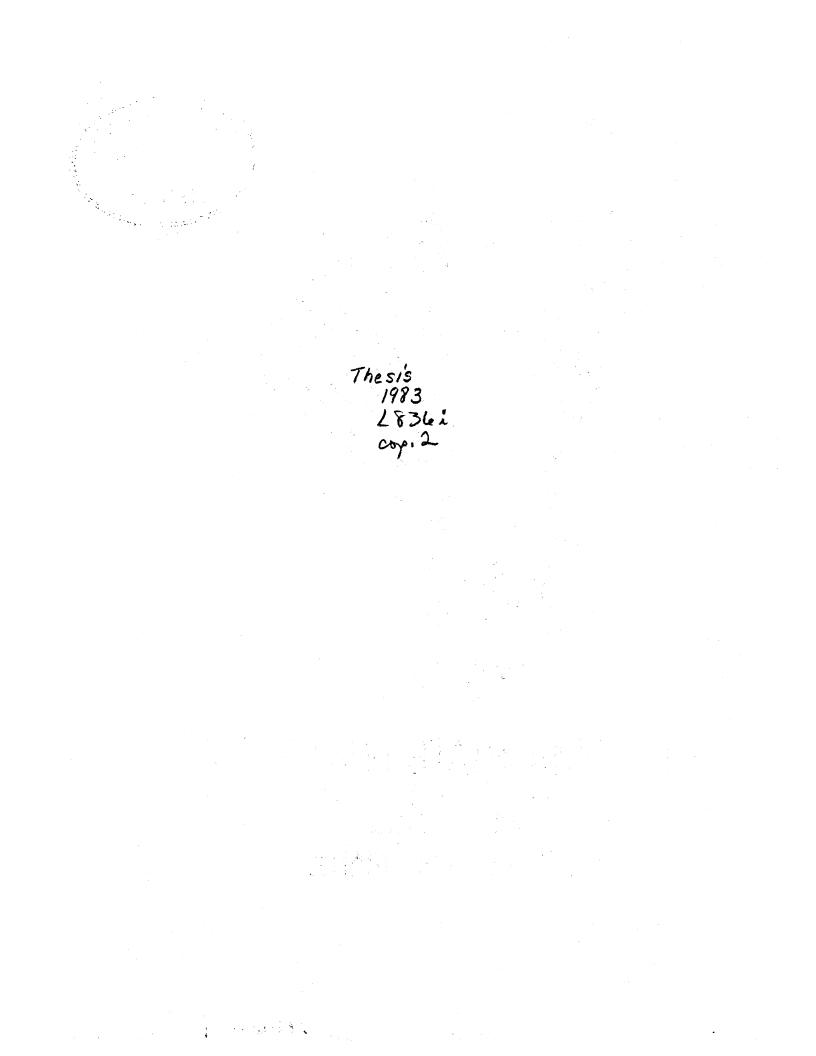
# INHERITANCE OF WOOD PROPERTIES IN LOBLOLLY PINE (<u>PINUS TAEDA</u> L.)

Ву

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### INTRODUCTION

Loblolly pine (<u>Pinus taeda</u> L.) is an important commercial timber species in the southern United States. It exhibits rapid early growth, good form and desirable wood properties. Current forestry practices are aimed at further reducing the rotation length while increasing the volume of wood harvested. This leads to an increase in the proportion of juvenile wood reaching the wood processors.

Juvenile wood is formed in the center of a tree throughout the length of the bole. Trees that grow faster allowing harvest at an earlier age than was possible in the past contain a larger proportion of juvenile wood. Juvenile wood is inferior to mature wood for most end products. A possible solution to the problem may be to breed trees for a shorter juvenile wood phase. The objective of this study was to examine this possibility.

Each chapterin this thesis is a spearate and complete manuscript. The first "Genetic variation in the time of transition from juvenile to mature wood in loblolly pine (<u>Pinus taeda</u> L.)", will be submitted to Silvae Genetica and the second, "Juvenile-mature relationships and heritability estimates within and among traits in loblolly pine (<u>Pinus</u> <u>taeda</u> L.)", will be submitted to the Canadian Journal of Forest Research for publication

PART I

### GENETIC VARIATION IN THE TIME OF TRANSITION

FROM JUVENILE TO MATURE WOOD IN

LOBLOLLY PINE (<u>PINUS</u> <u>TAEDA</u> L.)

#### SUMMARY

Wood samples were collected from a 25-year old loblolly pine progeny test in east Texas. Specific gravity and tracheid length were determined for two-ring segments from the pith to ring 22. Values for each property were plotted against age to determine the age of transition from juvenile to mature wood. The mean ages of transition were 11.45 and 10.39 years for specific gravity and tracheid length respectively. There was no correlation between the age of transition for specific gravity and tracheid length. Narrow sense heritabilities estimated on a family mean basis for age of transition of each property were sufficiently high to suggest moderate gains are possible. Genetic correlations between the age of transition for each character and height and diameter of the trees at age 20 were negative, suggesting that fast growth may be related to early age of transition and whole core specific gravity and tracheid length were negative.

#### INTRODUCTION

Loblolly pine (<u>Pinus taeda</u> L.) is the primary timber species grown in the southern United States due to its extensive range, good growth characteristics, and desirable wood properties. The species is well suited to short rotation forestry because of rapid early growth exhibited during the sapling stage. Genetic improvement and silvicultural practices are designed to further reduce rotation length while increasing productivty. As the rotation age is reduced, however, the relative proportion of juvenile wood in the harvest increases.

Juvenile wood which is formed near the pith throughout the bole of a tree is significantly different from wood produced in outer rings, termed mature wood. Juvenile wood characteristically has low specific gravity, short tracheids, large fibril angle, and a lack-luster appearance when compared with mature wood, (Zobel <u>et al</u>. 1972, Pearson and Gilmore 1971, Bendtsen 1978). Specific gravity, tracheid length and fibril angle have been identified as key indicators of wood quality for various end products because of their impact on strength, pulping quality and shrinkage (Mitchell 1965, Wahlgren and Schumann 1972, McElwee 1963). Thus the relative proportion of juvenile and mature wood reaching a manufacturer significantly influences the quality of the finished product.

The relationship between wood properties and wood age (distance from the pith) in loblolly pine has been described

as a trend characterized by rapidly increasing specific gravity and tracheid length with age, levelling off at 7 to 15 rings from the pith (Zobel and McElwee 1958, Saucier and Tarras 1969, McMillin 1968, Pearson and Gilmore 1980). Bendtsen (1978) stated that it is possible for one character such as cell length to reach maturity before another character such as cell wall thickness. Zobel and McElwee (1958) indicated that both specific gravity and tracheid length, plotted against age produce curves of similar form.

Heritabilities reported for specific gravity and tracheid length in juvenile wood of loblolly pine are relatively high. Heritability estimates for specific gravity of trees from three to eight years of age range from .56 to 1.0 (Stonecypher and Zobel 1966, van Buijtenen 1962, Goggans 1964, Stonecypher et al. 1973). Heritability estimates for tracheid length from trees of the same age range were reported by Goggans (1964) and Stonecypher et al. (1973) to be .44 and .97 respectively. Thus it should be possible to develop trees with more desirable juvenile wood properties than is generally found in young trees if there is significant genetic variation in the population Zobel and Blair (1976) reported, however, that high density juvenile wood did not have comparable physical properties to mature wood. Αn alternative to breeding for trees with high specific gravity, long-fibered juvenile wood may be to breed trees for a shorter juvenile wood production phase.

The objective of this study was to examine the possi-

bility of breeding loblolly pine for a reduced juvenile wood phase. Genetic variation in the time of transition from juvenile to mature wood was estimated for a population of loblolly pine from east Texas.

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### MATERIALS AND METHODS

Twelve millimeter increment core samples were collected in Dec. 1981, from a 25-year old loblolly pine open-pollinated progeny test in east Texas. The test was planted at two locations with 16 families randomized within each of three blocks at location one, near Rusk, and two blocks at location two, near Nacodoches<sup>1</sup>. The parent trees had been selected from throughout east Texas for high or low specific gravity extremes. Each family consisted of a row of 26 trees in each block when the plantations were established. The rows have subsequently been thinned to an average of nine trees per row at location one and 12 trees per row at location two. The 15 families that were sampled for this study had at least five surviving trees in each of two blocks at each location. One radial increment core was taken from the north side of each of five trees per family from each block at a height of 1.4 meters above the ground. Cores were examined for branch or knotwood and were used only if they consisted entirely of clear wood

Each core was divided into two-ring segments beginning at the pith. Prior to specific gravity determination, extratives were removed using a modified ASTM (1970) procedure described by Goggans (1962) and a modified soxhlet extractor apparatus described by Browns <u>et al</u>. (1977). Specific

<sup>&</sup>lt;sup>1</sup> The material was made available by the Western Gulf Forest Tree Improvement Cooperative, the Texas Forest Service and Texas A&M University.

gravity was determined by the maximum moisture content method described by Smith (1954). A small section of latewood was removed from the second ring of each two year segment for determination of tracheid length. The sample was macerated following a procedure described by Buxton (1967) and the fibers were stained with safrannin 0 dye. Thirty whole tracheids per segment sample were selected at random and measured to the nearest .05 mm.

#### ANALYSIS

The time of transition from juvenile to mature wood was estimated separately for specific gravity and tracheid length. Initially it was assumed that both specific gravity and tracheid length, when plotted against age, would produce a curve as shown in Figure 1 (Zobel and McElwee 1958). Thus the point of transition could be identified by fitting two regressions to the data for each tree and finding the point of intersection for the two lines with best fit (smallest error sum of squares).

All data did not conform to the expected pattern, however, and the most reasonable value resulting from a combination of three methods was used as the age of transition. The first method involved fitting two regressions, without forcing an intersection of the lines. This was done eight times for each tree with each iteration dividing the samples into two groups beginning with rings less than or equal to age four in the juvenile group and rings greater than age four in the mature group up to rings less than or equal to

age 18 in the juvenile group and rings greater than age 18 in the mature group. Increments were by two years. The age of transition was estimated as the age at which the second group (mature wood) began for the model with best fit determined by the smallest error sum of squares.

A second method was applied in cases where the best fit using method one resulted in the mature group having negative slope. This occurred in about 15% of the cases. Method two differed from method one in that the slope of the mature group was held constant at zero, with the assumption that the mature wood values fluctuate around a constant mean. In several cases where the best fit resulted in the juvenile group having negative slope and the mature having a positive slope, the time of transition was estimated by visual examination of the data points plotted over age. The ages estimated by the regression methods were checked against the plots to ensure that the regression model used was the most reasonable with respect to the data.

Specific gravity and tracheid length values for each segment were averaged over all families and each was plotted against age to yield an average curve. Phenotypic correlations using Pearson's product moment method (Statistical Analysis System 1979) and genetic correlations (Falconer 1980) were computed for the following pairs of characters:

- Age of transition for specific gravity with age of transition for tracheid length.
- 2. Age of transition for each trait with the value of

that trait at transition.

- 3. Age of transition with height and diameter of the trees at age 20.
- 4. Age of transition for specific gravity with parent tree specific gravity.<sup>2</sup>
- 5. Specific gravity at the point of transition with parent tree specific gravity.

The mean age of transition for each parameter was calculated for each family. An analysis of variance was computed for age of transition for each trait (Table 1). Variance components were estimated from the analysis of variance and family mean and individual tree heritabilities were calculated for age of transition for each character and for tracheid length at the point of transition. Standard errors associated with the heritability estimates were approximated (Kendall and Stuart 1958). The estimated heritabilities were based on the assumption that the open-pollinated families consisted of half-sibs. Heritabilities were calculated as follows:

(1)  $h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + 1/2 \sigma_{f1}^2 + 1/4 \sigma_{fr(1)}^2 + 1/20 \sigma_e^2}$ (2)  $h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{f1}^2 + \sigma_{fr(1)}^2 + \sigma_e^2}$ Where  $h_f^2$  = estimated narrow sense heritability by family mean

<sup>&</sup>lt;sup>2</sup>Growth data from the trees at age 20 and parent tree specific gravity was made available by the Western Gulf Forest Tree Improvement Cooperative, The Texas Forest Service and Texas A&M University.

- $h_i^2$  = estimated narrow sense heritability by individual tree
- $\sigma_{\epsilon}^2$  = family variance component
- $\sigma_{f1}^2$  = family x location interaction variance component
- $\sigma_{fr(1)}^2$  = family x replicate in location variance component
  - $\sigma^2$  = among progeny variance component

Expected individual tree breeding values were calculated independently for specific gravity and tracheid length for the three trees having the shortest juvenile phase in each of the two families with the shortest average juvenile phase. Expected breeding values were calculated as follows (Falconer 1980):

(3) E(B.V.)=[(1-r)/(1-t)]Pw + [(1+(n-1)r)/(1+(m-1)t)]Pf
where E(B.V.) = Expected breeding value
 r = genetic correlation between
 individuals
 t = intraclass correlation; in this
 case, 1/4 additive variance divided
 by total variance
 Pw = deviation of individual from family
 mean
 n = number of individuals in each
 family
 Pf = deviation of family from population
 mean.

