SHOOT ELONGATION PATTERNS AND GENETIC CONTROL OF SECOND YEAR HEIGHT GROWTH IN *Pinus taeda* L. USING CLONALLY REPLICATED TRIALS

By

LILIANA MARTA PARISI

A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2006

To Elsa and Ruben, my parents

Javier, my brother

Fabian, my husband

Olga, my mother in-law

and Luisa.

To my friends

Laura, Laura, Natalia, Andrea, Tete, Claru and Doña Isabel

ACKNOWLEDGMENTS

I would like to thank Drs. Timothy Martin, Dudley Huber and Timothy White for serving on my advisory committee, sharing with me their time, knowledge and help during this program. In particular, I want to express my enormous gratitude to Dr. Huber for his guidance, support and encouragement and also for his immense disposition and patience explaining difficult concepts to me over and over again. I especially thank Dr. Martin, for always providing me with valuable help for collecting the large amount of data that this project demanded. Thanks also go to Mr. Greg Powell for his support in several aspects.

This research was done with the financial support of the Cooperative Forest Genetic Research Program (CFGRP) and the Forest Biology Research Cooperative (FBRC), and I really hope the results of this study contribute to the continued success of the cooperatives and the better knowledge of loblolly pine height growth.

I also would like to acknowledge the financial support of the Fulbright-Bunge&Born fellowship for giving me the opportunity to initiate my graduate studies here in the United States and to the CFGRP for additional funding. My thanks also go to INTA (National Institute of Agriculture Technology), my employer, for maintaining my position and salary all this time.

I further acknowledge Blanca Canteros, Sara Caseres and Juan A. López (h.) for their encouragement and support to continue my academic career.

Special thanks are extended to all the people who helped me with the data collection for this project: particularity, Dr. Huber and Mr. Greg Powell for their amazing job at Georgia site; my fellow graduate students: Brian Baltunis, Veronica Emhart, Salvador Gezan, and Alex Medina, who also gave me valuable tips for classes and other academic issues; my friends Bijay Tamang and Jorge Baldessari, who freely and willingly gave me a helping hand not only with the field work but also with classes; and the help of the FBRC field crew.

I want to thank Ms Debra Anderson and my "Fulbright friends" for being such great company on all those special dates that being with family is so important. My special thanks also go to Tirhani Manganyi who cheers my days with her friendship.

Finally, and most important, I thank my parents and brother for their love, help and support; and, last but not at least, I want to thank my husband, Fabian Hergenreder, who brought me joy and encouragement every day during this master's program and for bearing stoically my daily supervision during his amazing job of measuring flush length and number of stem units.

TABLE OF CONTENTS

page

LIST OF TABLES

LIST OF FIGURES

Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

SHOOT ELONGATION PATTERNS AND GENETIC CONTROL OF SECOND YEAR HEIGHT GROWTH IN *Pinus taeda* L. USING CLONALLY REPLICATED TRIALS

By

Liliana Marta Parisi

May 2006

Chair: Timothy A. Martin
Cochair: Dudley A. Huber
Major Department: Forest Resources and Conservation.

Height growth is one of the most commonly measured phenotypic traits for assessing volume production in tree improvement programs. This study focused on the genetic architecture of the phenological (initiation, cessation, duration and growth rate) and morphological (number of flushes, flush length, number of stem units (*NSU*), mean stem unit length (*MSUL*)) aspects of the second-year annual height growth, using approximately 900 clones and 61 seedling families of loblolly pine from 61 full-sib families and 3 provenances.

Rooted cuttings differed from seedlings for all phenological and morphological traits that were analyzed in this study. This difference was due to propagation effects since types were compared for common families.

The overall results of this study indicated that the average growth rate per day was the most important variable in determining second-year annual height increment. The

contribution of growing season duration to second year annual height increment was negligible. Both analogies were used to assign relative importance to the components of height growth. The narrow and broad-sense heritability estimates for the different dates for height growth increment during the growing season were moderate and decreased from initiation date to cessation date.

For the total population average flush length was the principal contributor to total annual height while number of flushes was a minor contributor.

NSU was by far the most important trait for the length of the first three flushes. For later flushes *NSU* and *MSUL* contributed equally to flush length. The genetic contribution of *MSUL* to flush length was relatively larger than the phenotypic contribution, becoming more important than *NSU* after flush 3, especially for seedlings.

Provenances demonstrated different shoot elongation patterns. *FL* provenance had higher growth at the beginning of the growing season while *ACC* and *LG* growth was slightly higher than *FL* seed source after the second flush. Length of the early flushes appeared to confer a significant advantage for *FL* cutting over the other seed sources. Florida-source loblolly pine also had a longer growing season and more flushes than the other provenances.

With an understanding of the relationship among the loblolly pine shoot growth components, their genetic parameters and their physiology, we can obtain the structural and functional clues about differences among propagule types, seed sources, family and clones for annual height growth performance.

CHAPTER 1
INTRODUCTION

Pinus taeda L. (loblolly pine) is the most important commercial tree species planted in the southern United States occupying approximately 12 million hectares (Jokela and Long 2000). The material planted over the last 50 years has been developed from bulk orchards, open-pollinated orchards, full-sib families and more recently clones. In the southern United States, state agencies and forest companies carry out tree improvement programs and some of them are initiating their third generation of breeding. The overall gains in volume per unit area range from 10 to 30 percent over unimproved material; depending the deployment strategies used; but, if just the best full-sib and clones are planted, gains of 35 to 50 percent are possible (McKeand *et al*. 2003).

Height growth is one of the most commonly measured phenotypic traits for assessing volume production in tree improvement programs (Kremer and Lascoux 1988) and also seems to be the most dependable and simplest trait for early selection in loblolly pine in the southeastern United States (Bridgwater and McKeand 1997). Annual apical growth in conifers is a compound trait and can be divided into multiplicative and additive components (Cannell 1978 and Ford 1980). Those components can be grouped into phenological and morphogenical aspects. Knowledge of pine shoot growth components is essential for understanding height growth.

Annual apical growth (annual height increment *AHI*) can be considered as the product of shoot growth duration (*D*) and the average shoot growth rate (*ASGR*). For estimation of *D* and *ASGR*, in addition to height growth, the phenological traits, timing of

initiation and cessation, have to be determined. Higher growth rate was responsible for the superior height growth of two interprovenance jack pine (*Pinus banksiana*) families (Magnussen and Yeatman 1989). Perry *et al.* (1966), determined for loblolly pine that growth rate accounted for about 60 percent of the height growth variation. Bollmann and Sweet (1977) suggested that one of the reasons for the high growth rate of *Pinus radiata* is its extensive growing season. For loblolly pine Jayawickrama *et al.*(1998), implied that large gains in growth rate can be obtained from north Florida material because of their genetically longer growing season. Dougherty *et al.* (1994) reported an almost 6 week difference in bud break timing in *P. taeda* from two localities which differ by 6° latitude (Gulf Coast 30.5° and North Carolina-Virginia border 36.5°N). Loblolly pine has a broad natural range (14 States in USA, Burns and Honkala 1990) which promotes the occurrence of diverse ecotypes.

Loblolly pine has a complex shoot morphogenesis, with the annual height increment including many flushes or cycles (Boyer 1970; Griffing and Elam 1971; Bridgwater *et al.* 1985; Bridgwater 1990; Harrington 1991). There are commonly 3 to 6 cycles, and two types of growth, predetermined and free (Lanner 1976). Height growth initiation is primarily related to temperature (Boyer 1970; Ford 1980) and it has been not determined if the overwintering bud goes through a true dormancy or only a chilling period is needed to burst (Carlson 1985). Apical height growth starts during the spring with the elongation of the stem units present in the overwintering bud and this constitutes the first flush. This is predetermined growth because all the stem units that constitute the first flush were formed during the previous growing season. Commonly the overwintering bud contains only one flush, but one or two cycles from the preformed bud

were noted by Greenwood (1980). Subsequent flushes are called free, summer or indeterminate growth. The main characteristic of this type of growth is that both the bud and the elongation of its components occur in the same growing season, generally during the summer. The number of free cycles varies from 1 to 7 (Lanner 1976). Griffing and Elam (1971) studied the height growth patterns of loblolly pine saplings and pointed out overlapping flush elongations. Usually two consecutive cycles elongate concomitantly. At the time that a succeeding flush is at its maximum elongation rate the growth rate of the previous flush decelerates. This repeated pattern occurs until the winter bud is formed, which takes place when a succeeding bud does not elongate even when the preceding flush is fully elongated. Several studies of shoot growth have assessed the relative contributions of predetermined and free growth (Pollard and Longan 1974; Cannell and Johnstone 1978; Bailey and Feret 1982). Zhang *et al*. (1997), in loblolly pine under nitrogen fertilization, found that on average the first flush contributed about 69% of the total leaf area. Measuring annual shoot growth Isik *et al.* (2002) concluded that summer shoot growth can serve as an explanatory variable to predict height growth in *Pinus brutia* populations. Thus, annual shoot length is the result of the summation of predetermined and indeterminate flushes. The number of flushes also has an influence on height growth. Under different levels of vegetation control and site preparation in 3-year-old loblolly pine, the individuals with superior height growth had a larger numbers of flushes and a greater length per flush (Allen and Wentworth 1993).

The length of each flush is the product of the number of stem units (*NSU*) and the mean stem unit length (*MSUL*). The partitioning of the shoot growth into its components allows a better understanding of the genetic variation in height growth through

phenological, morphological and physiological characteristics associated with shoot growth (Rehfeldt and Lester 1966; Magnussen and Yeatman 1989; Rweyongeza *et al.* 2003). Theoretically *NSU* and *MSUL* are inherited independently because the meristems for stem unit initiation and for stem unit elongation are physically different and are activated at different times by independent mechanisms (Cannell *et al.* 1976; Cannell 1978). The division of conifer shoot growth into its factors has been performed by several authors, providing a method for assessing genetic, phenotypic and environmental variation but with very diverse results. *NSU* has been shown to be more important contributor to shoot length in loblolly pine, *P. rigida* and their hybrids (Bailey and Feret 1982), in *P. pinaster* (Kremer and Lascoux 1988), in *Abies cephalonica* (Fady 1990), in *P. elliottii* under two nitrogen treatments (Smith *et al.* 1993b) and *P. palustris* (Allen and Scarbrough 1970). For Kremer and Xu (1989), *MSUL* was the component with the highest stability and also a better predictor of total height in *P. pinaster*. Kaya (1993) working with Douglas-fir obtained moderate correlations among *NSU, MSUL*, and height increment. In *P. patula*, Gómez-Cárdenas *et al.* (1998) found that both *MSUL* and *NSU* where influential components in shoot height with a low negative correlation between them. Negative correlation between *NSU* and *MSUL* was reported by several authors (Kremer and Larson 1983; Bongarten 1986; Kremer and Lascoux 1988; Magnussen and Yeatman 1989) who suggested that *NSU* and *MSUL* are not good selection criteria. Some studies show variation between provenances and families within provenances for *NSU* and MSUL. Kremer and Larson (1983) reported that *NSU* was a better predictor of annual height increment on a provenance level, whereas *MSUL* was a slightly better predictor on a family-within provenance level. Within provenances of Douglas-fir

(*Pseudotsuga menziesii*) and blue spruce (*Picea pungens*) the phenotypic variation in shoot length assigned equally to *MSUL* and *NSU*. In blue spruce the genetic variation was mostly due to *MSUL* and the environmental variation was caused primarily by *NSU* (Bongarten 1986). Rweyongeza *et al.* (2003) working with white spruce found that *MSUL* would give more expected gain from direct selection at 11 years than *NSU* for both of the sites in which they were working. Their path coefficient analysis indicated that branch length was primarily determined by *NSU*.

Assessing height growth variation for *NSU* and *MSUL* several studies have promoted differential genetic expression of juvenile traits for predicting field performance by creating different environments such as irrigation and/or fertilization with promising results in slash pine (DeWald *et al*. 1992; Smith *et al*. 1993b; Surles 1993) in loblolly pine (Li *et al*. 1992; Williams 1988; Waxler and van Buijtenen 1981).

Traits of shoot growth patterns (*NSU*, *MSUL*, annual height increment (*AHI*), number of cycles) have been evaluated as early selection criteria on genotypic and phenotypic age-age correlations with varying results (Williams 1987; Williams 1988; Bridgwater 1990; Li *et al*. 1991; Li *et al*. 1992; Smith *et al*. 1993a; Lu *et al*. 2003). In one study, second-year total annual height increment was found to be better correlated to 8-year height performance than *MSUL* or *NSU* in loblolly pine (Bridgwater 1990) while summer *NSU* and *AHI* of treatments with supplementary irrigation and fertilization had equal or better correlation with 8-year height (Li *et al*. 1992).

One of the advantages of working with clonal tests derived from full-sib families is the chance to estimate additive and non-additive genetic components of variance associated with a specific trait (Isik *et al*. 2003). Isik *et al*. (2003) working with a

clonally replicated trial of loblolly pine determined that additive variance was the major source of genetic variance in height growth. Dominance variance for height, diameter and volume was insignificant during the first year, but was important at age 6. Epistatic variance was not important for growth traits. Similar results for additive and dominance variance were obtained by Paul *et al* (1997) for height. The importance of dominance at age 5 indicates the likelihood of additional genetic gains through clonal testing (Carson 1986; Paul *et al* 1997). Isik *et al* (2003) arrived at a similar conclusion and suggested that clonally replicated progeny tests may provide special advantages for loblolly pine tree improvement programs. In clonal tests the efficiency of testing is increased by averaging the microenviromental variance and a more precise estimation of genetic parameters can be obtained.

This study examined loblolly pine shoot growth patterns in clones in two different environments, and provided the opportunity to examine the genetic mechanisms controlling tree growth strategies, and to examine the adaptability of Florida material to cooler environments. The present study contains large numbers of clones (around 900) from full-sib families derived from a partial diallel mating design. The objectives were to: (i) Determine whether propagule types, seed sources, families or clones differ in the timing of growth initiation or cessation; (ii) Estimate genetic parameters, genetic architecture, propagule type and seed source effects for phenological and morphological traits; (iii) Determine the relative contributions of the number of flushes to total height growth; and (iv) Determine the relative contributions of the different components of the flush to flush length.

CHAPTER 2
MATERIALS AND METHODS

Study Area Characteristic

Two loblolly pine sites of the Forest Biology Research Cooperative (FBRC) CCLONES (Comparing Clonal Lines On Experimental Sites) study were measured during their second growing season. The intensive silvicultural treatment portion of those tests was chosen for this study. Site 1 was on Plum Creek land in Putnam County, Florida (approximate latitude 29° 38' 24" N, longitude 81° 49' 27" W; elevation: 7m.) and Site 2 was on MeadWestvaco land in Randolph County, Georgia (approximate latitude 31° 47' 59" N, longitude 84° 41' 32" W; elevation: 137m).

