-pollinated (OP) family. The cultural control treatment had no herbicide applications until age five and no fertilizer treatments (Table 1). The herbicide treatment consisted of early woody and herbaceous competition control and all treatments were aerially released at age five. The fertilization treatment was ground applied up until age nine (Table 1).

Genetic Materials

There were 25 OP loblolly pine families arranged as 6-tree noncontiguous subplots in a randomized complete-block design. In this study, some pedigree relationships were known to exist among parents (Table 2). These relationships included some OP parents being the same genotype as a grand parent of other OP parents.

Table 2. OP family codes, relationships among OP families, and generation for the 25 families involved in the GxC study.

Family	Grandparent 1	Grandparent 2	Generation
A	FF	GG	2
B	*	*	1
C	*	*	1
D	*	*	1
E	C	Z	2
F	AA	Z	2
G	HH	B	2
H	II	JJ	2
I	KK	AA	2
J	LL	BB	2
K	MM	AA	2
L	C	BB	2
M	D	B	2
N	NN	B	2
O	OO	PP	2
P	CC	DD	2
Q	QQ	DD	2
R	RR	SS	2
S	TT	DD	2
T	UU	CC	2
U	VV	WW	2
V	XX	YY	2
W	ZZ	AAA	2
X	C	EE	2
Y	BBB	EE	2

*Indicates grandparent is unknown.

Bold text indicates the individual also occurs elsewhere in the pedigree.

Sampling Procedures

Generally, 40 individuals were sampled from each of the 25 families, approximately 10 from each cultural treatment. Approximately two trees from each family (subplot) were sampled in each treatment plot. Around 50 trees total were sampled in each treatment plot (main plot). There were five blocks with about 200 trees per block total. Fifteen trees were excluded, because of missing measurements, yielding a total sample size of 985 stems. Some

plots had poor survival that required sampling fewer individuals of a single family in some blocks and more in others. Survival was especially poor in the fertilizer + no-herbicide treatment due to competing vegetation. At the time of planting, filler trees were planted in planting spots located in atypical areas such as gopher-tortoise holes and stumps. None of these filler trees were measured.

Two trees from each family were sampled from each plot using three criteria. First, selection was based on survival and defects that occurred below a three-inch top. Defects, such as forking, ramicorn branches, and rust galls, interfered with normal diameter growth and were excluded when possible. Second, trees were selected based on position in the treatment plot. Trees from the interior of the plot were favored over individuals on the plot edge. This criterion was used to minimize a border effect. Lastly, crop-tree competition was assessed to select trees with as many competitors as possible, to ensure uniformity of stocking. The three criteria were used to sample the most appropriate trees for assessment of typical growth. Although minimized, trees with defects, poor location, and fewer competitors were sometimes included for balance. Tree size was excluded as a criterion and sample-tree selection was conducted offsite to reduce bias toward a particular size class.

Destructive Sample

In total, 985 trees were felled in the 13th growing season. The purpose of the destructive sample was to obtain accurate inside- and outside-bark diameter measurements along the main stem. Each treatment plot was measured by two crews. Each crew consisted of a measurer and a recorder. Each crew randomly chose stems to measure from the selected stems in each treatment plot so that measurement bias among OP families could be avoided. The measurement duties remained the same throughout the sample, except one of the two

measurers was different in one whole block. The measurer effect was not confounded by block, cultural treatment, or family effects.

Before felling, each tree's breast height (BH) (4.5 feet above the ground level) was marked as a reference point for subsequent measurements. Each tree was cut at approximately 0.5 feet above the ground line. Once felled, each stem was measured at heights of 0.5, 2, 4.5, and 8 feet, and every 4 feet above the 8-foot height to a three-inch outside-bark (o.b.) top. Branches were avoided by moving the measurement point up two inches above the branch swell. At each height, outside-bark diameter (to the nearest 0.04 inch) and bark thickness (to the nearest 0.05 inch) were measured with aluminum calipers and punch-style bark gauges, respectively. Two caliper and two bark-gauge measurements were made at 90-degree angles at each height. Each pair of measurements was averaged arithmetically and the average bark thickness was doubled and subtracted from the average outside-bark diameter to yield an inside-bark diameter. Inside-bark diameters were used in Smalian's log volume equation (Avery and Burkhart 2002) to calculate the inside-bark volume of each stem section. Smalian's log volume equation was:

$$V = \left(\frac{B+b}{2} \right) L \quad (1)$$

Where:

V = total section volume, cu ft

L = length of bolt, ft

B = cross sectional area of bolt's large end, sq ft

b = cross sectional of bolt's small end, sq ft

The top-section volume above a three-inch o.b. top was estimated using the volume formula for a cone in Equation 2 (Avery and Burkhart 2002). The stem-section volumes were summed to calculate a whole-tree, inside-bark volume.

$$V = \left(\frac{B}{3} \right) L \quad (2)$$

Mean percent deviation (MPD) was calculated with this measured total inside-bark volume and a predicted total inside-bark volume from the Warner and Goebel (1963) combined-variable equation (Pederick 1970) (Equation 3). This deviation was analyzed as a measure of the bias between the previously used Warner-Goebel equation and data collected in this present study (refer to Chapter 3 for more information on MPD.)

$$MPD = \left(\frac{\hat{V}_{ib} - V_{ib}}{V_{ib}} \right) 100 \quad (3)$$

Where:

MPD = mean percent deviation, %

$\hat{V}_{ib}$ = estimated inside-bark volume from Warner-Goebel equation, cu ft

V_{ib} = measured inside-bark volume using the sum of individual sections for each measured stem, cu ft

In addition to diameter measurements, total height and height to live crown were measured to the nearest 0.1 ft. From these two measurements, crown ratio can be calculated (Burkhart and Walton 1985) as:

$$C = \left(\frac{H - H_{LC}}{H} \right) 100 \quad (4)$$

Where:

C = crown ratio, %

H = total height, ft

H_{LC} = height from the ground line to the first live branch, ft

Conventional Mixed Models

Mixed models were created to assess the conventional genotype and treatment effects on various traits. Variance components were evaluated as a percentage of the total variance and fixed effects were tested with Wald-type significance tests. The Wald-type significance tests took into account the split-plot design of the present study. The initial analysis involved conventional mixed models with measured total inside-bark volume, total inside-bark volume estimated using the Warner-Goebel equation, H, D, and bark thickness at breast height as dependent variables (Equation 5). Measured and estimated volumes were square-root transformed to reduce heterogeneity in the error variance. These models demonstrate family and treatment effects on growth.

$$\begin{aligned} Y_{ijklmn} = & \mu + H_i + N_j + (HN)_{ij} + M_k + R_l + (RH)_{il} + (RN)_{jl} + (RHN)_{ijl} \\ & + F_m + (RF)_{lm} + (FH)_{im} + (FN)_{jm} + (FHN)_{ijm} + (FRH)_{ilm} + (FRN)_{jlm} \\ & + (RFHN)_{ijlm} + \epsilon_{ijklmn} \end{aligned} \quad (5)$$

Where:

Y_{ijklmn} = the dependent variable

μ = mean

H_i = fixed herbicide treatment effect

N_j = fixed fertilizer treatment effect

$(HN)_{ij}$ = fixed herbicide by fertilizer interaction

M_k = random field measurer effect

R_l = random block effect

$(RH)_{il}$ = random block by herbicide interaction

$(RN)_{jl}$ = random block by fertilizer interaction

$(RHN)_{ijl}$ = random block by herbicide by fertilizer interaction

F_m = random family effect

$(RF)_{lm}$ = random block by family interaction

$(FH)_{im}$ = random family by herbicide interaction
 $(FN)_{jm}$ = random family by fertilizer interaction
 $(FHN)_{ijm}$ = random family by herbicide by fertilizer interaction
 $(FRH)_{ilm}$ = random family by block by herbicide interaction
 $(FRN)_{jlm}$ = random family by block by fertilizer interaction
 $(RFHN)_{ijlm}$ = random within plot effect
 ϵ_{ijklmn} = random error

Mixed-Model Analysis of Volume-Related Relationships and Traits

The following models were used to analyze traits in the context of the objective, where deviations from expected trait values were important. These models were analyzed with the same methods as those used for the conventional model analysis. Some of these models involved a continuous regressor to account for an applicable quantitative factor in the analysis. The first four of these models, volume relationship, height-diameter relationship, taper, and form models were created using the methods of Amateis and Burkhart (1987). Amateis and Burkhart (1987) analyzed these four models as fixed-effects models to test for site-preparation effects on prediction models. Schmidting and Clark (1988) followed a similar process when describing loblolly pine provenance differences in a 35-year-old study in Georgia. In contrast, the present study analyzed variance components and fixed effects in a mixed-model situation.

Volume Relationship Model

A volume model was used to analyze the significance of various effects after accounting for D^2H . The square-root of the total inside-bark volume measured from the destructive sample was the dependent variable and the square-root of D^2H was the continuous regressor. These two variables were square-root transformed to homogenize the

error variance. The family effect was interpreted as an intercept term and the D²H by family interaction as a partial slope. Family by treatment effects represented the genotype by environment interaction. Treatment effects were partitioned to represent both aspects of the factorial design, weed control and nutrition. The volume relationship model used was:

$$Y_{ijklmn} = \mu + \beta X_{ijklmn} + H_i + N_j + (HN)_{ij} + M_k + R_l + (RH)_{il} + (RN)_{jl} + (RHN)_{ijl} + F_m + \beta_m (XZ)_{ijklmn} + (RF)_{lm} + (FH)_{im} + (FN)_{jm} + (FHN)_{ijm} + (FRH)_{ilm} + (FRN)_{jlm} + (RFHN)_{ijlm} + \epsilon_{ijklmn} \quad (6)$$

Where:

Y_{ijklmn} = the dependent variable

X_{ijklmn} = the continuous regressor

β = regression coefficient for the square-root of D²H

β_m = random deviation of the square-root of D²H slope for family m

$$Z_m = \begin{cases} 1 & \text{family } m \\ 0 & \text{otherwise} \end{cases}$$

Height-Diameter Relationship Model

A height-diameter model was used to describe the effects of family, treatment and other environmental effects on H after accounting for D. The family effect represented an intercept term and the H by family interaction represented a partial slope. This model had the same format as Equation 6, with H as the dependent variable and D as the continuous regressor. H and D were both square-root transformed to homogenize the error variances.

Stem Taper Model

The taper model described narrowing of stem diameter up the stem. This model was analyzed differently because of the autocorrelation of stem diameters measured on the same stem. Autocorrelation was acknowledged by fitting a simple linear regression to each individual stem (Equation 7). The inside-bark diameters (d) at height h were squared so that

they represented the cross-sectional area. The regression (slope) and intercept coefficients from each regression were used in two mixed models. The first model was the intercept model, which described stem size. The second model used the regression coefficient as the dependent variable to represent the average rate of taper along the stem. The taper equation fit to each stem was:

$$d^2 = \beta_0 + \beta_1 h + \epsilon \quad (7)$$

Where:

d = inside-bark diameter measured at height h

h = height above ground line at which d was measured

β_0, β_1 = parameters to be estimated and used in the two taper mixed models

ϵ = error

The two taper models took the form of Equation 5, but with either the intercept or regression coefficient as the dependent variable.

Form Model

The form model describes stem shape. It is defined by the inside-bark cross-sectional area of the stump (A) multiplied by the total tree height (H). The relationship between the $A \cdot H$ term and inside-bark volume characterizes the geometric shape of the inside-bark volume. Like the other models described previously, family was interpreted as an intercept term and family by AH interaction was interpretable as a partial slope. The form model was analyzed as Equation 6, where measured total inside-bark volume was the dependent variable and AH was the continuous regressor. Both total inside-bark volume and AH were square-root transformed because of heteroscedasticity.

Bark Thickness Relationship Model

Bark thickness at BH is directly related to volume estimation procedures with a combined-variable equation. Any family differences not associated with the size of the stem may create a bias when estimating the volume of individual families. To account for size, a diameter inside-bark (d.i.b.) at BH was used as a continuous regressor. Adding this continuous regressor gave an indication of bark thickness independent of the stem size. The bark thickness relationship model was:

$$\begin{aligned} Y_{ijklmn} = & \mu + \beta X_{ijklmn} + H_i + N_j + (HN)_{ij} + M_k + R_l + (RH)_{il} + (RN)_{jl} + (RHN)_{ijl} \\ & + F_m + (RF)_{lm} + (FH)_{im} + (FN)_{jm} + (FHN)_{ijm} + (FRH)_{ilm} + (FRN)_{jlm} \\ & + (RFHN)_{ijlm} + \epsilon_{ijklmn} \end{aligned} \quad (8)$$

Where:

Y_{ijklmn} = bark thickness at BH

X_{ijklmn} = d.i.b. at BH

Crown-Ratio Model

Crown ratio (Equation 4) was analyzed as a mixed model because it is thought to be related to stem taper (Larson 1963). The crown-ratio mixed model followed the format of Equation 5, except crown ratio was the dependent variable.

Form-Quotient Model

A form-quotient model was used to describe stem taper. Form quotients are generally described as a ratio of an upper-stem diameter to D (Avery and Burkhart 2002). The form quotient used in this research was calculated by a ratio of outside-bark diameters at the fixed heights of 16 ft and BH (Equation 9). For some observations with short stems, the diameter

at 16 feet had to be estimated by linear interpolation between the uppermost diameter measured and H. All stems had total heights greater than 16 ft.

$$FQ = \left(\frac{D_{16}}{D} \right) \quad (9)$$

Where:

FQ = form quotient

D_{16} = outside-bark diameter 16 feet above the ground level

D = outside-bark diameter at BH

The form quotient mixed model was analyzed in the format of Equation 5, where form quotient was the dependent variable.

Mean Percent Deviation Model

Mean percent deviation (MPD) (Equation 3) is a measure of bias between predictions from the Warner-Goebel equation and the measured volumes in this study. The MPD mixed model was analyzed in the form of Equation 5, where MPD was the dependent variable.

RESULTS

Descriptive statistics for the dataset utilized in this study are presented in Table 3. The effects of silvicultural treatments on volume, D, H, and crown ratio are apparent. Family and treatment effects were found for measured total inside-bark volume, estimated inside-bark volume with the Warner-Goebel equation, D, H, and bark thickness (except for weed control main effects on bark thickness) (Table 4). Estimated and measured volumes were square-root transformed to increase the homogeneity of the error variance. The interaction of weed control and fertilization treatments was not significant for any of the traits at the 0.05 significance level. The measurer effect was small for the traits except for bark thickness, where it was 9.6% of the overall variance.

Table 3. Descriptive statistics for the data considered in this research. Total inside-bark volume, D, H, bark thickness at BH, and crown ratio are reported by treatments and over the whole dataset.

Fertilizer and herbicide treatment						Herbicide, no fertilizer treatment					
Trait*	N	Mean	Std dev	Minimum	Maximum	Trait*	N	Mean	Std dev	Minimum	Maximum
Total inside-bark volume	241	4.6	1.9	0.5	11.1	Total inside-bark volume	250	3.2	1.6	0.1	9.6
H	241	46.0	4.5	24.0	54.4	H	250	42.6	5.8	18.2	56.2
D	241	7.3	1.3	3.2	10.6	D	250	6.3	1.3	1.6	9.7
Bark thickness	241	0.6	0.1	0.3	1.0	Bark thickness	250	0.6	0.1	0.1	0.9
Crown ratio	241	0.56	0.07	0.32	0.77	Crown ratio	250	0.60	0.08	0.34	0.83

Fertilizer, no herbicide treatment						Control					
Trait*	N	Mean	Std dev	Minimum	Maximum	Trait*	N	Mean	Std dev	Minimum	Maximum
Total inside-bark volume	245	3.3	1.6	0.2	9.0	Total inside-bark volume	249	2.5	1.3	0.1	8.6
H	245	40.4	5.0	16.0	51.2	H	249	39.1	5.7	17.2	52.7
D	245	6.6	1.4	2.0	9.8	D	249	5.8	1.3	1.5	9.2
Bark thickness	245	0.6	0.1	0.2	1.0	Bark thickness	249	0.6	0.1	0.2	1.0
Crown ratio	245	0.61	0.08	0.15	0.76	Crown ratio	249	0.63	0.07	0.43	0.83

Combined statistics from all treatments					
Trait*	N	Mean	Std dev	Minimum	Maximum
Total inside-bark volume	985	3.4	1.8	0.1	11.1
H	985	42.0	5.9	16.0	56.2
D	985	6.5	1.4	1.5	10.6
Bark thickness	985	0.6	0.1	0.1	1.0
Crown ratio	985	0.60	0.08	0.15	0.83

*Volume, H, D, bark thickness, and crown ratio were reported in cubic feet, feet, inches, inches, and percentage of total height, respectively.

Table 4. Variance components for random effects and Wald-type tests for fixed effects with five conventional mixed models (Equation 5).

Variance parameter	Measured volume				Estimated volume				D			
	Variance parameter estimates				Variance parameter estimates				Variance parameter estimates			
	Estimate		Relative amount*		Estimate		Relative amount*		Estimate		Relative amount*	
R	0	.	0.0		0	.	0.0		0.00000	.	0.0	.
M	0.00750	(0.00807)	3.6		0.00019	(0.00144)	0.1		0.00219	(0.01240)	0.1	.
R*H	0.00579	(0.00738)	2.8		0.01129	(0.00964)	5.3		0.03410	(0.05098)	1.9	
R*N	0	.	0.0		0	.	0.0		0	.	0.0	
R*H*N	0.01022	(0.00683)	4.9		0.00897	(0.00627)	4.2		0.06887	(0.04999)	3.8	
F	0.01004	(0.00536)	4.8		0.01132	(0.00567)	5.3		0.10030	(0.05070)	5.6	
R*F	0	.	0.0		0	.	0.0		0	.	0.0	
F*H	0.00049	(0.00285)	0.2		0.00098	(0.00323)	0.5		0.01761	(0.03137)	1.0	
F*N	0.00415	(0.00372)	2.0		0.00268	(0.00339)	1.3		0.01681	(0.02760)	0.9	
F*H*N	0	.	0.0		0	.	0.0		0	.	0.0	
R*F*H	0.00135	(0.00506)	0.6		0.00342	(0.00546)	1.6		0.04389	(0.04878)	2.4	
R*F*N	0	.	0.0		0	.	0.0		0.00000	.	0.0	
R*F*H*N	0	.	0.0		0	.	0.0		0	.	0.0	
Residual	0.16870	(0.00904)	81.0		0.17460	(0.00936)	81.8		1.51800	(0.08140)	84.3	
Fixed effect	Type III tests of fixed effects**				Type III tests of fixed effects**				Type III tests of fixed effects**			
	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F
H	1	4	13.31	0.0218	1	4	10.55	0.0314	1	4	10.74	0.0306
N	1	4	33.08	0.0045	1	4	36.98	0.0037	1	4	41.36	0.003
H*N	1	4	0.93	0.3895	1	4	1.2	0.3349	1	4	0.38	0.5697

See Equation 5 for variable definitions.

*Relative amount is the percentage of the total variance.

**Wald -type tests for fixed effects.

Table 4 (continued). Variance components for random effects and Wald-type tests for fixed effects with five mixed models (Equation 5).

Variance parameter	H			Bark thickness at BH		
	Variance parameter estimates			Variance parameter estimates		
	Estimate		Relative amount*	Estimate		Relative amount*
R	0	.	0.0	0	.	0.0
M	0	.	0.0	0.00165	(0.00145)	9.6
R*H	5.4628	(3.2706)	18.5	0.00057	(0.00046)	3.3
R*N	1.0350	(1.1568)	3.5	0.00009	(0.00026)	0.5
R*H*N	0.6374	(0.7626)	2.2	0.00016	(0.00031)	0.9
F	0.9767	(0.4399)	3.3	0.00118	(0.00048)	6.9
R*F	0	.	0.0	0.00026	(0.00039)	1.5
F*H	0	.	0.0	0	.	0.0
F*N	0	.	0.0	0	.	0.0
F*H*N	0	.	0.0	0.00020	(0.00029)	1.2
R*F*H	0	.	0.0	0.00022	(0.00059)	1.3
R*F*N	0	.	0.0	0	.	0.0
R*F*H*N	0	.	0.0	0.00043	(0.00080)	2.5
Residual	21.3591	(0.9847)	72.5	0.01243	(0.00080)	72.4

Fixed effect	Type III tests of fixed effects**				Type III tests of fixed effects**			
	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F
H	1	4	8.55	0.0431	1	4	0.84	0.4115
N	1	4	9.13	0.0391	1	4	8.64	0.0424
H*N	1	4	5.29	0.0828	1	4	0.44	0.5445

See Equation 5 for variable definitions.

*Relative amount is the percentage of the total variance.