An expected breeding value provides a means for estimating the deviation of an individual's future progeny from the population mean. In the above form it can be used to predict a response to combined family and individual tree selection.

#### RESULTS AND DISCUSSION

Individual plots for specific gravity and tracheid length over age varied considerably from the expected shape. The plots could be divided into four categories based on the configuration of the points (Figure 2). Forty-five percent of the specific gravity plots and 65% of the tracheid length plots fit the expected curve. Twenty-five percent of the specific gravity plots showed a discontinuity or a very abrupt change from juvenile to mature wood and a large number of the plots for both traits, 16% of specific gravity and 29% of tracheid length, continued to increase consistently through ring 20. Due to the construction of the regression models, age 20 was used as the age of transition in the latter cases. In some cases, the rate of increase in tracheid length abruptly slowed but a constant "mature" tracheid length was not attained. Here the age of transition was identified as the point where the rate of increase in tracheid length declined. Thirty-one specific gravity plots and nine tracheid length plots showed a tendency for decreasing values with age in the mature wood. This was assumed to be a random fluctuation around an actual slope equal to zero.

Specific gravity, averaged over all trees, was plotted over age and produced a sigmoid curve, with a period of juvenile wood extending to age six, a transition period of rapidly increasing specific gravity extending from age six to approximately age 14 and mature wood from age 14 to age

22 (Figure 3). Average tracheid length, when plotted over age (Figure 4) yielded a picture that was similar to the expected shape with rapidly increasing tracheid length from age two to age 10 and a more gradual increase in length from age 10 through age 22.

Phenotypic and genetic correlations were computed for a number of pairs of characters, and are presented in Table 2. Phenotypic and genetic correlations between age of transition for specific gravity and the age of transition for tracheid length were very low. The data indicate that there is not a specific age where all wood properties express maturity. The onset of mature wood production in a loblolly pine tree must be considered relative to the wood property of interest. Phenotypic correlations for the age of transition with height and diameter of the trees at age 20 were not significant at the .05 level for either specific gravity or tracheid length. Genetic correlations were strong and negative, however, indicating that selection for fast growing trees may have the effect of shortening the juvenile phase of wood specific gravity and tracheid length. Phenotypic correlations were significant and positive between the age of transition for each wood property and the value of that property at the point of transition, but genetic correlations were less than .10. This would suggest that selection for early maturity should not have a negative effect on mature values for specific gravity or tracheid length.

There was no correlation between the age of transition for specific gravity and the parent tree specific gravity.

Thus the mode of selection of the parents should not cause bias in heritability estimates for age of transition for specific gravity. The age of transition for specific gravity was negatively correlated with whole core specific gravity. The phenotypic correlation  $(r_p)$  was -.12 and the genetic correlation  $(r_A)$  was -.68. Mature wood specific gravity had a positive phenotypic correlation  $(r_p=.13)$  but a negative genetic correlation  $(r_A=-.22)$  with the time of transition. The time of transition for tracheid length was negatively correlated with whole core tracheid length  $(r_p=.25)$  and with mature tracheid length  $(r_p=.08)$ . The correlations are low but indicate a tendency for the whole core or mature wood specific gravity and tracheid length to increase as age of transition decreases.

The mean age of transition for specific gravity was 11.5 years (Table 3). The mean age of transition for tracheid length was 10.4 years with a minimum of six years and a maximum of 20 years. The wide range in the age of transition for both properties indicates broad phenotypic variability. The mean specific gravity at the age of transition was .53 and the mean tracheid length at transition was 4.09. Family means ranged from 9.8 to 13.0 for age of transition of specific gravity (Table 4). Family means for age of transition for tracheid length ranged from 8.7 to 12.3 years. Texas family 4041001 had the earliest age of transition for both specific gravity and tracheid length.

Analysis of variance results are presented in Table 5. Although the among family variance pooled over locations was

not significant at the .05 level for specific gravity transition age, it was the closest to significance among the sources of variance. There was significant family x location interaction for transition age of tracheid length, resulting from several changes in family ranking between the two locations. When each location was analysed separately the family variation was significant at each location.

Variance components were estimated as shown in Table 1 and narrow sense heritabilities were calculated on a family mean  $(h_{f}^{2})$ , and an individual tree  $(h_{i}^{2})$  basis for age of transition for specific gravity over locations, and age of transition of tracheid length both over locations and by individual locations. Heritabilities with associated estimates of standard errors are presented in Table 6. The heritability estimate for specific gravity at the age of transition may be biased upward since there was a significant phenotypic correlation between this trait and parent tree specific gravity. The heritability estimate for tracheid length at the age of transition was negative and is therefore assumed to be close to zero.

Family mean heritability estimates for age of transition for both characters appear sufficiently high to allow moderate gains through family selection or combined selection based on family and individual tree heritabilities. Expected breeding values were calculated for the three individuals having the shortest juvenile wood phase in the two top ranked families for each property. The mean expected breeding

value for the three top individuals for specific gravity from the families ranked first and second were 4.10 and 3.45 respectively. Thus, theoretically, progeny produced from a mating of one of the three trees from the first family with the population at random could be expected to have a juvenile wood phase 2.05 years shorter for specific gravity than the population mean. If these three trees were mated with the three trees in the second ranked family, the progeny could be expected to have a juvenile wood phase lasting 3.77 years less thn the population mean of 11.45 years.

The mean expected breeding value for age of transition of tracheid length for the three best trees in the two top ranked families were 4.37 and 4.48 respectively, implying a possible reduction in juvenile wood phase among progeny of a cross between these two groups of trees of 4.42 years.

The selection intensities implied by the above estimates are improbably high, but it serves to demonstrate that considerable gains could be made. It is important to realize that the reported heritability estimates are based on the assumption that all of the open pollinated progeny are half-sibs. Further, the assumptions that there are no correlations among pollen parents and no correlations between pollen and seed parents, are implicit in the genetic models. Any or all of these assumptions may be violated when open pollinated progeny are used to estimate half-sib covariances, with the probable result that heritabilities will be slightly over-estimated (Squillace 1974, Namkoong 1966).

#### CONCLUSIONS

The age of transition from juvenile wood to mature wood in loblolly pine can be estimated only with reference to a particular wood property, such as specific gravity or tracheid length. When each character is considered independently, there is evidence of additive genetic variance influencing the time of transition among loblolly pine of east Texas. Estimated family mean heritabilities of transition age for specific gravity (.36) and tracheid length (.34-.51) are sufficiently high to suggest moderate gains can be achieved by selection on a family mean basis or be combined selection based on family mean and individual tree information.

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Table 1. Estimation of variance components from an analysis of variance, (a) over locations and (b) by indivdual locations.

<u>(a)</u>				
Source	Degrees of	freedom	Expected mean	squares
Location	1			
Reps in Location	2			
Family	14	•	$o_{e}^{2} + 5 o_{fr(1)}^{2} + 10 d_{fr(1)}^{2}$	$p_{f1}^2 + 20 o_f^2$
Family x location	14		$\sigma_{e}^{2} + 5\sigma_{fr(1)}^{2} + 10\sigma_{fr(1)}^{2}$	o <sup>2</sup> f1
Family x rep (loc	) 28		$o_e^2 + 5\sigma_{fr(1)}^2$	
Progeny	240		o <sup>2</sup> e	•
(b)	·····			
Source	Degrees of	freedom	Expected mean	squares
Reps	. 1			
Family	14		$\sigma_e^2 + 5\sigma_{fr}^2 + 10\sigma_f^2$	
Family x rep	14		$\sigma_e^2 + 5\sigma_{fr}^2$	
Progeny	120		$\sigma_e^2$	
Where $\sigma_e^2 = var$	riance among	g progeny	y within famili	es .
$\sigma_{fr(1)}^2 = far_{cor}$	nily x repli nponent	icate in	location varia	ance
2				

 $\sigma_{f1}^2$  = family x location variance component  $\sigma_{fr}^2$  = family x replicate variance component

 $\sigma_f^2$  = family variance component

Table 2. Phenotypic (r ) and genetic (r ) correlations among age of transition for specific gravity (SG AGE) and tracheid length (TL AGE), the values of the parameters at the point of transition (SG,TL), specific gravity of the parent trees (PSG) and height (Ht20) and diameter (Dia20) of the trees at age 20.

	TL Age	SG	TL	PSG	Ht20	Dia20
SG Age						
r p	.03	.51*	.06	04	10	06
r <sub>A</sub>	12	.07	.00		-1.37	61
TL Age		14			•	
r p		.02	.56*	.07	09	03
r <sub>A</sub>		.10	.00		43	.01
SG	. · ·		•.			
r p		•	04	.26*	25*	26*
r <sub>A</sub>			.00		-1.08	-1.07
TL						
r p		:		02	.11	.04
r <sub>A</sub>					.00	.00

\* significant at the P=.05 level

Table 3. Means, standard deviations and maximum and minimum values for age of transition for specific gravity (SG Age) and tracheid length (TL Age), and values of each parameter at transition.

Character	Mean	S.D.	Max	Min
SG Age	11.45	3.20	20	4
SG	.53	.06	0.73	0.40
TL Age	10.39	3.61	20	6
TL	4.09	.48	5.54	2.94

SG Age	Family	TL Age	Family	
9.8	4041001	8.7	4041001	
10.1	4401034	9.0	4021002	
10.8	4061001	9.4	4051002	
10.8	4051002	9.6	4051001	
10.9	4021001	9.8	4061003	
11.1	4011001	9.8	4021004	
11.4	4051001	10.0	4031002	
11.4	4031001	10.2	4061001	
11.4	4021003	10.7	4031001	
11.6	4031002	10.9	4201001	
11.9	4201001	11.0	4021001	
12.2	4021002	11.2	4011001	
12.6	4031004	11.5	4401034	
12.8	4061003	11.7	4021003	
13.0	4021004	12.3	4031004	

Table 4. Family mean ranking for age of transition for specific gravity (SG Age) and tracheid length (TL Age).

Table 5. Analysis of variance for age of transition for specific gravity, (a), tracheid length over locations, (b), and for tracheid length by locations, location 1, (c), and location 2, (d).

(a) Specific		·		
Source	d.f.	Mean square	F	P F
Location	1	6.4533	0.48	0.56
Replication	2	13.3333	1.38	0.25
Family	14	17.3676	1.80	0.14
Family x loc	14	9.6533	0.82	0.65
Family x rep()	loc) 28	11.8190	1.22	0:21
Error	240	9.6667	1.22	0.21
(b) Tracheid	longth			
	d.f.	Maan aquara	F	P F
Source	<u> </u>	Mean square	Г	<u> </u>
Location	1	65 2222	1.81	0.31
		65.3333		
Replication	2	36.0533	2.81	0.06
Family	14	21.7962	1.53	0.22
Family x loc	14	14.2762	2.37	0.03
Family x rep(		6.0248	0.47	0.99
Error	240	12.8333		
		Location 1		
Source	d.f.	Mean square	F	P F
D 1	1	0.0000	0 00	1 00
Replication	1	0.0000	0.00	1.00
Family	14	20.4267	3.08	0.02
Family x rep	14	6.6286	0.50	0.93
Error	120	13.3333		
(d) Tracheid	length	Location 2		
Source	d.f.	Mean square	F	ΡF
Replication	1	71.1066	13.30	0.00
Family	14	15.6457	2.89	0.03
Family x rep	14	5.4209	0.44	0.95
Error	120	12.3333		

Table 6.	Family mean and individual tree heritability est-
	imates for specific gravity at the age of transi-
	tion (SG) and for the age of transition for
	specific gravity (SG Age) and tracheid length (TL
	Age) in loblolly pine wood.

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Character	h <sup>2</sup> <sub>f</sub>	s.e.	h <sup>2</sup> i	s.e.
SG				
Over locations SG Age	.52	.11	.30	.04
Over locations TL Age	.36	.38	.12	.06
Over locations Location l Location 2	.34 .51 .45	.57 .15 .16	.11 .37 .31	.14 .20 .22

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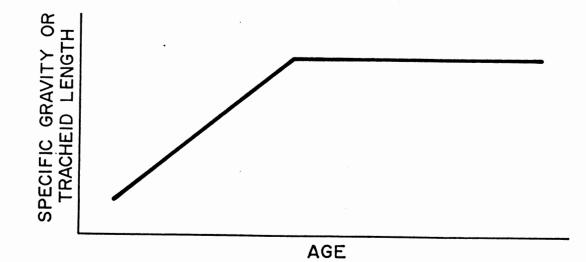


Figure 1. Expected form of the transition from juvenile to mature wood in loblolly pine. Adapted from Zobel and McElwee (1958).