The soils at Site 1 belong to Pomona fine sand soil series with slopes from 0 to 2 percent. Their taxonomic classification is sandy, siliceous, hyperthermic Ultic Alaquods. These soils are very deep and have a surface layer of black fine sand of about 18 cm. The subsurface layer is gray and light-gray fine sand with a depth of about 50 cm. The upper part of the subsoil is dark reddish brown loamy fine sand of a depth of 70 cm. Below that layer is dark brown and light brownish gray fine sand at an approximate depth of 105 cm. At around 180 cm the lower layer is gray and light gray fine sandy loam. The substratum as deep as 200 cm is greenish gray fine sandy loam. The water table under natural conditions is within 15 to 45 cm of the surface for one to three months and is at a depth of 25 to 100 cm for six months or more during most years. The natural fertility of these soils is low (Readle 1990). The average annual precipitation for the test area is around

1250 mm. The average high and low temperatures in summer are 33.4°C and 24.2°C, respectively. The average high and low temperatures in winter are 16.3°C and 6.6°C.

Soils at Site 2, Randolph County, GA, are classified as the Red Bay soils series. The Red Bay series consists of very deep, well drained, moderately permeable soils that formed in thick beds of unconsolidated, loamy marine sediments on uplands of the Coastal Plain. Slopes range from 0 to 15 percent. The taxonomic classification is fine-loamy, kaolinitc, thermic Rhodic Kandiudults. The typical sequence of horizons of this series is a dark reddish-brown sandy loam Ap horizon of about 15 cm, from approximately 15 to 120 cm this soils has a series of Bt horizons (Bt1, Bt2 and Bt3) dark red sandy loam to sandy clay loam (Monroe 2005). The average annual precipitation for the test area is around 1340 mm. The average high and low temperatures in summer are 33.5°C and 18.8°C, respectively. The average high and low temperatures in winter are 10.6°C and 3.5°C.

Plant Material and Experimental Design

The study population consisted of 61 genetically-improved full-sib loblolly pine families. The families were generated from 30 selected parents from the Atlantic Coastal Plain of South Carolina and Georgia, the flatwoods of Florida and the Gulf Coastal Plain of Mississippi and Alabama. Two slow-growing parents were included as connectors with other studies (FBRC 2000). The 32 parents were mated in a partial diallel design creating 70 full-sib families but just 61 full-sib families where in this two test. The material was propagated at the International Paper Company greenhouse in Jay, Florida (Baltunis *et al*. 2005).

The experimental design is an Alpha lattice with 4 complete replications per treatment. Each replication had 1,120 and 1,100 trees at Site 1 and 2, respectively. Weed

control, pesticides and the addition of macro and micro nutrients constitute the intensive silvicultural treatment. The tests were planted in 2002 with a chemical site preparation prior to planting. At Site 1 the chemical site preparation was done with a combination of triclopyr, glyphosate and imazapyr. Vegetation competition was controlled with directed spray application of glyphosate during the first and second growing season. In May 2003 the test received a broadcast application of 280 kg ha^{-1} of diammonium phosphate. During April 2004 560 kg ha^{-1} of 10-10-10 and micronutrients were applied and in June 2004 the test received 4.17 kg ha^{-1} of copper supplement. At Site 2, before the bed preparation the area was broadcast sprayed with glyphosate. During the first year the site was sprayed with sulfometuron methyl and later released with glyphosate applied with backpack sprayers. The fertilizer application was applied before bedding preparation and consisted of 11.2 kg ha^{-1} micronutrients blend and 902 kg ha^{-1} of 15-07-13.

The total number of clones tested was 941 in Site 1 and 868 in Site 2 (FBRC 2003). This allowed us to compare the genetic performance of 30 elite parents, 61 full-sib families, and about 900 clones within the full-sib families.

Traits Measured

Initiation and Cessation

Height growth increment was assessed to estimate timing of initiation and cessation using repeated measurements during the 2004 growing season. Before the trees of Site 1 started their second growing season all the trees were marked on their east side with an orange paint as near to the top as possible. The distance from the orange paint mark to the top was measured and used as a reference. Consecutive measurements were taken every fifteen to twenty days during the spring and fall for growth initiation and cessation and every thirty to forty days during the summer for monitoring height increment. The

first and the last measurement were performed on day of year 44 and 323, respectively. Four replications of each test (4440 trees) were measured. While the top of the trees could be reached easily, measurements were accomplished using a tape graduated in cm (Lufkin® Executive thinline 2m W606PM). After May 2004 a T-form graduated pole was used. The T form was used to place the tip of the tree under one of the T's arms with the objective of having more accurate measurement knowing that the pole was exactly at the top of tree. Height increment was measured to the nearest 0.1 cm. During 2004 the State of Florida was hit by three major hurricanes. None of them hit the study sites directly but their proximity affected Site 1, especially with flooding and wind damage. Trees which were leaning greater than 20-25 degrees from the vertical were not included in the determination of cessation. The final number of trees measured at Site 1 was 4,038. From late August to early December 2004 (day of year 243 to 348) measurements for determining timing of growth cessation were done at Site 2, initially on 3,252 trees. With the help of a trailer pulled by an All Terrain Vehicle (ATV) the top of the trees were reached and the painted reference measurement was placed 20 cm from the tip. Site 2 was relatively unaffected by the hurricanes but many trees suffered from tip die-back which reduced the cessation data. The final number of trees measured at Site 2 was 3,049.

Percent of cumulative height was calculated to observe the proportional distribution of the height growth over the growing season using total second year increment and periodic summer measurements (Allen and Wentworth 1993). The cumulative height increment was plotted by day of year and the dates of height growth initiation and cessation were estimated by interpolation to determine the dates of which 5% and 95% of

the total annual height were reached (Mirov *et al*. 1952; Hanover *et al*. 1963; Cannell and Willett 1976; Jayawickrama *et al*. 1998). At Site 1 the second growing season duration (*D*) was determined by subtracting the initiation date from the cessation date and the average rate of shoot growth (*ASGR*) (cm day^{-1}) was calculated dividing 90% of the *AHI* by *D*.

Flush Descriptors

Traits involving flush length (*FLn*), number of flushes (*NF*) and number of stem units (*NSU*) were measured, in 2005 once the shoots were fully elongated. When those traits were measured mean stem unit length (*MSUL*) and annual height increment (AHI_{FLn}) were calculated. AHI_{FLn} was computed as the sum of the flush lengths of the annual shoot. This height increment was slightly different from *AHI* described above. The number of trees evaluated was 2,132 at Site 1 and 2,101 at Site 2. Flush length and number of stem units were measured for each flush of the main leader. A 2.4 m ladder was used to reach and measure the flush length and count the number of stem units. Each flush whether predetermined or free growth is characterized by a whorl of branches at the bottom followed by a sterile bract zone, the fertile bract zone (needle-fascicles) and another whorl of branches (or branches buds) at the top. Thus, flush length was measured from the whorl of branches at the bottom to the other whorl of branches at the top with a graduated pole to the nearest 0.1 cm. Annual height increment was obtained by adding the flush length of each cycle for each tree. Also the proportion of AHI_{FLn} attributable to each flush (*PFLn*) was calculated by dividing the length of each flush by the AHI_{FLn} and multiplying the result by 100.

The term “stem unit” was introduce by Doak in 1935 and has been used by several authors with different meanings since then (Critchfield 1985). Stem unit in this study is

as defined by Doak (1935): A pine stem unit is comprised of four components 1) a node, 2) the internode below it, 3) a lateral appendage at the node (usually a needle fascicle), and 4) structures in the axial of the lateral appendage. The first three components are always present. *NSU* are the number of needles and sterile bracts which are in a spiral disposition along the flush or stem. One of the nondestructive ways to assess the number of stem units is through the leaf arrangement (needle-fascicles and sterile bracts) on the tree stem (phyllotaxis). *Pinus* species present phyllotactic parastichies (spiral or helix). These can be illustrate as imaginary lines that join adjacent stem units (Doak 1935; Kremer and Roussel 1982; Kremer *et al*. 1989, Fredeen *et al*. 2002) (Figure 2-1). Those helical arrangements on each pine flush can be followed in either clockwise (left) or counterclockwise (right) direction (Zagörska-Marek 1985; Fredeen *et al*. 2002) and are also known as opposed parastichy pairs (Figure 2-1). The number of stem units was determined by counting the stem units on one of the ascending parastichy (*n*) and multiplying that number by the number of parastichies on each flush (*np*) (Allen and Scarbrough 1970; Fady 1990 and Bridgwater 2004, personal communication) (Figure 2-1, Equation [2-1]).

$$NSU = n * np \qquad [2\text{-}1]$$

where NSU are the number of stem units *n* are the number of stem units on a single parastichy and *np* are the number of parallel parastichies

A permanent marker was used to follow the spirals from the bottom to the top of the flush. To avoid systematic errors the same person evaluated the number of the stem units at both sites.

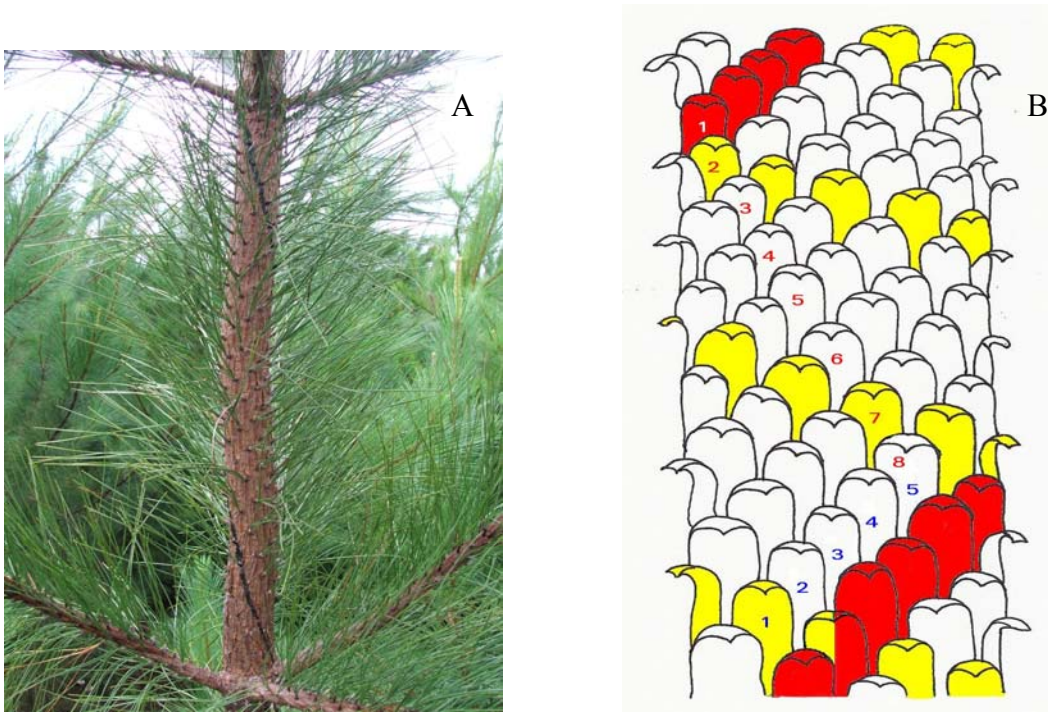

Figure 2-1. Loblolly pine parastichy arrangement. A) The line marked in black shows a clockwise parastichy. B) The lines in color show two opposing parastichies: the clockwise in yellow and the counterclockwise in red. The numbers illustrate a way to obtain the number of parastichies on each flush. For example: counting the stem units in a clockwise manner (yellow) the number of parastichies on that flush is five. Counting in the counterclockwise direction the number of parastichies is eight, so for this flush the number of opposing parastichies is 5:8. (Drawing adapted from Kremer and Roussel 1982).

Mean stem unit length (MSUL) was obtained by dividing the flush length (mm) by number of stem units (NSU) (Equation 2-2).

$$MSUL = \frac{Flush\,length(mm)}{NSU} \qquad [2\text{-}2]$$

Even though determining helical phyllotactic patterns (*PPs*) was not one of the objectives of this study, the way that NSU were measured provided a pattern of arrangement in terms of recognizable contact parastichies. Different helical phyllotaxis series can be typified by the number of opposing parastichies and the value of the divergence angle (angle between successive fascicles on the stem). The helical

phyllotactic series classification adopted in this study was the one proposed by Zagörska-Marek (1985) (Table 2-1), who followed the earlier proposal of Richards (1951) and differs little from Jean (1988). *PPs* were analyzed as an additional trait.

Table 2-1. Phyllostatic series identification.

Phyllotactic patterns	*Divergence angle (°)*	*Sequence of opposed parastichy numbers*
Monojugate pattern		
Fibonacci (principal)	≈ 137.5	2:3:5:8 …
First accessory	≈ 99.5	3:4:7:11 …
Second accessory	≈ 77.9	4:5:9:14 …
Third accessory	≈ 64.08	5:6:11:17 …
.	.	
.	.	
Seventh accessory	≈ 132.2	3:8:11:19 ...
Multijugate patterns		
Bijugy	≈ 137.5/2	2:4:6:10 …
Trijugy	≈ 137.5/3	3:6:9:15 …

Adapted from Zagörska-Marek (1985)

Statistical Analyses and Genetic Parameters

Phenological Traits

The phenological and growth variables were analyzed in ASREML (Gilmour *et al.* 2002). Analyses were first run for each propagule type and site separately. A parental model was used to estimate the genetic variances components. Equations 2-3 and 2-4 show the linear models for cuttings and seedlings respectively.

$$Y_{ijklm} = \mu + R_i + incblk_{j(i)} + gca_k + gca_l + sca_{kl} + clone_{m(kl)} + rgca_{ik} + rgca_{il} + rsca_{ikl} + \varepsilon_{ijklm} \quad [2\text{-}3]$$

Y_{ijklmn} is the measured trait of the m^{th} clone within the kl^{th} full-sib family in the j^{th} incomplete block within the i^{th} replication.
μ is an overall mean
R_i is the fixed effect of replication, i = 1,2,3,4
$incblk_{j(i)}$ is random incomplete block ~ (0, Diag $\hat{\sigma}^2_{incblk(i)}$)
gca_k and gca_l are the random female (k) and male (l) general combining ability respectively ~ N (0, A $\hat{\sigma}^2_{GCA}$) where A is the numerator relationship matrix
sca_{kl} is the random specific combining ability ~ NID (0, $\hat{\sigma}^2_{SCA}$)

$clone_{m(kl)}$ is the random clone within full-sib family ~ NID (0, $\hat{\sigma}^2_{CLONE}$)
$rgca_{ik}$ and $rgca_{il}$ are the random replication by female and male general combining ability and replication respectively ~ N [0, Diag (A $\hat{\sigma}^2_{REPxGCA}$)]
$rsca_{ikl}$ is the random replication by SCA interaction ~ NID (0, $\hat{\sigma}^2_{REPxSCA}$)
ε_{ijklm} is the random error term ~ NID (0, $\hat{\sigma}^2_{ERROR}$)

$$Y_{ijklm} = \mu + R_i + incblk_{j(i)} + gca_k + gca_l + sca_{kl} + rfam_{ikl} + \varepsilon_{ijklm} \quad [2\text{-}4]$$