**Wald-type tests for fixed effects.

The dependent and continuous independent variables in the volume relationship, height-diameter relationship, and form models were square-root transformed because of non-constant error variance (see APPENDIX I for residual plots after transformations were performed). Outliers were evaluated and all 985 observations were kept in the dataset because the outliers showed low influence. The coefficient of determination (R^2) values for the taper equation (Equation 7) fit to each individual stem varied from 0.572 to 0.997 with a mean R^2 value of 0.948. Most R^2 values were greater than 0.91, however smaller trees tended to have more eccentric diameter profiles resulting in poor fit. Consequently, a linear equation was the best fit for the majority of stems.

Family, treatment, and plot effects generally represented small proportions or none of the overall variance in the mixed models (Table 5). All the models showed that the residual or within-plot variances accounted for much of the variance. The continuous regressors in the volume relationship, height-diameter relationship, form, and bark thickness relationship models were all highly significant ($P\text{-value} \leq 0.0001$).

Table 5. Variance components for the random effects and Wald-type tests for the fixed effects in nine mixed models to analyze important relationships and characteristics related to volume estimation.

Volume relationship (6)					Height-diameter relationship (6)				Stem taper - intercept (5)			
Variance parameter estimates					Variance parameter estimates				Variance parameter estimates			
Variance parameter	Estimate		Relative amount*		Estimate		Relative amount*		Estimate		Relative amount*	
R	0	.	0		0.003339	(0.01098)	3.9		0	.	0	
M	0.001695	(0.00144)	22.0		0	.	0.0		0.001926	(0.00311)	0.8	
R*H	0	.	0		0.01465	(0.01108)	17.3		0.001978	(0.00501)	0.9	
R*N	0	.	0		0.003883	(0.00351)	4.6		0	.	0	
R*H*N	0.00029	(0.00015)	3.8		0.000756	(0.00139)	0.9		0.007433	(0.00582)	3.2	
F	0	.	0		0.001815	(0.00286)	2.1		0.01127	(0.00540)	4.9	
R*F	0	.	0		0.002649	(0.00151)	3.1		0	.	0	
F*H	0	.	0		0	.	0.0		0.001981	(0.00381)	0.9	
F*N	0	.	0		0	.	0.0		0	.	0	
F*H*N	0	.	0		0	.	0.0		0	.	0	
R*F*H	0	.	0		0	.	0.0		0.001402	(0.00607)	0.6	
R*F*N	0.000147	(0.00022)	1.9		0	.	0.0		0	.	0	
R*F*H*N	0.000449	(0.00033)	5.8		0	.	0.0		0	.	0	
Residual	0.005127	(0.00033)	66.5		0.05753	(0.00281)	67.9		0.2048	(0.01075)	88.7	
D ² H*Z	1.584E-07	(0)	0									
D*Z					0.000054	(0.00043)	0.1					
Type III tests of fixed effects**					Type III tests of fixed effects**				Type III tests of fixed effects**			
Fixed effect	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F
H	1	4	0.23	0.6584	1	4	7.23	0.0548	1	4	12.42	0.0244
N	1	4	1	0.3742	1	4	0.18	0.6927	1	4	46.09	0.0025
H*N	1	4	0.18	0.696	1	4	10.19	0.0331	1	4	0	0.9557
D ² H	1	24	26648.7	<.0001								
D					1	24	1387.85	<.0001				

See Equations 5 and 6 for variable definitions.

*Relative amount is the percentage of the total variance.

**Wald-type tests for fixed effects.

Equation numbers are in parenthesis.

Table 5 (continued). Variance components for the random effects and Wald-type tests for the fixed effects in nine mixed models to analyze important relationships and characteristics related to volume estimation.

Stem taper - slope (5)					Form (6)					Bark thickness relationship (8)				
Variance parameter	Variance parameter estimates				Variance parameter	Variance parameter estimates				Variance parameter	Variance parameter estimates			
	Estimate		Relative amount*			Estimate		Relative amount*			Estimate		Relative amount*	
R	1.773E-06	(0.00002)	0.7			0	.	0			0.000282	(0.00036)	2.1	
M	2.833E-07	(0.00000)	0.1			0.001128	(0.00118)	7.2			0.002811	(0.00237)	21.4	
R*H	0.000016	(0.00001)	6.2			0	.	0			0.00004	(0.00026)	0.3	
R*N	0.00002	(0.00002)	7.8			0	.	0			0.000028	(0.00025)	0.2	
R*H*N	0	.	0			0.000358	(0.00025)	2.3			0.000275	(0.00033)	2.1	
F	1.662E-06	(0.00000)	0.6			0	.	0			0.000636	(0.00026)	4.8	
R*F	1.863E-06	(0.00001)	0.7			0.000245	(0.00028)	1.6			0	.	0	
F*H	0	.	0			0	.	0			0	.	0	
F*N	0	.	0			0.000328	(0.00030)	2.1			0	.	0	
F*H*N	2.398E-06	(0.00000)	0.9			0.000051	(0.00030)	0.3			0	.	0	
R*F*H	2.839E-06	(0.00001)	1.1			0	.	0			0.000277	(0.00033)	2.1	
R*F*N	1.376E-06	(0.00001)	0.5			0	.	0			0	.	0	
R*F*H*N	0	.	0			0	.	0			0.000035	(0.00050)	0.3	
Residual	0.000208	(0.00001)	81.2			0.01342	(0.00069)	85.9			0.008756	(0.00056)	66.6	
AH*Z						0.0001	(0.00004)	0.6						
Type III tests of fixed effects**					Type III tests of fixed effects**					Type III tests of fixed effects**				
Fixed effect	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F		Num df	Den df	F value	Pr > F	
H	1	4	4.02	0.1155	1	4	1.43	0.2982		1	4	2.98	0.1596	
N	1	4	0.14	0.7239	1	4	0.9	0.3962		1	4	3.59	0.131	
H*N	1	4	8.73	0.0418	1	4	0.02	0.9065		1	4	0.03	0.8711	
AH					1	24	9779.29	<.0001						
d.i.b.										1	485	477.62	<.0001	

See Equations 5 and 6 for variable definitions.

*Relative amount is the percentage of the total variance.

**Wald-type tests for fixed effects.

Equation numbers are in parenthesis.

Table 5 (continued). Variance components for the random effects and Wald-type tests for the fixed effects in nine mixed models to analyze important relationships and characteristics related to volume estimation.

Variance parameter	Crown ratio (5)				Form quotient (5)				MPD (5)			
	Variance parameter estimates				Variance parameter estimates				Variance parameter estimates			
	Estimate		Relative amount*		Estimate		Relative amount*		Estimate		Relative amount*	
R	0.000298	(0.00047)	5.1		0.000077	(0.00033)	1.0		0	.	0.0	
M	0	.	0		0.000059	(0.00013)	0.8		35.5586	(30.22880)	21.5	
R*H	0.000445	(0.00035)	7.6		0.000218	(0.00021)	2.9		0	.	0	
R*N	0.000115	(0.00013)	2.0		0.000268	(0.00024)	3.5		0.4163	(2.11600)	0.3	
R*H*N	8.582E-06	(0.00007)	0.1		0	.	0		2.86	(2.72420)	1.7	
F	0.000081	(0.00008)	1.4		0.000201	(0.00011)	2.7		3.4884	(2.02160)	2.1	
R*F	0.000112	(0.00011)	1.9		0.000051	(0.00018)	0.7		0	.	0	
F*H	0	.	0		0	.	0		0	.	0	
F*N	0	.	0		0	.	0		0	.	0	
F*H*N	0.000112	(0.00010)	1.9		0	.	0		0	.	0	
R*F*H	0	.	0		0	.	0		0	.	0	
R*F*N	0	.	0		0.000043	(0.00025)	0.6		3.1447	(4.32900)	1.9	
R*F*H*N	0	.	0		0	.	0		1.4002	(6.86030)	0.8	
Residual	0.004683	(0.00024)	80.0		0.006739	(0.00036)	88.9		118.29	(7.60340)	71.6	
Type III tests of fixed effects**					Type III tests of fixed effects**				Type III tests of fixed effects**			
Fixed Effect	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F	Num df	Den df	F value	Pr > F
H	1	4	6.77	0.0599	1	4	1.65	0.2679	1	4	0.61	0.4785
N	1	4	9.86	0.0348	1	4	2.81	0.169	1	4	8.65	0.0423
H*N	1	4	1.04	0.3647	1	4	0.9	0.3969	1	4	1.13	0.3474

See Equations 5 and 6 for variable definitions.

*Relative amount is the percentage of the total variance.

**Wald-type tests for fixed effects.

Equation numbers are in parenthesis.

The volume relationship mixed model (Equation 6) shows plot effects and measurer as having noticeable impacts on volume after accounting for D^2H (Table 5). One of the most prominent effects involved the person measuring the bark thickness. The standard errors were high for all of these effects except the residual.

The height-diameter relationship model (Equation 6) demonstrated the strong blocking effect on this site (Table 5). The blocking variable and many of the interactions with blocks had a large estimated effect in this model, but with high standard errors. The family effect accounted for only a small portion of the overall variance and had a large estimated standard error. The residual or within-plot effect was large in this model. The interaction between herbicide and fertilizer was significant at the 0.05 significance level (P-value = 0.0331).

There were noticeable family effects on the intercept (Equation 5) but not the slope (Equation 5) for stem taper (Table 5). Herbicide and fertilization main effects were significant at the 0.05 significance level (P-values of 0.0244 and 0.0025, respectively) in the intercept model. The interaction between herbicide and nutrition treatments was significant for the slope model at the 0.05 significance level.

The variance of the partial slope, family by AH, was small in the form (stem shape) mixed model (Equation 6) (Table 5). There were no important family or treatment effects in this model. The measurer had a high percentage of the variance but had a relatively high standard error.

Family effects on bark thickness were modest after accounting for the inside-bark diameter (Equation 8) (Table 5). Treatment main effects and interactions were not

significant at the 0.05 level for bark thickness. The measurer was one of the most pronounced effects in this model but had a relatively high standard error.

Crown ratio (Equation 5) was not strongly affected by family (Table 5). Some of the plot effects were noticeable but had high standard errors. The fertilization treatment was significant at the 0.05 significance level.

Family effects were small with high standard errors in the form-quotient mixed model (Equation 5) (Table 5). Treatment main effects were not significant at the 0.05 significance level. There are some interactions with the blocking variable that were noticeable; however, the standard errors for these were large.

There was a strong measurer effect with a high standard error in the MPD model (Equation 5) (Table 5). The family effect was small with a high standard error. The fertilization treatment was significant at the 0.05 level.

DISCUSSION

The conventional analysis of measured total inside-bark volume, estimated total inside-bark volume with the Warner-Goebel equation, D, H, and bark thickness at BH demonstrated important main effects of family and cultural treatments on growth. Control over OP families, competition, and nutrition give the forest manager the ability to increase the amount of wood for a given acre over a period of time. Significant measurer effects for bark thickness demonstrated low precision and measurement bias with the use of a bark gauge.

The within-plot variances in all the mixed models accounted for a large percentage of the total variance. The presence of large residual variances indicates that major factors affecting the various traits of interests are not fully captured in the factors considered in this

study. Another common trend in all the models was the minor importance of GxC. The GxC effects were reduced by the use of continuous regressors in four of the models. For example, the volume relationship model indicated that the genotype and environment did not interact to change the volume after accounting for D^2H . The models without continuous regressors also showed mild GxC interactions. These models indicate that GxC was unimportant for taper, crown ratio, form quotient, and MPD.

The estimated measurer variance was large in the volume relationship, form, bark thickness relationship, and MPD models, which all involved bark thickness measurements. In the field, it was noticed that the force applied by different measurers to the bark gauge varied. This issue demonstrated an inherent bias when using different field workers in the same genetic trial. For this study, two crews measured each block for logistical reasons. The standard errors of the estimated variability among measurers were also large, indicating there is low precision with this measurement in general. This was probably the result of bark thickness being a highly variable trait (Pederick 1970) and measurements with a bark gauge being imprecise. The addition of the continuous regressors in the mixed-model analysis of volume-related relationships and traits increased the relative size of the measurer variance. The continuous regressors removed much of the main growth effects, such as cultural treatment and family effects on volume, D, and H.

The volume relationship model results indicated that the estimated volume from a combined-variable equation is an appropriate predictor of total inside-bark volume. The variable D^2H removed the family and treatment effects on volume, which signifies that this single combined-variable is adequate when comparing many genotypes in a variety of environments.

The stem-taper intercept model was characterized by stem size and demonstrated the presence of family and treatment effects. These main family and treatment factors affected the stem size but did not contribute to the stem-taper slope model. The stem-taper slope model characterized the rate of stem narrowing. The main family and treatment factors and the family by treatment interactions did not change this rate. This finding is contrary to Larson (1963) who noted that nutrition and genetics affected stem taper. While the main effects were unimportant, the interaction of herbicide and fertilization treatments affected both the stem-taper slope model and the height-diameter relationship model. This indicates that only the most intensive silvicultural regime considered in this research affected stem taper and the relationship of H and D. In this present study, family was found to have little effect on the intercept or slope in the height-diameter relationship model. This was in contrast to Buford and Burkhardt (1987), where they found evidence of differences in the intercept term for OP families and seed sources, but not the shape of the relationship. The methods of Buford and Burkhardt (1987) differed from the present study. Buford and Burkhardt (1987) fit a height-diameter model to each seed source or OP family, and used the parameter estimates to evaluate block, and seed source or OP family effects in an analysis of variance.

There was a family effect on bark thickness not related to D. This indicates that bark thickness is genetically controlled when the influence of stem size on bark thickness is removed. Therefore, bark thickness should be considered a candidate for improving volume estimates through measurements beyond H and D. There was no strong treatment influence on bark thickness after accounting for D. This means that when predicting volume growth, the silvicultural treatment will not affect bark thickness other than by affecting stem size.

Therefore, there is no need to measure bark thickness in silvicultural experiments to estimate inside-bark diameter or volume.

Crown ratio was affected by stand conditions related to silvicultural treatments and blocking. Crown ratio is influenced by stand conditions (Larson 1963, Newberry and Burkhardt 1986). Plots may have had a variety of stand structures to influence crown ratio. Likewise, fertilization advances stand conditions and accelerates lifting of the live crown. Crown ratio is thought to be phenotypically correlated with stem taper (see Chapter 3). Branch whorls are thought to contribute to diameter growth below the branches, so that longer crowns spread diameter growth more evenly over the stem (Labyak and Schumacher 1954, Newberry and Burkhardt 1986). Shorter crowns tend to create a more cylindrically shaped bole (Larson 1963). Crown ratio did not vary greatly among families. This is contrary to the examples given by Larson (1963), although he did not quantify inheritance of crown ratio in loblolly pine.

The fertilization treatment significantly affected the MPD because of its influence on the size of the stem; larger trees had smaller MPD's. Family effects were small on MPD, which demonstrates that volume predictions with the Warner-Goebel equation were not systematically erroneous with respect to family-mean volume estimates.

CONCLUSION

Total volume differences among families not accounted for in a D^2H equation are small. The combined-variable equation is an effective predictor of total inside-bark volume, even when fit to small data sets (Spurr 1952), and is widely used. Evaluation of the Warner-Goebel combined-variable equation can be found in Chapter 3.

Similar to volume, no large family differences were found for height-diameter relationship, stem taper, form, crown ratio, form quotient, or MPD. These findings give further support that a combined-variable equation captures all of the important total inside-bark differences between families. Since there was little family variation in the height-diameter relationship, stem taper coefficient, and form quotient, family differences in taper are probably small.

There was a noteworthy family effect on bark thickness after accounting for stem size. Although not enough to show a strong family effect in the combined-variable model, bark thickness variation among families could affect the actual total inside-bark volume of selected individuals in future breeding cycles. Further investigation into the variation and measurement of bark thickness should be considered. The measurer effect was relatively large for bark thickness so the use of a bark gauge may be inappropriate for field experiments. Conceivably, a more precise bark thickness measurement could be obtained by bucking stems and measuring bark thickness with a ruler.

3. EVALUATING AND IMPROVING VOLUME ESTIMATION IN TREE IMPROVEMENT TRIALS

INTRODUCTION

Tree breeding programs around the world select for volume more than any other trait. These programs commonly estimate volume using a combined-variable equation that uses diameter at breast height (D) squared multiplied by total tree height (H) as a regressor on inside-bark volume. The North Carolina State University–Industry Cooperative Tree Improvement Program (TIP) has a long history using the Warner and Goebel (1963) combined-variable equation (Warner-Goebel equation). The Warner-Goebel equation was derived from 74 loblolly pine trees from the upper South Carolina Piedmont with least-squares regression. Combined-variable equations have been effective in fitting prediction equations for total inside-bark volume to small data sets (Spurr 1952). However, differences in taper and bark thickness among individuals or families are not accounted for with a combined-variable equation. The objective of this chapter is to evaluate selection with the Warner-Goebel equation, evaluate our volume estimates for gain, and to analyze methods for improving accuracy of volume estimates.

MATERIALS AND METHODS

A genotype by cultural treatment (GxC) study at Bainbridge, GA was destructively sampled in the 13th growing season. There were 25 open-pollinated (OP) families (Table 2) sampled in a 2 x 2 factorial of herbicide and fertilization treatments (Table 1). Total inside-bark volume was calculated using stem diameter and bark thickness measurements along the stems (Equations 1 and 2). Measurements were made at 0.5, 2, 4.5, and 8 ft heights above ground level and at four-foot intervals starting at the 8 ft height and continuing to a three-

inch outside-bark (o.b.) top. In addition to diameter measurements, total height, height to live crown, and height to a three-inch top were measured. All measurements were described in detail in Chapter 2.

Volume Estimation

Volumes estimated from the Warner-Goebel equation were compared to those determined by stem analysis of the felled tress. The Warner-Goebel equation is:

$$\hat{V}_{ib} = 0.03371 + 0.196128 \left(\frac{D^2 H}{10} \right) \quad (10)$$

Where:

$$\hat{V}_{ib} = \text{estimated total inside-bark volume, cu ft}$$

Genetic Parameters

The computer program, ASReml (Gilmour 2003), was used to calculate variance components and their corresponding standard errors. ASReml uses residual maximum likelihood for fitting linear mixed models and estimating variance components. The pedigree was used from Table 2 to account for relatedness among families. Variance components were estimated from a mixed linear model describing genotype and environmental effects (Equation 11).

$$Y_{ijkl} = \mu + R_i + T_j + RT_{ij} + F_k + FR_{ik} + FT_{jk} + FRT_{ijk} + \epsilon_{ijkl} \quad (11)$$

Where:

$$\begin{aligned} Y_{ijkl} &= \text{trait of interest} \\ R_i &= \text{fixed block effect} \\ T_j &= \text{fixed treatment effect} \\ F_k &= \text{random family effect} \\ \epsilon_{ijkl} &= \text{random tree-to-tree error} \end{aligned}$$

Individual-tree and family-mean heritabilities were calculated with formulae adapted from Zobel and Talbert (1984) and Namkoong et al. (1966), respectively. Individual-tree heritabilities were calculated using the following equation:

$$h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{fr}^2 + \sigma_{ft}^2 + \sigma_{ftr}^2 + \sigma_e^2} \quad (12)$$

Where:

h_i^2 = individual-tree heritability

σ_f^2 = family variance

σ_{fr}^2 = family by rep interaction variance

σ_{ft}^2 = family by treatment interaction variance

σ_{ftr}^2 = family by rep by treatment interaction variance

σ_e^2 = error variance

Family-mean heritability calculations used coefficients from expected mean square for the random family effect to adjust for imbalances in the dataset. To relieve the confounding effect of tree size on bark thickness, heritabilities for bark thickness were calculated after including inside-bark diameter as a continuous regressor. Family-mean heritabilities were computed using the following equation:

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \frac{k_2\sigma_{fr}^2}{k_1} + \frac{k_3\sigma_{ft}^2}{k_1} + \frac{k_4\sigma_{ftr}^2}{k_1} + \frac{\sigma_e^2}{k_1}} \quad (13)$$

Where:

h_f^2 = family-mean heritability

k_1 to k_4 are the coefficients for σ_f^2 , σ_{fr}^2 , σ_{ft}^2 and σ_{ftr}^2 , respectively, in the expected mean squares for the family effect. These coefficients were 37.764, 7.554, 9.442, and 1.908, respectively.

Several traits were transformed to increase the homogeneity of the error variances. Measured total inside-bark volume, measured total outside-bark volume, total inside-bark volume estimated with the Warner-Goebel equation, and D²H were square-root transformed and total height was squared for both the estimation of heritabilities and genetic correlations. The residual plots for these traits after transformations can be seen in Appendix II.