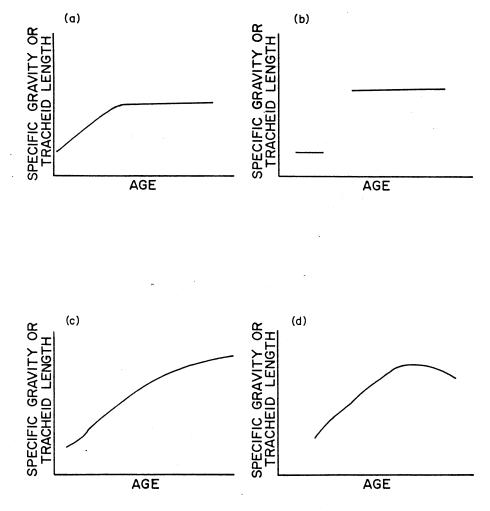


Figure 2. Generalized shapes of the plots of specific gravity and tracheid length over age: (a) 45% of specific gravity plots and 65% of tracheid length plots, (b) 25% specific gravity and 1% tracheid length plots, (c) 16% of specific gravity and 29% of tracheid length plots, and (d) 10% of specific gravity and 3% of tracheid length plots.

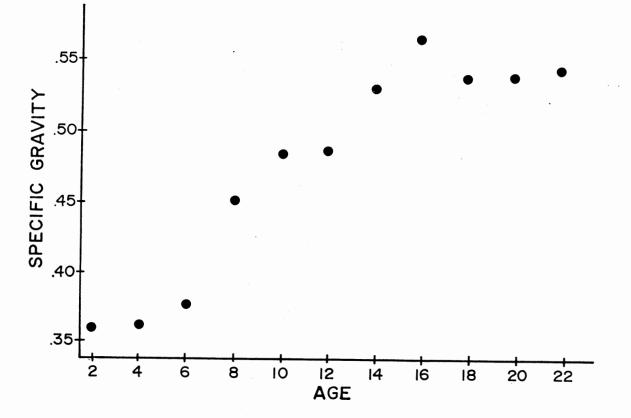


Figure 3. Specific gravity averaged over 300 trees plotted against age.

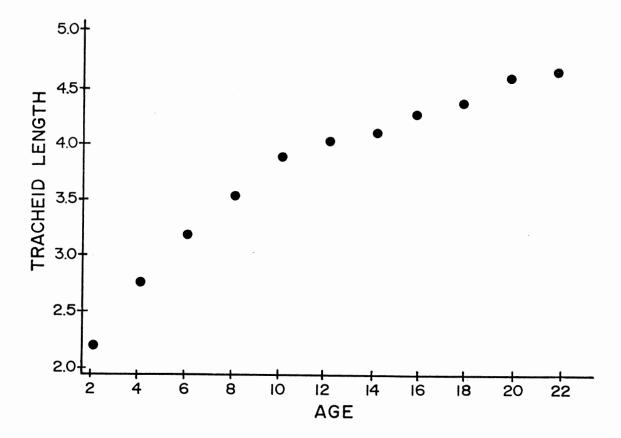


Figure 4. Tracheid length averaged over 300 trees plotted against age.

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## PART II

# JUVENILE-MATURE RELATIONSHIPS AND HERITABILITY

# ESTIMATES FOR SEVERAL TRAITS IN

LOBLOLLY PINE (<u>PINUS</u> <u>TAEDA</u> L.)

#### ABSTRACT

Heritability estimates for wood specific gravity of loblolly pine in east Texas were high and relatively constant for all ages of wood sampled, but tracheid length was found to have low heritability at all ages. Heritability estimates for tracheid length declined with age after age four. Coefficients of genetic prediction indicated that specific gravity of age two wood is a reliable predictor of wood specific gravity at age twenty-five. Genetic covariances between juvenile and mature tracheid length were approximately zero. Coefficients of genetic prediction and genetic correlations between specific gravity and height and diameter at age twenty indicated a strong negative relationship.

#### INTRODUCTION

Genetic gains per unit time are inversely proportional to the length of a selection cycle, thus the value of the juvenile form of a trait in predicting the mature form is an important consideration in a breeding program. Studies by Nicholls (1966) and Namkoong <u>et al</u>. (1972) have demonstrated that the degree of genetic control for certain characters may change with age. Assessing juvenile-mature relationships may be difficult when the two phases have very different properties. In particular, specific gravity of juvenile wood may be considered to be a genetically different trait from specific gravity of mature wood (Jett and Talbert 1982).

Measures of juvenile-mature relationships include genetic and phenotypic correlations, parent-offspring regression and the coefficient of genetic prediction as described by Earadat (1976). A genetic correlation is recognized as a more reliable predictor than a phenotypic correlation since the magnitude and direction of environmental correlations are usually not known (Falconer 1980). The presence of a genetic correlation suggests that a relationship between the two traits is inherent. A parentoffspring regression is useful if the juvenile and mature forms of the trait are similar and are controlled by the same genes (Jeff and Talbert 1980). The coefficient of genetic prediction seems ideally suited to measuring the expected response in the mature phase resulting from

selection during the juvenile phase for a given trait. When the phenotypic mean of one trait is shifted by one standard deviation, the breeding value of the other trait changes by an amount equal to the product of the coefficient of genetic prediction and the phenotypic standard deviation of the trait (Baradat 1976).

The coefficient of genetic prediction of any trait with itself would equal heritability. If the degree of genetic control remains constant throughout the life of an organism, the coefficient of genetic prediction for a juvenile and mature form of the same trait should be very similar to the heritability of the trait during either phase. Similarly, a parent-juvenile offspring regression should be very close to both the coefficient of genetic prediction and heritability estimated from variance components, if the juvenile trait is closely related to the corresponding mature trait.

High positive phenotypic and genetic juvenile-mature correlations for wood specific gravity and tracheid length have been reported by Zobel <u>et al</u>. (1959), Stonecypher and Zobel (1966), and Jackson and Greene (1958). The relationship between these wood properties and growth of loblolly pine have been studied extensively, but results vary from strong positive to strong negative correlations (Stonecypher <u>et al</u>. 1973, McKinley <u>et al</u>. 1982, Bendtsen 1978, Zobel <u>et</u> <u>al</u>. 1960, Namkoong <u>et al</u>. 1969). The relaionship between tracheid length and specific gravity is not clear. Zobel

et al. (1961), McMillan (1968) and Goggans (1964) reported negative or zero correlations between the two properties.

The objectives of this study were to examine age trends in heritability of specific gravity and tracheid length, to examine juvenile-mature relationships with respect to the predictive value of the juvenile wood phase for specific gravity and tracheid length of mature loblolly pine wood, and to examine relationships among wood specific gravity, tracheid length and measures of tree growth at age twenty.

## MATERIALS AND METHODS

Wood samples were collected from a 25-year old loblolly pine open-pollinated progeny test planted at two locations. Location one is near Rusk and location two is near Nacodoches, Texas<sup>1</sup>. The parent trees had been selected from throughout east Texas for high and low specific gravity. Sixteen families were randomized within each of three blocks at location one and two blocks at location two. The fifteen families that were sampled for this study had at least five surviving trees in each of two blocks at each location. One radial 12-millimeter increment core was taken from the north side of each of five trees per family from each block at the height of 1.4 meters above the ground. Cores were examined for branch or knot wood and were used only if they consisted entirely of clear wood.

Cores were divided into two-year segments beginning at the pith. Extractives were removed from the wood segments using a modified ASTM (1970) procedure described by Goggans (1962) and a modified soxhlet extractor apparatus described by Browns <u>et al</u>. (1977). Wood specific gravity was determined by the maximum moisture content method (Smith 1954). A small section of latewood was removed

<sup>&</sup>lt;sup>1</sup> The material was made available by Western Gulf Forest Tree Improvement Cooperative, the Texas Forest Service and Texas A&M University.

from the second ring of each segment for determination of tracheid length. The sample was macerated following a procedure outlined by Buxton (1967) and the fibers were stained with Safrannin O dye. Thirty whole tracheids were selected at random from each latewood sample and measured to the nearest .05 mm.

Specific gravity and average tracheid length were calculated for each age segment of the cores representing different ages of wood. The center of the pith to the end of ring two represented wood from a two year old tree. The pith to the end of ring four represented a four year old tree. Specific gravity and mean tracheid length were also calculated for six, eight, and ten-year core segments in the same manner. Whole core values and values for each property for the segments from ring sixteen to ring twenty-two, representing mature wood (Loo, <u>et al</u>. 1984), were calculated. Analyses of variance were computed for each age group and each property. Heritability estimates were calculated on a family mean and individual tree basis using variance components (Table 1) as follows:

(1) 
$$h_{f}^{2} = \frac{\sigma_{f}^{2}}{\sigma_{f}^{2} + 1/2 \sigma_{f1}^{2} + 1/4 \sigma_{fr(1)}^{2} + 1/20 \sigma_{e}^{2}}$$

(2) 
$$h_{i}^{2} = \frac{\sigma_{f}^{2} + \sigma_{f1}^{2} + \sigma_{fr(1)}^{2} + \sigma_{e}^{2}}{\sigma_{f}^{2} + \sigma_{f1}^{2} + \sigma_{fr(1)}^{2} + \sigma_{e}^{2}}$$

Where  $h_f^2$  = estimated narrow sense heritability by family mean

 $h_i^2$  = estimated narrow sense heritability by individual tree

 $\sigma_f^2$  = family variance component

 $\sigma_{f1}^2$  = family x location interaction variance component

 $\sigma_e^2$  = among progeny variance component Coefficients of genetic prediction were calculated to estimate the value of specific gravity and tracheid length at each age (2, 4, 6, 8 & 10) in predicting specific gravity or mean tracheid length of the mature wood and of the whole core at age 25. The coefficient of genetic prediction is:

(3) 
$$CGP_{i} = \frac{cov (A_{i}, A_{j})}{\sigma_{pi} \sigma_{pj}}$$

Where

CGP<sub>i</sub> = coefficient of genetic prediction for trait i calculated on a family mean basis

 $Cov(A_{j}, A_{j}) = covariance between the breeding values of traits i and j$ 

 $\sigma_{pj}, \sigma_{pi}$  = square root of phenotypic variance of trait i or trait j.

Parent-offspring regressions were calculated for specific gravity. Phenotypic and genetic correlations were computed for each age of wood with the mature wood and with the whole core for each property.

Coefficients of genetic prediction as well as genetic and phenotypic correlations were calculated for specific gravity of juvenile wood (rings 1 - 6), mature wood (rings 16 - 22) and whole core with height and diameter of the trees at age  $20^2$ . Phenotypic correlations were computed for

<sup>&</sup>lt;sup>2</sup> Parent tree specific gravity and progeny height and diameter data were made available by the Texas Forest Service and Texas A&M University.

juvenile, mature and whole core tracheid length with the growth characters and with specific gravity of each phase.

Standard errors associated with heritability estimates, coefficients of genetic prediction, and genetic correlations were approximated (Kendall and Stuart 1958) as follows:

s.e. (E) = 
$$([(E/Mi)^2][2(Mi)^2]/ki)^{-2}$$

where E = expression for the estimate of interest

- Mi = ith mean square

when more than two mean squares were involved in the calculation, and:

s.e.(E) = 
$$[Mi/Mj]^2[Var(F)]$$

where

e Mj = jth mean square

Var(F) = the variance of an F distribution,

when the calculation could be reduced to a ratio of two mean squares.

#### RESULTS AND DISCUSSION

The analysis of variance indicated highly significant differences among family means for specific gravity at all ages. Family differences for tracheid length were not significant at any age. Both family and individual tree heritabilities for specific gravity at all ages are very high (Table 2). This might be expected since the seed parents were selected for high or low specific gravity, thus violating the assumption of random selection implicit in the statistical model.

Parent-offspring regressions provide a valid estimate of heritability regardless of the mode of selection of the parents when the same trait is considered in each group. By doubling the regression of mature wood specific gravity on specific gravity of parent trees a valid estimate of heritability should be obtained. This estimate is low  $(2b_{op}=.57\pm.14)$  in comparison with the individual tree and family mean heritability estimates of 1.03±.37, and .80±.14 respectively for mature wood specific gravity. It is also low compared with many published family mean heritability estimates (Stonecypher and Zobel 1966, Namkoong et al. 1969, van Buijtenen 1962, and Goggans 1964). The parentoffspring regression may be the more reliable estimate since the assumptions of random selection of parents and of the .25 half-sib correlation among progeny are involved in the estimation of heritability by variance components but are not in parent-offspring regression estimates. The dis-

parity between parent-offspring regression estimates and the variance component heritability estimates for rings two to ten may support the view that specific gravity of juvenile wood is genetically a different trait from that of mature wood.