Y_{ijklm} is the measured trait of the m^{th} seedling within the kl^{th} full-sib family in the j^{th} incomplete block within the i^{th} replication.
μ is the seedling population mean
R_i is the fixed effect of replication, i = 1,2,3,4
$incblk_{j(i)}$ is the random incomplete block ~ (0, Diag $\hat{\sigma}^2_{incblk(i)}$)
gca_k and gca_l are the random female (k) and male (l) general combining ability respectively ~ N (0, A $\hat{\sigma}^2_{GCA}$)
sca_{kl} is the random specific combining ability ~ NID (0, $\hat{\sigma}^2_{SCA}$)
$rfam_{ikl}$ is the random replication by full-sib family ~ NID (0, $\hat{\sigma}^2_{REPxFAM}$)
ε_{ijklm} is the random error term ~ NID (0, $\hat{\sigma}^2_{ERROR}$)

The estimates of additive ($\hat{V}_A$) and total genetic variance for clonal ($\hat{V}_{G_C}$) and seedling ($\hat{V}_{G_S}$) population were calculated by the Equations 2-5, 2-6 and 2-7 respectively.

$$\hat{V}_A = 4\hat{\sigma}^2_{GCA} \quad [2\text{-}5]$$

$$\hat{V}_{G_C} = 2\hat{\sigma}^2_{GCA} + \hat{\sigma}^2_{SCA} + \hat{\sigma}^2_{CLONE} \quad [2\text{-}6]$$

$$\hat{V}_{G_S} = 4\hat{\sigma}^2_{GCA} + 4\hat{\sigma}^2_{SCA} \quad [2\text{-}7]$$

Equations 2-8 and 2-9 were used to compute the estimates of the phenotypic variance for clonal ($\hat{V}_{P_C}$) and seedling ($\hat{V}_{P_S}$) population.

$$\hat{V}_{P_C} = 2\hat{\sigma}^2_{GCA} + \hat{\sigma}^2_{SCA} + \hat{\sigma}^2_{CLONE} + 2\hat{\sigma}^2_{REPxGCA} + \hat{\sigma}^2_{REPxSCA} + \hat{\sigma}^2_{ERROR} \quad [2\text{-}8]$$

$$\hat{V}_{P_S} = 2\hat{\sigma}^2_{GCA} + \hat{\sigma}^2_{SCA} + \hat{\sigma}^2_{REPxFAM} + \hat{\sigma}^2_{ERROR} \quad [2\text{-}9]$$

Individual tree-narrow-sense heritability (h^2) and broad-sense heritability (H^2) were calculate using the estimated variance components for the phenological and growth traits for each propagule type. Equations 2-10 and 2-11 were used for assessing clonal heritabilities.

$$h^2 = \frac{\hat{V}_A}{\hat{V}_{P_C}} \qquad [2\text{-}10]$$

$$H^2 = \frac{\hat{V}_{G_C}}{\hat{V}_{P_C}} \qquad [2\text{-}11]$$

Equation 2-12 and 2-13 were used for obtaining seedling heritabilities.

$$h^2 = \frac{\hat{V}_A}{\hat{V}_{P_S}} \qquad [2\text{-}12]$$

$$H^2 = \frac{\hat{V}_{G_S}}{\hat{V}_{P_S}} \qquad [2\text{-}13]$$

Standard errors for narrow and broad-sense heritabilities were estimated using ASREML as a Taylor series approximation for the variance of a ratio (Gilmour 2002).

Atlantic Coastal Plain (*ACC*), Florida (*FL*), and Lower Gulf (*LG*) were the loblolly pine provenances present in this study. The analysis of provenance effect was performed using ASREML (Gilmour 2002). The mean of the population was partitioned into the provenance effect since provenances effects were included as fixed variable in models [2-3] and [2-4]. Least square means for the phenological and growth traits of each provenance were calculated adding the estimated mean, the provenance effects and the average of the replication values. The effects of the provenance and their standard errors were also computed using ASREML (Gilmour 2002).

Genetic correlations among phenological traits and growth rate were calculated for each propagule type and genetic component using Equation 2-14 (Falconer and Mackay 1996):

$$r_{xy} = \frac{\mathrm{cov}_{xy}}{\sqrt{\sigma_x^2 \sigma_y^2}} \qquad [2\text{-}14]$$

where cov_{xy} is the genetic component covariance between two traits, and σ_x^2 and σ_y^2 are the product of the genetic component variance for traits x and y, respectively. Standard error for genetic correlations was estimated using ASREML (Gilmour 2002).

Differences between propagule types for shoot length and phenological traits were calculated using ASREML (Gilmour 2002). The propagule types were considered different when their F value was greater than $F_{\alpha\ 0.05\,(2,4)} = 6.94$.

Path coefficient analysis (Wright 1968) was used in order to determine the relative contribution of *D* and *ASGR* to the *AHI*. The method has been fully described (Kremer and Larson 1983; Kremer 1985; Bongarten 1986; Magnussen and Yeatman 1989; Rweyongez *et al*. 2003). The following is a short summary of the method

The data is standardized by dividing each trait by its mean. With the standardization each trait has a mean of 1 and makes it possible for the variances to be compared when the path coefficients are computed (Bongarten 1986; Rweyongeza *et al*. 2003).

Shoot elongation (*AHI*) also can be described as the product of *D* and *ASGR*

$$AHI = (D)(ASRG) \qquad [2\text{-}15]$$

Applying a logarithmic transformation to equation 2-15 the resultant relationship is:

$$\log(AHI) = \log(D) + \log(ASRG) \quad [2\text{-}16]$$

In terms of variances

$$\sigma^2_{AHI} = \sigma^2_D + \sigma^2_{ARSG} + 2\,\mathrm{cov}(D, ASRG) \quad [2\text{-}17]$$

As the correlation of *D* and *ASRG* is: $r_{(D,ASRG)} = \dfrac{\mathrm{cov}(D, ASRG)}{\sigma_D \sigma_{ASRG}}$ replacing cov(*D,ASRG*) by $\sigma_D \sigma_{ASRG} r_{(D,ASRG)}$ then equation 2-18 is obtained

$$\sigma^2_{AHI} = \sigma^2_D + \sigma^2_{ASRG} + 2\sigma_D \sigma_{ASRG}\, r_{(D,ASRG)} \quad [2\text{-}18]$$

Replacing and dividing each term by σ^2_{AHI} in equation [2-17], equation [2-18] is obtained

$$p^2_{AHI} = p^2_D + p^2_{ASRG} + 2p_D\, p_{ASRG}\, r_{(D,ASRG)} \quad [2\text{-}19]$$

where p^2_{AHI} is equal to 1 because it is the path coefficient of $\log(AHI)$ to itself. p_D and p_{ASRG} are the path coefficients for $\log(D)$ and $\log(ARSG)$ respectively to $\log(AHI)$. The relative contribution of *D* to *AHI* can be determined as

$$c_D = p_D\, r_{(AHI,D)} \quad [2\text{-}20]$$

where c_D is the degree of determination of *D* to *AHI* and $r_{(D,ASRG)}$ is the correlation coefficient between *AHI* and *D*. The relative contribution of *ASGR* to *AHI* can be calculated as

$$c_{ASRG} = p_{ASRG}\, r_{(AHI,ASRG)} \quad [2\text{-}21]$$

where c_{ASRG} is the degree of determination of *ASGR* to *AHI* and $r_{(AHI,ASRG)}$ is the correlation coefficient between *AHI* and *ASGR*.

$$c_D + c_{ASRG} = 1 \quad [2\text{-}22]$$

Flush Descriptors

The flush descriptors, *FLn, NSU, MSUL*, number of flushes of each shoot leader (*NF*), *PFLn, AHI_{FLn}* and second-year total height (TH_2) traits were analyzed in ASREML (Gilmour *et al.* 2002). Analyses were run for each propagule type and site separately. A parental model was used to estimate the genetic variances components and the linear model used for cuttings and seedlings were detailed in equations [2-3] and [2-4] respectively. *NSU* and *MSUL* were analyzed for each flush. The numbers of replications measured for shoot components were 2 for Site 1 and 3 for Site 2.

Genetic parameter ($\hat{V}_A, \hat{V}_{G_C}, \hat{V}_{G_S}, \hat{V}_{P_c}, \hat{V}_{P_S}, h^2$, and H^2) were calculated according equations [2-5] to [2-13] respectively. Standard errors for narrow and broad-sense heritabilities were estimated using ASREML (Gilmour 2002).

Provenance differences and genetic correlations were computed to explain phenological traits.

Differences between propagule types were also computed for shoot components and growth traits as for phenological traits using ASREML (Gilmour 2002). The propagule types were considered different when their F value was greater than $F_{\alpha\ 0.05\,(2,2)}=19.0$ for Site 1 and $F_{\alpha\ 0.05\,(2,3)}=9.55$ for Site 2.

Shoot components, *PFLn, AHI_{FLn}* and TH_2 traits were also analyzed across the two sites separately by propagule type. The mixed model is described in equation [2-23] for clones population and equation [2-24] for seedlings respectively. Different residual variances were allowed by site.

$$Y_{ijklmn} = \mu + S_i + R_{ij} + incblk_{k(ij)} + gca_l + gca_m + sca_{lm} + clone_{n(lm)} + sgca_{il} + sgca_{im} + ssca_{ilm} + sclone_{in(lm)} + rgca_{ijl} + rgca_{ijm} + rsca_{ijlm} + \varepsilon_{ijklmn} \quad [2\text{-}23]$$

Y_{ijklmn} is the measured trait of the n^{th} clone within the lm^{th} full-sib family in the k^{th} incomplete block within the j^{th} replication of the i^{th} site.
μ is the clonal population mean
S_i is the fixed effect of site i=1,2
R_{ij} is the fixed effect of replication, i= 1,2 j = 1,2,3,4
$incblk_{k(ij)}$ is the random incomplete block ~ (0, Diag $\hat{\sigma}^2_{incblk(i)}$)
gca_l and gca_m are the random female (l) and male (m) general combining ability respectively ~N (0, A $\hat{\sigma}^2_{GCA}$)
sca_{lm} is the random specific combining ability ~ NID (0, $\hat{\sigma}^2_{SCA}$)
$clone_{n(lm)}$ is the random clone within full-sib family ~ NID (0, $\hat{\sigma}^2_{CLONE}$)
$sgca_{il}$ and $sgca_{im}$ are random site by replication by female and male general combining ability and replication respectively ~ NID (0, $\hat{\sigma}^2_{SITExGCA}$)
$ssca_{ilm}$ is the random site by *SCA* interaction ~ NID (0, $\hat{\sigma}^2_{SCA}$)
$sclone_{n(lm)}$ is the random site by clone within full-sib family interaction ~ NID (0, $\hat{\sigma}^2_{SITExCLONE}$)
$rgca_{ijl}$ and $rgca_{ijm}$ are the random site by replication by female and male general combining ability and replication interaction respectively ~ N (0, A $\hat{\sigma}^2_{GCA}$)
$rsca_{ijlm}$ is the random site by replication by SCA interaction ~ NID (0, $\hat{\sigma}^2_{REPxSCA}$)
ε_{ijklmn} is the random error term ~ [0, Diag ($\hat{\sigma}^2_{ERROR_{(i)}}$)]

$$Yijklmn = \mu + Si + Rij + incblkk(ij) + gcal + gcam + scalm + sgcail + sgcaim + sscailm + rfamijlm + \varepsilon ij_{klmn} \quad [2\text{-}24]$$

Y_{ijklmn} is the measured trait of the n^{th} seedling within the lm^{th} full-sib family in the k^{th} incomplete block within the j^{th} replication and the i^{th} site.
μ is the clonal population mean
T_i is the fixed effect of site i=1,2
R_{ij} is the fixed effect of replication, i= 1,2 j = 1,2,3,4
$incblk_{k(ij)}$ is the random incomplete block ~ (0, Diag $\hat{\sigma}^2_{incblk(i)}$)
gca_l and gca_m are the random female (l) and male (m) general combining ability respectively ~NID (0, $\mathbf{A}\hat{\sigma}^2_{GCA}$)
sca_{lm} is the random specific combining ability ~NID (0, $\hat{\sigma}^2_{SCA}$)
$sgca_{il}$ and $sgca_{im}$ are random site by female and male general combining ability respectively ~ NID (0, $\hat{\sigma}^2_{SITExGCA}$)
$ssca_{ilm}$ is the random site by SCA interaction ~ NID (0, $\hat{\sigma}^2_{SITExSCA}$)
$rfam_{ijlm}$ is the random site by replication by full-sib family interaction ~ NID (0, $\hat{\sigma}^2_{REPxFAM}$)
ε_{ijklmn} is the random error term ~ [0, Diag ($\hat{\sigma}^2_{ERROR_{(i)}}$)]

From the across sites analyses type B correlations for each of the traits were calculated. A type B genetic correlation gives us an indication of how consistently the trait is expressed in two different environments (Yamada 1962). When the correlation is near 1 the trait-by-environment interaction is small and genetic entries rank the same in both environments. When the genetic correlation is low the genetic entries rank differently in the two environments.

The formulae to calculate the type B correlation were the follow:

$$r_{B_{CLONE}} = \frac{2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{CLONE}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{CLONE} + 2\sigma^2_{SITExGCA} + \sigma^2_{SITExSCA} + \sigma^2_{SITExCLONE}} \quad [2\text{-}25]$$

$r_{B_{CLONE}}$ is the type B genetic correlation for clonal value across trials

$$r_{B_{GCA}} = \frac{\sigma^2_{GCA}}{\sigma^2_{GCA} + \sigma^2_{SITExGCA}} \quad [2\text{-}26]$$

$r_{B_{GCA}}$ is the type B genetic correlation for parents across the two sites

$$r_{B_{FAMILY}} = \frac{2\sigma^2_{GCA} + \sigma^2_{SCA}}{2\sigma^2_{GCA} + \sigma^2_{SCA} + 2\sigma^2_{SITExGCA} + \sigma^2_{SITExSCA}} \quad [2\text{-}27]$$

$r_{B_{FAMILY}}$ is the type B genetic correlation for full-sib families across trials

In order to estimated the degree of determination of the *AHI* by the number of flushes (*NF)* and the average flush length (*AvFLn)* as well as the estimate the contribution of the *MSUL* and the *NSU* to each flush length *FLn,* a path coefficient analysis (Wright 1968) was computed for each case (Bongarten 1986; Rweyongeza *et al*. 2003).