The genetic correlation between two traits is described by the ratio of the family covariance to the square-root product of the family variances (Falconer and Mackay 1996) (Equation 14). A bivariate model was used to build an unstructured variance matrix between pairs of traits for family and error random effects in ASReml (Gilmour 2003). Both family and error effects were assumed to be independent Gaussian variables with means of zero. Each pair of traits had two 2 x 2 unstructured matrices for both family and error effects.

$$r_G = \frac{COV(xy)}{\sqrt{VAR(x)*VAR(y)}} \quad (14)$$

Where:

r_G = genetic correlation between traits x and y
 $COV(xy)$ = family covariance between traits x and y
 $VAR(x)$ = family variance of trait x
 $VAR(y)$ = family variance of trait y

The genetic correlation between bark thickness and D was calculated with bark thickness values adjusted for the stem size. This adjustment for bark thickness was accomplished by regressing inside-bark diameter on bark thickness and adding the individual residual values to the bark-thickness grand mean. Phenotypic correlations were calculated

similarly, but with the phenotypic covariance and variances as Pearson's correlation coefficient.

Form quotients were calculated using the following equation:

$$FQ = \left(\frac{d_{h1}}{d_{h2}} \right) \quad (15)$$

Where:

FQ = form quotient

d_{h1} = diameter at height 1

d_{h2} = diameter at height 2

Table 6 identifies the two heights representing the locations of diameters used to calculate three form quotients (Equation 15). Two form quotients were calculated for each set of heights, one with inside-bark diameters and the other with outside-bark diameters.

Table 6. Description of heights where diameters were used to calculate three form quotients.

Form Quotient	Height 1	Height 2
16-BH	16 ft	BH
8-2	8 ft	2 ft
8-0.5	8 ft	SH

BH = breast height, 4.5 feet above ground level.

SH = stump height, 0.5 feet above ground level.

The regression coefficient (slope) from the stem-taper regression on each individual stem (Equation 7) was used to calculate genetic parameters as an indicator of average stem taper.

Evaluating Selection for Total Volume

Total inside-bark stem volume is extremely difficult to assess directly from standing trees, so selection on estimated volume may be considered a form of indirect selection.

Estimated inside-bark volumes were predicted with the Warner-Goebel equation. The

selection efficiency of indirect selection was then calculated using Equations 16-18 (Falconer and MacKay 1996). Selection efficiency can be thought of as the gain expected from indirect selection divided by the gain expected from direct selection of a trait. In this case, the trait of interest is the true total inside-bark volume (y) and the trait we actually select for is the predicted total inside-bark volume (x).

$$CR_y = ih_x h_y r_A \sigma_{py} \quad (16)$$

$$R_y = ih_y^2 \sigma_{py} \quad (17)$$

$$S = \frac{CR_y}{R_y} \quad (18)$$

Where:

CR_y = correlated response of indirect selection for trait y

i = selection intensity

$h_x = \sqrt{\text{heritability of trait } x}$

$h_y = \sqrt{\text{heritability of trait } y}$

r_A = genetic correlation between traits x and y

σ_{py} = phenotypic standard deviation of trait y

R_y = response from direct selection

h_y^2 = heritability of trait y

S = selection efficiency

The average Type-B genetic correlation among treatments was calculated for each trait using Equation 19. These correlations described the interaction of the genotype with several different environments (Yamada 1962). The error variance in each of the four treatments is assumed constant with this formula (Burdon 1975). If the interaction variance was greater than half the size of the family variance (Type-B correlation < 0.67) then GxC was said to be large (Shelbourne 1972).

$$r_{G_B} = \frac{\sigma_A^2}{\sigma_A^2 + \sigma_{AT}^2} \quad (19)$$

Where:

r_{G_B} = average Type-B genetic correlation

σ_A^2 = additive genetic variance

σ_{AT}^2 = additive genetic by treatment interaction variance

Evaluating Accuracy of Volume Estimates

To evaluate current and experimental volume estimation models, the range in family-mean percent deviations (MPD) (Pederick 1970), coefficient of determination (R^2), and root mean-square error (RMSE) were used to compare the relative accuracy of the models. The formula for MPD and bias are as follows:

$$MPD = \left(\frac{\hat{V}_{ib} - V_{ib}}{V_{ib}} \right) 100 \quad (20)$$

$$Bias = \left(\hat{V}_{ib} - V_{ib} \right) \quad (21)$$

Where:

$Bias$ = differences in predicted and measured volumes, cu ft

$\hat{V}_{ib}$ = Estimated inside-bark volume from Warner-Goebel equation, cu ft

V_{ib} = Measured inside-bark volume using the sum of the measured stem sections, cu ft

An analysis of the Warner-Goebel combined-variable equation was performed using the range in family MPD to evaluate model estimates. A similar combined-variable equation was fit to the study dataset to create a base range in MPD and fit from which to compare

alternative models. This fitted combined-variable equation can also be compared to the results from the Warner-Goebel equation to determine whether having a local volume equation results in an improvement in volume estimates.

Data transformations were performed to reduce heteroscedasticity for the prediction models. The total inside-bark volume and D^2H were always square-root transformed in the prediction models. Residual plots after transformations can be seen in Appendix III. Also, ten stems were removed from the measured dataset because of missing data. Outliers were evaluated and, as none were identified, all 985 observations were used.

Additional Measurements to Improve Volume Estimates

Capturing some of the family differences not accounted for in a combined-variable equation required further measurements related to inside-bark volume estimation. Some measurements considered included bark thickness, crown ratio, form quotients, and height to a three-inch top.

Bark thickness was obtained using a punch-style bark gauge to measure the bark thickness at BH, and thus determine diameter inside-bark (d.i.b.) at BH. However, there are two obstacles when measuring bark thickness with a bark gauge. First, bark thickness varies dramatically in loblolly pine due to fissures and peaks (Pederick 1970). The second hurdle is that of measurer error and bias. The inconsistent nature of measuring bark thickness is problematic. Evaluation of bark thickness involved an adjustment of inside-bark volume by measurer to account for the bias that the measurer may have introduced. This was accomplished by regressing bark thickness on measurer, taking the individual residual values, and adding the residuals to the grand mean for bark thickness. A prediction model was created to evaluate bark thickness as an accuracy-improving measurement. Bark

thickness was put into relative terms to minimize multicollinearity between independent variables that may affect standard errors. This was accomplished by dividing bark thickness by D (Persson and Downie 1992). This volume prediction model was:

$$Y = \beta_0 + \beta_1 X + \beta_2 B + \beta_3 XB + \epsilon \quad (22)$$

Where:

Y = the square-root of total inside-bark volume

X = the square-root of D^2H

$$B = \left(\frac{\text{bark thickness, adjusted for measurer}}{d.i.b. at BH} \right)$$

$\beta_0, \beta_1, \beta_2, \beta_3$ = parameters to be estimated

ϵ = error

Crown ratio is conveniently calculated as the percentage of stem occupied by live crown. This measurement is practical because total height is routinely measured in genetic tests and height to live crown would not require any effort to set up for an additional clinometer or height-pole reading. The crown ratio calculation was:

$$C = \left(\frac{H - H_{LC}}{H} \right) 100 \quad (23)$$

Where:

C = Crown Ratio, %

H_{LC} = height from the ground line to the first live branch, ft

A volume prediction model was used to predict total inside-bark volume with D^2H and crown ratio as independent variables so that improvements in volume estimates from adding crown ratio could be evaluated. The volume prediction model with crown ratio was:

$$Y = \beta_0 + \beta_1 X + \beta_2 C + \beta_3 XC + \epsilon \quad (24)$$

Form quotients can be used to describe taper differences among individuals. Two form quotients were used as independent variables in the volume prediction models; both were ratios of outside-bark diameters. One was calculated from diameters at 8 and 2 ft above ground level, and the other at 16 and 4.5 ft. These form quotients were chosen because they are easy to apply in operational settings. On the young stems commonly assessed in genetic tests, diameter measurements at 8 and 2 ft may create a similar form quotient to the Girard form quotient (Mesavage and Girard 1946) used on larger stems but with two outside-bark diameters. The two volume prediction models including a form quotient took the following form (Spurr 1952):

$$Y = \beta_0 + \beta_1 X + \beta_2 F + \beta_3 XF + \epsilon \quad (25)$$

Where:

F = form quotient

Others terms described previously

Similarly, a model including a term for height to a three-inch o.b. top diameter follows a similar form to the form quotient model (Equation 26). The height to a three-inch o.b. top variable was expressed as a proportion of total height. This variable gives an indication of taper by expressing the portion of stem below a three-inch o.b. top. In operational settings with standing trees, this would require an optical dendrometer set to three inches and used to scan until the appropriate location on the stem was found. The height to a three-inch o.b. top diameter was put into relative terms to minimize multicollinearity between independent variables that may affect standard errors. The height to a three-inch o.b. top diameter was divided by H and can be interpreted as a ratio describing the proportion of stem below a three-inch o.b. top diameter. The equation used was:

$$Y = \beta_0 + \beta_1 X + \beta_2 T + \beta_3 XT + \epsilon \quad (26)$$

Where:

$$T = \left(\frac{\text{height to three-inch o.b. top}}{H} \right)$$

Creating a More Efficient Volume Prediction Model

Other than adding variables, simply creating new models may improve predicted volume estimates. One possible model comes from Schumacher and Hall (1933). The Schumacher-Hall model was:

$$Y = \beta_0 D_r^{\beta_1} H_r^{\beta_2} + \epsilon \quad (27)$$

Where:

D_r = reciprocal of D
 H_r = reciprocal of H

In this case D and H are reciprocal transformed because of heteroscedasticity. This nonlinear model has been extensively used as a total-volume prediction model. Pseudo- R^2 was used to evaluate this nonlinear model in place of the R^2 for linear models. The formula for Pseudo- R^2 from Schabenberger and Pierce (2002) was:

$$\text{Pseudo-}R^2 = 1 - \frac{SSR}{SST_m} \quad (28)$$

Where:

SSR = residual sum of squares
 SST_m = total sum of squares corrected for the mean

Another candidate volume prediction model includes all significant relationships between D and H. The independent variables, D and H, were tested up to the second-order polynomial with all interactions included. Only second- and first-order terms were tested to

make the selection process simple and reduce the complexity of the final model. The model was reduced and most second-order terms were dropped in backward model selection procedures. The full (Equation 29) and reduced (Equation 30) models fit to this dataset were:

$$Y = \beta_0 + \beta_1 D + \beta_2 H + \beta_3 DH + \beta_4 D^2 + \beta_5 H^2 + \beta_6 D^2 H + \beta_7 DH^2 + \beta_8 D^2 H^2 + \epsilon \quad (29)$$

$$Y = \beta_0 + \beta_1 D + \beta_2 H + \beta_3 DH + \beta_4 D^2 + \epsilon \quad (30)$$

Where:

Y = square-root of total inside-bark volume

β_i = parameters to be estimated, $i = 0, \dots, 8$

Other terms are as defined previously

RESULTS

Genetic Parameters

Table 7 shows the variance components for various traits from Equation 11. For many traits, the family variance component is about five percent of the overall phenotypic variance. If these OP families are assumed to be half-sibs, the family variance represents one quarter of the additive genetic variance. Many traits show a small percentage of genotype by environment interaction in the form of family by treatment or family by block interactions. The crown ratio, taper coefficient, and form quotient (i.b., 8ft/0.5ft) traits have family by treatment and family by block interaction components that are larger than family components. The error variance components were always large.

Table 7. Variance components used in the calculation of heritabilities for 16 traits (standard errors in parentheses) (Equation 11).

Trait	Component	Variance		Percentage of phenotypic variance
Total volume (i.b.)	Family	0.01140	(0.00479)	6.1
	Family*Treatment	0.00224	(0.00340)	1.2
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0	(0)	0.0
	Error	0.17290	(0.00829)	92.7
Total volume (o.b.)	Family	0.01315	(0.00537)	6.6
	Family*Treatment	0.00206	(0.00357)	1.0
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0	(0)	0.0
	Error	0.18410	(0.00883)	92.4
Estimated volume (i.b.)	Family	0.01301	(0.00523)	6.7
	Family*Treatment	0.00148	(0.00337)	0.8
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0	(0)	0.0
	Error	0.17840	(0.00856)	92.5
D ² H	Family	6.72100	(2.70300)	6.7
	Family*Treatment	0.74990	(1.74300)	0.8
	Family*Block	0.00002	(0)	0.0
	Family*Trt*Blk	0.00006	(0)	0.0
	Error	92.33000	(4.42800)	92.5
D	Family	0.11630	(0.04680)	6.9
	Family*Treatment	0.01667	(0.03014)	1.0
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0	(0)	0.0
	Error	1.56300	(0.07495)	92.2
d.i.b. at BH	Family	0.07927	(0.03300)	6.0
	Family*Treatment	0.00820	(0.02304)	0.6
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0	(0)	0.0
	Error	1.23700	(0.05933)	93.4
Bark thickness	Family	0.00059	(0.00028)	5.1
	Family*Treatment	0	(0)	0.0
	Family*Block	0.00036	(0.00027)	3.1
	Family*Trt*Blk	0.00017	(0.00052)	1.5
	Error	0.01039	(0.00066)	90.3
H	Family	6530	(2856)	4.7
	Family*Treatment	0.01473	(0.00068)	0.0
	Family*Block	0.03214	(0.00148)	0.0
	Family*Trt*Blk	0.05053	(0.00233)	0.0
	Error	131500	(6062)	95.3

Table 7 (continued). Variance components used in the calculation of heritabilities for 16 traits (standard errors in parentheses) (Equation 11).

Trait	Component	Variance		Percentage of phenotypic variance
Crown ratio	Family	0.00008	(0.00008)	1.6
	Family*Treatment	0.00011	(0.00010)	2.2
	Family*Block	0.00011	(0.00011)	2.2
	Family*Trt*Blk	0	(0)	0.0
	Error	0.00468	(0.00024)	93.9
Taper coefficient	Family	0.000002	(0.000003)	0.7
	Family*Treatment	0.000002	(0.000004)	1.1
	Family*Block	0.000004	(0.000005)	1.6
	Family*Trt*Blk	0	(0)	0.0
	Error	0.000211	(0.000011)	96.5
Form quotient (i.b., 8ft/2ft)	Family	0.00013	(0.00007)	3.7
	Family*Treatment	0.00005	(0.00008)	1.2
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0.00024	(0.00017)	6.7
	Error	0.00324	(0.00021)	88.4
Form quotient (o.b., 8ft/2ft)	Family	0.00011	(0.00006)	4.3
	Family*Treatment	0.00003	(0.00005)	1.1
	Family*Block	0	(0)	0.0
	Family*Trt*Blk	0.00007	(0.00012)	2.6
	Error	0.00242	(0.00015)	92.0
Form quotient (i.b., 8ft/0.5ft)	Family	0.00007	(0.00007)	1.4
	Family*Treatment	0.00008	(0.00009)	1.7
	Family*Block	0.00008	(0.00010)	1.6
	Family*Trt*Blk	0	(0)	0.0
	Error	0.00460	(0.00023)	95.3
Form quotient (o.b., 8ft/0.5ft)	Family	0.00015	(0.00008)	4.4
	Family*Treatment	0.00006	(0.00007)	1.8
	Family*Block	0.00003	(0.00007)	0.8
	Family*Trt*Blk	0	(0)	0.0
	Error	0.00325	(0.00017)	93.1
Form quotient (i.b., 16ft/BH)	Family	0.00019	(0.00013)	2.4
	Family*Treatment	0.00002	(0.00015)	0.2
	Family*Block	0.00000	(0.00016)	0.0
	Family*Trt*Blk	0	(0)	0.0
	Error	0.00807	(0.00041)	97.4
Form quotient (o.b., 16ft/BH)	Family	0.00020	(0.00011)	2.8
	Family*Treatment	0	(0)	0.0
	Family*Block	0.00006	(0.00014)	0.9
	Family*Trt*Blk	0	(0)	0.0
	Error	0.00680	(0.00033)	96.3

Individual-tree heritabilities for many growth traits were between 0.19 and 0.27 (Table 8). The heritability of bark thickness was 0.21 after accounting for d.i.b. at BH. Crown ratio, the taper coefficient, and several of the form quotients had a low heritability (≤ 0.17). Form quotients involving inside-bark diameters tended to have lower heritabilities than their outside-bark counterparts. This phenomenon was likely a result of increased error associated with additional traits; i.e. inside-bark diameters involved variation associated with outside-bark diameter and bark thickness measurements. The outside-bark form quotients with diameters at 8 and 2 foot and 8 and 0.5 foot had the highest estimated heritability among form quotients.

Table 8. Individual Tree (h_i^2) heritability (Equation 12), family-mean (h_f^2) heritability (Equation 13), and average Type B genetic correlation (r_{G_B}) (Equation 19) (standard errors in parentheses) for 16 traits across four treatments.

Trait	h_i^2	h_f^2	r_{G_B}
Total volume (i.b.)	0.24 (0.10)	0.69 (0.10)	0.84 (0.23)
Total volume (o.b.)	0.26 (0.10)	0.71 (0.10)	0.86 (0.22)
Estimated volume (i.b.)	0.27 (0.10)	0.72 (0.09)	0.90 (0.22)
D ² H	0.27 (0.10)	0.72 (0.09)	0.90 (0.22)
D	0.27 (0.10)	0.72 (0.09)	0.87 (0.21)
d.i.b. at BH	0.24 (0.10)	0.69 (0.10)	0.91 (0.25)
Adjusted bark thickness	0.21 (0.09)	0.62 (0.12)	1 (0)
Total height	0.19 (0.08)	0.65 (0.10)	1 (0)
Crown ratio	0.06 (0.06)	0.32 (0.23)	0.42 (0.37)
Form quotient (i.b., 8ft/2ft)	0.15 (0.08)	0.55 (0.15)	0.75 (0.35)
Form quotient (o.b., 8ft/2ft)	0.17 (0.08)	0.60 (0.13)	0.79 (0.31)
Form quotient (i.b., 8ft/.5ft)	0.06 (0.06)	0.30 (0.24)	0.45 (0.44)
Form quotient (o.b., 8ft/.5ft)	0.17 (0.09)	0.59 (0.14)	0.71 (0.27)
Form quotient (i.b., 16ft/BH)	0.09 (0.06)	0.47 (0.19)	0.92 (0.65)
Form quotient (o.b., 16ft/BH)	0.11 (0.06)	0.50 (0.16)	1 (0)
Taper coefficient	0.03 (0.05)	0.19 (0.28)	0.40 (0.68)

d.i.b. = inside-bark diameter.
BH = breast height.
o.b. = outside-bark.
i.b. = inside-bark.

Many of the growth traits had a family-mean heritability between 0.65 and 0.72. Bark thickness had a heritability of 0.62 after accounting for d.i.b. at BH. Crown ratio and some of the form quotients had low heritabilities. The taper coefficient had an extremely low heritability relative to the other traits.

The genetic correlations between characters are shown in Table 9. Estimated total inside-bark volume and D^2H were both highly correlated with the measured total inside-bark volume from destructively sampling. Bark thickness, adjusted for inside-bark diameter, had a genetic correlation of 0.66 with D . Crown ratio had low phenotypic and genetic correlation with almost every trait measured, except for a modest positive genetic correlation with total height.

Table 9. The genetic and phenotypic correlations between pairs of traits with associated standard errors or p-values, respectively, in parenthesis.

	Measured total volume (i.b.)	Measured total volume (o.b.)	D ² H	D	Adjusted bark thickness	Estimated total volume (i.b.)	Crown ratio	Total height	Form quotient (o.b., 8ft/ 2ft)	Form quotient (o.b., 16ft/ BH)	Taper coefficient
Measured total volume (i.b.)			0.99 (0.0054)			0.99 (0.0056)	0.51 (0.273)				
Measured total volume (o.b.)			1.00 (0.0029)				0.48 (0.28)				
D ² H	0.98 (<.0001)	0.99 (<.0001)									
D					0.66 (0.1851)			0.77 (0.1206)			
Adjust bark thickness				0.15 (<.0001)							
Estimated total volume (i.b.)	0.98 (<.0001)										
Crown ratio	0.00 (0.976)	0.01 (0.8687)						0.61 (0.2825)	0.49 (0.3073)	0.50 (0.3305)	0.52 (0.4624)
Total height				0.75 (<.0001)			-0.11 (0.0004)				
Form quotient (o.b., 8ft/ 2ft)							0.05 (0.11)				
Form quotient (o.b., 16ft/ BH)							0.07 (0.0294)				
Taper coefficient							-0.08 (0.0077)				

Values above the diagonal are genetic correlations and below are phenotypic correlations.

d.i.b. = inside-bark diameter.

BH = breast height.

o.b. = outside-bark.

i.b. = inside-bark.

Evaluating Selection for Total Volume

Selection efficiency was high (1.01) for indirect selection for true total inside-bark volume using the total inside-bark volume estimated by the Warner-Goebel equation. The selection efficiency was greater than one because the heritability for estimated volume from the Warner-Goebel equation was slightly higher than that for the measured volume. This value was also a result of the high correlation between estimated and measured total inside-bark volumes. Table 10 shows the selection efficiencies for alternative prediction models. Increases in selection efficiency with these prediction models were trivial. The genetic correlation between estimated and measured total inside-bark volumes were already 0.99 with the Warner-Goebel equation. The other prediction equations either slightly improved or did not improve the genetic correlation. Heritabilities of the estimated volumes were similar with all the prediction equations.