Tracheid length heritability estimates indicate that the character may be under little genetic control, but there is an apparent age dependency. The estimated family mean heritability was highest at age four  $(h^2_{f}=.30)$ , but declined to .14 at age ten. This corresponds to a trend in <u>Pinus</u> <u>radiata</u> (D. Don) discussed by Nicholls (1967). Published heritability estimates for tracheid length in loblolly pine are much higher, however, ranging from .44 to .97 (Namkoong <u>et al</u>. 1969, Goggans 1964, and Stonecypher <u>et al</u>. 1973). The estimated heritabilities for tracheid length in mature wood and for the whole core were 0 and .04 respectively. The standard errors were high at all ages suggesting that a sample size of twenty tracheids may not have been adequate for accurate estimates.

The estimated coefficients of genetic prediction (CGP) between specific gravity of each age of wood and whole core specific gravity presented in Table 3 are very similar to the family mean heritability estimates. Wood from a twoyear-old tree appears to be as valuable in predicting the specific gravity of a twenty-five-year-old tree as an ageten wood sample. The CGP varied only from .75 to .79 over ages. Based on these data, selection for high specific

gravity at age two should result in high specific gravity at age twenty-five. The CGP estimate for specific gravity of each age with mature wood may be a more reliable predictor than the CGP for each age with the whole core specific gravity if the projection is for trees old enough to contain a large proportion of mature wood. The best age for selection based on this criterion is six years.

Genetic and phenotypic correlations for wood specific gravity of two, four, six, eight and ten-year-old wood with mature and whole core specific gravity are presented in Table 3. Genetic correlations are very high; in all cases higher than the phenotypic correlations. Phenotypic correlations, especially between juvenile and mature wood, appear to have relatively low predictive value for early selection purposes.

Genetic covariances involving mean tracheid length of the mature wood or of the whole core where approximately zero. Thus, the length of tracheids in juvenile wood apparently has no value in a genetic sense in predicting tracheid length in the mature wood or in the whole core. The only correlations that were not zero were phenotypic correlations (Table 4). Although phenotypic correlations are positive and relatively high, results of this study indicate that they may be misleading, reflecting mostly environmental relationships.

Coefficients of genetic prediction as well as genetic correlations were negative and relatively high for both

height and diameter with specific gravity (Table 5). This relationship was most apparent for mature wood specific gravity. The data indicate that selection for high specific gravity in juvenile trees, age six in this example, may result in a significant negative response in both height and diameter growth at age twenty. Similar results were reported by McKinley et al. (1982) for age-ten loblolly pine.

Phenotypic correlations seem to have low reliability as predictors, since the environmental correlations between growth characters and specific gravity appear to have an opposite effect from genetic correlations. Phenotypic correlations between tracheid length and growth parameters were all positive and significant but low. Phenotypic correlations between specific gravity and tracheid length from juvenile wood, mature wood and whole core samples were all negative and low. The highest correlation was between mature wood specific gravity and juvenile tracheid length, but it only explained 10% of the variation.

#### CONCLUSIONS

Heritability estimates for specific gravity are high and relatively constant at all ages, but are very low and have an age trend for tracheid length. Coefficients of genetic prediction indicate that selection for high specific gravity trees at age two should result in high specific gravity at age twenty-five. Wood specific gravity may be negatively correlated with height and diameter of the trees at age twenty. Phenotypic correlations between specific gravity and tracheid length are negative but weak.

The results of this study indicate that specific gravity can be improved in a breeding program by selection at an early age. Care must be exercised, however, to avoid a concurrent negative impact on tree volume. Tracheid length can probably not be changed easily by selection.

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Table 1. Analysis of variance for estimation of variance components for the loblolly pine open-polinated progeny test.

Source	Degrees of	freedom	Expected mean squares
Location	1		
Reps in location	n 2		
Family	14		$\sigma_{e}^{2} + 5\sigma_{fr(1)}^{2} + 20\sigma_{f1}^{2}20\sigma_{f}^{2}$
Family x location	on 14		$\sigma_{e}^{2} + 5\sigma_{fr(1)}^{2} + 10\sigma_{f1}^{2}$
Family x rep(lo	c) 28		$o_{e}^{2} + 5 o_{fr(1)}^{2}$
Progeny	240		° <sup>2</sup> <sub>e</sub>

Where  $o_e^2$  = variance among progeny within families  $o_{fr(1)}^2$  = family x rep in location variance component  $o_{f1}^2$  = family x location variance component  $\sigma_f^2$  = among family variance component

		nce comp		estimate	Regression			
Frait	h <sup>2</sup> <sub>f</sub>	s.e.	h <sup>2</sup> i	s.e.	2 b <sub>o p</sub>	s.e.		
SG Age 2	.80	.12	.77	.30	.29	.09		
SG Age 4	.74	.14	.82	.35	.30	.08		
SG Age 6	.76	.17	.85	.25	.30	.08		
SG Age 8	.76	.17	.89	.35	.30	.08		
SG Age 10	.76	.17	.87	.35	.32	.08		
SG Mature*	.80	.14	1.03	.37	.57	.14		
SG Whole Core	.81	.14	1.08	.30	.38	.09		
TL Age 2	.00	.54	.00	.11				
TL Age 4	.32	.49	.15	.21				
TL Age 6	.24	.54	.13	.18				
TL Age 8	.21	.56	.12	.20				
TL Age 10	.18	.58	.09	.19				
TL Mature*	.00	1.02	.00	.10				
TL Whole Core	.04	.68	.02	.14				

Table 2. Heritability estimates for specific gravity (SG) and tracheid length (TL) of loblolly pine at various ages, calculated from variance components on an individual tree ( $h_i$ ) and family mean basis ( $h_f$ ), and parent-offspring regressions (2b op) for specific gravity.

\* rings 16-22

Table 3. Phenotypic (r ) and genetic (r ) correlations, and coefficients of genetic prediction (CGP) for specific gravity (SG) of wood cores of various ages with mature specific gravity and whole core specific gravity (age 25) of loblolly pine.

		SG Ma	nture	*			SG Wł	nole C	ore
Trait	CGP	s.e.	rA	s.e.	rp	CGP	s.e.	rA	s.e. r
SG Age 2	.58	.17	.73	.18	.27	.77	.10	.96	.08 .65
SG Age 4	.70	.14	.90	.12	.40	.75	.12	.97	.12 .76
SG Age 6	.77	.11	.99	.10	.44	.78	.11	1.00	.03 .83
SG Age 8	.77	.11	.99	09	.45	.78	.11	1.00	.02 .88
SG Age 10	.74	.12	.95	.09	.45	.79	.20	1.00	.01 .91
SG Mature	×					.74	.12	.92	.09 .60

\* rings 16 - 22

Trait	TL Mature rp	TL Whole Core p
TL Age 2	.30	.55
TL Age 4	.39	.69
TL Age 6	.45	.77
TL Age 8	.51	.81
TL Age 10	.54	.84
TL Mature		.73

Table 4. Phenotypic correlations (r ) for mean tracheid length (TL) from various ages of wood with mature (rings 16 - 22) and whole core tracheid length means of loblolly pine.

54	24* 77			.34	.20*	
54				.34	.20*	0 F X
	77	46				.35*
29		40				
	.21	.31				
40 -	59	36				
23	.19	.24				
02 -	36*	.03		.21*	.11*	.23*
45 -	73	39				
29	.19	.30				
34 -	56	31				
23	.18	.24				
d = r	ings 1 -	6				
	23 02 45 29 34 23	23 .19 0236* 4573 29 .19 3456 23 .18	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$

Table 5. Phenotypic  $(r_{p})$  and genetic  $(r_{A})$  correlations and coefficients for genetic prediction (CGP) between

APPENDIX

# PRINTOUT OF SPECIFIC GRAVITY AND TRACHEID LENGTH DATA

		5, 201						L LINGII	DATA					
FAM	REP	TREE	CHAR	AGE2	AGE4	AGE6	AGE8	AGE 10	AGE 12	AGE 14	AGE 16	AGE 18	AGE20	AGE22
1 1 1 1	2 2 2 2 2 2 2 2	1 2 2 3	SG TL SG TL SG	1.92 0.30 2.04	2.39 0.30 2.14	2.65 0.37 2.46	0.39 2.94 0.32 2.57 0.55	3.55 0.41 2.89	0.50 3.52 0.48 3.53 0.49	0.48 3.73 0.52 3.89 0.58	0.55 3.82 0.59 3.84 0.60	0.50 4.16 0.68 3.92 0.51	0.52 4.07 0.65 3.98	0.57 4.50 0.76 3.79
, 1 1 1 1	4 2 2 2 2 2 2 2 2	3 3 4 4 5 5	TL SG TL SG TL	2.15 0.36 1.46 0.36	2.92 0.35 1.51 0.37	2.50 0.48 1.65 0.42	3.80 0.37 2.43 0.60	3.94 0.38 2.66 0.56	3.84 0.54 2.98 0.57	4.02 0.53 3.22 0.56	4.06 0.54 3.43	4.63 0.56 3.74	0.54 4.80 0.54 4.12	0.50 4.92 0.55 4.08
1 1 1	3333	1 1 2 2 3	SG TL SG TL	0.32 2.11 0.41 2.12	0.31 1.87 0.47 2.66	0.37 2.07 0.57 2.89	3.71 0.33 1.92 0.61 3.25	0.36 2.49 0.64 2.97	3.97 0.38 2.89 0.65 2.90	3.96 0.52 4.39 0.50 4.97	0.53 3.99 0.58 4.56	0.56 4.60 0.65 4.19	0.64 4.37 0.59 4.66	
1 1 1 1	3 3 3 3 3 3	3 4 5	SG TL SG TL SG	2.20 0.41 1.81 0.36	2.17 0.39 2.49 0.41	2.78 0.48 3.20 0.50	0.32 3.85 0.54 3.61 0.59	3.55 0.56 4.32 0.55	0.49 4.06 0.60 3.95 0.62	0.64 3.28 0.69 3.57 0.60	0.63 3.25 0.65 4.35 0.65	0.68 3.59 0.62 5.12 0.55	0.65 3.94 0.55 5.17 0.53	0.71 4.13 0.60
1 1 1	4 4 4	51122	TL SG TL SG TL	0.38 2.27 0.34 2.03	0.38 2.58 0.39 2.99	0.42 3.10 0.34 3.52	3.51 0.50 3.74 0.44 3.78	0.46 4.31 0.44 3.96	3.96 0.51 4.23 0.46 3.93	4.97 0.55 4.39 0.55 3.98	3.99 0.57 4.50 0.59 4.32	4.19 0.48 4.32 0.50 4.57	4.64 0.56 4.62 0.57 4.81	4.79 0.60 4.67
1 1 1	4 4 4 4 4	3 3 4 5	SG TL SG TL SG	2.09 0.32 2.05 0.34	2.19 0.36 2.46 0.33	2.99 0.39 3.04 0.34	0.41	3.54 0.49 0.50	0.48 3.46 0.57 4.39 0.44	0.59 2.91 0.54 4.67 0.56	0.62 3.18 0.68 4.64 0.54	C.56 4.13 0.70 4.80 0.46	0.50 4.29 0.55 4.72	0.52 4.29
1 1 1 1 1	4 5 5 5 5 5 5	5 1 2 2 3	TL SG TL SG TL SG	0.36 2.21 0.37 2.69	0.39 2.78 0.41 3.48	0.42 3.27 0.44 3.91	3.91 0.49 3.40 0.54 4.38 0.51	0.60 3.70 0.59 4.87	4.35 0.50 4.19 0.55 4.41 0.55	4.19 0.62 4.06 0.61 4.66 0.58	4.75 0.67 4.22 0.64 5.30 0.57	4.83 0.59 4.54 0.53 5.31 0.58	0.63 4.28 0.56 4.92 0.64	0.60 4.87
1 1 1 1	ទំភេទទំភ	3 4 5 5	TL SG TL SG TL	2.12 0.40 2.21 0.38	3.07 0.41 2.81 0.34	3.48 0.36 3.74 0.40	4.34 0.47 4.14 0.51 3.74	3.27 0.56 5.23 0.53	3.45 0.49 4.64 0.53 4.47	4.00 0.55 4.67 0.54 3.98	4.27 0.65 4.67 0.62 4.38	4.71 0.57 5.14 0.57 4.25	4.73 0.55 4.92	0.62 5.00
2 2 2 2 2 2	2 2 2 2 2 2 2 2 2	1 2 2 3	SG TL SG TL SG	0.36 2.14 0.35 1.95	0.38 2.61 0.37 2.68	0.47 3.18 0.33 2.81	0.55 4.31 0.38 3.56 0.47	0.56 4.46 0.50 3.81	0.60 4:26 0.50 4.42 0.50	0.61 4.28 0.60 4.08 0.53	0.62 4.77 0.62 4.55 0.52	0.58 4.90 0.60 4.45 0.48	0.57 4.81 0.54 4.52 0.50	0.66 4.82
2 2 2 2 2 2 2	2 2 2 2 2 3	3 4 5 5 1	TL SG TL SG TL SG	0.38 1.79 0.38 2.00	0.37 3.06 0.41 3.26	0.40 3.53 0.46 4.03	3.40 0.54 3.43 C.49 3.97 0.42	C.47 3.72 C.54 4.28	4.17 0.56 4.61 0.57 4.78 0.54	4.72 0.55 4.68 0.60 4.73 0.60	4.56 0.57 4.13 0.59 4.39	4.53 0.54 4.41 0.57 4.67	4.83 0.59 4.75 0.58 5.06	4.73 0.60 4.60 0.55 4.93
2 2 2 2 2 2	3 3 3 3 3 3	1 2 2 3 3	TL SG TL SG TL	1.61 C.36 1.67 O.54	1.71 0.35 1.82 0.44	3.22 0.32 1.81 0.37	2.94 0.37 2.14 0.36 3.04	4.32 0.35 2.01 0.42	4.17 0.38 2.60 0.58 3.78	4.37 0.50 3.39 0.53 3.82	0.58 3.53 0.55 4.49	0.56 3.97 0.58 4.37	0.66 3.77 0.63 4.39	0.62 3.84 0.53 4.07