The *FLn* of each flush is the result of the product of *NSU* and *MSUL* and *AHI* can be described as the product of *NF* and *AvFLn.* With logarithmic transformation those multiplicative relationships became additive. Following the steps described from

equations [2-16] to [2-19] we obtain for *FLn* and AHI_{FLn} equations [2-28] and [2-29] respectively

$$p_{FLn}^2 = p_{NSU}^2 + p_{MSUL}^2 + 2p_{NSU}p_{MSUL}r_{(MSUL,NSU)} \quad [2\text{-}28]$$

$$p_{AHI_{FLn}}^2 = p_{NF}^2 + p_{AvFLn}^2 + 2p_{NF}p_{AvFLn}r_{(NF,AvFLn)} \quad [2\text{-}29]$$

From [2-28] and [2-29] p_{FLn}^2 and $p_{AHI_{FLn}}^2$ are equal to 1 because they are the path coefficients of $\log(FLn)$ and $\log(AHI_{FLn})$ with themselves. p_{NSU} and p_{MSUL} are the path coefficients for $\log(NSU)$ and $\log(MSUL)$ to $\log(FLn)$ as well as p_{NF} and p_{AvFLn} are the path coefficients for $\log(NF)$ and $\log(AvFLn)$ to $\log(AHI_{FLn})$, respectively. The relative contribution of *NSU* and *MSUL* to *FLn*, and *NF* and *AvFLn* to AHI_{FLn} can be determined with the equation [2-30], [2-31], [2-32] and [2-33] respectively

$$c_{NSU} = p_{NSU}r_{(FLn,NSU)} \quad [2\text{-}30]$$

$$c_{MSUL} = p_{MSUL}r_{(FLn,MSUL)} \quad [2\text{-}31]$$

$$c_{NF} = p_{NF}r_{(AHI_{FLn},NF)} \quad [2\text{-}30]$$

$$c_{AvFLn} = p_{AvFLn}r_{(AHI_{FLn},AvFLn)} \quad [2\text{-}31]$$

where c_{NSU} and c_{MSUL} are the degree of determinations of *NSU* and *MSUL* to *FLn* and c_{NF} and c_{AvFLn} are the degree of determinations of *NF* and *AvFLn* to AHI_{FLn}. $r_{(FLn,NSU)}$, $r_{(FLn,MSUL)}$, $r_{(AHI_{FLn},NF)}$, and $r_{(AHI_{FLn},AvFLn)}$ are the correlation coefficients between *FLn* and *NSU*, *FLn* and *MSUL*, AHI_{FLn} and *NF*, and AHI_{FLn} and *AvFLn*, respectively.

Genetic correlations among shoot components traits were calculated for each propagule type and genetic effect using equation [2-14] (Falconer and Mackay 1996).

Standard error for genetic correlations was estimated using ASREML (Gilmour 2002).

The number of trees involved in each analysis is detailed in Table 2-2.

Table 2-2. Number of trees involved in each of the analyses by site and propagule type.

Flush descriptors by flush number		*Site 1*		*Site 2*	
		Cuttings	*Seedlings*	*Cuttings*	*Seedlings*
FLn					
	1	1730	402	1678	423
	2	1729	402	1674	421
	3	1727	401	1666	416
	4	1702	397	1635	404
	5	1493	329	1471	337
	6	732	132	746	133
	7	134	18	130	21
PFL					
	1	1727	400	1657	419
	2	1727	400	1655	418
	3	1727	400	1651	415
	4	1702	397	1623	404
	5	1493	329	1464	337
	6	732	132	746	133
	7	134	18	129	21
NSU, MSUL Parastichy pattern	1	1730	402	1674	423
	2	1729	402	1670	421
	3	1727	401	1662	416
	4	1702	397	1631	404
	5	1492	329	1469	337
	6	730	131	745	133
	7	134	17	130	21
NF		1727	400	1657	419
AHI_{FLn}		1727	400	1657	419
TH_2		1769	404	1680	426
Phenological traits		3352	731	2432	618

CHAPTER 3
RESULTS AND DISCUSSION

Phenological Traits

Least Square Means for Phenological Traits by Provenance and Propagule Type

Significant differences ($p<0.05$) between propagule types were found for all the phenological and growth traits (Appendix A). For Site 1 the average difference for initiation date for seedling and cutting was 4 days. In contrast to Site 1, Site 2 seedling material had earlier cessation dates than cutting material.

Cuttings provenances were significantly different ($p<0.05$) for initiation, cessation and duration at Site 1 and for cessation at Site 2, but were not significantly different for *ASRG* and *AHI* (Table 3-1). *ACC* provenance height growth initiation started growing latter than *FL* and *LG* which had the same least square mean initiation date. Although *LG* and *FL* started together for both propagule types, *FL* provenance cuttings grew later in the season while *ACC* and *LG* had stopped growing by a similar date. There were no significant differences in cessation date for seedlings among provenances. Although there were significant differences in initiation, cessation and duration for provenance for Site 1, no significant differences were obtained for *AHI*. *FL* was the provenance with the longest growing season and *ACC* had the shortest growing periods for both propagule types. *LG* was the provenance with the smallest *AHI,* because of its lower *ASRG*. *FL* and *ACC* presented similar initiation dates and *ASRG*. In Site 2 again *FL* is the provenance which the latest cessation date. These results are in partial agreement with Jayawickrama *et al*. (1998) on height growth pattern of loblolly pine in Southwest Georgia. They found

significant differences among provenance for height growth cessation but no significant differences for height growth initiation. For Jayawickrama *et al*. (1998) Atlantic Coastal Plain, Lower Gulf and Florida provenance grew until day 241, 233 and 248 in 1993 and 244, 240 and 253 in 1994, respectively. Also their Florida material (Gulf Hammock) had the longest growing season and greatest height. McCrady and Jokela (1996), in South Carolina, reported a mean bud-break Julian Date of 73 to 84 for their different families and planting spacings. Those dates are in accordance with the ones found in this report. Also the average shoot rate growth reported in this study for cuttings was in agreement with McCrady and Jokela (1996) of 0.58-0.65 cm·day^{-1}. The duration of the shoot growth in this study in North Central Florida (Table 3-1) is shorter than the one reported by McCrady and Jokela (1996) (191 versus 201 days).

Table 3-1. Least square means for second-year phenological traits and annual height increments by provenances and propagule type for 2004 growing season in Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

	INITIATION (days)		CESSATION (days)		DURATION (days)		ASRG (cm day^{-1})		AHI (cm)	
	C	S	C	S	C	S	C	S	C	S
Site 1										
LG	79	84	248	263	170	180	0.56	0.67	108.9	121.3
FL	79	83	252*	266	174*	183*	0.65	0.72	128.7	131.2
ACC	84*	87*	247	261	165	175	0.65	0.72	121.0	125.8
Site 2										
LG			269	255						
FL			277*	257*						
ACC			263	248						

Note: LG, FL and ACC are Lower Gulf, Florida and Atlantic Coastal Plain provenances, respectively. C= cuttings; S= seedlings.
Initiation and cessation are days after January 1 to complete 5 and 95% of total AHI.
(*) indicates significant differences between the provenances ($p<0.05$)

Provenances were also significantly different for shoot growth pattern during the growing season. Least square means were calculated for each of the measurement days (Figure 3-1) for average cumulative apical height growth increment and apical height growth increment by propagule type and provenance. Fewer significant points in

seedlings than in cuttings are attributable to lower numbers of seedlings present in the study (Table 2-2).

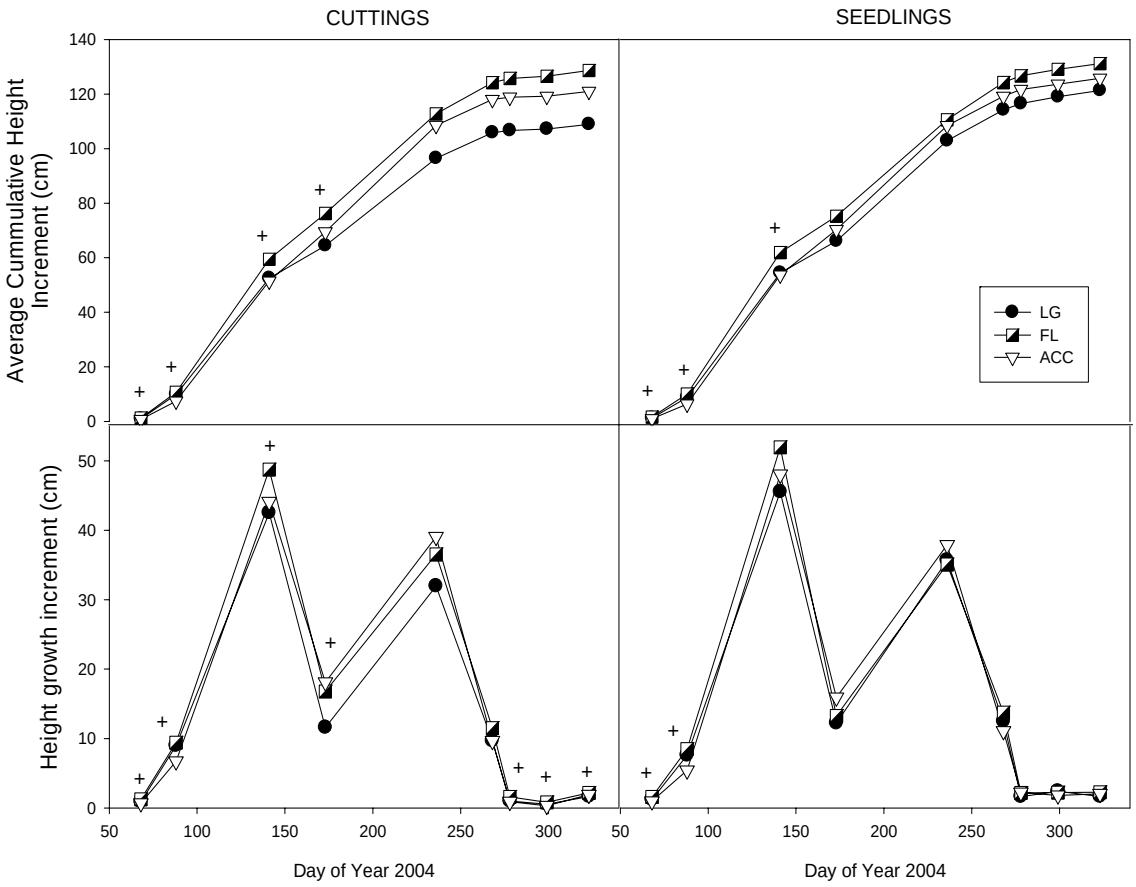

Figure 3-1. Least square means for average cumulative apical height growth increment and apical height growth increment by provenance and propagule type at Site 1 (North Central Florida). (+) indicates significant differences between provenances ($p<0.05$).

Seedlings and cuttings have a similar general growth pattern for height increment with two peaks, one later in the spring and the other in later summer. Even though no significant difference between provenances were found for the second half of the growing season for cumulative height increment, the cutting curve shape shows how cumulative growth increment by provenance becomes distinct whereas for seedlings provenances differences of cumulative height increment at the end of the growing season are subtle.

Peaks of height increment are larger in seedlings than in cuttings. It seems that the differences in height increment occurred in cuttings during the second half of the growing season are responsible for the evident (but not significant) differences in cumulative height increment. Heritabilities values for cumulative height increment and height increment are shown in Table 3-2 and 3-3 by day of measure.

Heritability Estimates

Height Growth Increment

Narrow sense heritability for incremental height growth was always greater for cuttings than for seedlings except for dates 141 and 268 (Table 3-2). Seedling values for broad sense heritability were more inconsistent than cutting values. Cuttings show a declining trend after day 68 except for day 141 which was smaller than expected. Narrow sense heritabilities also decreased during the growing season after day 68 and cutting heritability values were more inconsistent than seedling values. Larger standard errors are associated with seedlings than with cuttings heritabilities. After day 268 narrow and broad sense heritabilities for both cuttings and seedling become constant and almost zero. The decreasing and small values of heritabilities are attributable to growth cessation. There was little or no additive variance for day 68 (h^2 was 0.00 and 0.07 for seedlings and cuttings, respectively) but moderate non-additive variance for both propagule types (H^2 was 0.35 and 0.26 for seedlings and cuttings, respectively) for height increment, cumulative height increment and cumulative percentage height increment. The total genetic variance evaluated in H^2 is primarily due to clonal variation; $2\sigma^2_{GCA}$ is a distant second while the *SCA* variance contribution is almost negligible (Table 3-2).

These contributions are also consistent for cumulative height growth increment (Table 3-3) and average cumulative percent height growth (Table 3-4).

Table 3-2. Incremental height growth: narrow (h^2) and broad-sense (H^2) heritabilities on measurement days during 2004 growing season by propagule type at Site 1 (North Central Florida).

Day	Seedlings		Cuttings				
No.[+]	h^2	H^2	h^2	H^2	*Clone/Vp**	2*GCA/Vp**	*SCA/Vp**
68	0.00 (0.00)	0.35 (0.16)	0.07 (0.03)	0.26 (0.02)	0.218	0.035	0.011
88	0.22 (0.11)	0.26 (0.14)	0.25 (0.08)	0.40 (0.03)	0.259	0.124	0.016
141	0.17 (0.08)	0.17 (0.08)	0.07 (0.03)	0.11 (0.02)	0.074	0.033	0.002
173	0.15 (0.13)	0.41 (0.17)	0.21 (0.06)	0.22 (0.03)	0.109	0.104	0.005
236	0.13 (0.09)	0.13 (0.09)	0.23 (0.06)	0.22 (0.03)	0.103	0.113	0.000
268	0.14 (0.10)	0.20 (0.15)	0.09 (0.04)	0.11 (0.02)	0.058	0.046	0.010
278	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.01 (0.01)	0.000	0.008	0.006
299	0.00 (0.00)	0.12 (0.12)	0.01 (0.01)	0.01 (0.02)	0.000	0.007	0.003
323	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.021	0.000	0.003

[+] Day of the year 2004 when the height increment was recorded.
** *Clone/Vp*, 2*GCA/Vp* and *SCA/Vp*, are the relative contribution of clonal, GCA and SCA variances to broad-sense heritability (H^2). Standard errors are given in parentheses.

Cumulative and Cumulative Percentage Height Growth Increment

Cumulative broad sense heritability values (Table 3-3) were generally smaller for cuttings than for seedlings. The decreasing pattern during the growing season is also present for both narrow and broad-sense heritabilities for all traits except height growth increment. After day 268 (end of the growing season) heritability values became constant. Non-additive variance seems to be larger for seedlings than for cuttings, with larger standard errors associated with seedlings than cuttings

For cumulative percentage of height growth the decreasing pattern in both narrow and broad-sense heritability values started at day 88 and becoming close to zero after day 236.

Table 3-3. Cumulative height growth: narrow (h^2) and broad-sense (H^2) heritabilities on measurement days during 2004 growing season by propagule type at Site 1 (North Central Florida).