Table 10. Selection efficiencies for indirect selection using the Warner-Goebel equation and the other prediction models. Family-mean heritabilities and genetic correlations (with standard errors in parentheses) are also shown.

Model*	h_f^2	r_G	r_G	Selection efficiency
Warner-Goebel (10)	0.72 (0.09)	0.99	(0.01)	1.01
D ² H equation (31)	0.72 (0.09)	0.99	(0.01)	1.01
Adjusted bark thickness (22)	0.71 (0.09)	1.00	(0.00)	1.01
Crown ratio (24)	0.72 (0.09)	0.99	(0.01)	1.01
Form quotient (16 ft/BH) (25)	0.72 (0.09)	1.00	(0.00)	1.01
Form quotient (8 ft/2 ft) (25)	0.72 (0.09)	0.99	(0.00)	1.02
Top limit ratio (26)	0.71 (0.10)	1.00	(0.00)	1.01
Nonlinear (27)	0.72 (0.09)	0.99	(0.01)	1.01
D and H (30)	0.72 (0.09)	0.99	(0.01)	1.01

*Equation numbers in parentheses.

Table 11 demonstrates only minor rank changes between total inside-bark volume estimated with the Warner-Goebel equation and the measured total inside-bark volume from

the destructive sample. Rank changes that occur can be related to stem taper and bark thickness differences. For example, family C is ranked lower for measured volume than for estimated volume. This rank change is due to family C having higher average stem taper and relatively thicker bark than the other families with which it changes rank.

Table 11. Comparison of family rankings for volume estimated with the Warner-Goebel equation, the measured volume from the destructive sample, the taper coefficient (Equation 7), and the ratio of bark thickness to inside-bark diameter at breast height.

Family	Estimated volume (cu ft)	Family	Measured volume (cu ft)	Family	Taper coefficient	Family	Bark thickness at BH
E	4.69	E	4.27	Y*	-0.0742	S	0.1264
W	4.61	W	3.99	S	-0.0742	W	0.1217
B*	4.60	M*	3.96	I	-0.0741	T*	0.1202
M*	4.50	B*	3.94	H	-0.0735	I	0.1197
K	4.34	K	3.91	W	-0.0717	V*	0.1195
C*	4.25	X*	3.79	P	-0.0714	H	0.1191
H	4.23	H	3.65	G	-0.0702	B*	0.1157
X*	4.15	F*	3.63	R*	-0.0701	G	0.1147
F*	4.01	C*	3.59	U	-0.0699	Q	0.1143
J	4.00	J	3.55	O*	-0.0698	O*	0.1133
N	3.91	N	3.52	D	-0.0698	C*	0.1114
U	3.91	U	3.47	T*	-0.0697	F*	0.1113
D	3.91	D	3.45	Q	-0.0692	N	0.1109
L	3.88	L	3.41	L	-0.0686	P	0.1104
O*	3.69	A*	3.25	M*	-0.0686	K	0.1101
V*	3.64	O*	3.24	C*	-0.0680	J	0.1100
A*	3.47	V*	3.23	J	-0.0678	R*	0.1098
S	3.46	S	3.01	A*	-0.0674	U	0.1093
P	3.37	P	2.93	E	-0.0672	M*	0.1090
R*	3.27	Y*	2.92	F*	-0.0669	X*	0.1078
T*	3.27	R*	2.90	K	-0.0669	D	0.1060
Y*	3.25	T*	2.79	B*	-0.0666	Y*	0.1041
Q	3.21	Q	2.76	V*	-0.0659	L	0.1038
G	3.16	G	2.76	X*	-0.0648	A*	0.1036
I	2.83	I	2.46	N	-0.0633	E	0.1009

*Indicates a rank change between estimated and measured volumes.

Figure 1 shows the estimation line for the Warner-Goebel equation in contrast to the prediction line (Equation 31) fit to the study data. The intercepts of the prediction lines differ only slightly but the slopes are noticeably different. The Warner-Goebel equation generally

overestimated the volumes measured through destructive sampling. However, for selection and gain estimation purposes overall precision is more important than overall bias because individuals or groups of individuals are being compared. The difference in slopes between the two equations suggests the Warner-Goebel equation inflated the volumes of larger stems proportionally more than smaller stems. See the results on evaluating the accuracy of volume estimates for a detailed description of MPD.

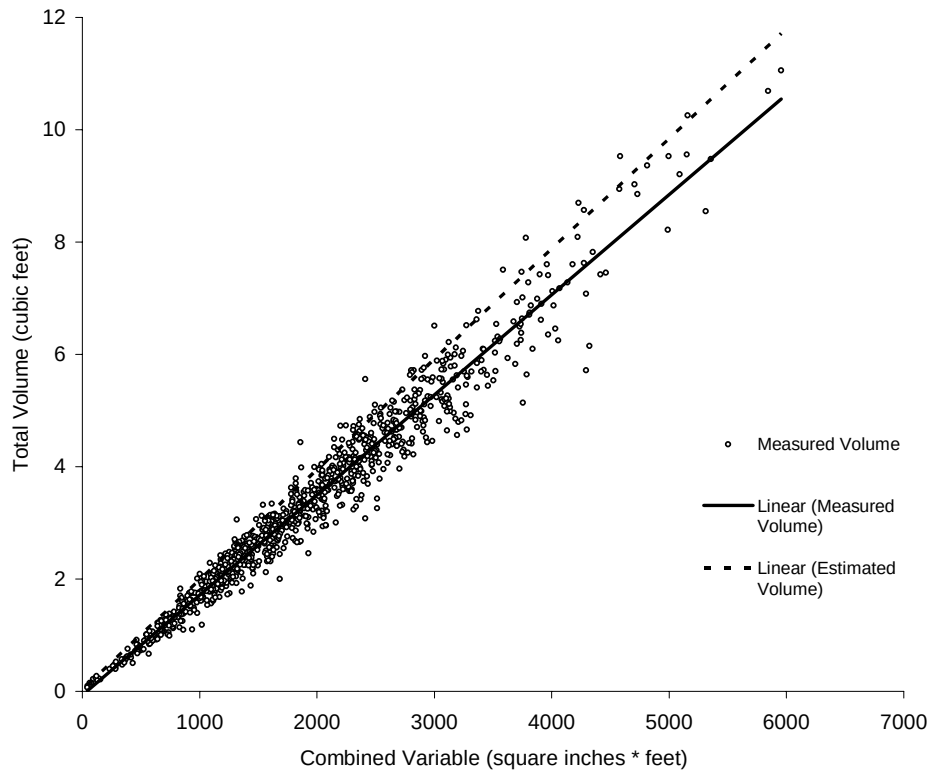


Figure 1. Comparison of prediction lines for estimated and measured inside-bark volumes from the Warner-Goebel equation and the back-transformed Equation 31, respectively.

The total inside-bark volume equation fit to the dataset from the present study required square-root transformations on both the independent and dependent variables to reduce heteroscedasticity (Equation 31).

$$\sqrt{V_{ib}} = -0.0378994028 + 0.042573971\sqrt{D^2H} \quad (31)$$

The average Type-B genetic correlation across treatments was used to evaluate the GxC effect. Only crown ratio, the taper coefficient, and one of the form quotients had average Type-B genetic correlation values below 0.67 (Table 8). Figure 2 shows five families that represent the extremes, central, and quarter values of family-mean inside-bark volume over the entire study. GxC is relatively small in this figure, with the largest family differences occurring at the highest mean for the treatment plots.

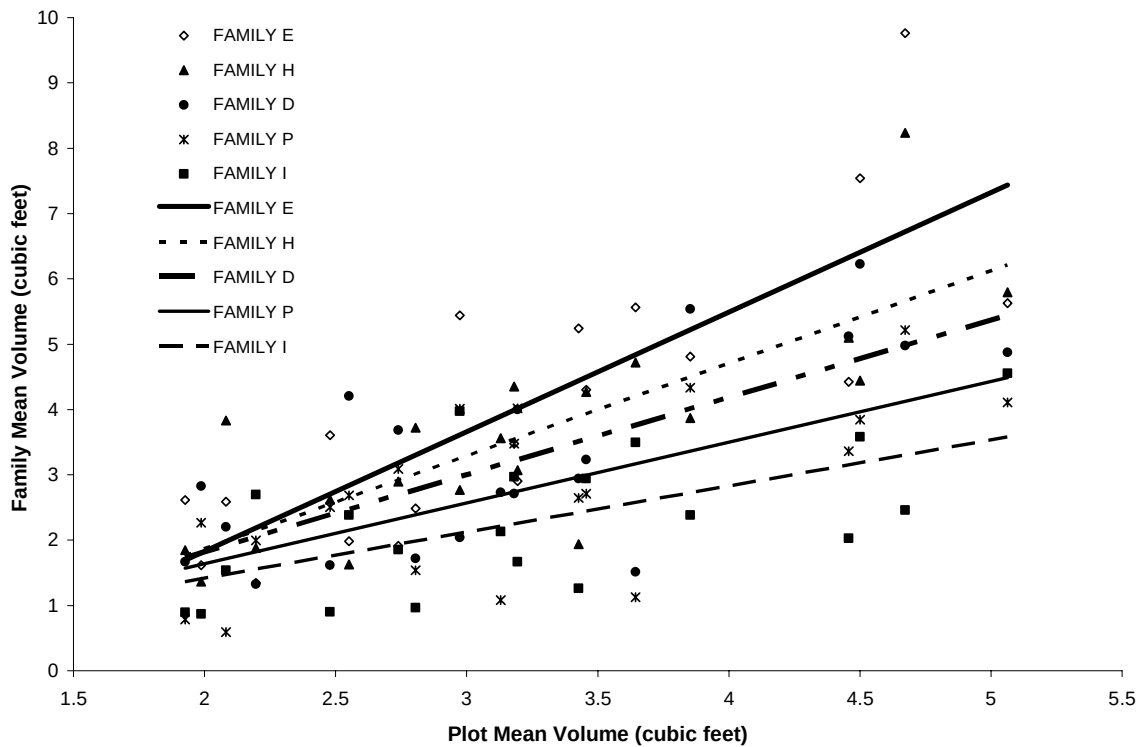


Figure 2. Regression of family plot mean on plot mean volume for five representative families. This graph demonstrates some genotype by environment interaction for total inside-bark volume.

Evaluating Accuracy of Volume Estimates

Fitting a combined-variable equation to the study dataset resulted in family MPDs that varied from -4.9 to 4.4 %. Fitting a combined-variable equation to the destructively sampled dataset had a range in MPD of 9.4 %, compared to 9.9 % with the Warner-Goebel

equation. This can be viewed as a small difference in site, stand, and age between the stems measured in this present study and those assessed by Warner and Goebel (1963).

There was overall bias associated with using the Warner-Goebel equation. The values of family MPDs from the Warner-Goebel combined-variable equation varied from 9.8 to 19.7% (Figure 3), which are biased upwards. In Figure 3, there was no systematic deviation for any particular size of stems. Also, the spread of family MPD values was reasonably constant over the range of measured inside-bark volumes.

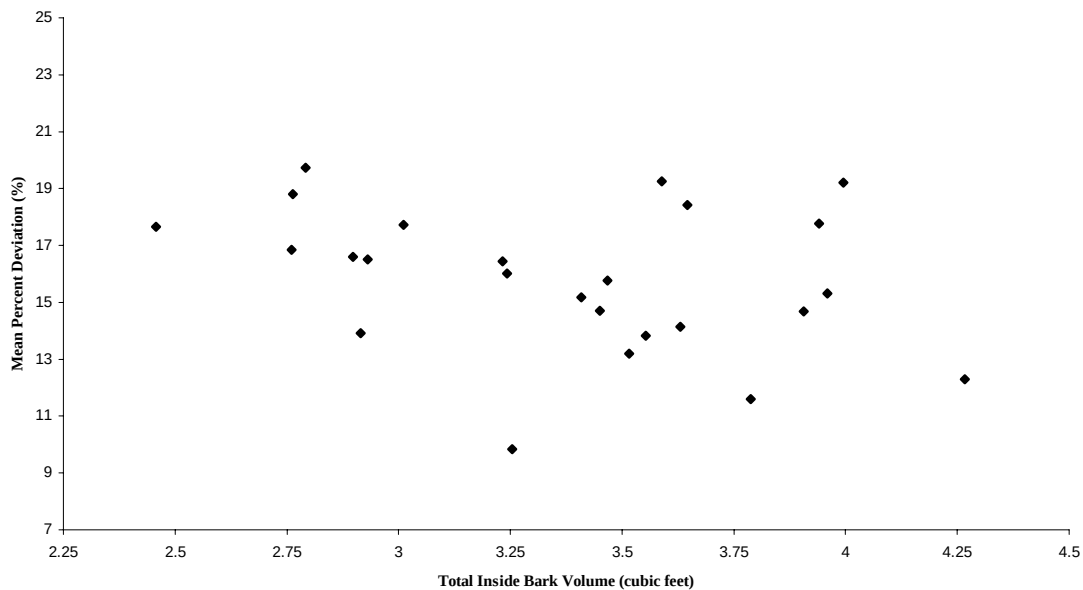


Figure 3. Mean percent deviation using the Warner-Goebel equation and measured inside-bark total volume for family means. This figure represents patterns of bias related to family-mean volume.

Figures 4 and 5 depict the variation in individual-tree total inside-bark volumes compared to the estimated total inside-bark volume predicted with the Warner-Goebel equation. Figure 4 shows the MPD values for individual trees in the dataset. Larger stems in the dataset varied less in MPD. Greater uniformity in MPD could be a result of less variation in stem taper and bark thickness. The profiles of some smaller stems were especially

eccentric as demonstrated by low R^2 values when a linear taper model (Equation 7) was fit to each individual stems. Figure 5 shows the bias for each individual stem when volume was estimated with the Warner-Goebel equation.

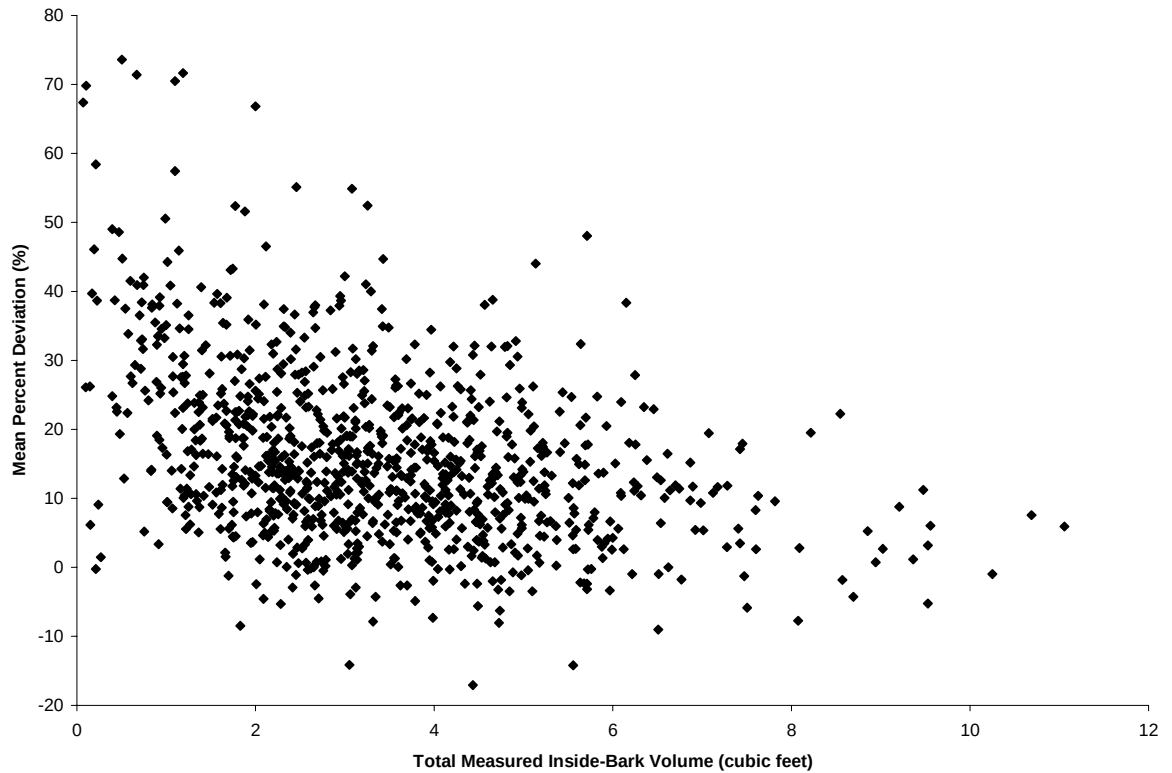


Figure 4. Relationship between mean percent deviation from the Warner-Goebel equation and measured total inside-bark volume for individual trees. This figure represents patterns of bias related to individual-stem size.

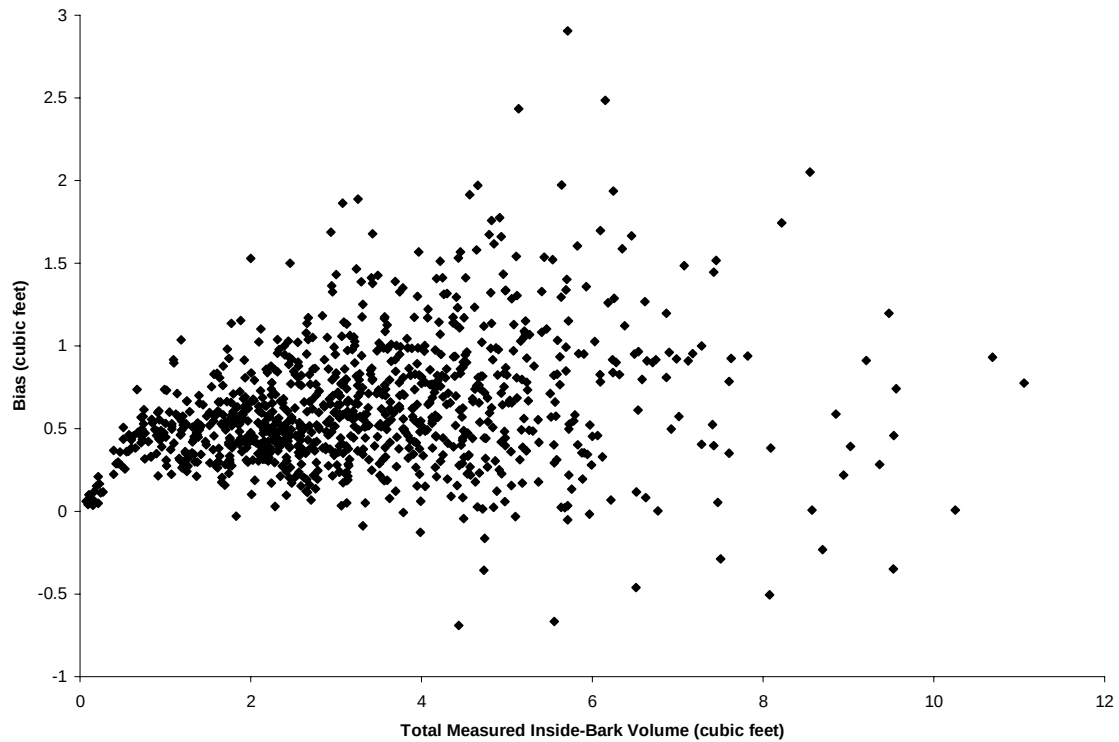


Figure 5. Relationship between bias from the Warner-Goebel equation and measured total inside-bark volume for individual trees. This figure represents patterns of bias related to individual-stem size.

Additional Measurements to Improve Volume Estimates

Models that included additional measurement terms were fit to evaluate their effectiveness in predicting volume in forest genetic trials. Each model's predicted volumes were used to calculate the MPDs in Table 12. Bark thickness, crown ratio, two form quotients, and top-limit ratio variables were used in attempts to reduce deviations from the measured volume due to family differences. All the models reduced the family MPD range and standard deviation except the model using crown ratio. Only the bark thickness and one form-quotient measurement with diameters at 16 ft and BH demonstrated major reductions in MPD. The bark thickness model with adjusted volume predictions reduced the family MPD range from 9.37 to 7.24%. The ideal model for this dataset was the form quotient of

diameters at 16 feet and BH, which reduced the range in family MPD from 9.37 to 6.77%.

See Table 13 for fit statistics and a summary of parameter estimates for these models.

Table 12. The mean percent deviations for each OP family from nine prediction models compared to the measured total inside-bark volume with descriptive statistics.