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22

FAM	REP	TREE	CHAR	AGE2	AGE4	AGE6	AGE8	AGE 10	AGE 12	AGE 14	AGE 16	AGE 18	AGE20	AGE22
3 3 3 3 3	5 5 5 5 5	2 2 3 3 4	SG TL SG TL SG	2.05 0.32 2.74	2.53 0.33 2.57	0.33 2.95 0.42 2.55 0.40	3.02 0.34 3.36	3.79 0.37 3.90	0.41 4.20 0.50 3.75 0.55	0.54 3.70 0.50 3.96 0.44	0.57 3.70 0.48 4.31 0.58	C.48 4.44 0.54 4.23 0.56	0.48 4.18 0.56 4.24 0.50	0.54 4.26 0.43 4.31 0.63
3 3 4 4	5 5 5 2 2	4 5 1 1	TL SG TL SG TL	2.66 0.33 2.00 0.38	3.05 0.34 2.60 0.39	3.26 0.35 3.43 0.46 3.13	4.09 0.45 3.46 0.51	4.23 0.55 3.89 0.50	4.39 0.46 3.96 0.56 3.62	4.32 0.53 4.31 0.57 3.75	4.40 0.50 4.23 0.60 3.54	4.41 0.52 4.45 0.57 4.36	4.57 0.57 4.80 0.56 4.85	4.82 0.55 4.53 0.65 4.66
4 4 4 4	2 2 2 2 2 2 2	2 2 3 3 4	SG TL SG TL SG	0.39 1.66 0.40 1.62	0.39 2.30 0.37 2.36	0.43 2.69 0.41 3.09 0.40	0.57 3.00 0.51 2.83	0.53 3.04 0.57 3.32	0.56 3.27 0.48 3.70 0.52	0.53 3.97 0.65 3.47 0.63	0.58 3.53 0.62 4.01 0.63	0.55 3.52 0.64 4.31 0.64	0.57 4.31 0.57 4.81 0.60	0.57 4.68 0.54 4.37
4 4 4 4 4	2 2 3 3	4 5 1 1	TL SG TL SG TL	0.42 1.65 0.37	0.39 2.64 0.39	3.07 0.50 2.67 0.46 3.03	0.53 3.75 0.44	0.52 3.52 0.54	3.72 0.55 3.35 0.50 3.73	3.80 0.60 3.96 0.60 4.88	4 36 0.63 4.11 0.63 4.28	3.80 0.59 4.30 0.62 5.42	4.51 0.70 4.46 0.64 4.81	•
4 4 4 1	3333	2 2 3 3 4	SG TL SG TL SG	1.69 0.38 2.10	2.03 0.34 2.59	0.37 2.58 0.40 2.54 0.45	2.89 0.41 3.10	3.44 0.46 3.78	0.51 4.00 0.56 4.18 0.55	0.51 4.19 0.59 3.70 0.57	0.64 3.89 0.59 3.95 0.64	0.56 4.54 0.66 4.34 0.65	0.62 4.83 0.59	0.64 4.90
4 4 4 4 4	33344	4 5 1 1	TL SG TL SG TL	0.38 2.26 0.37 3.01	2.37 0.41 2.66	0.38 3.17 0.39 2.83	3.70 0.53 2.88	0.57 3.58 0.57 2.97	3.87 0.51 4.60 0.49 3.43	4.43 0.57 4.52 0.56 3.42	4.00 0.60 4.58 0.62 4.59	4.44 0.64 4.72 0.62 4.76	4.84 0.54 4.32 0.55 5.06	0.59 4.72
4444	4 4 4 4	2 2 3 3 4	SG TL SG TL SG	2.14 0.42 2.29 0.36	2.70 0.41 2.50 0.33	0.50 3.24 0.41 2.55 0.34	3.33 0.44 3.21 0.50	3.38 0.51 3.16 0.53	0.58 3.73 0.56 3.32 0.53	0.62 3.60 0.53 3.85 0.60	0.60 4.17 0.66 3.92 0.62	0.52 4.21 0.60 4.10 0.56	0.64 4.61 0.60 3.93 0.54	
44444	44410101	4 5 1 1	TL SG TL SG TL	0.40 2.44 0.39 2.16	0.45 3.32 0.41 2.79	3.60 0.53 3.41 0.42 3.03	0.60 3.95 0.51 3.61	0.60 4.22 0.53 3.61	4.14 0.50 4.21 0.46 3.32	4.34 0.59 4.01 0.60 3.62	4.06 0.67 4.38 0.56 3.79	4.13 0.58 4.30 0.50 3.74	4.43 0.67 4.29 0.52 4.65	0.52 4.50
4 4 4 4 4	555555	2 2 3 3 4 4	SG TL SG TL SG TL	1.97 0.35 2.19 0.40	2.85 0.34 2.98 0.42	0.34 3.28 0.37 3.32 0.44 3.50	3.82 0.48 3.19 0.54	4.31 0.47 3.69 0.54	0.49 4.47 0.44 4.08 0.55 4.53	0.39 4.87 0.58 3.94 0.65 4.31	0.53 4.90 0.58 4.16 0.67 4.28	0.60 4.05 0.56 4.65 0.54 4.54	0.54 4.15 0.58 4.76 0.57 4.97	0.57 4.58 0.56 4.75 0.57 5.06
r 4 4 5 5 5	55222	7 5 1 1 2	SG TL SG TL SG	0.39 2.52 0.39 2.02	0.41 2.96 0.39 2.75	0.45 3.27 0.45	0.46 3.59 0.53 3.27	0.46 4.11 3.60	4.03 0.48 4.01 0.58 3.75 0.44	4.31 0.50 4.07 0.57 3.91 0.64	4.28 0.51 4.36 0.58 4.01 0.54	4.54 0.53 4.48 0.55 3.82 0.47	4.97 0.50 5.10 0.56 3.94 0.46	0.57 3.83 0.46
555555	222222	2 3 3 4 4	TL SG TL SG TL	1.90 0.35 1.96 0.39	2.59 0.34 2.56 0.37	3.25 0.36	3.75 C.50 3.32 O.39	3.64 0.44 3.22 0.48	4.08 C.40 3.28 O.52 3.72		4.00 0.56 3.80 0.54 4.05	4.56 0.48 3.88 0.57 4.19	4.73 0.58 4.36 0.56 3.86	4.50 0.60 4.10 0.46 4.29

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FAM	REP	TREE	CHAR	AGE2	AGE4	AGE6	AGE8	AGE 10	AGE 12	AGE 14	AGE 16	AGE 18	AGE 20	AGE22
5	2	5	SG	0.38	0.35	0.39	0.53	0.51	0.49	0.48	0.54	0.53	0.49	0.53
5	2	5	ΤL		2.64				3.52	3.22	3.87	5.06	3.63	3.56
5	3	1	SG		0.44				0.67	0.58	0.59	0.51	•	•
5 5	3 3	1	TL SG		3.05 0.36				4.52 0.47	3.90 0.52	4.44 0.49	4.07	0.00	0.60
5	3	2	TL		2.79				3.72	4.05	4.07	0.51 4.17	0.60 3.41	0.60 3.96
5	3	3	SG		0.45				0.46	0.47	0.57	0.59	0.67	
5	З	з	TL		1.74				3.78	4.36	4.22	4.51	4.72	
5	З	4	SG		0.33				0.40	0.50	0.46	0.63	0.56	
5	3	4	TL		1.78				2.98	3.80	4.04	3.80	4.68	
5 5	3 3	5 5	SG TL		0.40 2.84				0.54 3.83	0.55 4.13	0.57 4.80	0.55 4.65	0.60 4.96	0.53 4.79
5	4	1	SG		0.37				0.47	0.56	0.56	0.50	0.53	4.75
5	4	1	TL		2.74				4.17	4.19	4.61	4.11	4.28	
5	4	2	SG		0.35				0.38	0.50	0.52	0.55	0.46	0.53
5	4	2	TL		2.58				4.38	4.02	4.29	4.59	4.63	4.76
5 5	4 4	3 3	SG TL		0.37 2.81				0.43 4.58	0.58 3.94	0.63 4.59	0.53 4.70	0.63 4.18	·
5	4	4	SG		0.34				0.39	0.49	0.58	0.49	0.43	0.53
5	4	4	TL		3.07				4.63	4.67	4.72	4.57	4.80	5.01
5	4	5	SG		0.34				0.47	0.57	0.60	0.48	0.54	0.58
5 5	4 5	5 1	TL SG		3.14 0.38				4.52	4.60	4.46	4.61	4.93	4.68
5	5	1	TL		2.74				0.50 4.09	0.51 3.70	0.51 3.84	0.49 4.42	0.51 4.41	•
5	5	2	SG		0.38				0.48	0.56	0.59	0.51	0.58	0.58
5	5	2	TL		3.56				3.91	4.14	4.20	4.25	4.04	4.85
5	5	3	SG		0.35				0.44	0.55	0.52	0.43	0.54	0.53
5 5	5 5	3 4	TL SG		3.39				4.31	4.56	4.49	5.12	5.19	5.20
5	5	4	TL		0.34 2.93				0.46 3.73	0.49 4.16	0.58 4.57	0.49 4.78	0.46 4.93	0.50 4.77
5	5	5	SG		0.36				0.50	0.51	0.59	0.51	0.49	
5	5	5	ΤL		2.89				4.39	3.84	4.56	4.58	4.58	
6	2	1	SG		0.40				0.47	0.49	0.57	0.58	0.51	0.55
6 6	2 2	1	TL SG		2.14 0.36				3.55 0.57	3.97 0.56	3.73 0.59	4.13 0.52	4.15 0.60	4.74 0.52
6	2	2	TL		3.04				3.60	3.64	3.64	3.52	3.91	4.04
6	2	з	SG		0.42				0.46	0.45	0.60	0.57	0.53	0.46
6	2	3	TL		2.10				3.94	4.78	4.76	5.33	5.24	5.63
6	2 2	4 4	SG		0.36				0.50	0.52	0.63	0.61	0.61	0.55
6 6	2	5	TL SG		2.88 0.34				3.96 0.52	3.93 0.51	4.28 0.61	4.22 0.55	4.35 0.56	4.26 0.55
6	2	5	TL		2.56				4.18	4.44	4.50	4.58	4.42	4.10
6	з	1	SG		0.37				0.53	0.60	0.63	0.60	0.56	0.57
6	3	1	TL		2.39				4.47	4.73	4.93	4.75	5.10	5.25
6	3	2 2	SG TL		0.36 2.41				0.49	0.56 4.13	0.57 4.35	0.53 4.40	0.44 5.00	0.50
6	3	2	SG		0.35				3.67 0.50	0.55	4.35 0.53	4.40 0.54	0.48	4.50 0.51
6	3	3	TL		2.67				3.81	3.63	4.30	4.38	4.76	4.65
6	З	4	SG		0.36				0.43	0.53	0.55	0.49	0.52	0.48
6	3	4	TL		2.29				3.93	4.48	4.59	4.72	4.58	4.42
6 6	3 3	5 5	SG TL		0.39 2.80				0.63 4.14	0.61 4.41	0.69 4.50	0.55 4.84		·
6	4	1	SG		0.42				0.44	0.48	4.50 0.63	4.84 0.51	0.41	:
6	4	1	TL		2.87				4.22	4.33	4.37	4.22	4.00	
6	4	2	SG		0.34				0.50	0.56	0.59	0.52		•
6	4	2	TL	3.03	3.46	4.16	4.29	4.37	4.12	4.40	4.63	4.75		