Day	Seedlings		Cuttings				
No.+	h^2	H^2	h^2	H^2	*Clone/Vp**	2*GCA/Vp**	*SCA/Vp**
68	0.00 (0.00)	0.35 (0.16)	0.07 (0.03)	0.26 (0.02)	0.218	0.035	0.011
88	0.22 (0.11)	0.31 (014)	0.24 (0.07)	0.41 (0.03)	0.274	0.120	0.018
141	0.18 (0.10)	0.28 (0.14)	0.09 (0.03)	0.14 (0.02)	0.096	0.043	0.000
173	0.22 (0.12)	0.31 (0.15)	0.14 (0.05)	0.17 (0.03)	0.101	0.070	0.002
236	0.14 (0.12)	0.24 (0.16)	0.19 (0.06)	0.19 (0.03)	0.087	0.095	0.004
268	0.21 (0.12)	0.23 (0.15)	0.20 (0.06)	0.20 (0.03)	0.087	0.099	0.008
278	0.19 (0.12)	0.22 (0.15)	0.20 (0.06)	0.19 (0.03)	0.083	0.100	0.009
299	0.17 (0.12)	0.21 (0.15)	0.20 (0.06)	0.19 (0.03)	0.082	0.102	0.010
323	0.11 (0.12)	0.23 (0.16)	0.20 (0.06)	0.20 (0.03)	0.084	0.102	0.009

+ Day of the year 2004 when the height increment was recorded.
* *Clone/Vp*, 2*GCA/Vp* and *SCA/Vp*, are the relative contribution of clonal, GCA and SCA variances to broad-sense heritability (H^2). Standard errors are given in parentheses.

Table 3-4. Cumulative percentage of height growth: narrow (h^2) and broad-sense (H^2) heritabilities on measurement days during the 2004 growing season by propagule type in Site 1 (North Central Florida).

Day No.	Seedlings		Cuttings				
	h^2	H^2	h^2	H^2	*Clone/Vp**	2*GCA/Vp**	*SCA/Vp**
68	0.00 (0.00)	0.35 (0.17)	0.05 (0.02)	0.14 (0.02)	0.115	0.026	0.003
88	0.33 (0.14)	0.43 (0.15)	0.18 (0.06)	0.27 (0.03)	0.148	0.090	0.030
141	0.31 (0.14)	0.47 (0.17)	0.20 (0.06)	0.21 (0.03)	0.105	0.100	0.003
173	0.20 (0.11)	0.24 (0.16)	0.15 (0.05)	0.19 (0,03)	0.117	0.075	0.000
236	0.09 (0.09)	0.17 (0.16)	0.02 (0.02)	0.08 (0.02)	0.046	0.012	0.017
268	0.01 (0.04)	0.01 (0.04)	0.00 (0.00)	0.05 (0.02)	0.036	0.000	0.011
278	0.02 (0.05)	0.02 (0.05)	0.00 (0.00)	0.03 (0.02)	0.025	0.000	0.007
299	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.018	0.000	0.005

+ Day of the year 2004 when the height increment was recorded.
* *Clone/Vp*, 2*GCA/Vp* and *SCA/Vp*, are the relative contribution of clonal, GCA and SCA variance to the broad-sense heritability (H^2). Standard errors are given in parentheses.

Phenological Traits and *AHI*

Little non-additive variance was present for cutting height growth initiation (Table 3-5). Height growth cessation had little genetic variance in cuttings and seedlings at Site 1. In contrast, for Site 2 seedling height growth cessation was highly controlled by non-additive variance (h^2 is 0.02; H^2 is 0.58). More moderate values for narrow and broad-sense heritabilities were present for cutting height growth cessation (h^2 is 0.29; H^2 is

0.39). This study also reports low narrow and broad-sense heritabilities for seedlings and cuttings for growing season duration. Cutting growing season duration seemed to be influenced by non-additive genetic variance. Narrow-sense heritabilities for initiation, cessation and duration obtained in this study are smaller than those reported by Li and Adams (1993) in 15 year-old pole-size Douglas-fir. They estimated strong narrow-sense heritabilities for bud burst and bud set and low to moderate values for growing season duration (h^2 are 0.73, 0.81 and 0.17, respectively). *ASGR* was not influenced by non-additive variance for cuttings. Seedling *ASGR* heritabilities are higher than cuttings heritabilities. Clonal variation was the greatest contributor to the total genetic variance; $2\sigma^2_{GCA}$ made a small contribution while *SCA* variance contribution was almost negligible (Table 3-5).

Table 3-5. Individual narrow (h^2) and broad-sense (H^2) heritabilities for phenological traits and *AHI* by propagule type for the 2004 growing season in Site 1 (North Central Florida) and 2 (Southwest Georgia)

Variable	Seedlings		Cuttings				
	h^2	H^2	h^2	H^2	*Clone/Vp*	2*GCA/Vp*	*SCA/Vp*
Site 1							
Initiation	0.40 (0.13)	0.40 (0.13)	0.29 (0.08)	0.39 (0.03)	0.228	0.143	0.018
Cessation	0.07 (0.07)	0.07 (0.07)	0.00 (0.00)	0.07 (0.02)	0.058	0.000	0.011
AHI	0.11 (0.12)	0.23 (0.16)	0.20 (0.06)	0.20 (0.03)	0.084	0.102	0.009
Duration	0.10 (0.07)	0.10 (0.07)	0.02 (0.02)	0.08 (0.02)	0.060	0.008	0.007
ASGR	0.26 (0.14)	0.33 (0.16)	0.18 (0.06)	0.19 (0.03)	0.090	0.093	0.009
Site 2							
Cessation	0.02 (0.11)	0.58 (0.24)	0.22 (0.07)	0.34 (0.03)	0.216	0.110	0.017

Clone/Vp, 2*GCA/Vp* and *SCA/Vp*, are the relative contribution of clonal, GCA and SCA variances to broad-sense heritability (H^2). Standard errors are given in parentheses.

Correlations Among Phenological Traits.

Genetic correlations were not estimated for those components whose genetic variance was 0.

Initiation-Duration Correlation

Genetic correlations between initiation and duration at Site 1 were significantly strong and negative for both propagule types, which indicated that the material which initiated height growth later tended to have a shorter growing season and the material which had early height growth initiation tended to grow longer (Table 3-6). Phenotypic and microsite initiation-duration correlations were negatively low and significant. Also initiation-duration correlations for seedlings were in general lower than those for cuttings. *GCA* initiation-duration correlation was the strongest negatively and significant correlation.

Cessation-Duration Correlation

Cessation-duration correlations were significant and strongly positive. Phenotypic and environmental cessation-duration correlations were positive and even larger than the genetic correlations. The positive correlation between cessation and duration indicated that the material with the latest cessation date will have the longest growing season.

Phenotypic and environmental correlations between initiation and cessation were significant and low for both cuttings and seedlings. The clonal initiation-cessation correlation was also low. The significant positive correlation between initiation and cessation implies that the material which started growing later also stopped growing later in the season and vice versa.

Initiation-*AHI* and Initiation-Cessation Correlations

For Site 1 the standard errors associated with initiation-*AHI* and cessation-*AHI* genetic correlations were many times larger than the estimates whereas phenotypic and environmental initiation-*AHI* and cessation-*AHI* correlation were positive low and significant. Lower correlation values were estimated for cuttings than for seedlings and

cessation-*AHI* correlation were lower than initiation-*AHI* correlations. Positive correlation for initiation-*AHI* meant that material which initiated later in the growing season had larger height increments. At Site 2, standard errors associated with genetic cessation-*AHI* correlation for seedlings were larger than the estimate also microsite standard errors were larger than the estimated correlations for both propagule types. The phenotypic and environmental correlations were low and positive, clonal and total genetic correlation for cessation-*AHI* at Site 2 were moderate but with high standard errors. Positive correlation for cessation-*AHI* indicates that material which grew longer in the season had the largest *AHI*.

Initiation-*ASRG* Correlations

Phenotypic, environmental and genetic correlations for initiation-*ASRG* were positive, moderate-to-low and significant for cuttings, except for the *SCA* correlations where the standard error which was four times larger than the estimate (Table 3-6). Seedling genetic correlations also had high standard errors whereas the phenotypic correlations were positive, significant and moderate. Seedling microsite initiation-*ASRG* correlation was also moderate, significant and negative. Positive correlations indicate that materials with later initiation dates would have higher growth rate. The negative correlation for microsite initiation-*ASGR* meant that a particular microsite promoting early height growth initiation tended to promote higher growth rate.

Table 3-6. Genetic, phenotypic and environmental (microsite) correlations between phenological traits and annual height increment (*AHI)* by propagule type for 2004 growing season in Site 1 (North Central Florida) and 2 (Southwest Georgia).

Variables		*Cuttings*				*Seedlings*			
		C	*AHI*	*D*	*ASGR*	*C*	*AHI*	*D*	*ASGR*
	Site 1								
I	r_{GCA}	-0.49 (0.50)	0.25 (0.21)	-0.91 (0.08)	0.49 (0.17)	-0.16 (0.33)	0.31 (0.44)	-0.71 (0.18)	0.38 (0.23)
	r_{SCA}	0.66 (0.46)	0.36 (0.73)	***	0.18 (0.82)	***	***	***	***
	r_{Clone}	0.29 (0.11)	0.06 (0.09)	-0.41 (0.10)	0.21 (0.09)	---	---	---	---
	$r_{Genetic}$	0.14 (0.10)	0.16 (0.11)	-0.60 (0.08)	0.35 (0.10)	-0.11 (0.23)	0.19 (0.26)	-0.48 (0.20)	0.38 (0.23)
	$r_{Phenotypic}$	0.11 (0.02)	0.29 (0.03)	-0.29 (0.02)	0.38 (0.03)	0.13 (0.04)	0.89 (0.13)	-0.25 (0.05)	0.42 (0.04)
	$r_{Microsite}$	0.12 (0.02)	0.35 (0.02)	-0.21 (0.02)	0.40 (0.02)	0.18 (0.04)	0.37 (0.04)	-0.23 (0.04)	-0.43 (0.03)
C	r_{GCA}		0.56 (0.31)	0.84 (0.27)	0.26 (0.37)		-0.23 (0.41)	0.81 (0.12)	-0.45 (0.31)
	r_{SCA}		0.32 (0.77)	0.97 (0.22)	0.12 (0.86)		***	***	***
	r_{Clone}		-0.11 (0.17)	0.77 (0.05)	-0.35 (0.14)		---	---	---
	$r_{Genetic}$		0.11 (0.13)	0.73 (0.05)	-0.14 (0.13)		-0.23 (0.41)	0.81 (0.12)	-0.31 (0.23)
	$r_{Phenotypic}$		0.09 (0.02)	0.93 (0.00)	-0.24 (0.02)		0.16 (0.04)	0.92 (0.01)	-0.23 (0.04)
	$r_{Microsite}$		0.08 (0.02)	0.95 (0.00)	-0.26 (0.02)		0.18 (0.05)	0.93 (0.01)	-0.22 (0.04)
	Site 2								
C	r_{GCA}		***				***		
	r_{SCA}		***				0.36 (0.24)		
	r_{Clone}		0.53 (0.24)				---		
	$r_{Genetic}$		0.47 (0.20)				0.36 (0.24)		
	$r_{Phenotypic}$		0.12 (0.05)				0.09 (0.04)		
	$r_{Microsite}$		0.06 (0.04)				0.06 (0.04)		

Note: *I*= Initiation; *C*=Cessation; *D*=Duration; *ASRG*=average shoot growth rate.

***Correlation could not estimated because σ^2_{SCA} was 0.

(---) was not included in the model.

Standard errors are given in parentheses.

Cessation-*ASGR* Correlations

Genetic cessation-*ASGR* correlations were associated with large standard errors for both propagule types. Phenotypic and environmental correlations for both cuttings and seedlings were negative significant and low, which means that the material which stopped growing early tends to have a higher growth rate. Phenological and growth correlation results were in agreement with those reported by Li and Adam (1993) for Douglas-fir. They found positive correlation between bud set and growth. Also they reported negative moderate (-0.30 ± 0.24) and negative low (-0.07 ± 0.28) correlations between bud burst and bud set with duration for their first year of analyses. For their second year of analysis the duration-bud set correlation became a strong correlation (-0.87 ± 0.07). Ekberg *et al.* (1994) working with Norway spruce (*Picea abies*) seedlings did not find any strong correlation between total height or shoot elongation with any of the bud phenological traits or shoot elongation period. They also could not strongly associate the shoot elongation period with bud burst and bud set.

Path Analysis

Table 3-7 presents the phenotypic and genetic path coefficients, correlation coefficients and degrees of determination for the second-year *AHI* from duration and average shoot growth rate for both propagule types. For both propagule types average shoot growth rate was the principal contributor to *AHI*. The genetic and phenotypic degree of determination of *AHI* by *ASRG* was almost 1 for cuttings and 0.86 and 0.72 for seedlings. Both phenotypic and genetic correlations between *AHI* and *ASRG* were positive strong and significant, indicating that material which has higher average shoot rate growth has larger *AHI*.

Table 3-7. Values of phenotypic and genetic path coefficients, correlation coefficients and degrees of determination for annual height increment (*AHI*) by growth duration (*D*) and average shoot growth rate (*ASRG*) by propagule type for Site 1 (North Central Florida).

Prop. type	*AHI Components (Log)*	*Path Coeff.* p^2_{AHI}	*Path coefficients components*			*Correlation Coefficient*		*Degree of determination*
			p^2_D	p^2_{ASRG}	* $2p_y p_z r_{yz}$	$r_{(AHI,D)}$ $r_{(AHI,ASRG)}$	$r_{(D,ASRG)}$	c_D c_{ASRG}
Phenotypic								
Cuttings								
	D	1.004	0.086	1.133	-0.215	-0.053	**-0.344**	-0.016
	ASRG					**0.907**		0.965
Seedlings								
	D	0.999	0.139	1.113	-0.253	0.036	**-0.322**	0.134
	ASRG					**0.814**		0.859
Genetic								
Cuttings								
	D	0.986	0.112	1.177	-0.303	-0.098	**-0.418**	-0.033
	ASRG					**0.891**		0.967
Seedlings								
	D	0.998	0.111	1.198	-0.310	-0.134	-0.426	-0.045
	ASRG					**0.656**		0.718

Note: Path coefficient formula: $p^2_{AHI} = p^2_D + p^2_{ASRG} + 2p_D\, p_{ASRG}\, r_{(D,ASRG)}$

*$2p_D\, p_{ASRG}\, r_{(D,ASRG)}$. $c_D = p_D\, r_{(AHI,ASRG)}$; $c_{ASRG} = p_{ASRG}\, r_{(AHI,ASRG)}$

Numbers in bold are significant ($p<0.05$)

These results were in agreement with those obtained by Magnussen and Yeatman (1989) in jack pine, who found that rate of shoot extension was a better predictor for within-family shoot length than the duration of the shoot elongation. Some reports for loblolly pine were in concordance with our results like: Perry *et al.* (1966), who through regression analyses reported that growth rate accounted for approximately 60 percent of the height growth variation while duration growth rate accounted for 30 percent. McCrady and Jokela (1996) attributed the differences in *AHI* between families to the height growth rate, and Boyer (1970) suggested that the flush growth variation in loblolly is attributable to growth rate and not to length of the growth season.

Duration and average growth rate were moderately and negatively correlated meaning that materials with shorter growing period had high growth rates. Phenotypic and genetic correlations were significantly different except for the seedling genetic correlation.