Family	N	Family mean percent deviation*								
		Warner-Goebel Equation (10)	D ² H equation fit to dataset (31)	Adjusted Bark Thickness equation (22)	Crown ratio equation (24)	Form quotient (16 ft/BH) equation (25)	Form quotient (8 ft/2 ft) equation (25)	Top limit ratio equation (26)	Nonlinear equation (27)	D and H equation (30)
A	40	9.83	-4.93	-3.02	-4.93	-3.13	-4.17	-3.97	-4.61	-4.69
B	40	17.77	3.58	2.32	3.58	3.33	4.25	2.29	3.66	3.55
C	39	19.27	4.28	4.23	4.28	1.24	4.52	1.57	4.79	4.72
D	40	14.69	0.20	0.83	0.20	-1.26	-0.24	-0.50	0.13	0.03
E	39	12.30	-1.63	-0.87	-1.63	-0.82	-1.40	-2.11	-1.57	-1.69
F	40	14.14	-0.95	-0.19	-0.95	1.16	0.47	0.22	-0.64	-0.82
G	40	16.85	-0.33	1.90	-0.33	2.26	0.11	4.56	0.05	-0.53
H	39	18.42	3.34	2.65	3.34	0.97	2.36	1.56	3.26	3.09
I	40	17.67	1.19	2.46	1.19	-0.16	0.44	0.14	1.37	1.36
J	40	13.82	-0.66	-0.63	-0.66	-0.19	-0.41	1.00	-0.70	-0.88
K	40	14.69	0.05	0.29	0.05	1.56	0.48	0.19	0.28	0.23
L	40	15.18	-0.33	1.34	-0.33	-0.96	-0.45	2.43	0.21	-0.16
M	40	15.32	1.39	0.94	1.39	0.85	1.28	0.78	1.15	0.93
N	39	13.19	-0.79	-1.10	-0.79	-0.20	-0.50	-0.27	-0.60	-0.70
O	40	16.00	0.56	1.27	0.55	0.58	0.86	1.19	0.86	0.61
P	40	16.51	0.21	2.02	0.22	0.87	0.23	1.54	0.96	0.90
Q	40	18.80	3.05	3.78	3.05	0.78	1.93	-0.56	3.42	3.35
R	38	16.60	1.22	2.26	1.22	-0.37	0.51	-1.05	1.61	1.53
S	36	17.72	2.27	1.47	2.28	-1.07	0.49	1.88	1.92	1.75
T	38	19.73	3.06	3.89	3.06	2.71	3.00	3.78	3.55	3.39
U	40	15.77	1.43	1.30	1.43	-1.03	1.62	2.34	0.91	0.85
V	40	16.44	0.88	0.99	0.88	2.77	1.02	1.00	1.27	1.08
W	39	19.21	4.44	2.97	4.44	3.65	3.65	3.87	4.16	4.03
X	38	11.59	-2.37	-2.08	-2.38	0.91	-1.89	-2.30	-1.84	-1.91
Y	40	13.92	-2.76	-0.17	-2.76	-2.23	-3.24	2.02	-2.49	-2.98
Mean		16.01	0.75	1.24	0.76	0.50	0.53	1.06	0.94	0.79
Max		19.73	4.44	4.23	4.44	3.65	4.52	4.56	4.79	4.72
Min		9.83	-4.93	-3.02	-4.93	-3.13	-4.17	-3.97	-4.61	-4.69
Range		9.90	9.37	7.24	9.37	6.77	8.70	8.53	9.40	9.41
Std dev		2.54	2.29	1.82	2.29	1.69	2.07	1.98	2.23	2.26

*Equation numbers are in parenthesis.

Table 13. Model information and parameter estimates with standard errors for the eight total inside-bark volume prediction models.

	Inside-bark volume prediction equations*							
	D ² H equation fit to dataset (31)	Adjusted bark thickness equation (22)	Crown ratio equation (24)	Form quotient (16 ft/BH) equation (25)	Form quotient (8 ft/2 ft) equation (25)	Top limit ratio equation (26)	Nonlinear equation (27)	D and H equation (30)
N	985	985	985	985	985	985	985	985
RMSE**	0.086	0.076	0.086	0.064	0.083	0.075	0.085	0.085
R ²	0.970	0.977	0.970	0.983	0.972	0.977	0.970***	0.970
Parameter estimates								
$\hat{\beta}_0$	-0.0379 (0.0105)	0.0151 (0.0414)	-0.0374 (0.0232)	0.2200 (0.0320)	-0.0077 (0.1118)	0.1689 (0.0391)		-0.1298 (0.0637)
$\hat{\beta}_1$	0.0426 (0.0002)	0.0437 (0.0010)	0.0426 (0.0002)	0.0176 (0.0011)	0.0314 (0.0029)	0.0226 (0.0015)	0.0319 (0.0017)	0.1226 (0.0126)
$\hat{\beta}_2$		0.1908 (0.3338)	-0.0008 (0.0348)	-0.2063 (0.0459)	-0.0023 (0.1385)	0.0472 (0.0649)	-0.9919 (0.0104)	0.0053 (0.0030)
$\hat{\beta}_3$		-0.0263 (0.0085)		0.0299 (0.0015)	0.0126 (0.0036)	0.0224 (0.0020)	-0.5754 (0.0171)	0.0029 (0.0004)
$\hat{\beta}_4$								0.0017 (0.0018)

*Equation numbers are in parenthesis.

**Root mean-square error.

***Psuedo-R² (Equation 28).

Creating a More Efficient Volume Prediction Model

There were two regression models fit to the study dataset that did not use additional measurements (Equations 27 and 30). Both these models failed to show improvement in MPD over the combined-variable equation fit to the present dataset (Table 12). The fit statistics for these models are given in Table 13.

DISCUSSION

Genetic Parameters

Bark thickness at BH had heritability estimates similar to those of many other growth traits after accounting for the size of the stem. This indicates that bark thickness is under similar levels of genetic control as many growth traits. The heritability estimates for crown ratio and the taper coefficient were a great deal lower than for most other traits. This low genetic component for crown ratio was probably due to the stand condition effect on crown characteristics (Larson 1963, Newberry and Burkhart 1986). The low heritability estimate for the taper coefficient indicates that average taper of stems is not strongly genetically controlled. The heritability estimates for form-quotient traits varied dramatically. The heritabilities for form quotients calculated from outside-bark diameters were always higher than for inside-bark diameters, because of additional variance associated with bark thickness measurements. The form quotient with diameters at 16 ft and BH had a moderate heritability estimate, probably because some of the 16 foot diameters were estimated by interpolation. The form quotients with outside-bark diameters at 8 and 2 ft and at 8 ft and stump height tended to have the highest heritabilities of the form quotients calculated. It is probable that the stump-height diameter measurement would involve butt swell variation in 13-year-old loblolly pine which reduced the heritability estimate for this form quotient. It is not clear whether the form quotients evaluated were confounded by the size of the stem.

Crown ratio had a low genetic correlation with most of the traits evaluated; the strongest positive genetic correlation was with H. This indicates that selection for H will result in a higher percent crown, which could lower value for quality wood products. However, this finding may be deceiving because of differences in stand conditions between a

genetic test and the deployment of family blocks. If genetic tests have more variation in total height than family-block plantings, a family who performs well in height growth may have a longer crown in a genetic test due to a more dominant crown position, whereas the same family planted in a block might reach crown closure earlier and develop a lower percentage of live crown. Phenotypic correlations between crown ratio and many other taper-related traits such as form quotients and the taper coefficient were negligible. This is contrary to many other reports (Baldwin et al. 2000, Larson 1963, Newberry and Burkhart 1986), possibly because of age or stand condition differences between the present study and others.

Evaluating Selection for Total Volume

Combined-variable equations are commonly used to estimate volume in many research applications. For TIP trials, individual stems are generally compared using the Warner-Goebel total inside-bark volume prediction equation. Selection for true inside-bark volume by estimating volume with this equation has been an effective practice based on selection efficiency. In fact, family selection for volume estimated by prediction equations was slightly more favorable than by destructively sampling (Table 10). This high selection efficiency may have resulted from less error variance being associated with estimated volume than with the detailed volume measurement. The measured volume may have had more error variance due to variation in stem taper, bark thickness, environmental variation, and unknown factors. Nonetheless, D and H measurements capture a great deal of the genetic variation in total inside-bark volume. Differences in volume not accounted for by estimating volume with the combined-variable equation are probably small enough for indirect selection to be effective. Also, Figures 1 through 3 did not show strong patterns, which indicates any errors for family-mean or individual tree volume estimates are not systematic. The selection

efficiencies for the alternative prediction models were similar to that of the D^2H equation. This indicates any further measurements or improved models will not improve the selection of families for total inside-bark volume. Table 11 demonstrated that there are rank changes caused by family differences in bark thickness and stem taper, but these rank changes are generally small. In this example, selection of the highest-ranking five or highest-ranking ten families would not have changed between estimated volume with the Warner-Goebel equation and the measured volume.

Thicker bark results from selection of higher volume families due to a positive genetic correlation of bark thickness and D in loblolly pine. The genetic correlation of D and bark thickness was similar to Pederick (1970) where the correlation between bark thickness and d.i.b. at BH was estimated as 0.66. Thicker bark could be important in disease, insect, mechanical damage, and fire resistance, but no commercial value has been explored. In fact, thicker bark individuals may result in slightly increased transportation and processing cost. The largest effect from the correlation of bark thickness and D may be from a biometrical standpoint. Bark thickness variation can confound the inside-bark D and increase the error associated with volume estimation and forecasting. This would indicate that updated models may be needed to prevent overestimation of wood volume for the genetic material that is being characterized. The bark thickness variation probably has a minimal effect on estimates due to the high correlation of estimated and measured total inside-bark volume.

GxC interaction was noticeable only for crown ratio and two form quotients (Table 8). These findings were similar to Chapter 2, where GxC was small or negligible. Crown ratio is highly influenced by stand conditions related to silvicultural treatments (Larson 1963).

GxC had a relatively minor effect on volume production. This indicates that genotype deployment and silvicultural treatments do not have to be coordinated to maximize total inside-bark volume. This finding is similar to the stability across environments captured by McKeand et al. (2000) for loblolly pine and by Zhelev et al. (2003) for Scots pine (*Pinus sylvestris* L.). Other literature dealing with genotype by environment interaction indicates that it would be preferable to plant the best-performing individuals when high-intensity silvicultural regimes are implemented (McKeand et al. 1997).

Stem taper could be a trait selected in future tree-breeding programs. The taper coefficient heritability was low for the taper model but most form quotients had moderate heritability estimates. This indicates the average taper over the stem did not have a strong genetic component but there was a strong genetic component for taper in some stem sections. Since the form quotients were calculated at fixed heights, stem size may have had an impact on the taper for the respective stem section. For example, two stems with different heights and diameters and the same age may have different ratios of diameters at 16 ft and BH, but have the same relative stem profile. The relative heights of these measurements may be misleading. Stem taper and crown ratio would probably not be easily selected as a pair of traits because crown ratio was not genetically correlated with stem taper. Other quality traits are probably more important in value than stem taper, although it may have some economic value for solid products.

Evaluating Accuracy of Volume Estimates

The Warner-Goebel equation generally overestimated volume in this study. The data used to derive this equation were from different genetic material, with different soil characteristics, and different ages. Using an equation that was fit to the specific data set

reduced the range in family MPDs from 9.90 to 9.37%. This small reduction in MPD suggests that locally-derived volume equations are not necessary in estimating volume for genetic trials. It is still recommended that local volume equations be used in genetic tests for similar age material in like environments, when available. Deriving volume equations for the sole purpose of local genetic trials may not be cost-effective in a tree-breeding situation with trials spread over large geographic areas.

Figure 3 shows that selection of the top few genotypes would provide an average MPD similar to the MPD of all the families measured. However, the volume estimates for single families and individual trees can be imprecise (Figures 4 and 5). Each deviation from the expected volume could be related to combinations of height-diameter relationship, stem taper, form, and bark thickness variation not captured with the combined-variable equation.

Additional Measurements to Improve Volume Estimates

Collecting data for single families to create tailored volume prediction equations would be too costly to be practical. However, differences among loblolly pine families may be captured through measurements that supplement D and H. These measurements must capture some of the variation in stem taper or bark thickness and be practical for field use.

All of the models used to predict total inside-bark volume fit the dataset well (Table 13). The differences in model performance were most apparent when looking at single-family volume estimates. The form quotient with diameters at 16 ft and BH added the greatest improvement to a combined-variable model. This prediction model may exclude the variation in butt swell to give a better indication of form in 13-year-old trees. The other form quotient, with diameters at heights of 8 and 2 ft, improved family volume estimates but not as much as the first. This result was surprising since the form quotient with diameters at 8 and

2 ft had a higher heritability estimate than the first form quotient considered. This second form quotient variable would be less expensive to collect, because it only requires measurements at 8 and 2 ft above the ground line. This measurement could be made with calipers and a height pole if the measurer is tall enough or if light-weight specialized calipers could be obtained. For the first form quotient, diameters at 16 ft are required which would involve more time and cost.

Upper-stem diameters can be hard to measure optically. The author's experience with non-magnified optical devices resulted in low precision. Care must be taken to make certain that the device used is sufficiently precise to make the measurement cost effective and valuable. Even at best, optical devices can only estimate outside-bark diameters. It is recommended that specialized calipers be used to measure upper-stem diameters at or below 16 feet when possible. The calipers must give the researcher an ability to estimate the height of the measurement from ground level, as well as the o.b. diameter at that height.

The bark thickness variable added to a combined-variable prediction model also improved the family volume estimates. It should be noted that there was a strong measurer effect on bark thickness measured in the field. This should be taken into consideration and care must be taken when measuring bark thickness with any device, so as to minimize overall error and make this an effective measurement.

The three-inch o.b. top height to H ratio improved the volume estimates but may not be practical. The costs for this measurement could be high because an optical dendrometer may have to be used to estimate the height to a given stem diameter.

The addition of crown ratio into a prediction equation gave the least improvement in precision. Crown ratio is easily measured when H is measured; however, this measurement

did not improve the model enough to warrant even the relatively small cost associated with its measurement. This finding is contradictory to the findings of Muhairwe et al. (1994) where crown ratio improved volume, diameter, and merchantable height models in lodgepole pine. The difference between Muhairwe et al. (1994) and the present study could be related to different species, different aged material, or the use of only dominant or co-dominant lodgepole pine trees.

Creating a More Efficient Volume Prediction Model

Combined-variable equations were created to facilitate graphic interpretation of equations and least-squares regression (Spurr 1952). With the processing power of current personal computers, regression techniques are not limited by hand calculations. More sophisticated models could allow for a better representation of H and D within the volume model. Also, the simplest way to enhance our estimates of volume in genetic trials is to create a better model without additional measurements. The expense of extra field measurements can be restrictive, but using an effective model with D and H variables only can be financially attractive.

The combined-variable model from Spurr (1952) has been widely used to predict total volume. The two models evaluated that did not include any additional measures performed similarly to the combined-variable equation fit to the dataset. In Spurr (1952), the Schumacher and Hall (1933) model performed less desirably than the combined-variable equation. The findings from this present study implies that the combined-variable equation is as useful and effective as other total inside-bark prediction equations without additional measurements.

CONCLUSION

Indirect selection for estimated volume using the Warner-Goebel equation was appropriate to make gains in true inside-bark volume because of a high selection efficiency. Thicker bark results from selection of higher volume families due to a positive genetic correlation of bark thickness and D , after accounting for the confounding effect of tree size on bark thickness. Over time, thicker bark may cause volume prediction models to overestimate the amount of wood volume for a given outside-bark measurement. Crown ratio showed positive genetic correlation with total height, although this may have resulted from the single-tree study design. Simultaneous selection of crown ratio and stem taper using one of the two traits to indirectly select the other would not be efficient due to the low genetic correlation between them. Stem taper could be a trait selected for in future tree breeding programs but its relatively low economic importance may discourage this. Selection for stems with a more cylindrically-shaped lower bole may be more easily accomplished and economically desirable as opposed to improving the taper over the entire stem. The lower heritability for the stem taper coefficient supports this idea because it could be considered an average rate of taper over the whole stem.

Volume estimates for single OP families and individuals could have dramatic error. Using the combined-variable equation fit to the present dataset, individual families had mean volume estimates, that were in error by as much as 5%. Volume estimates were not improved through the use of other models with D and H terms. Volume estimates were improved the most by the addition of a form quotient using outside-bark diameters at 16 ft and BH. Further research would be needed on multiple sites closer to selection age to effectively evaluate the use of form quotient measurements in tree improvement trials.

Younger stems may not require form quotients with diameters as far up the stem as was required in this dataset to optimally improve volume estimates.

The ability to improve the precision through further measurements suggested that the combined-variable equation excludes variation in stem taper and bark thickness. However, the range in family MPD remained above 6% for every model evaluated. This indicates that variation not accounted for with a combined-variable equation may have resulted from measurement error, heterogeneous stocking, stem profile differences, branch swell issues, and unknown factors. Stem profile may have differed by stem section, which would have introduced additional variability in volume estimates that may be difficult to capture with the methods used in this study. Depending on the location of the diameter measurements on the stem, stem-diameter estimates may have varied by each measurement's relative position to a former or living branch whorl. The genetic correlation between estimated and measured total inside-bark volume was high. This correlation implies that the stem taper, bark thickness, measurement effects, and stem profile effects on wood volume estimates are small. Selection using a combined-variable equation resulted in only minor differences in family rankings between measured and estimated total inside-bark volume. The alternative prediction models did not improve selection dramatically. Therefore, a combined-variable equation is adequate for selection of total inside-bark volume.

4. GENERAL CONCLUSION

Twenty-five open-pollinated (OP) first- and second-generation loblolly pine families were destructively sampled in a genotype by cultural treatment study at age 13.

Measurements included diameter and bark thickness along the stem to assess total inside-bark volume. Total inside-bark volume is the most important selection criterion for productivity in tree breeding programs in the Southeastern U.S. Tree breeding programs typically estimate total inside-bark volume based on diameter at breast height (D) and total stem height (H) with a combined-variable equation. This equation assumes that stem taper and bark thickness is constant across genotypes. In the present study, it was found that taper and bark thickness factors have relatively small impacts on volume estimation. The North Carolina State University–Industry Cooperative Tree Improvement Program (TIP) has a history of using the Warner-Goebel combined-variable equation for the estimation of inside-bark volume using D and H measurements in genetic trials. The genetic correlation of this estimated total inside-bark volume to the measured total inside-bark volume from the destructive sample was high (0.99). This indicates that selection for estimated volume is sufficient to make the desired gains in actual wood volumes. The combined-variable equation is an effective predictor of total inside-bark volume when fitting a model to small datasets (Spurr 1952).

Further investigation indicated that family-mean and individual-tree volume estimates using the Warner-Goebel equation were biased and demonstrated moderate precision.

Models were investigated to explain some of the imprecision. The form quotient model with diameters at 16 ft and BH was ideal for improving the precision of the volume estimates.

The addition of a lower form quotient, bark thickness, or three-inch o.b. top height ratio also

showed improvement in precision over the combined-variable equation. Data are needed from 6-year old genetic trials to validate these models. Furthermore, the site and regional variation of stem taper and bark thickness needs to be assessed to determine the need for local or regional inside-bark volume prediction equations.

Not all of the sources of imprecision were explained. The range in family MPD could not be reduced below 6 %. It is likely that measurement error, mortality, stem profile differences, and the impacts of branch whorls on diameter measurements contributed to the unexplained imprecision. Stem profile may have differed by stem section, which would have introduced additional variability in volume estimates that may be difficult to capture with the methods used in this study. Depending on the location of the diameter measurements on the stem, stem diameter estimates may have varied by each measurement's relative position to a former or living branch whorl. The high genetic correlation between estimated and predicted total inside-bark volume implies that stem taper, bark thickness, measurement effects, and stem profile effects on wood volume estimates are small. Due to the extra cost of additional measurements considered in the present study, the inability to explain a higher portion of the imprecision involved in volume estimates, and the high selection efficiency of the combined-variable equation, it is not recommend that additional measurements be utilized for total inside-bark volume predictions.

Analyses were conducted for height-diameter relationship, stem taper, form, crown ratio, form quotient, or MPD in a mixed-model situation. Family effects in the mixed models suggested that the OP family was a minor component of variation in each trait. Low heritabilities for crown ratio, the taper coefficient from a regression on stem taper, and several form quotients indicate that the genetic components of these traits were smaller than

for growth traits like D and H. These findings give further support to the notion that a combined-variable equation captures all the important total inside-bark differences between families. Crown ratio was not found to be phenotypically or genetically correlated with stem taper. This was contradictory to many other studies that related these two traits (Baldwin et al. 2000, Larson 1963, Newberry and Burkhart 1986). Perhaps the difference from these other studies is due to their evaluation under different stand conditions, while the present study analyzed one site with a variety of genotype and cultural constitutions. Crown ratio was genetically correlated with H. This was probably a result of the single-tree plot design, where taller trees had a higher proportion of crown due to a more dominant canopy position.