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22

0 0 <b>0 0 0 0 0 0 0 0 0</b> 0	4 4 4 4 4 5 5 5 5 5 5 5	3344551122334	SG L S	0.37 0.39 2.32 3.05 0.34 0.29 2.50 3.71 0.33 0.35	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	3.49 0.49 3.39 0.44 4.02 0.54 4.33 0.48 4.46 0.48 4.50	0.47 4.22 3.31 0.48 4.39 0.46 4.56 0.50 4.27 0.46 4.48 0.51	0.57 3.81 0.61 3.43 0.51 4.14 0.56 4.50 0.54 4.66 0.46 4.37 0.55	0.61 4.52 0.56 3.84 4.57 0.55 4.72 0.54 4.98 0.53 4.93 4.93 4.93 4.55	0.62 3.70 0.63 4.14 0.45 4.79 0.54 4.78 0.47 4.53 0.45 4.89 0.47	$\begin{array}{c} 0.51\\ 4.42\\ 0.58\\ 4.07\\ 0.56\\ 4.40\\ 0.50\\ 4.92\\ 0.52\\ 4.83\\ 0.52\\ 5.43\\ 0.57\end{array}$	0.56 4.77 0.55 5.10 0.53 5.10 0.60
6667777	5552222	455122	TL SG TL SG TL SG TL	0.34 0.32 2.07 2.89 0.34 0.31 1.93 2.66	0.36 0.45 3.71 4.11 0.37 0.45 2.80 3.80 0.35 0.40 3.47 4.08	0.42 4.04 0.43 3.62 0.38 3.24	3.65 0.43 4.29 0.48 3.30 0.46 3.80	3.94 0.43 3.47 0.49 4.29 0.56 4.57	3.96 0.47 4.04 0.49 4.17 0.53 4.05	4.09 0.43 4.47 0.46 4.19 0.49 3.94	4.59 0.46 5.11 0.48 3.71	4.60 0.51 4.45
7 7 7 7 7 7 7	2 2 2 2 2 3 0	3344551	SG TL SG TL SG TL SG	0.40 0.37 1.98 2.39 0.35 0.35 2.15 3.33 0.32 0.31 2.58 2.77 0.32 0.34	2.79 3.10 0.34 0.49 3.95 4.20 0.46 0.46 3.07 3.14 0.34 0.49	<ul> <li>3.40</li> <li>0.47</li> <li>4.48</li> <li>0.43</li> <li>4.03</li> <li>0.52</li> </ul>	0.46 3.40 0.41 4.99 0.46 4.02 0.50	0.69 4.23 0.54 5.35 0.54 4.22 0.53	0.60 4.21 0.67 5.40 0.46 4.26 0.52	0.57 5.22 0.49 3.86 0.57	0.52 5.25 0.49 4.31 0.53	0.62
7 7 7 7 7 7 7 7 7	3333333	1 2 2 3 3 4 4	TL SG TL SG TL SG TL	0.38 0.32 1.46 2.64 0.37 0.37 1.68 1.84 0.33 0.39 2.11 2.54	2.42 3.62 0.31 0.33 1.92 1.83 0.40 0.51 3.23 3.45	0.51 3.98 0.34 2.86 0.55 3.90	4.26 0.54 4.60 0.35 3.31 0.49 3.54	4.21 0.41 4.07 0.46 3.29 0.60 3.59	4.70 0.55 5.03 0.42 4.17 0.62 4.22	4.36 0.56 4.24 0.45 4.22 0.55 4.61	4.66 0.54 4.95 0.55 4.86 0.50 4.90	4.69 0.54 4.58
7 7 7 7 7 7 7	3 3 4 4 4 4 4	5511223	SG TL SG TL SG TL SG	0.36 0.32 2.43 2.79 0.34 0.36	3.59 3.61 0.33 0.41 3.56 3.57 0.31 0.44 3.22 3.55 0.32 0.42	4.15 0.42 3.34 0.49 3.24 2.0.41	0.45 4.49 0.39 4.11 0.44 3.66 0.42	0.48 4.76 0.44 3.89 0.54 3.71 0.46	0.49 4.34 0.49 4.17 0.58 4.42 0.45	0.46 4.69 0.46 4.22 0.48 4.32 0.41	0.41 4.49 0.44 4.29 0.51 4.68 0.49	0.46 4.96 0.41
7 7 7 7 7 7 7	4 4 4 5 5 5 5	3 5 1 1 2 2	TL SG TL SG TL SG TL	-	0.37 0.31 3.54 4.01 0.34 0.39 3.67 3.78 0.34 0.36 4.43 4.53	0.49 4.25 0.39 3.07 50.42 84.47	3.83 0.45 4.49 0.42 3.64 0.39 4.13	4.11 0.47 4.30 0.51 3.83 0.47 4.13	4.08 0.55 4.47 0.58 3.32 0.45 4.50	4.46 0.51 4.32 0.51 3.53 0.45 4.28	4.91 0.48 4.50 0.51 4.11 0.49 4.65	5.02 0.52 4.64 0.54 4.61 0.50 5.02
7 7 7 7 7 8 8	5 5 10 10 10 10 10	3 3 4 4 5 5 1 1	SG TL SG TL SG L SG L	0.37 0.37 2.59 3.36 0.39 0.36 2.66 3.34 0.30 0.33 2.17 3.13 0.41 0.39 1.66 1.79	3.47 3.76 0.35 0.43 3.36 3.78 0.35 0.42 3.90 4.17 0.41 0.40	5 3.88 3 0.47 3 3.54 2 0.62 7 4.28 0 0.47	0.43 3.86 0.45 3.78 0.42 4.27 0.50 3.64	0.51 4.08 0.51 4.17 0.46 4.31 0.47 3.52	0.57 4.24 0.54 4.36 0.49 4.88 0.51 3.75	0.49 4.33 0.49 4.00 0.53 4.94 0.49 3.77	0.55 4.45 0.49 4.16 0.47 5.11 0.43 3.67	0.59 4.66 0.53 4.47 0.60 5.56 0.48 4.24

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22 SG 0.38 0.31 0.37 0.44 0.42 0.47 0.50 0.50 0.48 C.52 8 2 2 0.46 2.46 2.67 2.88 3.22 3.52 3.90 3.91 4.54 4.93 5.01 8 2 TL 4.27 2 8 2 3 SG 0.38 0.37 0.31 0.31 0.41 0.39 0.60 0.51 0.53 0.44 0.44 2 1.65 2.08 3.19 2.82 3.58 4.21 4.58 8 З TL 4.18 4.39 4.64 4.62 4 0.34 0.34 0.36 0.31 0.33 0.30 8 2 SG 0.31 0.40 0.42 0.38 8 2 4 TL 1.64 1.89 1.68 1.73 2.26 2.94 2.83 3.03 3.36 3.21 2 0.37 0.28 0.47 0.34 0.33 0.70 0.69 8 5 SG 0.46 0.57 0.42 0.67 8 2 5 TL 1.80 2.04 2.02 2.41 2.79 3.39 3.81 3.70 3.98 3.72 4.03 8 з 1 SG 0.36 0.36 0.45 0.48 0.48 0.50 0.52 0.51 0.47 0.47 0.45 з 1.98 2.86 3.20 3.39 3.80 3.96 4.70 4.68 4.51 8 1 TL 5.12 4.68 8 з 2 SG 0.37 0.31 0.37 0.47 0.45 C.49 0.51 0.62 0.56 0.54 0.62 2 2.18 2.85 2.53 3.01 3.78 8 з TL 4.00 4.22 4.23 4.54 4.59 5.03 8 з з SG 0.33 0.31 0.41 0.46 0.39 0.40 0.48 0.56 0.46 0.45 . 8 з з TL 2.30 2.82 2.85 3.83 4.12 4.12 4.38 4.73 4.75 5.09 0.49 0.56 8 4 0.34 0.34 0.32 0.44 0.50 0.39 0.51 0.48 з SG 0.36 8 З 4 τL 1.73 2.19 2.56 2.82 2.67 3.09 3.74 4.05 3.80 4.62 0.54 8 з 5 SG 0.36 0.38 0.40 0.43 0.47 0.47 0.54 0.51 0.53 0.57 5 1.66 2.30 2.63 3.40 3.39 3.51 4.56 8 з TL 3.90 4.19 4.36 4.46 8 4 1 SG 0.35 0.33 0.33 0.42 0.44 0.45 0.49 0.54 0.53 0.46 0.53 2.33 2.95 3.44 2.89 4.15 4.04 8 4 1 TL 4.35 4.35 4.05 4.77 4.64 4 2 0.36 0.33 0.27 0.47 0.51 8 0.46 0.49 0.54 0.52 SG 0.59 • 8 1 2 TL 2.99 3.49 3.52 3.82 3.77 4.10 4.11 4.31 4.66 4.37 0.51 8 4 з SG 0.35 0.35 0.35 0.33 0.40 0.45 0.47 0.60 0.46 0.52 8 4 З TL 2.05 2.40 2.60 3.06 3.21 3.70 3.87 4.22 4.62 4.24 3.95 4 8 4 SG 0.38 0.37 0.35 0.36 0.49 0.56 0.53 0.60 0.58 0.51 0.53 8 4 4 ΤL 2.40 2.98 3.34 3.76 3.79 5.08 4.28 4.13 4.57 4.44 5.10 8 4 5 SG 0.41 0.37 0.34 0.46 0.40 0.43 0.46 0.56 0.41 0.44 . 4 1.75 2.48 2.58 3.63 3.78 3.70 8 5 TL 3.95 4.70 4.64 4.85 8 5 1 SG 0.34 0.32 0.32 0.40 0.49 0.43 0.50 0.55 0.43 0.51 0.47 5 2.39 2.93 3.05 3.44 4.10 4.37 8 1 TL 4.15 4.31 4.78 4.14 3.94 8 5 2 0.37 0.36 0.34 0.46 0.48 0.45 SG 0.38 0.56 0.58 0.51 0.53 8 5 2 TL 2.30 3.19 3.71 3.85 3.85 4.60 4.88 5.10 5.15 4.75 4.68 8 5 З 0.35 0.33 0.36 0.47 0.44 0.45 0.52 0.53 0.50 0.51 SG 0.47 8 5 З TL 2.13 2.87 2.99 3.74 4.33 4.59 4.92 4.98 4.80 4.87 4.66 8 5 4 SG 0.34 0.36 0.38 0.43 0.52 0.52 0.54 0.57 0.53 0.56 8 5 4 TL 2.27 2.73 3.57 3.94 4.18 4.16 4.50 4.80 4.84 5.06 8 5 5 SG 0.36 0.35 0.36 0.49 0.50 0.47 0.54 0.58 0.52 0.57 0.58 5 5 2.20 3.04 3.31 3.89 4.13 8 TL 4.41 4.64 4.91 5.08 4.82 5.24 9 2 1 SG 0.39 0.39 0.35 0.39 0.56 0.52 0.56 0.65 0.62 0.58 0.57 2 1.85 1.80 2.73 2.93 3.51 4.00 9 1 TL 3.86 4.16 4.31 4.58 4.52 9 2 2 0.43 0.35 0.44 0.57 0.56 0.54 0.61 0.61 0.63 0.54 0.56 SG 9 1.87 2.47 3.01 3.20 3.41 2 2 ΤL 3.43 3.90 3.89 4.37 4.24 4.28 9 2 З SG 0.36 0.35 0.33 0.51 0.41 0.45 0.57 0.58 0.54 0.58 0.55 9 2 з ΤL 2.33 2.86 3.37 3.66 3.70 3.75 3.83 3.77 4.05 4.26 4.03 0.58 9 2 4 0.38 0.37 0.33 0.37 0.47 0.46 0.53 0.53 0.52 0.45 SG 9 2 4 TL 1.53 2.07 3.33 3.67 3.78 4.23 4.16 4.25 4.60 4.51 4.80 9 2 5 SG 0.38 0.40 0.40 0.44 0.58 0.56 0.58 0.59 0.60 0.55 0.55 9 2 5 TL 2.13 2.20 2.70 2.89 3.76 3.80 4.17 4.34 4.09 4.53 4.56 9 З 1 SG 0.40 0.40 0.47 0.54 0.51 0.51 0.57 0.63 0.53 0.60 0.57 1.90 2.92 3.60 3.73 3.53 4.43 4.45 4.37 4.60 4.34 9 З 1 TL 5.24 9 0.38 0.39 0.40 0.54 0.54 0.54 0.56 0.63 0.61 0.58 0.59 З 2 SG 1,94 2.62 3.52 3.29 3.14 2 3.71 S з TL 3.78 3.67 4.04 4.37 9 З 0.36 0.36 0.38 0.53 0.56 0.52 0.58 0.63 0.64 0.55 0.56 з SG З 9 З TL 2.37 3.06 3.38 3.64 3.59 4.00 3.70 4.45 4.80 4.80 4.40 9 з 4 0.37 0.34 0.40 0.35 0.37 0.58 0.58 0.59 0.64 0.67 0.62 SG 9 з 4 TL 1.98 1.80 1.97 2.60 2.98 3.10 3.10 4.10 4.30 4.03 4.41