Flush Descriptors

Heritability Estimates

Significant differences ($p<0.05$) between propagule types were found for all the flush descriptors (*FLn*, *PFL*, *NSU* and *MSUL*), *NF* and growth traits (AHI_{FLn} and TH_2) (Appendix A).

On Site 1 additive variance was the primarily genetic variation associated with seedlings and cuttings for most of the flushes for *FLn*, *NSU*, *MSUL*, and *PFL* (Table 3-8) whereas non-additive genetic variance was the principal genetic variation associated with *NF* and TH_2 for seedlings. Additive genetic variance was the main genetic variation for TH_2 cuttings and AHI_{FLn} for cuttings and seedlings. There was non-additive variance for seedlings except for *FLn* flush 1, *PFL* flush 1 and 4, *NSU* flush 3 and *MSUL* flush 2.

On Site 2, as well, additive variance was the primarily genetic variation associated with seedlings for most of the flushes by *FLn*, *NSU*, *MSUL*, and *PFL* (Table 3-9) whereas non-additive genetic variance was the principal genetic variation associated with *NF*, TH_2 and AHI_{FLn}. There was less non-additive variance associated with *NF*, TH_2 and AHI_{FLn} in cuttings than in seedlings. Seedlings had no non-additive variance except for flush 2 for *FLn, PFL* and *NSU.*

Non-additive genetic variance was more frequent in with cuttings for Site 2 than for Site 1 (Table 3-8 and Table 3-9). On Site 2 for several flushes and different traits, H^2 was at least twice as large as h^2.

At both sites total genetic variance for cuttings was due primarily to clonal genetic variance. Two times *GCA* variance was the next highest contributor to the total genetic variance while *SCA* variance was generally small.

Seedling heritabilities were slightly larger and more inconsistent among the flushes than cuttings and also had larger standard errors than cuttings, which is attributable to the small seedling population (Table 2-2). Site 2 cutting heritabilities in general were slightly larger than in Site 1. There was no clear pattern of decreasing/increasing heritabilities values with the increasing/decreasing flush number for either propagule type or site. Heritabilities for flushes 6 and 7 are probably not reliable due to the small number of trees that produced 6 or 7 flushes.

NF AHI_{FLn} and TH_2 narrow and broad-sense heritabilities values were larger for Site 2 than for Site 1 for both cuttings and seedlings (Table 3-8 and 3-9).

For both Site 1 and 2, additive genetic variance was the primary genetic variance for seedlings and cuttings across site for most of the flushes for *FLn*, *PFL*, *NSU* and *MSUL*. Across sites cuttings had little to no non-additive variance; for a few flushes non-additive variance was twice as large as the additive variance.

Non-additive genetic variance was associated with *NF*, and seedlings TH_2. Additive genetic variance was the main genetic variance for AHI_{FLn} and cutting TH_2. Across-site *NF*, AHI_{FLn} and TH_2 cutting heritability values were two to five times larger than seedlings heritabilities values.

Table 3-8. Site 1 (North Central Florida): individual-tree narrow (h^2) and broad-sense (H^2) heritabilities for growth and shoot components by propagule type for the 2004 growing season.

Variable by flush #		*Seedlings*		*Cuttings*				
		h^2	H^2	h^2	H^2	$\frac{2GCA}{V_P}$	$\frac{SCA}{V_P}$	$\frac{Clone}{V_P}$
FLn	1	0.00 (0.00)	0.21 (0.26)	0.07 (0.03)	0.22 (0.04)	0.03	0.00	0.19
	2	0.14 (0.10)	0.14 (0.10)	0.16 (0.06)	0.22 (0.04)	0.08	0.01	0.12
	3	0.23 (0.12)	0.23 (0.12)	0.19 (0.06)	0.22 (0.04)	0.10	0.00	0.12
	4	0.25 (0.15)	0.27 (0.22)	0.16 (0.05)	0.17 (0.04)	0.08	0.00	0.09
	5	0.00 (0.00)	0.00 (0.00)	0.21 (0.07)	0.20 (0.05)	0.11	0.00	0.09
	6	0.03 (0.00)	0.03 (0.00)	0.10 (0.08)	0.12 (0.09)	0.05	0.00	0.07
	7	---	---	0.00 (0.00)	0.00 (0.00)	0.00	0.00	0.00
PFL	1	0.12 (0.13)	0.33 (0.23)	0.17 (0.06)	0.27 (0.04)	0.08	0.00	0.18
	2	0.08 (0.08)	0.08 (0.08)	0.08 (0.04)	0.13 (0.04)	0.04	0.02	0.08
	3	0.19 (0.10)	0.19 (0.10)	0.09 (0.04)	0.16 (0.04)	0.04	0.01	0.11
	4	0.09 (0.13)	0.45 (0.30)	0.10 (0.04)	0.13 (0.04)	0.05	0.00	0.09
	5	0.07 (0.10)	0.07 (0.10)	0.13 (0.06)	0.15 (0.05)	0.07	0.03	0.05
	6	0.73 (0.42)	0.73 (0.42)	0.14 (0.09)	0.21 (0.09)	0.07	0.00	0.14
	7	---	---	0.00 (0.00)	0.00 (0.00)	0.00	0.00	0.00
NSU	1	0.00 (0.00)	0.00 (0.00)	0.12 (0.04)	0.20 (0.04)	0.06	0.00	0.14
	2	0.13 (0.09)	0.13 (0.09)	0.13 (0.05)	0.21 (0.04)	0.06	0.01	0.14
	3	0.12 (0.11)	0.19 (0.25)	0.22 (0.07)	0.33 (0.04)	0.11	0.00	0.21
	4	0.13 (0.10)	0.13 (0.10)	0.17 (0.06)	0.17 (0.04)	0.08	0.01	0.07
	5	0.00 (0.00)	0.00 (0.00)	0.15 (0.06)	0.22 (0.04)	0.07	0.00	0.15
	6	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.12 (0.09)	0.00	0.00	0.12
	7	---	--	0.00 (0.00)	0.18 (0.34)	0.00	0.18	0.00
MSUL	1	0.10 (0.09)	0.10 (0.09)	0.11 (0.05)	0.16 (0.04)	0.06	0.00	0.10
	2	0.08 (0.10)	0.11 (0.20)	0.10 (0.06)	0.14 (0.04)	0.05	0.01	0.08
	3	0.42 (0.15)	0.42 (0.15)	0.29 (0.08)	0.32 (0.04)	0.14	0.00	0.17
	4	0.28 (0.13)	0.28 (0.13)	0.21 (0.06)	0.28 (0.04)	0.11	0.01	0.16
	5	0.27 (0.16)	0.27 (0.16)	0.22 (0.08)	0.30 (0.05)	0.11	0.03	0.16
	6	0.52 (0.42)	0.52 (0.42)	0.21 (0.08)	0.21 (0.08)	0.11	0.00	0.10
	7	---	--	0.00 (0.00)	0.00 (0.00)	0.00	0.00	0.00
NF		0.06 (0.12)	0.24 (0.22)	0.14 (0.07)	0.32 (0.04)	0.07	0.05	0.20
AvFL		0.00 (0.00)	0.00 (0.00)	0.18 (0.08)	0.31 (0.06)	0.09	0.00	0.22
AHI_{FLn}		0.00 (0.00)	0.00 (0.29)	0.26 (0.08)	0.20 (0.05)	0.13	0.00	0.06
TH_2		0.01 (0.08)	0.11 (0.26)	0.21 (0.07)	0.22 (0.04)	0.11	0.01	0.109

Note: *FLn*=flush length; *PFL*=flush contribution to annual height increment in percent; *NSU*=number of stem units; *MSUL*=mean stem unit length; *NF*= number of flushes; *AvFL*= average flush length; AHI_{FLn}=annual height increment as summation of the flush length; TH_2=second year total height. Standard errors are given in parentheses.

Table 3-9. Site 2 (Southwest Georgia): individual tree narrow (h^2) and broad-sense (H^2) heritabilities for growth and shoot components by propagule type for 2004 growing season.

Variable by flush #		*Seedlings*		*Cuttings*				
		h^2	H^2	h^2	H^2	$\frac{2GCA}{V_P}$	$\frac{SCA}{V_P}$	$\frac{Clone}{V_P}$
FLn	1	0.10 (0.09)	0.10 (0.09)	0.13 (0.05)	0.30 (0.04)	0.06	0.01	0.23
	2	0.16 (0.14)	0.50 (0.26)	0.20 (0.06)	0.42 (0.04)	0.10	0.00	0.32
	3	0.00 (0.00)	0.00 (0.00)	0.16 (0.06)	0.26 (0.04)	0.08	0.00	0.18
	4	0.16 (0.11)	0.16 (0.11)	0.19 (0.06)	0.28 0.04)	0.10	0.00	0.18
	5	0.00 (0.00)	0.23 (0.35)	0.21 (0.07)	0.28 (0.05)	0.10	0.00	0.17
	6	0.10 (0.63)	1.00 (1.21)	0.20 (0.09)	0.33 (0.09)	0.10	0.00	0.23
	7	---	---	0.00 (0.00)	0.18 (13.9)	0.00	0.00	0.15
PFL	1	0.14 (0.11)	0.14 (0.11)	0.13 (0.05)	0.30 (0.04)	0.06	0.01	0.23
	2	0.19 (0.15)	0.42 (0.25)	0.22 (0.06)	0.40 (0.04)	0.11	0.00	0.29
	3	0.00 (0.00)	0.00 (0.00)	0.10 (0.05)	0.20 (0.04)	0.05	0.02	0.14
	4	0.12 (0.10)	0.12 (0.10)	0.16 (0.05)	0.28 (0.04)	0.08	0.00	0.20
	5	0.06 (0.12)	0.06 (0.12)	0.16 (0.06)	0.25 (0.05)	0.08	0.00	0.17
	6	0.28 (0.47)	0.28 (0.47)	0.11 (0.08)	0.31 (0.09)	0.06	0.00	0.25
	7	---	---	0.00 (0.00)	0.59 (27.1)	0.00	0.00	0.59
NSU	1	0.09 (0.09)	0.09 (0.09)	0.14 (0.05)	0.32 (0.04)	0.07	0.00	0.24
	2	0.16 (0.15)	0.50 (0.26)	0.17 (0.06)	0.39 (0.04)	0.09	0.00	0.30
	3	0.03 (0.07)	0.03 (0.07)	0.18 (0.06)	0.26 (0.04)	0.09	0.01	0.16
	4	0.08 (0.08)	0.08 (0.08)	0.09 (0.04)	0.21 (0.04)	0.04	0.02	0.15
	5	0.08 (0.12)	0.08 (0.12)	0.11 (0.06)	0.28 (0.05)	0.05	0.02	0.21
	6	0.00 (0.00)	0.75 (1.29)	0.03 (0.05)	0.21 (0.10)	0.02	0.00	0.19
	7	---	---	0.00 (0.00)	0.33 (0.33)	0.00	0.08	0.24
MSUL	1	0.13 (0.11)	0.13 (0.11)	0.18 (0.06)	0.23 (0.04)	0.09	0.00	0.14
	2	0.03 (0.08)	0.03 (0.08)	0.20 (0.07)	0.34 (0.04)	0.10	0.02	0.22
	3	0.28 (0.13)	0.28 (0.13)	0.29 (0.08)	0.39 (0.04)	0.14	0.00	0.25
	4	0.05 (0.09)	0.05 (0.09)	0.26 (0.08)	0.40 (0.04)	0.13	0.00	0.27
	5	0.36 (0.18)	0.36 (0.18)	0.22 (0.07)	0.38 (0.04)	0.11	0.01	0.26
	6	0.00 (0.00)	1.00 (1.44)	0.16 (0.09)	0.46 (0.07)	0.08	0.00	0.38
	7	---	---	0.00 (0.00)	0.00 (0.00)	0.00	0.00	0.00
NF		0.20 (0.15)	0.46 (0.25)	0.29 (0.08)	0.41 (0.04)	0.14	0.01	0.26
AvFL		0.09 (0.09)	0.09 (0.09)	0.10 (0.05)	0.22 (0.05)	0.05	0.00	0.17
AHI_{FLn}		0.07 (0.12)	0.44 (0.27)	0.20 (0.07)	0.33 (0.04)	0.10	0.02	0.21
TH_2		0.03 (0.11)	0.53 (0.27)	0.31 (0.09)	0.41 (0.04)	0.15	0.01	0.25

Note: *FLn*=flush length; *PFL*=flush contribution to annual height increment in percent; *NSU*=number of stem units; *MSUL*=mean stem unit length; *NF*= number of flushes; *AvFL*= average flush length; AHI_{FLn}=annual height increment as summation of the flush length; TH_2=second year total height. Standard errors are given in parentheses.

Narrow and broad-sense heritabilities values were in general lower for across-site analysis than for single-site analyses. Individual-tree narrow and broad-sense heritabilities for cuttings are slightly larger than narrow and broad-sense heritabilities for seedlings.

These study findings are not in complete agreement with other studies of shoot growth components. Heritability values for second-year total height are in concordance with Paul *et al.* (1997) from two different factorial loblolly pine clonal tests. The h^2 values from their two factorial tests were 0.08 and 0.26. H^2 values ranged from 0.12 to 0.25 in their factorial tests.

In general, cutting heritability estimates in this study for second-year total height were larger than those estimates for the components (*FLn*, *NSU* and *MSUL*) and almost equal for *NF*. Heritabilities estimates for *NSU* and *MSUL* indicated that they are both under similar genetic control. Several other studies reported greater heritability values than the ones found in this study, with values ranging from 0.1 to nearly 1.0 for growth and growth component traits in loblolly pine and other conifers (Kremer and Larson 1983, Bongarten 1986, Li *et al*. 1991; Li *et al*. 1992, Smith *et al.* 1993b, Kaya 1993, Rweyongeza *et al.* 2003).

Type B Correlation

The stability of families and parents across site were compared for seedlings and cuttings (Table 3-11). Also clonal stability across site was analyzed for cuttings.

Table 3-10. Across site individual narrow (h^2) and broad-sense (H^2) heritabilities for growth and shoot components by propagule type for 2004 growing season for Site 1(North Central Florida) and Site 2 (Southwest Georgia).