There was a noteworthy family effect on bark thickness after accounting for stem size. Although not enough to show a strong family effect in the combined-variable model, bark thickness variation among families could affect the actual total inside-bark volume of selected individuals in the advancement of breeding cycles. In this present study and in Pederick (1970), it was concluded that thicker bark results from selection of larger diameter genotypes. This is because of a positive genetic correlation of bark thickness and D, even after accounting the confounding effect of stem size on bark thickness. Over time, thicker bark may cause volume prediction models to overestimate the amount of wood volume for a given outside-bark measurement. Further investigation into the variation and measurement of bark thickness should be explored. The measurer effect was relatively large for bark thickness so the use of a bark gauge may be inappropriate for field experiments. It is possible that a more precise bark thickness measurement could be obtained by sectioning stems and measuring bark thickness with a ruler.

Stem taper could be a trait selected in future tree breeding programs but its relatively low economic importance may discourage interest from breeding programs. Selection for stems with a more cylindrically shaped lower bole may be more easily accomplished and economically desirable as opposed to improving the taper over the entire stem. The low heritability for the stem taper coefficient supports this idea because it could be considered an average rate of taper over the whole stem. Form quotients from diameters on the lower bole seemed to have a higher heritability than the taper coefficient. Simultaneous selection of crown ratio and stem taper using one of the two traits to indirectly select the other would not be efficient due to the low genetic correlation between them.

The lack of stem taper and bark thickness effects on volume estimates found in the present study indicates that growth and yield modeling for loblolly pine may not require data for individual OP families. Although not shown in this study, the rates stands develop are probably influenced by the rates at which families grow. Further research would be needed to quantify stem taper and bark thickness variation over time for commonly deployed families. Age-age correlations are also unknown for stem taper and bark thickness in loblolly pine. Age-age correlation may be especially important in stem taper where stand development can change the trait dramatically.

In conclusion, it is not recommended that the TIP change its current estimation system for total inside-bark volume. It is recommended that TIP use the combined-variable equation (Equation 31) fit to this present dataset because it had slightly better precision, had much less overall bias in volume estimates, and was derived from mostly second-generation genetic material with known ages and sizes. Adding variables did improve volume estimates, but the expense of adding further measurements and the high efficiency of indirect

volume selection with a combined-variable equation make the benefits from additional measurements small. Inaccuracy in volume estimates used in gain calculations are minor errors compared to erroneous selection of families or individual trees, which was not found to occur in the present study. Future analysis of genetic correlations between bark thickness or stem taper with commonly selected traits should be considered in selection-age material. This would acknowledge and investigate the potential for counter-productive selection that could reduce the actual wood volume and value. For example, a positive correlation between straightness and stem taper could result in a systematic over-prediction of total inside-bark volume in future breeding cycles.

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APPENDIX I: Mixed Model Residual Plots

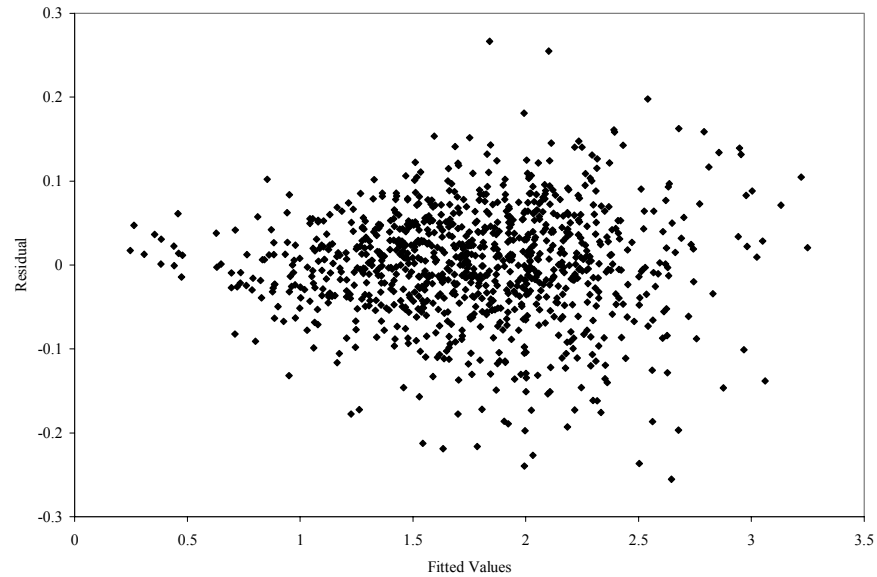


Figure 6. Residual and estimated values for the volume relationship mixed model with the square-root of total inside-bark volume as the dependent variable and the square-root of D^2H as the continuous regressor (Equation 6).

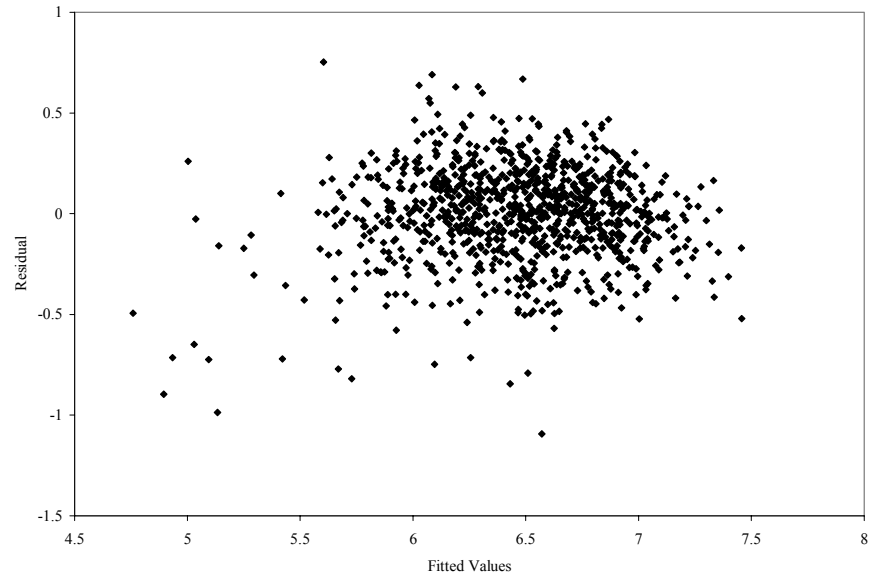


Figure 7. Residual and estimated values for the height-diameter relationship mixed model with total stem height as the dependent variable and diameter at breast height as the continuous regressor (Equation 6).

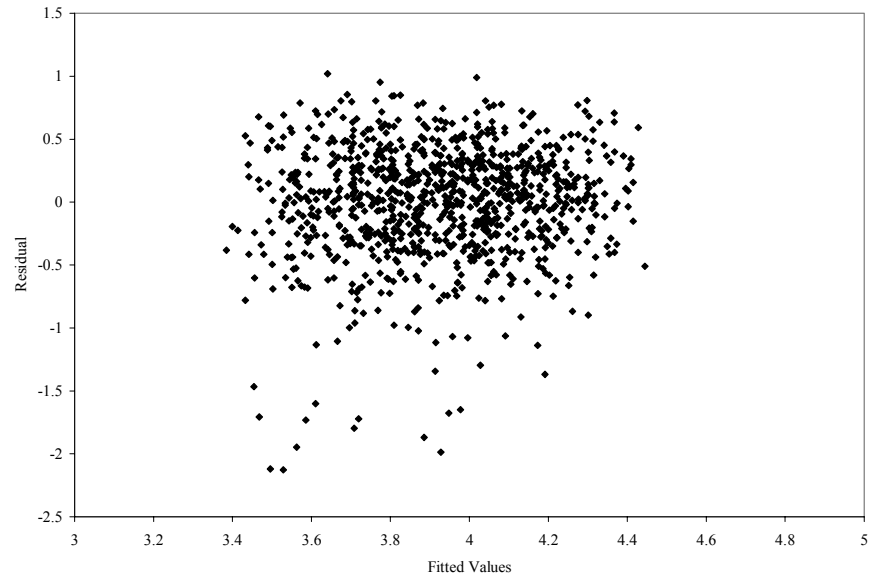


Figure 8. Residual and estimated values for the taper mixed model with the intercept coefficient for stem taper as the dependent variable (Equation 5).

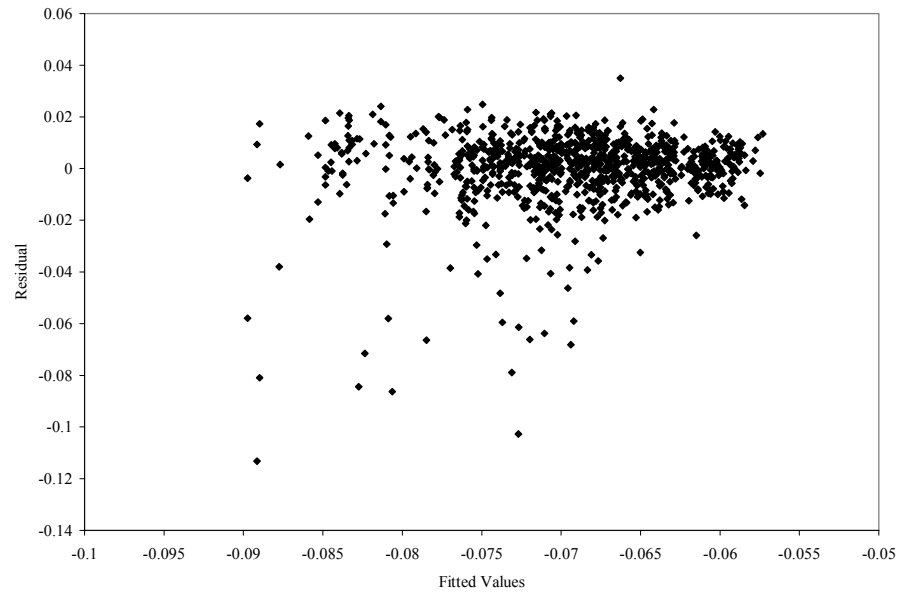


Figure 9. Residual and estimated values for the taper mixed model with the taper coefficient as the dependent variable (Equation 5).

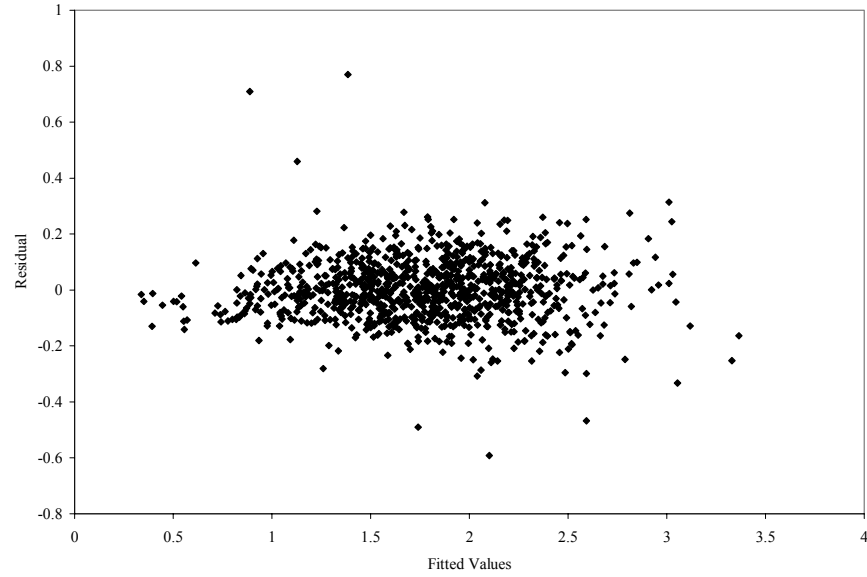


Figure 10. Residual and estimated values for the form mixed model with the square-root of total inside-bark volume as the dependent variable and the square-root of the inside-bark stump cross-sectional area multiplied by total stem height as the continuous regressor (Equation 6).

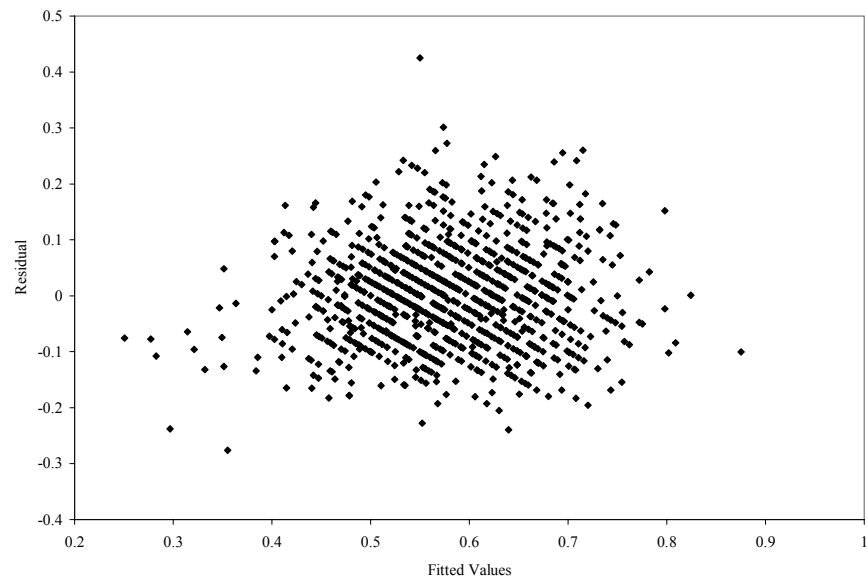


Figure 11. Residual and estimated values for the bark thickness relationship mixed model with the inside-bark diameter continuous regressor (Equation 8).

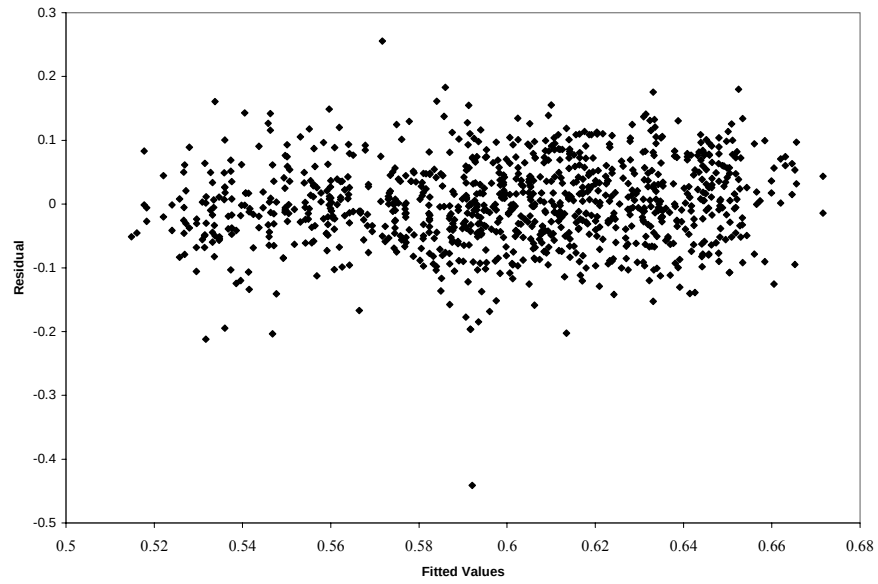


Figure 12. Residual and estimated values for the crown ratio mixed model (Equation 5).

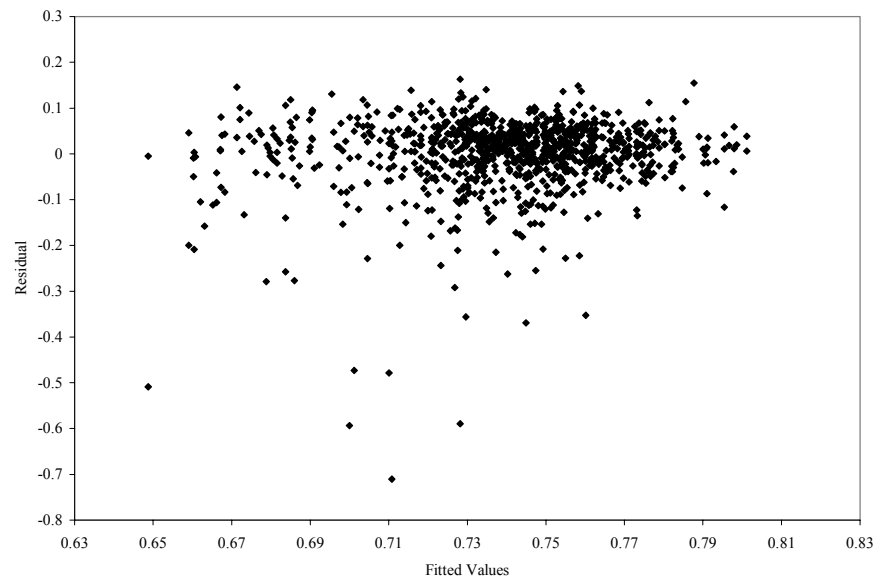


Figure 13. Residual and estimated values for the form quotient mixed model with the dependent variable as a ratio of diameters at 16 ft and breast height (Equation 5).

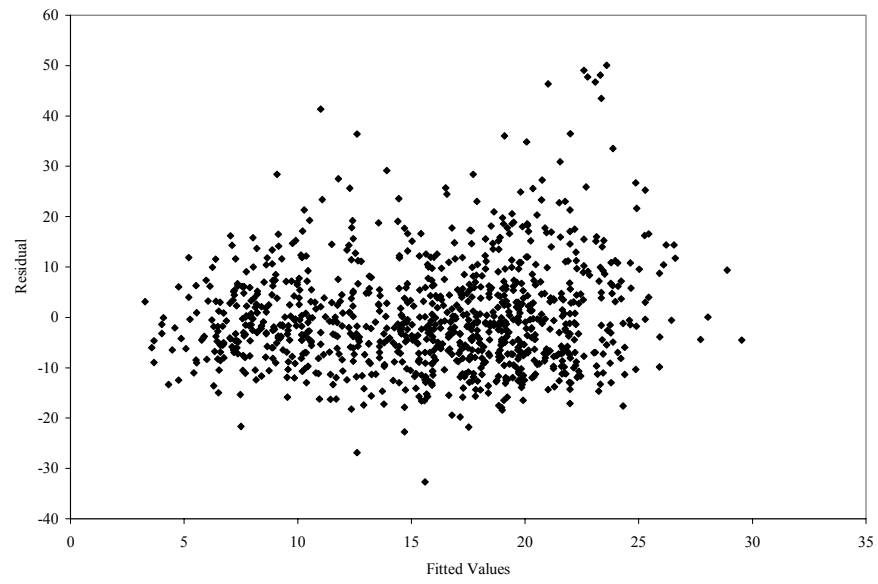


Figure 14. Residual and estimated values for the mean percent deviation mixed model (Equation 5).

APPENDIX II: Residual Plots for Models used to Estimate Genetic Parameters

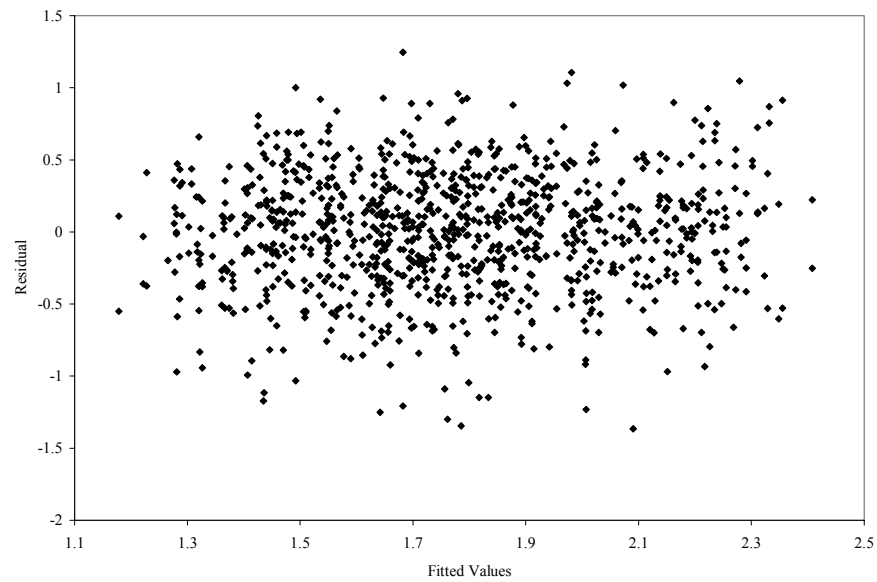


Figure 15. Residual and predicted values for the square-root of total inside-bark volume model (Equation 11).