SG 0.38 0.38 0.46 0.53 0.53 0.63 0.56 0.66 9 з 5 0.61 0.62 0.62 9 З 5 1.59 2.95 2.64 3.81 4.45 TL 3.82 3.91 3.78 3.74 4.54 4.63 9 4 SG 0.42 0.43 0.42 0.40 0.60 0.52 1 0.60 0.59 0.62 0.54 0.53 9 4 2.10 2.85 3.25 3.42 3.40 1 TL 3.87 3.87 3.81 3.77 3.77 3.98 9 4 2 SG 0.40 0.38 0.37 0.49 0.54 0.45 0.50 0.54 0.54 0.45 0.58 9 4 2 TL 2.43 3.19 3.51 3.74 3.82 3.93 4.00 4.10 4.22 4.96 4.99 9 4 з 0.41 0.34 0.44 0.44 0.38 SG 0.47 0.50 0.47 0.39 0.52 . 9 4 З TL 2.55 3.36 3.93 3.61 3.46 4.18 3.86 3.59 4.40 4.28 9 4 4 SG 0.36 0.34 0.36 0.47 0.53 0.49 0.56 0.60 0.51 0.44 . 9 4 4 2.68 3.19 3.81 3.87 4.52 TL 4.01 4.17 4.39 4.05 4.43 9 4 5 SG 0.45 0.40 0.40 0.50 0.47 0.49 0.54 0.55 0.50 0.45 0.53 9 4 5 T1 2.13 3.08 3.22 3.82 3.64 4.05 4.04 4.27 4.62 4 49 4.65 9 5 0.38 0.34 0.41 0.43 0.47 1 SG 0.45 0.54 0.54 0.43 0.60 0.57 9 5 1 ΤĹ 3.21 3.30 3.77 4.11 4.20 4.48 4.57 4.36 4.68 4.82 4.66 9 5 2 SG 0.40 0.37 0.37 0.52 0.54 0.41 0.58 0.63 0.48 0.57 0.49 9 5 4.43 2 TL 2.93 3.18 3.83 4.22 4.17 4.64 4.80 4.78 4.96 4.80 9 5 з SG 0.37 0.36 0.36 0.51 0.49 0.46 0.53 0.59 0.52 0.51 0.47 9 5 З TL 2.76 3.14 3.85 4.17 4.63 4.47 4.78 4.69 4.68 4.78 4.69 9 5 4 0.37 0.33 0.35 0.49 0.47 SG 0.48 0.56 0.54 0.53 0.53 0.45 9 5 4 TL 2.97 2.90 4.31 3.82 4.22 4.33 4.24 4.46 4.40 4.74 4.71 9 5 5 SG 0.36 0.32 0.34 0.44 0.46 0.42 0.44 0.48 0.39 0.48 . 9 3.95 5 5 ΤL 2.39 3.36 3.63 3.67 4.37 4 41 4.12 4.63 4.82 10 2 1 SG 0.28 0.31 0.36 0.44 0.39 0.51 0.48 0.50 0.46 0.43 0.43 10 2 1 TL 2.13 3.12 3.48 4.14 4.20 4,48 4.37 4.19 4.21 4.51 4.72 2 10 2 SG 0.35 0.33 0.36 0.45 0.43 0.54 0.47 0.46 0.43 0.48 0.58 2 10 2 T! 2.01 3.14 3.44 3.89 4.01 4.20 4.05 4.36 4.34 5.08 4.87 10 2 з SG 0.32 0.33 0.37 0.40 0.38 0.45 0.46 0.50 0.41 0.43 0.47 10 2 з TL 2.07 3.14 3.28 4.05 4.11 4.39 4.67 4.80 5.19 5.34 5.08 10 2 0.32 0.31 0.42 0.49 0.49 4 SG 0.52 0.54 0.54 0.47 0.51 0.43 10 2 4 ΤL 2.25 3.13 3.58 4.04 5.54 4.60 4.23 4.78 4.68 4.78 4.76 10 2 5 0.31 0.29 0.41 0.49 0.47 SG 0.56 0.62 0.60 0.57 0.56 0.49 10 2 5 TL 2.36 3.02 3.57 3.95 4.27 3.53 3.64 4.16 4.44 4.31 4.45 10 з 1 SG 0.30 0.36 0.41 0.42 0.42 0.49 0.51 0.55 0.50 0.50 0.45 10 з ΤL 2.14 2.51 3.58 3.68 3.83 1 4.41 4.55 4.65 5.11 5.03 4.52 1C З 2 0.36 0.34 0.32 0.51 0.58 0.65 SG 0.52 0.60 0.50 0.50 0.53 10 з 2 TL 2.35 3.33 4.48 3.18 3.77 3.97 4.39 4.17 4.81 4.64 4.88 10 з З SG 0.32 0.30 0.39 0.49 0.45 0.45 0.51 0.62 0.51 0.51 0.45 10 з з TL 2.88 3.65 3.25 4.14 3.78 4.44 4.46 4.84 4.69 4.75 5.09 10 0.34 0.33 0.44 0.43 0.54 з 4 SG 0.50 0.50 0.54 C.48 0.50 0.49 10 з 4 TL 2.24 3.01 2.90 3.87 4.15 4.71 4.56 4.54 4.64 4.99 5.26 10 з 5 SG 0.33 0.37 0.43 0.46 0.47 0.52 0.47 0.51 0.51 0.60 10 з 5 TL 2.69 3.58 3.76 3.99 4.23 4.21 4.25 4.36 4.51 4.78 4 10 1 SG 0.34 0.33 0.36 0.42 0.46 0.54 0.57 0.54 0.46 0.58 0.51 10 4 2.34 2.79 3.59 4.01 4.32 1 TL 3.98 4.37 4.27 4.46 4.99 4.74 10 4 2 SG 0.38 0.33 0.33 0.50 0.46 0.56 0.61 0.59 0.59 0.60 10 4 2 TL 2.01 2.44 3.29 3.16 3.45 3.50 3.99 3.33 4.02 4.39 . 10 4 з 0.41 0.33 0.32 0.40 0.41 0.43 0.44 SG 0.49 0.48 0.49 . 4 10 з ΤL 2.52 3.32 3.67 3.97 4.22 4.19 3.97 4.26 4.49 4.50 10 4 4 SG 0.36 0.33 0.35 0.47 0.44 0.54 0.52 0.55 0.48 0.58 0.53 10 4 4 TL 2.35 2.51 3.28 3.49 4.03 3,82 3.76 3.95 4.94 4.11 4.02 10 4 5 SG 0.34 0.33 0.33 0.45 0.39 0.51 0.51 0.61 0.51 0.46 10 4 5 2.03 3.02 3.96 3.55 4.01 TL 3.88 3.82 3.96 3.78 4.26 5 10 1 SG 0.32 0.32 0.31 0.44 0.43 0.41 0.48 0.49 0.41 0.47 4.17 10 5 ΤL 3.07 3.44 3.81 3.49 1 2.30 4.22 4.70 4.76 4.60 . 10 5 2 SG 0.37 0.32 0.36 0.43 0.46 0.44 0.51 0.54 0.55 0.50 . 10 5 2 4.14 TL 2.66 3.15 3.62 3.98 4.10 4.22 4.48 4.75 4 57

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22 SG 0.35 0.31 0.30 0.38 0.41 0.37 0.42 0.48 0.45 0.45 0.55 10 5 З 10 5 з TI 1.94 2.84 3.57 4.19 4.04 4.17 4.06 4.11 4.29 4.58 4.79 10 5 0.37 0.34 0.33 0.48 0.51 4 SG 0.40 C.52 0.58 0.48 0.53 0.46 10 5 4 2.53 3.64 4.20 4.65 4.76 TL 4.82 4.81 5.24 5.10 5.10 5.28 5 10 5 SG 0.31 0.30 0.32 0.36 0.37 0.38 0.40 0.44 0.40 0.46 0.45 10 5 5 TL 2.76 3.23 3.73 4.14 4.19 4.93 5.12 4.64 4.82 4.97 5.03 11 2 0.39 0.36 0.45 0.56 0.54 1 SG 0.59 0.54 0.57 C.55 0.53 0.57 2 11 1 TI 1.90 2.83 3.54 4.25 4.34 4.78 4.59 4.44 4.79 5.26 5.27 11 2 2 0.38 0.31 0.32 0.49 0.57 SG 0.35 0.60 . . . . 11 2 2 1.74 2.68 2.56 3.52 4.02 TL 4.07 4.16 11 2 З SG 0.36 0.34 0.44 0.51 0.43 0.56 0.60 0.60 0.54 0.64 0.60 11 2 з 2.50 2.84 3.66 4.14 4.59 TL 4.28 4.61 4.88 4.85 4.94 4.89 11 2 4 0.38 0.34 0.49 0.52 0.60 SG 0.48 0.59 0.54 0.52 0.53 0.69 2 4 11 TL 2.22 2.85 3.90 3.85 4.44 4.53 4.35 4.43 4.44 4.64 4.43 11 2 5 0.37 0.37 0.46 0.48 0.51 SG 0.54 0.53 0.65 0.61 0.52 0.53 11 2 5 TL 1.94 2.67 3.27 3.31 3.43 3,90 4.30 4 51 4 70 4.85 4.50 11 з 0.33 0.34 0.40 0.47 0.47 1 SG 0.53 0.53 0.54 0.50 0.52 0.49 11 З 1 TL 2.23 2.93 3.77 4.01 3.86 4.52 4.56 4.24 4.65 4.58 4.76 11 З 2 SG 0.36 0.37 0.36 0.51 0.52 0.54 0.62 11 З 2 TL 2.10 2.76 3.18 3.69 3.66 4.06 3.83 11 з З SG 0.33 0.32 0.43 0.50 0.48 0.54 0.57 . . 11 з 2.43 3.03 3.96 4.38 4.67 з TL 4.78 4.55 11 З 4 0.38 0.44 0.54 0.62 0.60 0.67 SG 0.59 0.71 0.68 0.71 З 11 4 TL 2.14 2.96 3.70 3.72 3.77 4.21 4.58 4.24 4.55 5.12 11 З 5 SG 0.35 0.36 0.44 0.52 0.52 0.62 0.62 0.61 0.59 0.59 0.58 11 з 5 1.92 3.02 3.65 4.03 3.99 ΤL 4.50 4.03 4.71 4.13 4.61 4.36 0.34 0.38 0.43 0.48 0.49 11 4 1 SG 0.51 0.53 0.53 0.45 0.54 . 11 4 1 TL 2.75 3.11 3.43 3.77 4.09 4.15 4.20 4.51 4.26 4.33 11 4 2 SG 0.34 0.38 0.35 0.43 0.52 0.44 0.62 0.50 0.53 0.60 2 11 4 2.32 2.85 3.61 3.72 3.90 TI 4.13 4.16 4.60 4.60 0.52 11 4 З SG 0.35 0.32 0.30 0.39 0.47 0.43 0.52 0.48 0.47 0.54 11 4 з TL 1.92 2.97 3.46 3.51 4.07 3.98 4.15 4.22 4.31 4.70 4.38 0.31 0.27 0.33 0.47 0.50 4 11 4 SG 0.47 0.56 0.58 0.48 0.53 . Δ 11 Δ TL 2.15 2.28 2.58 3.13 3.44 4.00 4.56 4.47 4.78 4.56 11 4 5 SG 0.37 0.38 0.37 0.50 0.53 0.51 0.52 0.54 0.52 0.49 0.53 3.02 3.44 3.52 3.71 3.82 11 4 5 TL 4.12 4.10 4.22 4.63 4.37 4.19 5 11 1 SG 0.33 0.35 0.34 0.40 0.44 0.46 0.47 0.55 0.56 0.50 0.60 11 5 TL 2.60 3.00 3.72 3.52 4.28 -4 4.41 4.46 4.56 4.54 4.62 4.74 11 5 2 SG 0.36 0.41 0.34 0.37 0.48 0.50 0.59 0.64 0.60 C.62 5 11 2 ΤL 2.14 2.80 3.72 3.52 3.87 4.23 4.24 4.35 4.60 4.53 11 5 З SG 0.35 0.37 0.37 0.54 0.49 0.45 0.54 0.58 0.51 . 11 5 З TL 2.16 2.66 3.12 3.81 4.32 3.73 4.07 3.87 4.27 5 11 4 SG 0.37 0.37 0.38 0.36 0.52 0.55 0.47 0.54 0.54 0.56 0.52 11 5 2 TL 1.74 2.48 2.60 2.62 2.91 4.04 4.03 4.09 4.22 4.29 4.52 11 5 Ξ SG 0.39 0.41 0.41 0.48 0.49 0.45 0.47 0.53 0.52 0.46 0.56 11 5 5 2.10 2.78 3.13 3.66 4.02 TL 4.00 4.05 4.14 4.42 4.93 4.42 12 2 1 SG 0.31 0.34 0.34 0.44 0.48 0.44 0.54 0.54 0.62 0.59 0.61 2.23 2.55 3.14 3.33 4.11 12 2 1 TL 3.68 4.38 4.83 4.97 4.96 12 2 2 SG 0.35 0.34 0.44 0.50 0.48 0.51 0.50 0.54 0.55 0.58 0.45 12 2 2 TL 2.56 3.26 3.08 4.02 4.33 3.86 3.82 3.89 4.06 4.17 3.99 2 12 3 SG 0.34 0.32 0.34 0.42 0.51 0.34 0.54 0.59 0.55 0.51 0.54 12 2 З T1. 1.78 2.54 3.02 3.84 3.31 3.62 3.63 3.80 3.29 4 82 4.63 4 12 2 0.36 0.34 0.46 0.49 0.47 SG 0.49 0.56 0.60 0.48 0.45 0.48 2 12 4 TL. 2.44 3.43 3.49 4.02 4.67 4.46 4.07 4.77 4.75 4.70 4.60 12 2 5 SG 0.33 0.33 0.32 0.34 0.45 0.45 0.45 0.54 0.53 0.44 0.48 5 2.24 3.00 3.07 3.60 4.10 TL 4.25 4.24 4.21 4.84 5.08