Variable by flush #		*Seedlings*		*Cuttings*				
		h^2	H^2	h^2	H^2	$\frac{2GCA}{V_P}$	$\frac{SCA}{V_P}$	$\frac{Clone}{V_P}$
FLn	1	0.03 (0.04)	0.10 (0.07)	0.06 (0.03)	0.12 (0.02)	0.03	0.00	0.09
	2	0.08 (0.03)	0.08 (0.03)	0.11 (0.04)	0.14 (0.02)	0.06	0.00	0.08
	3	0.05 (0.04)	0.05 (0.04)	0.12 (0.05)	0.13 (0.03)	0.06	0.00	0.07
	4	0.10 (0.06)	0.11 (0.08)	0.10 (0.04)	0.14 (0.03)	0.05	0.00	0.09
	5	0.00 (0.00)	0.04 (0.09)	0.09 (0.06)	0.17 (0.03)	0.05	0.01	0.11
	6	0.00 (0.00)	0.00 (0.00)	0.11 (0.05)	0.06 (0.03)	0.06	0.00	0.00
	7	---	---	0.18 (0.12)	0.32 (0.12)	0.09	0.00	0.23
PFL	1	0.24 (0.10)	0.28 (0.10)	0.17 (0.06)	0.21 (0.03)	0.08	0.01	0.11
	2	0.15 (0.06)	0.15 (0.06)	0.11 (0.04)	0.16 (0.03)	0.06	0.00	0.11
	3	0.02 (0.04)	0.02 (0.04)	0.06 (0.03)	0.07 (0.02)	0.03	0.01	0.03
	4	0.10 (0.07)	0.10 (0.09)	0.06 (0.03)	0.11 (0.03)	0.03	0.00	0.08
	5	0.03 (0.07)	0.14 (0.10)	0.05 (0.05)	0.13 (0.03)	0.03	0.03	0.08
	6	0.06 (0.02)	0.00 (0.00)	0.11 (0.05)	0.06 (0.03)	0.06	0.00	0.00
	7	---	---	0.17 (0.11)	0.16 (0.12)	0.08	0.00	0.08
NSU	1	0.08 (0.07)	0.27 (0.11)	0.11 (0.04)	0.17 (0.03)	0.05	0.00	0.12
	2	0.05 (0.02)	0.05 (0.02)	0.08 (0.03)	0.13 (0.02)	0.04	0.00	0.09
	3	0.07 (0.03)	0.07 (0.03)	0.15 (0.02)	0.23 (0.02)	0.08	0.00	0.15
	4	0.08 (0.05)	0.08 (0.05)	0.13 (0.05)	0.19 (0.02)	0.06	0.02	0.11
	5	0.05 (0.04)	0.05 (0.04)	0.14 (0.05)	0.26 (0.03)	0.07	0.00	0.19
	6	0.01 (0.14)	0.24 (0.29)	0.05 (0.03)	0.08 (0.04)	0.02	0.00	0.06
	7	---	---	0.00 (0.00)	0.10 (0.19)	0.00	0.04	0.06
MSUL	1	0.16 (0.07)	0.27 (0.09)	0.13 (0.05)	0.17 (0.03)	0.06	0.00	0.10
	2	0.07 (0.07)	0.14 (0.09)	0.15 (0.05)	0.14 (0.03)	0.08	0.00	0.06
	3	0.28 (0.09)	0.28 (0.09)	0.26 (0.07)	0.26 (0.04)	0.13	0.00	0.14
	4	0.14 (0.07)	0.14 (0.07)	0.14 (0.06)	0.19 (0.03)	0.07	0.00	0.12
	5	0.18 (0.07)	0.18 (0.07)	0.17 (0.07)	0.22 (0.04)	0.09	0.02	0.12
	6	0.00 (0.00)	0.00 (0.00)	0.15 (0.06)	0.08 (0.03)	0.07	0.01	0.00
	7	---	---	0.21 (0.15)	0.24 (0.14)	0.11	0.01	0.12
NF		0.05 (0.08)	0.11 (0.12)	0.17 (0.07)	0.26 (0.03)	0.09	0.02	0.16
AvFL		0.00 (0.01)	0.00 (0.01)	0.05 (0.03)	0.10 (0.02)	0.03	0.00	0.07
AHI_{FLn}		0.04 (0.05)	0.04 (0.05)	0.21 (0.07)	0.22 (0.03)	0.10	0.01	0.11
TH_2		0.04 (0.05)	0.11 (0.12)	0.22 (0.07)	0.24 (0.04)	0.11	0.01	0.11

Note: *FLn*=flush length; *PFL*=flush contribution to annual height increment in percent; *NSU*=number of stem units; *MSUL*=mean stem unit length; *NF*= number of flushes; *AvFL*= average flush length; AHI_{FLn}=annual height increment as summation of the flush length; TH_2=second year total height. Standard errors are given in parentheses.

Table 3-11. Type B correlations for growth and shoot components by propagule type for 2004 growing season between Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

Variable by flush #		*Seedlings*		*Cuttings*		
		$r_{B_{Parents}}$	$r_{B_{Family}}$	$r_{B_{Clone}}$	$r_{B_{Parents}}$	$r_{B_{Family}}$
FLn	1	0.84 (0.88)	0.92 (0.46)	0.68 (0.12)	0.59 (0.20)	0.57 (0.19)
	2	1.00 (0.00)	1.00 (0.00)	0.80 (0.08)	0.69 (0.16)	0.61 (0.15)
	3	0.83 (0.52)	0.83 (0.52)	0.65 (0.12)	0.79 (0.14)	0.78 (0.13)
	4	0.65 (0.31)	0.66 (0.30)	0.72 (0.13)	0.63 (0.17)	0.59 (0.17)
	5	0.00 (0.00)	0.28 (0.54)	0.69 (0.12)	0.455 (0.21)	0.52 (0.18)
	6	0.00 (0.00)	0.00 (0.00)	0.24 (0.11)	0.72 (0.25)	0.72 (0.25)
	7	---	---	0.98 (0.13)	0.95 (0.44)	0.95 (0.44)
PFL	1	0.94 (0.15)	0.94 (0.14)	0.68 (0.08)	0.93 (0.09)	0.91 (0.08)
	2	1.00 (0.00)	0.98 (0.22)	0.64 (0.10)	0.70 (0.17)	0.60 (0.16)
	3	0.34 (0.68)	0.34 (0.68)	0.43 (0.15)	0.66 (0.21)	0.74 (0.16)
	4	0.60 (0.32)	0.60 (0.31)	0.51 (0.13)	0.485 (0.23)	0.42 (0.21)
	5	0.27 (0.56)	0.52 (0.35)	0.59 (0.13)	0.37 (0.26)	0.55 (0.17)
	6	0.00 (0.00)	0.005 (0.14)	0.23 (0.11)	0.72 (0.26)	0.72 (0.26)
	7	---	---	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
NSU	1	0.94 (0.44)	0.97 (0.22)	0.78 (0.11)	0.82 (0.13)	0.80 (0.13)
	2	1.00 (0.00)	1.00 (0.00)	0.81 (0.07)	0.67 (0.18)	0.58 (0.16)
	3	1.00 (0.00)	1.00 (0.00)	0.94 (0.09)	0.95 (0.01)	0.95 (0.01)
	4	0.78 (0.38)	0.78 (0.38)	0.97 (0.03)	0.92 (0.08)	0.94 (0.07)
	5	0.70 (0.67)	0.53 (0.52)	0.96 (0.04)	0.86 (0.12)	0.86 (0.12)
	6	1.00 (0.00)	1.00 (0.00)	0.49 (0.27)	1.00 (0.00)	1.00 (0.00)
	7	---	---	0.20 (0.40)	0.23 (0.00)	1.00 (0.00)
MSUL	1	0.99 (0.00)	0.99 (0.00)	0.82 (0.12)	0.77 (0.14)	0.77 (0.13)
	2	0.47 (0.38)	0.58 (0.30)	0.58 (0.10)	1.00 (0.00)	0.86 (0.11)
	3	0.89 (0.14)	0.89 (0.14)	0.73 (0.07)	0.89 (0.07)	0.89 (0.07)
	4	0.78 (0.25)	0.78 (0.25)	0.60 (0.08)	0.64 (0.16)	0.61 (0.15)
	5	1.00 (0.00)	1.00 (0.00)	0.67 (0.08)	0.76 (0.13)	0.79 (0.11)
	6	0.00 (0.00)	0.00 (0.00)	0.25 (0.08)	0.93 (0.18)	0.93 (0.17)
	7	---	---	0.99 (0.18)	0.97 (0.39)	0.97 (0.34)
NF		0.36 (0.49)	0.32 (0.29)	0.72 (0.07)	0.76 (0.14)	0.73 (0.11)
AvFL		1.00 (0.00)	1.00 (0.00)	0.82 (0.08)	0.59 (0.21)	0.55 (0.20)
AHI_{FLn}		0.89 (1.33)	0.40 (0.55)	0.81 (0.09)	0.88 (0.08)	0.89 (0.08)
TH_2		1.00 (0.00)	0.48 (0.39)	0.74 (0.08)	0.88 (0.10)	0.85 (0.09)

Note: *FLn*=flush length; *PFL*=flush contribution to annual height increment in decimal equivalents; *NSU*=number of stem units; *MSUL*=mean stem unit length; *NF*= number of flushes; *AvFL*= average flush length; AHI_{FLn}=annual height increment as summation of the flush length; TH_2=second year total height. Standard errors are given in parentheses.

Growth and Shoot Components

Cutting *NF*, AHI_{FLn} and TH_2 showed consistent clonal, parental and family ranking across site with type B correlations that ranged from 0.72 to 0.89 whereas seedling family and parental rankings across site were quite inconsistent for *NF*, and for family AHI_{FLn} and TH_2 were inconsistent. *AvFL* family and parental ranking across site was very consistent for seedlings, but not for cuttings. Only clonal ranking was very consistent for cuttings.

Flush Descriptors

The type B correlations reported in this study vary greatly from flush to flush, trait to trait, and with propagule type. While *FLn*, *PFL*, *NSU* and *MSUL* seedling flush 1 and 2 exhibited high strong parent and family correlations, cuttings flush 1 and 2 parental and family correlations were moderate, except for *MSUL* flush 2 for which cutting parental and family correlation are higher than seedlings.

Seedling *NSU* and *MSUL* exhibited consistent family and parental ($r_{B_{Parents}}$ =0.70 to 1.00; $r_{B_{Family}}$ =0.78 to 1.00) rankings across both sites for most of the flushes except family rankings for *MSUL* flush 2 and *NSU* flush 5 which were inconsistent with correlated values of 0.47 to 0.58 for either parental and family type B correlations (Table 3-11).

Parent type B correlations for seedling *FLn* were high and ranged from 0.83 to 1.00 for the first three flushes while the fourth flush had a moderated correlation and the remained flushes where low (0.28) to uncorrelated. *PFL* showed similar behavior to *FLn*, but just for the first two flushes. Flush 3 was low for both parental and family type B correlation. The other *PFL* flushes had moderate to nil family and parental correlations.

The majority of the type B correlations for cuttings along the flushes and traits were moderate to high ranging from 0.51 to 1. There were a small number of correlations which were lower than 0.50 and most of them were clonal type B correlations. Few flushes, flush 6 for example, exhibited consistent family and parental ranking across sites and inconsistent clonal ranking across sites for all the traits analyzed.

Seedling family type B correlations estimated in this study for loblolly pine second growing season were lower than those reported by Smith *et al.* (1993b), who reported 0.89 to 0.94 family type B genetic correlations for cycle length, number of cycles and *NSU* per cycle. The moderate correlations (0.64 to 0.72) for total height, total number of NSU and free growth stem unit length were more in accord to some of the correlations obtained in this study. Li *et al.* (1992) reported genetic correlations across their treatments (fertilized and irrigated against non- fertilized and non-irrigated) ranging from 0.61 to 0.80.

Path Analyses

Annual Height Increment with Number of Flushes and Average Flush Length

For sites 1 and 2 phenotypic and genetic path coefficients, correlation coefficients and degree of determination for second year AHI_{FLn} by *NF* and *AvFL* for both propagule types are show in Table 3-12.

For both sites and propagule type average flush length was the principal contributor to AHI_{FLn}. At Site 1, the phenotypic degrees of determination of AHI_{FLn} by *AvFL* were 0.80 for cuttings and 0.71 for seedlings. Seedling genetic path analysis could not be assessed due to the very low variance of the genetic components. Both phenotypic and genetic correlations between AHI_{FLn} and *AvFL* were larger than AHI_{FLn} and *NF* correlations. AHI_{FLn}-*AvFL* correlations were significant positive and moderate to strong

(0.63 to 0.86), indicating that material which has higher average flush length has larger AHI_{FLn}. AHI_{FLn}-*NF* phenotypic correlations were positive moderate and significant for both cuttings and seedlings whereas cutting genetic correlation was low and nonsignificant. Cuttings and seedlings *NF*-*AvFL* phenotypic correlations were negative low (-0.13 to -0.25) but significant, meaning that materials with fewer flushes had longer flushes.

Cutting genetic *NF*-*AvFL* correlation was much higher (-0.59) than cutting phenotypic correlations. On the other hand Site 2 cuttings and seedlings *NF*-*AvFL* phenotypic correlation were strongly negative and significant (-0.78 and -0.74). Although the seedling genetic correlation was also strong negative and significant, Site 2 cuttings genetic *NF*-*AvFL* correlation was low positive and significant. Site 2 cuttings and seedlings AHI_{FLn}-*AvFL* phenotypic correlation as well as Site 1 were moderate and positive. Genetic AHI_{FLn}-*AvFL* correlations were also moderate and positive but only the cutting correlation was significant. AHI_{FLn}.-*NF* correlation were low (0.003 to 0.26) and nonsignificant for both cuttings and seedlings and for phenotypic and genetic correlations; only the cutting genetic correlation was negative. The relatively larger phenotypic degree of determination for *AvFL* to AHI_{FLn} at Site 2 indicated a strong contribution of *AvFL* to AHI_{FLn} and a weak role for *NF* in that environment. Cutting genetic path analysis was not estimated correctly $p^2_{AHI_{FLn}}$ (the path estimated of AHI_{FLn} with itself has to be 1 and in this case the number obtained was 4.34).

Gómez-Cárdenas *et al.* (1998) found similar average number of flushes (4±1) in their two year study on *P. patula*, but in the second year their annual height increment was quite low (drought) due to shorter flushes. For Gómez-Cárdenas *et al.* (1998) average

flush length and *NSU* were the most important components in the shoot elongation pattern of *P. patula*.

Table 3-12. Phenotypic and genetic values for path coefficients components, correlations coefficients, and degree of determinations for annual height increment AHI_{FLn} by number of flushes (*NF*) and average flush length (*AvFL*) by propagule type for Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

Prop. type	*Flush Components (Log)*	*Path coeff.* $p^2_{AHI_{FLn}}$	*Path coeff. components* p^2_{NF}	p^2_{AvFL}	$2p_y p_z r_{yz}$ *	*Correlation coefficient* $r_{(AHI_{FLn}, NF)}$ / $r_{(AHI_{FLn}, AvFL)}$	$r_{(NF, AvFL)}$	*Degree of determination* c_{NF} / c_{AvFL}
Site 1								
Phenotypic								
Cuttings								
	NF	1.01	0.47	0.86	-0.32	**0.46**	**-0.25**	0.31
	AvFL					**0.86**		0.79
Seedlings								
	NF	1.05	0.44	0.77	-0.16	**0.56**	**-0.13**	0.37
	AvFL					**0.81**		0.71
Genetic								
Cuttings								
	NF	1.11	1.02	1.61	-1.52	0.26	**-0.59**	0.26
	AvFL					**0.63**		0.80
Seedlings								
	NF	---	---	---	---	---	---	---
	AvFL					---		---
Site 2								
Phenotypic								
Cuttings								
	NF	0.94	1.26	2.09	-2.41	0.09	**-0.74**	0.10
	AvFL					**0.64**		0.92
Seedlings								
	NF	0.99	1.52	2.53	-3.04	0.003	**-0.78**	0.003
	AvFL					**0.64**		1.01
Genetic								
Cuttings								
	NF	4.34	1.35	2.56	0.43	-0.09	**0.12**	-0.11
	AvFL					**0.69**		1.10
Seedlings								
	NF	1.01	166	2.04	-2.69	0.26	**-0.73**	0.33
	AvFL					0.47		0.67

Note: Path coefficient formula: $p^2_{AHI_{FLn}} = p^2_{NF} + p^2_{AvFL} + 2p_{NF}\ p_{AvFL}\ r_{(NF, AvFL)}$

*$2p_{NF}\ p_{AvFL}\ r_{(NF, AvFL)}$. $c_{NF} = p_{NF}\ r_{(AHI_{FLn}, NF)}$; $c_{AvFL} = p_{AvFL}\ r_{(AHI_{FLn}, AvFL)}$

(---) Could not estimated because at least one of the variances was 0

Numbers in bold are significant ($p<0.05$).