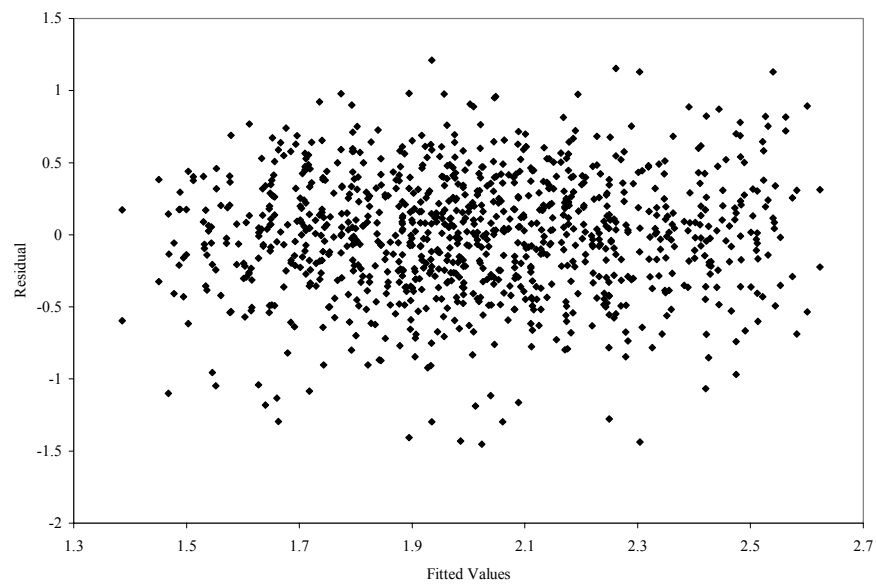


Figure 16. Residual and predicted values for the square-root of total outside-bark volume model (Equation 11).

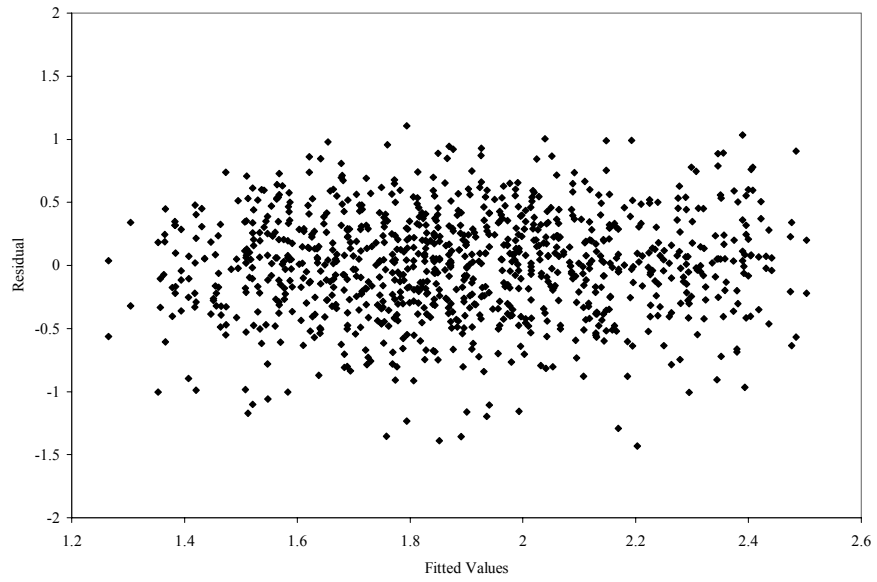


Figure 17. Residual and predicted values for the square-root of estimated total inside-bark volume model using the Warner-Goebel equation (Equation 11).

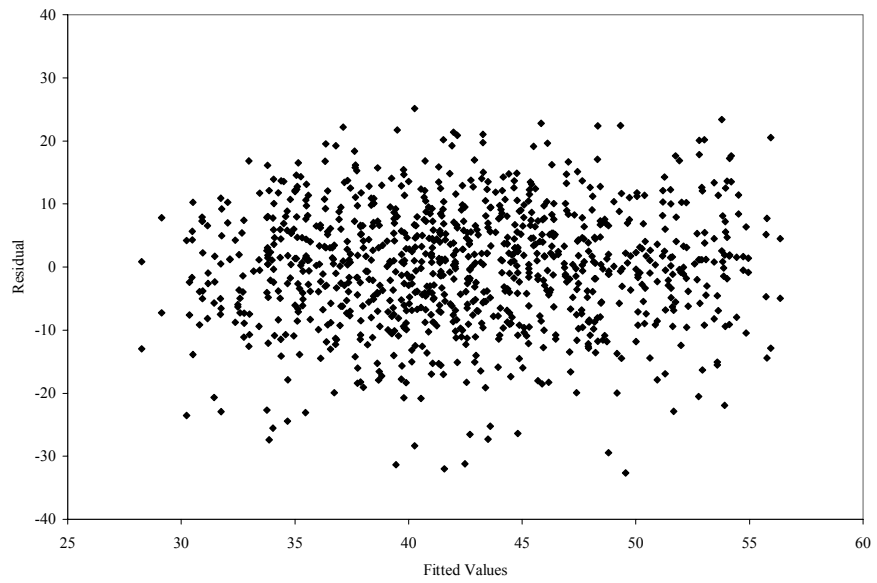


Figure 18. Residual and predicted values for the square-root of D^2H model (Equation 11).

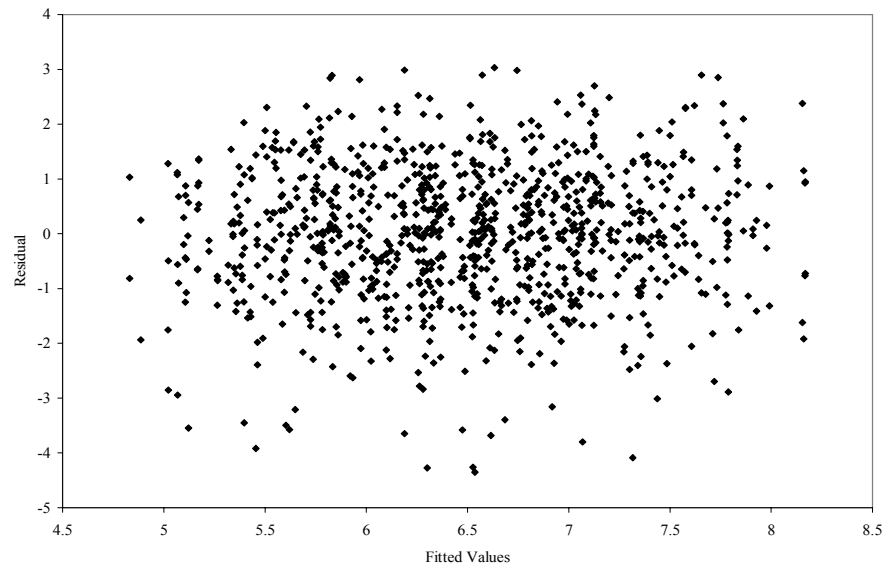


Figure 19. Residual and predicted values for the outside-bark diameter at breast height model (Equation 11).

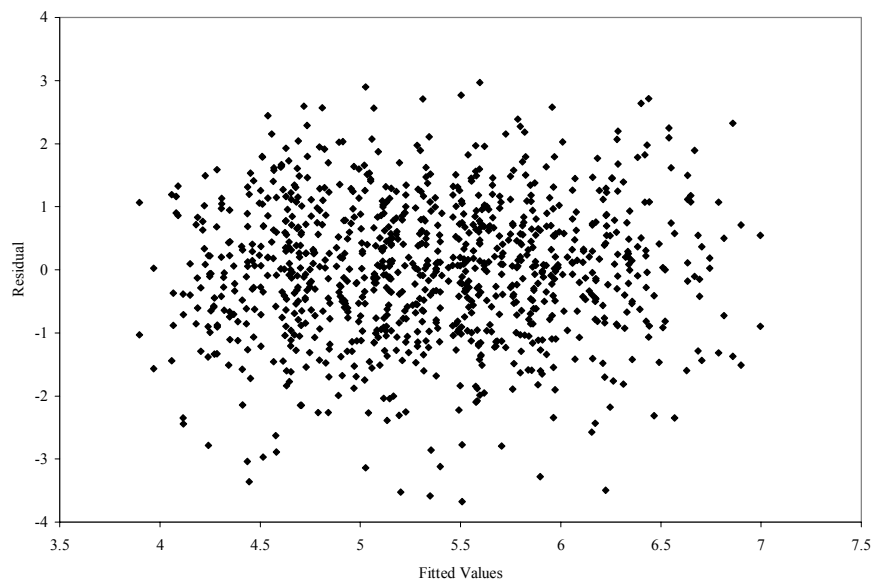


Figure 20. Residual and predicted values for the inside-bark diameter at breast height model (Equation 11).

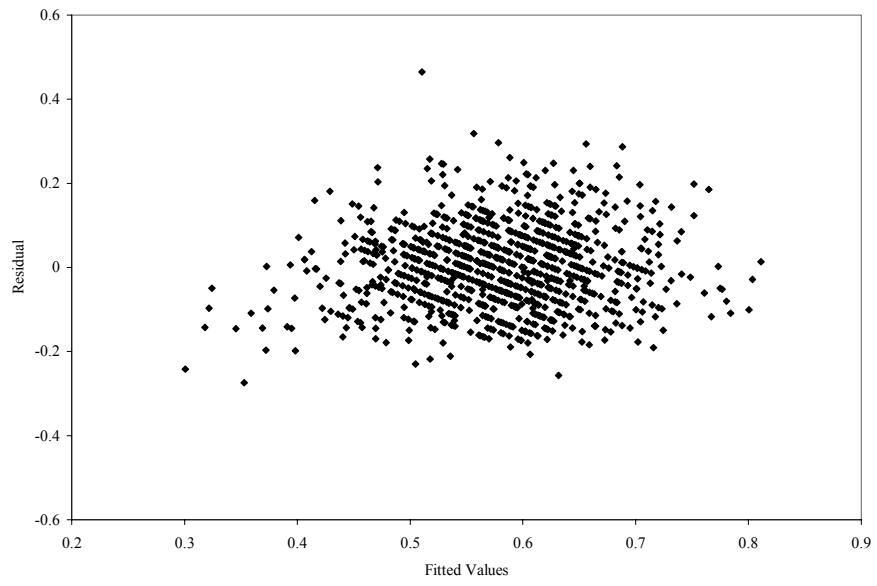


Figure 21. Residual and predicted values for the bark thickness model after accounting for the inside-bark diameter continuous regressor (Equation 11).

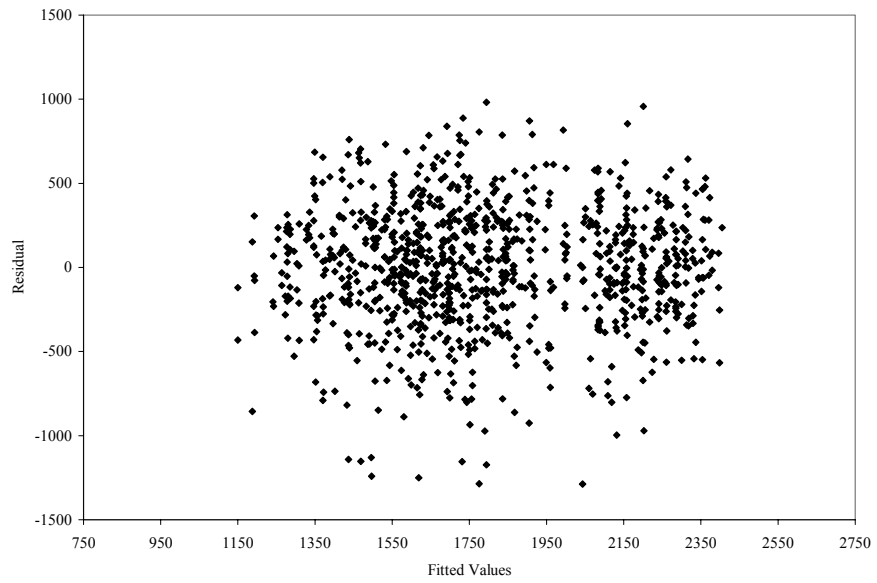


Figure 22. Residual and predicted values for the total height squared model (Equation 11).

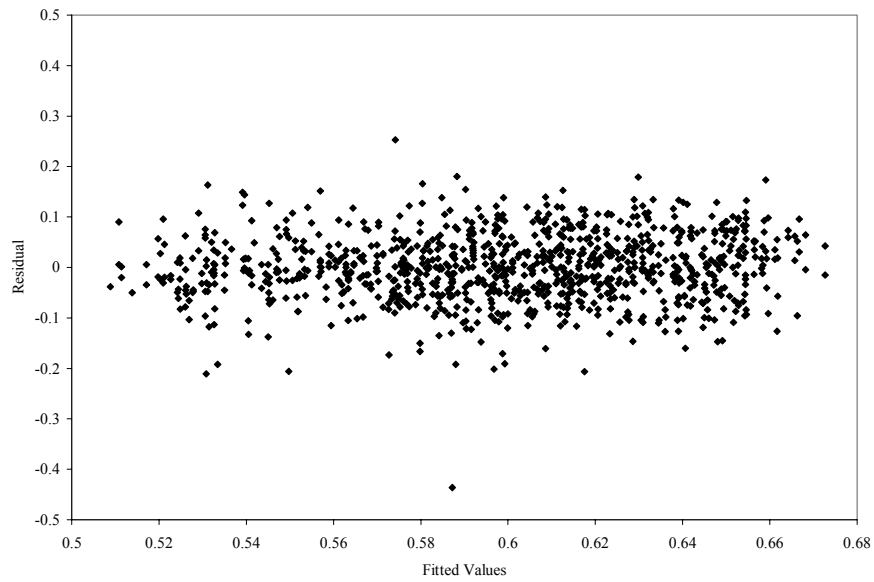


Figure 23. Residual and predicted values for the crown ratio model (Equation 11).

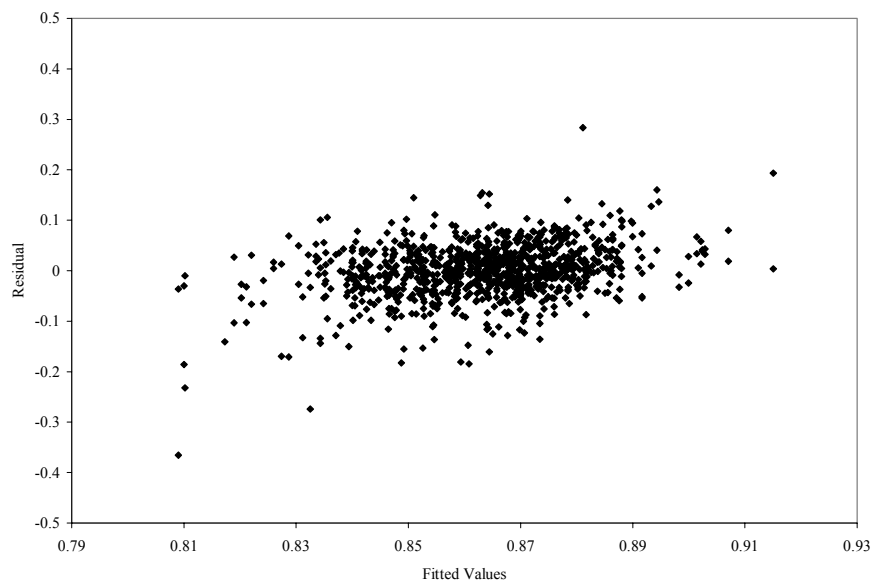


Figure 24. Residual and predicted values for the form quotient model (the ratio of inside-bark diameters at 8 and 2 ft) (Equation 11).

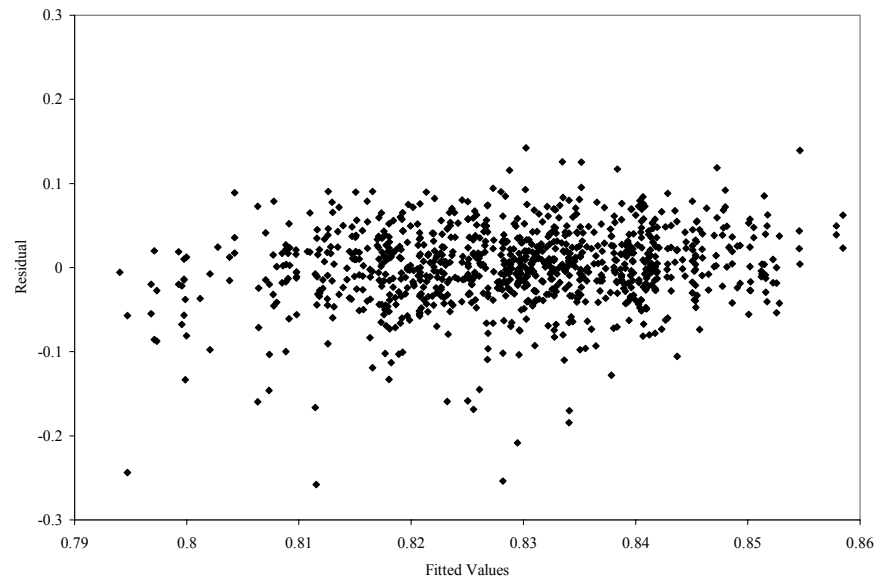


Figure 25. Residual and predicted values for the form quotient model (the ratio of outside-bark diameters at 8 and 2 ft) (Equation 11).

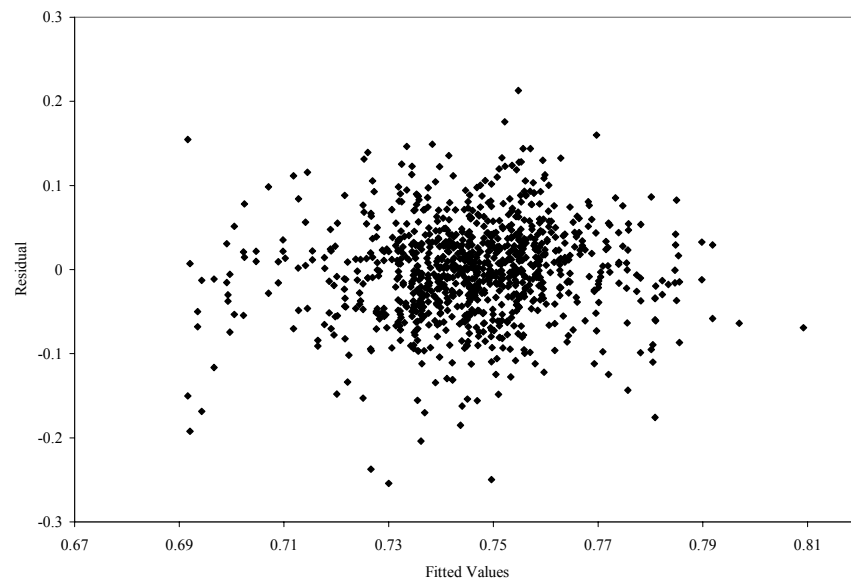


Figure 26. Residual and predicted values for the form quotient model (the ratio of inside-bark diameters at 8 ft and stump height) (Equation 11).

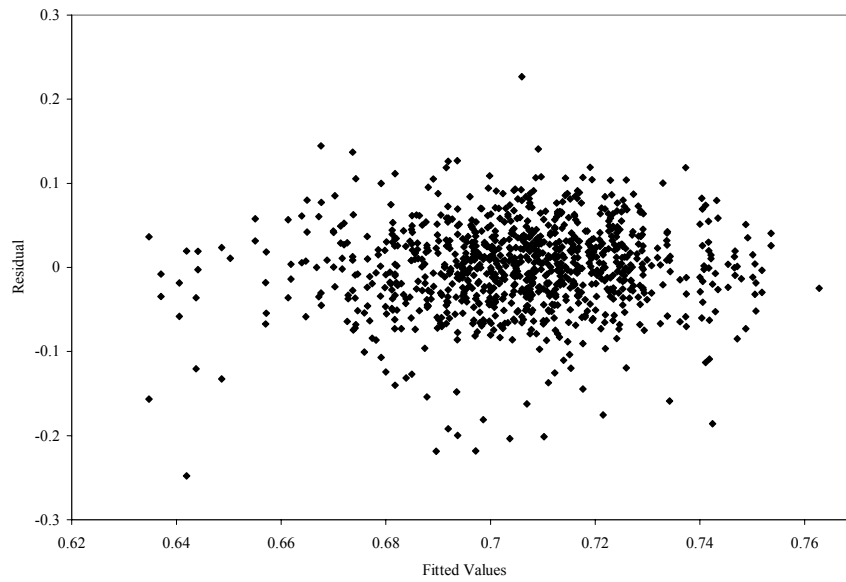


Figure 27. Residual and predicted values for the form quotient model (the ratio of outside-bark diameters at 8 ft and stump height) (Equation 11).