FAM REP TREE CHAR AGE2 AGE4 AGE6 AGE8 AGE10 AGE12 AGE14 AGE16 AGE18 AGE20 AGE22 13 SG 0.31 0.29 0.27 0.38 0.41 0.39 0.44 0.48 0.46 0.49 4 4 2.76 3.19 3.64 4.22 4.30 13 4 4 TL 4.31 4.42 4.41 4.52 4.52 13 4 0.37 0.33 0.31 0.36 0.44 0.45 0.48 0.46 0.46 0.55 5 SG 0.40 13 4 5 TL 2.04 3.76 3.81 4.06 4.24 4.44 4.45 4.87 4.52 4.94 5.21 13 5 1 SG 0.37 0.37 0.41 0.53 0.56 0.51 0.55 0.58 0.50 0.53 . 13 5 2.55 3.04 3.40 3.74 4.12 TL 3.88 4.17 4.27 4.40 1 4.14 0.55 13 5 2 SG 0.34 0.34 0.31 0.45 0.44 0.44 0.53 0.59 0.46 0.56 2.40 2.31 3.18 3.28 3.48 5 2 13 ΤL 3.76 3.75 3.83 4.11 4.64 4.16 SG 0.38 0.33 0.31 0.49 0.49 5 з 0.48 0.59 0.55 13 0.60 0.53 0.59 13 5 3 ΤL 2.18 3.18 3.30 3.41 3.64 4.27 3.67 4.13 3.90 4.25 4.58 5 4 0.35 0.30 0.33 0.42 0.48 13 SG 0.46 0.51 0.56 0.43 . . 13 5 4 TL 2.05 2.82 3.45 3.88 4.00 3.60 3.69 3.92 4.16 5 5 0.49 0.50 13 SG 0.38 0.33 0.37 0.49 0.53 0.47 0.52 0.55 0.50 5.00 13 5 5 2.16 3.05 3.66 3.92 4.07 4.25 4.45 4.62 4.43 ΤL 4.17 14 2 1 SG 0.33 0.37 0.31 0.31 0.48 0.55 0.53 0.60 0.66 . . 2 14 1.98 2.54 3.15 3.73 4.16 1 TL 4.18 4.33 4.52 4.56 14 2 2 SG 0.39 0.38 0.36 0.53 0.51 0.32 0.51 0.67 0.60 0.54 14 2 2 ΤL 2.05 2.58 2.91 3.20 3.28 3.47 4.20 4.19 4.47 4.66 2 14 з 0.60 SG 0.36 0.37 0.36 0.43 0.50 0.48 0.58 0.62 0.50 14 2 3 TL 2.00 2.64 3.16 3.55 4.10 3.84 4.20 4.43 4.30 4.53 14 2 4 SG 0.35 0.35 0.33 0.52 0.56 0.44 0.65 0.53 0.60 . 14 2 4 TL 2.11 2.58 3.53 3.57 3.94 4.01 4.48 4.16 4.60 2 0.57 14 5 SG 0.39 0.38 0.37 0.41 0.52 0.51 0.57 0.63 0.58 0.58 14 2 5 TL 2.09 2.48 3.56 3.92 4.12 4.61 4.57 4.73 4.42 4.93 5.13 з 14 SG 0.47 0.38 0.38 0.47 0.49 0.55 0.56 0.54 0.58 0.57 1 14 з ΤL 1.20 2.14 2.00 3.21 3.22 1 3.42 3.46 4.05 4.20 3.43 14 з 2 SG 0.33 0.38 0.33 0.36 0.45 0.53 0.45 0.52 0.60 0.55 . 14 З 2 ΤL 1.71 1.77 2.68 2.09 2.74 3.01 3.79 3.35 3.66 3.04 14 з SG 0.34 0.35 0.37 0.35 0.39 0.58 0.68 з 0.49 0.59 0.53 0.67 14 з з ΤL 1.99 2.49 2.60 2.41 3.38 3.48 3.56 4.15 3.82 4.31 4.13 14 З 4 SG 0.31 0.35 0.36 0.38 0.50 0.52 0.48 0.55 0.56 0.62 . 14 з 2.12 2.13 2.88 3.11 3.72 4.30 4 ΤL 4.04 4.22 3.76 4.28 . 14 з 5 SG 0.36 0.36 0.38 0.48 0.48 0.56 0.56 0.73 0.66 0.65 14 З 5 ΤL 1.72 2.25 3.16 3.54 3.58 4.36 3.84 3.97 4.11 4.15 14 4 SG 0.37 0.38 0.35 0.37 0.47 0.58 0.43 0.53 0.60 0.58 0.51 1 4 14 1 TL 1.92 2.28 2.90 3.09 3.25 4.09 4.01 4.06 3.71 3.99 4.28 14 4 2 SG 0.36 0.40 0.39 0.38 0.50 0.57 0.50 0.58 0.65 0.51 0.58 4 14 2 TL 2.46 2.62 3.09 3.29 3.41 3.73 3.93 3.88 4.14 4.67 4.76 14 4 3 SG 0.40 0.36 0.38 0.48 0.60 0.49 0.55 0.60 0.52 0.60 0.60 14 4 2.11 2.78 3.22 3.75 3.90 з TL 3.89 4.34 4.28 4.21 4.29 4.48 14 4 4 SG 0.35 0.35 0.35 0.50 0.50 0.50 0.57 0.51 0.49 0.48 . 14 4 4 ΤL 2.60 3.20 3.42 3.86 4.09 3.93 3.95 4.77 4.92 4.54 14 4 5 0.40 0.40 0.48 0.52 0.50 0.55 0.60 0.53 0.72 SG 0.65 . 14 4 5 ΤL 3.12 3.41 3.41 4.09 3.92 4.52 3.99 4.59 4.82 5.23 5 14 SG 0.34 0.34 0.37 0.40 0.49 0.47 0.55 0.55 0.43 0.55 0.58 1 14 5 TL 2.54 3.76 3.75 4.26 4.37 4.54 4.21 4.63 4 44 1 5.16 5.21 14 5 2 SG 0.37 0.37 0.43 0.53 0.52 0.50 0.58 0.62 0.52 0.60 0.58 14 5 2 2.98 3.65 3.64 4.19 4.46 TL 4.54 4.38 5.24 4.73 4.90 4.95 14 5 з 0.49 0.49 0.43 0.44 0.52 0.51 0.59 0.63 0.69 SG 0.49 . 1.02 1.74 2.85 3.55 3.93 14 5 з TL 4.12 4.06 4.17 4.53 4.74 14 5 4 SG 0.37 0.37 0.41 0.51 0.48 0.48 0.58 0.63 0.53 0.59 0.59 14 5 4 ΤL 2.54 2.81 2.87 3.46 4.63 4.05 4.16 4.35 4.31 4.58 4.85 5 5 0.31 0.40 0.34 0.46 0.52 0.50 0.50 0.65 14 SG 0.57 . . 14 5 5 ΤL 2.57 3.00 3.26 3.32 4.12 4.23 4.30 4.54 5.44 SG 0.37 0.38 0.45 0.56 0.48 0.50 0.56 0.58 0.48 0.55 0.51 15 2 1 15 TL 2.17 2.83 3.27 3.31 4.17 4.70 4.35 4.56 4.60 1 4.60 3.85

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FAM	REP	TREE	CHAR	AGE2	AGE4	AGE6	AGE8	AGE 10	AGE 12	AGE 14	AGE 16	AGE 18	AGE20	AGE22
15 15 15 15 15	2 2 2 2 2 2 2	2 2 3 3 4 4	SG TL SG TL SG TL	1.98 0.33 2.18 0.36	2.47 0.34 2.61 0.35	0.40 2.97 0.39 3.31 0.35 3.18	3.09 0.42 3.28 0.41	3.88 0.48 4.07 0.49	0.50 3.99 0.48 4.19 0.49 3.91	0.57 3.29 0.50 3.94 0.50 3.95	0.60 3.64 0.53 3.92 0.56 4.11	0.56 4.17 0.53 4.89 0.54 4.20	0.54 4.51 0.60 4.12 0.49 3.86	
15 15 15 15 15	2 2 3 3 3	5 5 1 2	SG TL SG TL SG	1.78 0.37 1.86	1.81 0.41 2.31	0.36 2.41 0.37 2.38 0.36	2.93 0.41 2.23	2.91 0.49 2.88	0.52 4.04 0.54 3.76 0.51	0.54 3.59 0.51 3.62 0.54	0.58 4.53 0.56 3.12 0.54	0.60 3.91 0.60 3.82 0.52	0.55 4.53 0.56 3.92 0.52	0.57 4.70 0.46 4.59 0.47
15 15 15	3 3 3 3	2 3 3 4	TL SG TL SG	1.96 0.36 1.97 0.33	2.78 0.33 2.06 0.37	2.61 0.33 3.12 0.43	3.65 0.40 3.08 0.45	3.16 0.49 3.90 0.44	4.10 0.48 3.18 0.52	3.90 0.47 4.13 0.50	4.75 0.52 4.24 0.52	4.57 0.65 4.11 0.49	4.53 0.53 3.82 0.50	4.36 0.58 5.31 0.50
15 15 15 15	3 3 3 4 4	4 5 1 1	TL SG TL SG TL	0.34 2.42 0.36	0.42 2.47 0.31	3.74 0.39 2.69 0:33 3 36	0.55 3.15 0.46	0.59 3.39 0.44	3.91 0.61 3.13 0.43 3.96	4.78 0.61 4.23 0.49 4.18	4.79 0.68 4.24 0.52 4.19	4.26 0.70 3.63 0.43 4.49	5.23 0.57 4.73 0.48 4.51	4.76 0.68 4.19 0.45 4.72
15 15 15	4 4 4	2 2 3 3	SG TL SG TL	0.35 1.86 0.34 2.45	0.32 2.62 0.32 2.76	0.29 2.46 0.34 3.32	0.31 3.23 0.42 3.37	0.46 3.49 0.48 3.96	0.49 3.56 0.39 3.85	0.46 3.46 0.46 4.06	0.51 3.77 0.51 3.26	0.50 4.14 0.49 4.14	0.47 3.92 0.44 4.62	0.49 3.78 0.49 5.39
15 15 15 15 15	44445	4 4 5 5	SG TL SG TL SG	2.55 0.40 2.33	3.06 0.39 3.09	0.37 3.40 0.38 3.27 0.42	3.54 0.38 3.39	3.98 0.53 3.93	0.47 3.69 0.54 4.30 0.50	0.49 4.00 0.51 4.24 0.52	0.55 4.12 0.54 4.13 0.57	O.48 4.26 O.55 4.18 O.48	0.54 4.88 0.46 4.22 0.55	0.48 4.54 0.50
15 15 15 15 15 15 15	ទេទទទទទទ	1 2 2 3 4 4	TL SG TL SG TL SG TL	2.70 0.36 2.66 0.33 2.95 0.35	2.74 0.29 3.16 0.33 3.12 0.35	3.56 0.31 3.37 0.31 4.13 0.32 3.80	3.34 0.44 3.59 0.43 4.12 0.43	3.73 0.43 4.11 0.43 3.66 0.52	3.90 0.40 3.93 0.40 4.59 0.46 5.02	4.44 0.50 4.05 0.49 3.76 0.51 5.11	4.15 0.52 4.41 0.52 4.06 0.52 5.16	4.02 0.45 4.03 0.48 4.53 0.50 5.24	3.17 0.48 4.04 0.50 5.46 0.58 5.52	3.92 0.53 3.78 0.46 5.12 0.55 5.45
15 15	5 5	5 5	SG TL			0.34 3.67			0.48 4.32	0.53 3.97	0.49 4.24	0.42 4.46	0.46 5.08	0.52 4.49

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# VITA

#### Judith Ardyce Loo

## Candidate for the Degree of

Master of Science

## Thesis: INHERITANCE OF WOOD PROPERTIES IN LOBLOLLY PINE (PINUS TAEDA L.)

Major Field: Forestry

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- Education: Graduated from Kensington Rural High School, Kensington, Prince Edward Island, June 1974; received Bachelor of Science in Forestry degree from the University of New Brunswick, New Brunswick, Canada, in May 1979. Completed the requirements for Master of Science degree at Oklahoma State University in December, 1983.

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