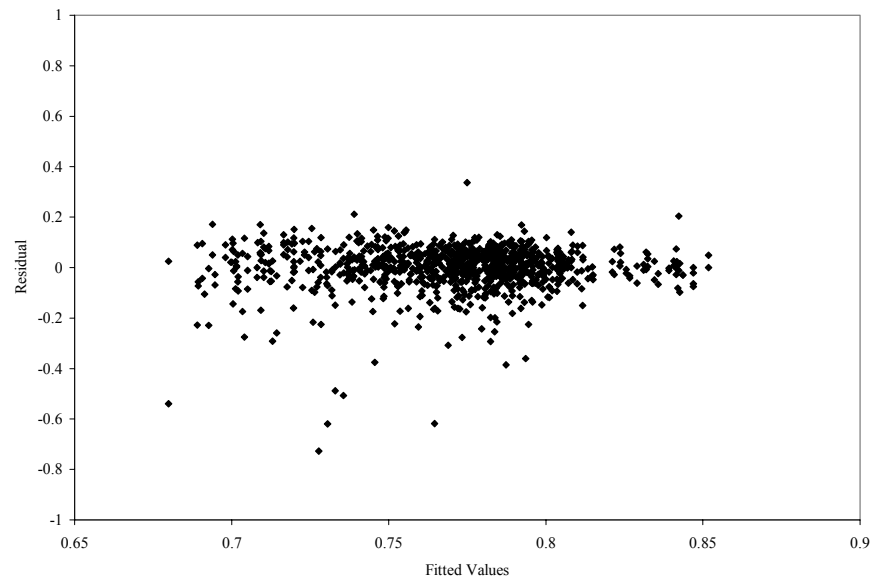


Figure 28. Residual and predicted values for the form quotient model (the ratio of inside-bark diameters at 16 ft and breast height) (Equation 11).

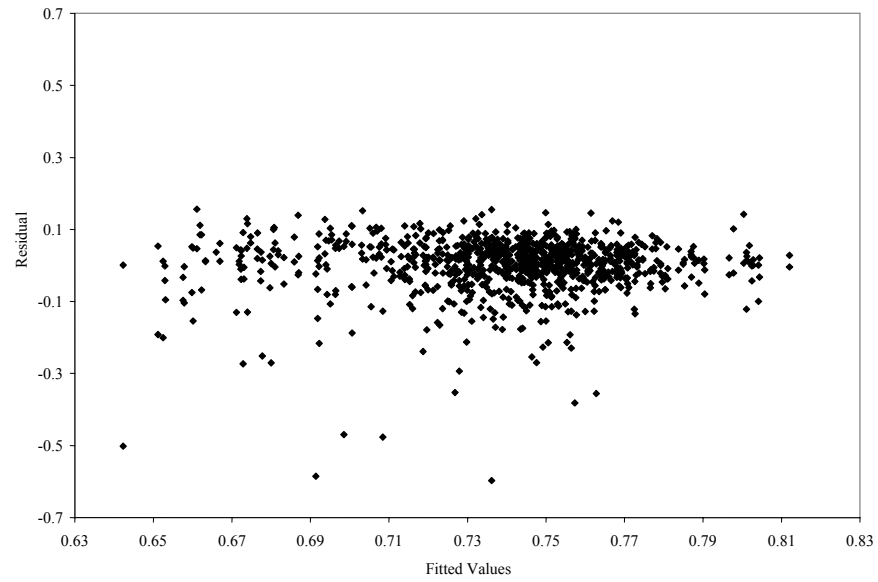


Figure 29. Residual and predicted values for the form quotient model (the ratio of outside-bark diameters at 16 ft and breast height) (Equation 11).

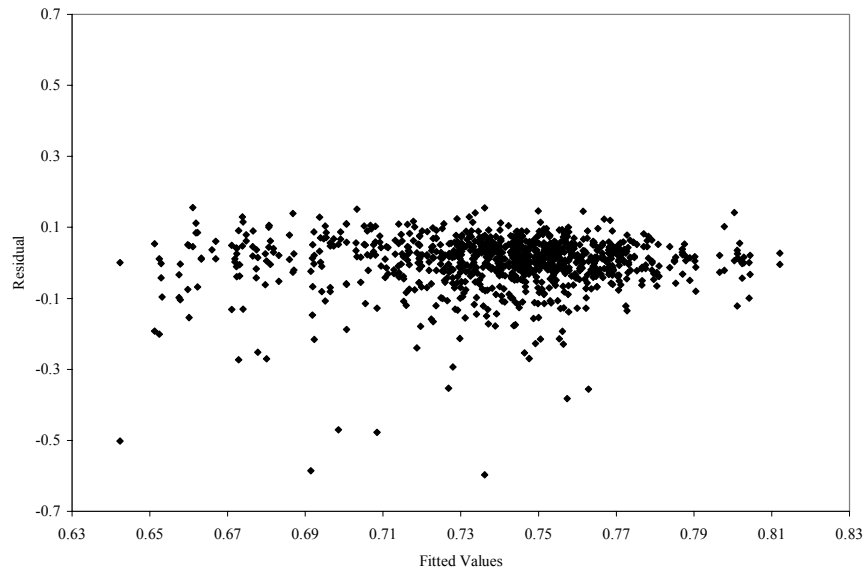


Figure 30. Residual and predicted values for the form quotient model (the ratio of outside-bark diameters at 16 ft and breast height) (Equation 11).

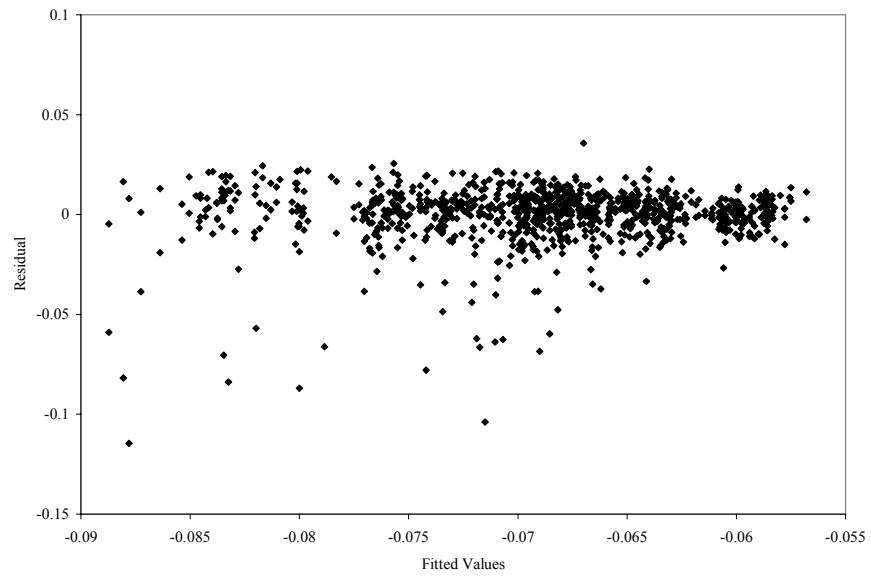


Figure 31. Residual and predicted values for the taper coefficient from the taper model (Equation 7 and 11) .

APPENDIX III: Prediction Model Residual Plots

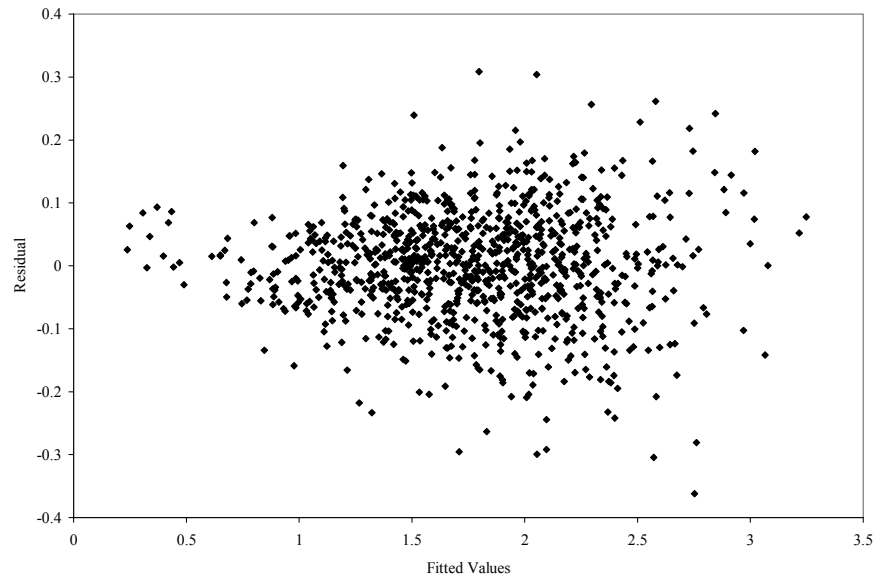


Figure 32. Residual and estimated values for the prediction model with the square-root of total inside-bark volume response variable and the square-root of D^2H explanatory variable (Equation 31).

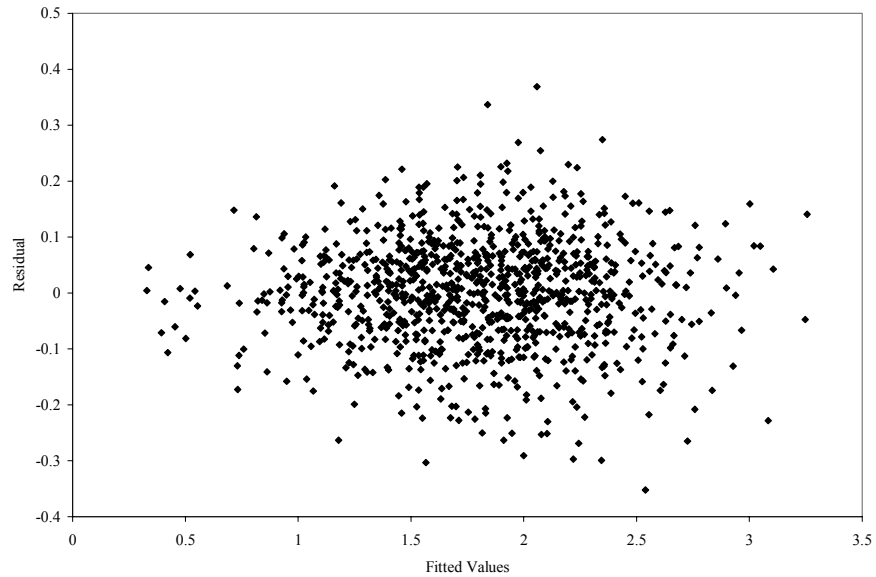


Figure 33. Residual and estimated values for the prediction model with the square-root of total inside-bark volume response variable and both the square-root of D^2H and the bark thickness to D ratio explanatory variables (Equation 22).

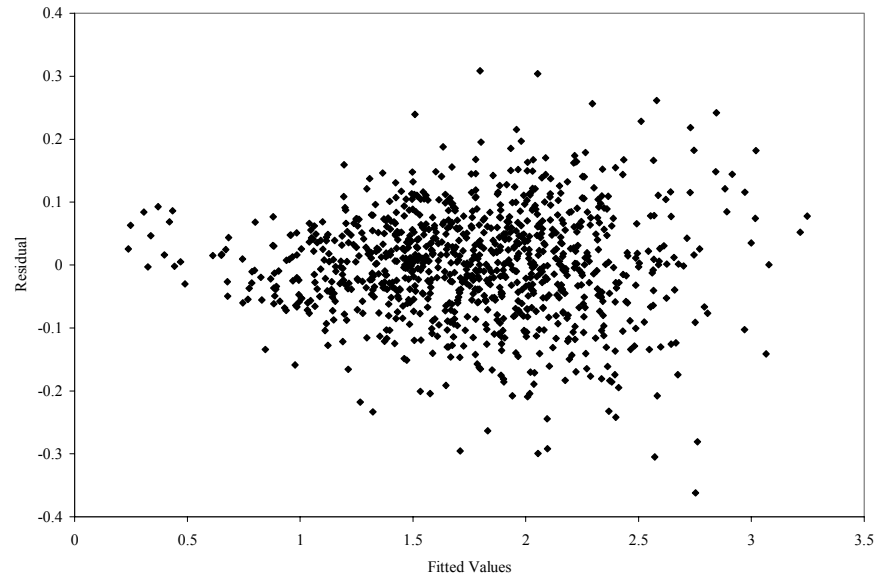


Figure 34. Residual and estimated values for the prediction model with the square-root of total inside-bark volume response variable and both the square-root of D^2H and crown ratio explanatory variables (Equation 24).

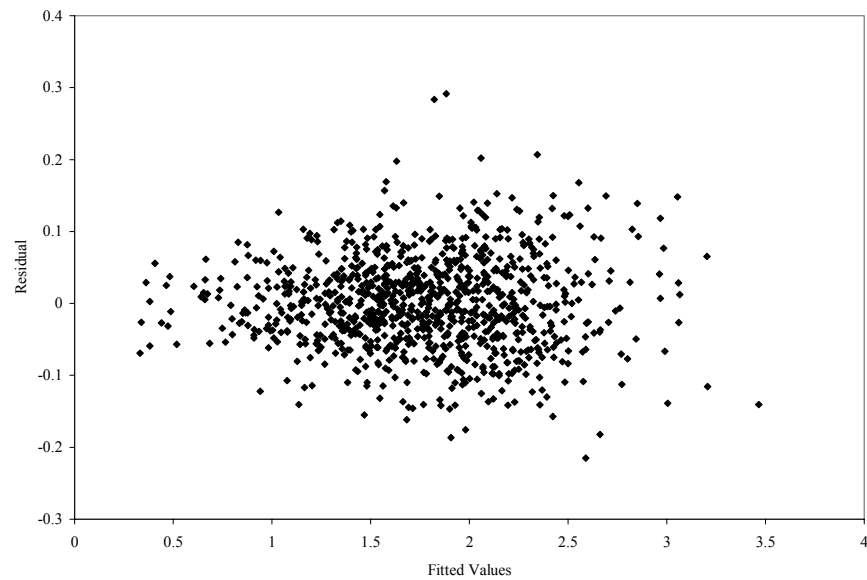


Figure 35. Residual and estimated values for the prediction model with the square-root of total inside-bark volume response variable and both the square-root of D^2H and the form factor (diameters at 16 ft and breast height) explanatory variables (Equation 25).

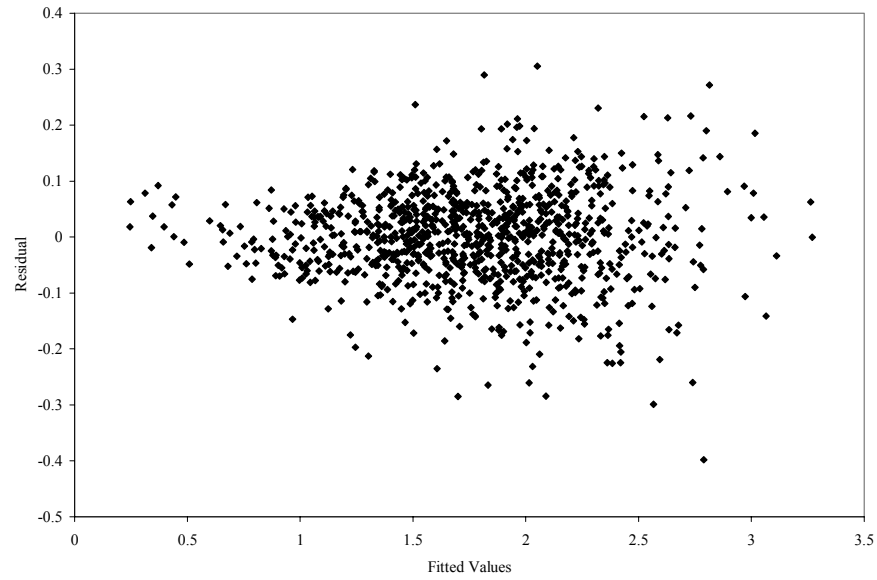


Figure 36. Residual and estimated values for the prediction model with the square-root of total inside-bark volume response variable and both the square-root of D^2H and the form factor (diameters at 8 and 0.5 ft) explanatory variables (Equation 25).

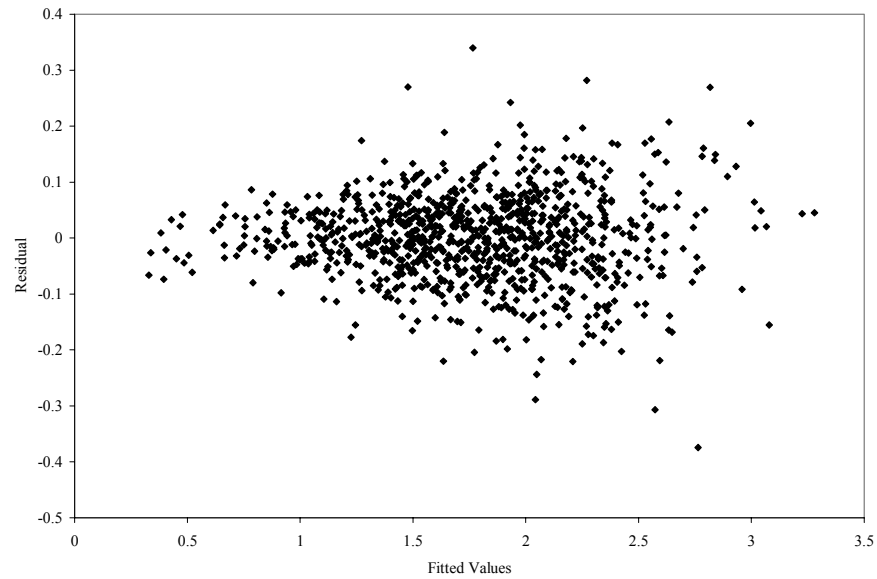


Figure 37. Residual and estimated values for the prediction model with the square-root of total inside-bark volume response variable and both the square-root of D^2H and the height to three-inch top ratio explanatory variables (Equation 26).

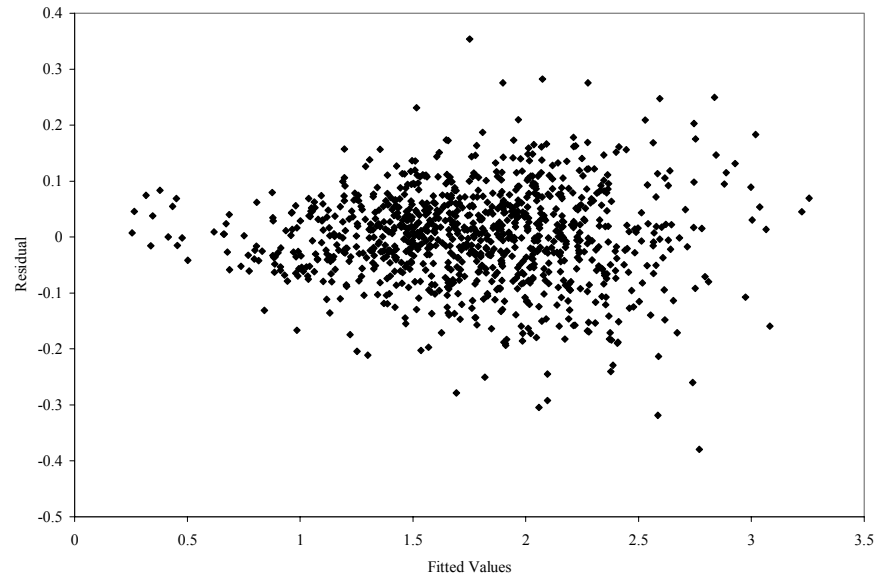


Figure 38. Residual and estimated values for the nonlinear prediction model with the square-root of total inside-bark volume response variable and both the reciprocal of D and the reciprocal of H explanatory variables (Equation 27).

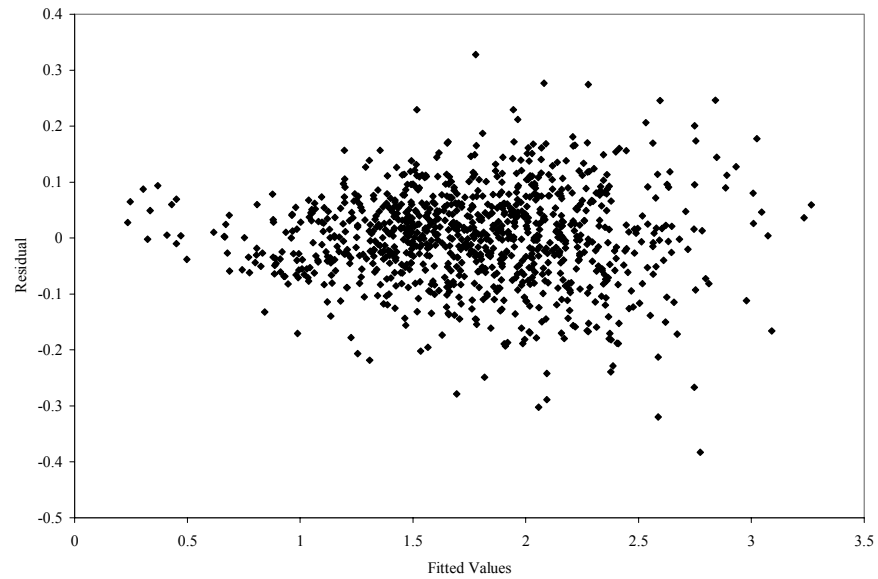


Figure 39. Residual and estimated values for the nonlinear prediction model with the square-root of total inside-bark volume response variable and D, H, D^2 , and DH explanatory variables (Equation 30).