Flush Length with Number of Stem Units and Mean Stem Unit Length.

For site 1 and 2 phenotypic and genetic path coefficients, correlation coefficients and degree of determination for second year height *FLn* by *NSU* and *MSUL* for both propagule types are show in Table 3-13, 3-14, 3-15 and 3-16.

At both sites in the phenotypic analysis and for both propagule types *NSU* was by far the principal contributor to *FLn* for the first and second flush with values of 1 for seedlings and cuttings in Site 2 and with values of 0.72-0.75 for flush 2 for both cuttings and seedlings in Site 1 (Table 3-13 and 3-14). From flush 4 onward, *NSU* and *MSUL* contribute in almost the same proportion to the *FLn*. In Site 1 for the last flushes evaluated in seedlings (5 and 6) the contribution of *MSUL* to *FLn* was slightly superior to NSU (Table 3-13).

The phenotypic correlations between *MSUL* and *NSU* at Site 2 (Table 3-14) were low to moderate negative and significant (-0.19 to -0.54) for cuttings and seedlings, indicating that material with shorter *MSUL* had a larger number of *NSU*. The lowest correlations were for flushes 4 and 5 for both propagule types. *FLn-NSU* correlations were positive moderate to high and significant (0.49 to 0.93), indicating that material with longer flushes had greater *NSU*. The results indicate that *FLn-NSU* correlations decreased in value from flush 1 to 7 and *FLn-MSUL* correlations increase in value from flush 1 to 7.

FLn-MSUL correlations were low and negative and not significant for the first two flushes in cuttings and seedlings, except for seedling flush 2 where the correlation was significant.

Table 3-13. Site 1 (North Central Florida): phenotypic values of path coefficients and path components, correlations coefficients and degree of determination for flush length (*FLn*) as the product of mean stem unit length (*MSUL*) and number of stem unit (*NSU*) by propagule type.

Prop. type	*Flush Components (Log)*	*Path coeff.* p^2_{FLn}	*Path coeff. components**			*Correlation coefficient*		*Degree of determination*
			p^2_{NSU}	p^2_{MSUL}	$2p_y p_z r_{yz}$ *	$r_{(FLn,\ NSU)}$ $r_{(FLn,MSUL)}$)	$r_{(MSUL,NSU)}$	c_{NSU} c_{MSUL}
Cuttings								
Flush								
1	NSU MSUL	0.95	1.48	0.41	-0.94	**0.88** **-0.07**	**-0.60**	1.07 -0.04
2	NSU MSUL	0.99	0.67	0.23	0.085	**0.88** **0.57**	**0.11**	0.72 0.28
3	NSU MSUL	0.97	0.79	0.61	-0.43	**0.67** **0.53**	**-0.31**	0.60 0.41
4	NSU MSUL	0.99	0.69	0.55	-0.24	**0.70** **0.59**	**-0.20**	0.58 0.44
5	NSU MSUL	0.997	0.64	0.49	-0.13	**0.73** **0.62**	**-0.12**	0.59 0.43
6	NSU MSUL	0.98	0.45	0.55	-0.02	**0.67** **0.74**	-0.02	0.45 0.55
7	NSU MSUL	0.99	0.76	0.66	-0.44	**0.64** **0.58**	**-0.31**	0.56 0.47
Seedlings								
Flush								
1	NSU MSUL	0.94	1.46	0.47	-0.99	**0.85** -0.04	**-0.60**	1.03 -0.03
2	NSU MSUL	1.00	0.72	0.26	0.02	**0.88** **0.55**	0.02	0.75 0.28
3	NSU MSUL	0.97	0.76	0.71	-0.50	**0.61** **0.55**	**-0.34**	0.53 0.46
4	NSU MSUL	1.08	0.68	0.56	-0.16	**0.71** **0.65**	**-0.13**	0.58 0.48
5	NSU MSUL	1.04	0.46	0.68	-0.10	**0.60** **0.76**	-0.09	0.40 0.63
6	NSU MSUL	0.93	0.365	0.66	-0.09	0.18 **0.78**	-0.09	0.11 0.63

Note: Path coefficient formula: $p^2_{FLn} = p^2_{NSU} + p^2_{MSUL} + 2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$

*$2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$. $c_{NSU} = p_{NSU}\ r_{(FLn,\ NSU)}$; $c_{MSUL} = p_{MSUL}\ r_{(FLn,MSUL)}$

Numbers in bold are significant ($p<0.05$).

Table 3-14. Site 2 (Southwest Georgia): phenotypic values of path coefficients and path components, correlations coefficients and degree of determination for flush length (*FLn*) as the product of mean stem unit length (*MSUL*) and number of stem unit (*NSU*) by propagule type.

Prop. type	*Flush Components (Log)*	*Path coeff.* p^2_{FLn}	*Path coeff. components*			*Correlation coefficient*		*Degree of determination*
			p^2_{NSU}	p^2_{MSUL}	$2p_y p_z r_{yz}$ *	$r_{(FLn,\ NSU)}$ $r_{(FLn,MSUL)}$	$r_{(MSUL,NSU)}$	c_{NSU} c_{MSUL}
Cuttings								
Flush								
1	NSU	0.98	1.38	0.34	-0.74	**0.87**	**-0.54**	1.03
	MSUL					-0.05		-0.03
2	NSU	1.00	1.21	0.17	-0.38	**0.93**	**-0.42**	1.02
	MSUL					-0.04		-0.02
3	NSU	0.98	1.11	0.63	-0.76	**0.70**	**-0.45**	0.74
	MSUL					**0.33**		0.26
4	NSU	1.00	0.65	0.58	-0.23	**0.67**	**-0.19**	0.54
	MSUL					**0.61**		0.47
5	NSU	1.00	0.85	0.62	-0.47	**0.67**	**-0.33**	0.63
	MSUL					**0.49**		0.38
6	NSU	1.03	0.96	0.95	-0.88	**0.53**	**-0.46**	0.52
	MSUL					**0.52**		0.51
7	NSU	1.00	0.84	0.99	-0.83	**0.49**	**-0.46**	0.44
	MSUL					**0.56**		0.56
Seedlings								
Flush								
1	NSU	0.99	1.29	0.25	-0.55	**0.85**	**-0.48**	1.01
	MSUL					-0.02		-0.01
2	NSU	1.01	1.30	0.17	-0.46	**0.86**	**-0.49**	1.06
	MSUL					**-0.14**		-0.06
3	NSU	1.00	1.02	0.51	-0.53	**0.57**	**-0.37**	0.75
	MSUL					**0.35**		0.25
4	NSU	1.00	0.64	0.65	-0.28	**0.70**	**-0.22**	0.49
	MSUL					**0.63**		0.51
5	NSU	1.00	0.72	0.62	-0.33	**0.62**	**-0.25**	0.55
	MSUL					**0.57**		0.45
6	NSU	0.69	0.69	0.76	-0.75	**0.64**	**-0.52**	0.56
	MSUL					**0.61**		0.53

Note: Path coefficient formula: $p^2_{FLn} = p^2_{NSU} + p^2_{MSUL} + 2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$

*$2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$. $c_{NSU} = p_{NSU}\ r_{(FLn,\ NSU)}$; $c_{MSUL} = p_{MSUL}\ r_{(FLn,\ MSUL)}$

Numbers in bold are significant ($p<0.05$).

The negative correlations between *FLn-MSUL* indicated that flushes with short *MSUL* had longer flushes. This is in concert with flushes 1 and 2 where the flush length was determined principally by *NSU*. At Site 2 *FLn-MSUL* correlation were no higher

than 0.63. Site 1 phenotypic correlations followed the general pattern indicated for Site 2 but with some particularities. *MSUL-NSU* correlations were in general lower but for flush 2 in both propagule type *MSUL-NSU* correlations were positive low and significant and the contribution of *NSU* to second flush *FLn* was lower than for Site 2.

FLn-MSUL correlations for flush 2 were moderate positive and significant (0.55 and 0.57) for both seedlings and cuttings. *FLn-MSUL* phenotypic correlations for seedling flushes 5 and 6 and for cutting flush 6 were large (0.74 to 0.78) while their *MSUL-NSU* correlation were low and nonsignificant; signifying the increasing contribution of *MSUL* to the *FLn* for those flushes. Seedling phenotypic flush 7 path analysis at both sites could not be estimated (Table 2-2).

NSU was reported to be the main contributor to total height by several authors like Allen and Scarbrough (1970) in *P. palustris*, Kremer (1985) in *P. pinaster*, Guyon (1986) in *P. nigra*, Kremer and Lascoux (1988) in *P. pinaster*, Magnussen and Yeatman (1989) in *P. banksiana*, Fady (1990) in *Abies cephalonica*, Smith *et al.* (1993b) in slash pine, Gómez-Cárdenas (1998) in *P. patula,* and Raweyongeza *et al* (2003) in white spruce. A mixed support for *NSU* and *MSUL* as primary contributors to flush length was reported by Kremer and Larson (1983) in jack pine, Bongarten (1986) in blue spruce and Douglas fir, and Kaya (1993) in Douglas fir

MSUL-NSU negative phenotypic and genetic correlations were reported in several shoot components studies like Kremer and Larson (1983), Kremer (1985), Bongarten (1986), Kremer and Lascoux (1988), Magnussen and Yeatman (1989), Fady (1990), Kaya (1993) Smith *et al.* (1993b) and Gómez-Cárdenas (1998) whereas Raweyongeza *et al* (2003) reported genetic, phenotypic and environmental as very low but positive

correlations between *MSUL* and *NSU*. Guyon (1986) in *P. nigra* obtained just one positive non significant MSUL-NSU correlation in the 6 years analyzed.

Genetic path analyses by flush for *FLn* as a product of *MSUL* and *NSU* could not be estimated for all the flushes at both sites due to the low variances for some of the traits (Table 3-15 and 3-16).

Cutting genetic path analyses for Site 2 followed the general characteristics described for the phenotypic path analyses for cutting for flush 1 and 2 in which *NSU* were the principal contributors for the *FLn* but after flush 3 *MSUL* became equal to or more important than *NSU* as a determinate of flush length. *MSUL* degree of determination values ranged from 0.50 to 0.90. Seedlings in Site 2 had the same genetic pattern as cutting but *MSUL* reached only one extreme value (0.99 in flush 3). Seedling genetic path for flush 5 analysis could not be estimated because at least one of the component variances was almost 0.

At Site 1 the cutting genetic path analysis had similar values to the phenotypic path analyses, even the low positive *MSUL-NSU* correlation for flush 2. Seedling genetic path analyses could not be assessed for flushes 1, 2 and 6 because the variance of at least of one of the components was almost 0. For flushes 3, 4 and 5 where the genetic path analyses could be estimated, *MSUL* was by far the main contributor to *FLn* with a degree of determination ranged from 0.74 to 1.38.

MSUL became more important in its contribution to *FLn* in the genetic analyses than in the phenotypic to the point that it became the primary contributor for many flushes at both sites for cuttings and seedling.

Table 3-15. Site 1 (North Central Florida): genetic values for path coefficients and path components, correlation coefficients and degrees of determination for flush length (*FLn*) as the product of mean stem unit length (*MSUL*) and number of stem unit (*NSU*) by propagule type.

Prop. type	*Flush Components (Log)*	*Path coeff.* p^2_{FLn}	*Path coeff. components**			*Correlation coefficient*		*Degree of determination*
			p^2_{NSU}	p^2_{MSUL}	$2p_y p_z r_{yz}$ *	$r_{(FLn,\ NSU)}$ $r_{(FLn,MSUL)}$	$r_{(MSUL,NSU)}$	c_{NSU} c_{MSUL}
	Cuttings							
Flush								
1	NSU	1.03	1.41	0.47	-0.85	**0.76**	**-0.52**	0.90
	MSUL					**0.07**		-0.05
2	NSU	0.98	0.70	0.21	0.07	**0.88**	0.10	0.73
	MSUL					**0.55**		0.26
3	NSU	1.02	1.22	1.08	-1.29	**0.52**	**-0.56**	0.58
	MSUL					**0.41**		0.55
4	NSU	1.01	0.96	0.97	-0.92	**0.54**	**-0.48**	0.51
	MSUL					**0.52**		0.58
5	NSU	1.03	0.77	0.70	-0.45	**0.62**	**-0.30**	0.55
	MSUL					**0.58**		0.52
6	NSU	1.03	0.36	0.74	-0.07	**0.55**	-0.07	0.33
	MSUL					**0.80**		0.64
7	NSU	---	---	---	---	---	---	---
	MSUL					---		---
	Seedlings							
Flush								
1	NSU	---	---	---	---	---	---	---
	MSUL					---		---
2	NSU	---	---	---	---	---	---	---
	MSUL					---		---
3	NSU	0.89	0.67	2.55	-2.34	-0.43	**-0.82**	-0.37
	MSUL					**0.87**		1.38
4	NSU	0.55	0.26	0.48	-0.19	0.31	-0.21	0.16
	MSUL					**0.84**		0.74
5	NSU	0.96	0.18	1.59	-0.81	-0.30	-0.66	-0.14
	MSUL					**0.94**		1.16
6	NSU	---	---	---	---	---	---	---
	MSUL					---		---

Note: Path coefficient formula: $p^2_{FLn} = p^2_{NSU} + p^2_{MSUL} + 2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$

*$2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$. $c_{NSU} = p_{NSU}\ r_{(FLn,\ NSU)}$; $c_{MSUL} = p_{MSUL}\ r_{(FLn,MSUL)}$

(---) Could not estimated because at least one of the variances was 0

Numbers in bold are significant ($p<0.05$).

Table 3-16. Site 2 (Southwest Georgia): genetic values for path coefficients and path components, correlation coefficients and degree of determination for flush length (*FLn*) as the product of mean stem unit length (*MSUL*) and number of stem units (*NSU*) by propagule type.

Prop. type	*Flush*	*Components (Log)*	*Path coeff.* p^2_{FLn}	*Path coeff. components* p^2_{NSU}	p^2_{MSUL}	$2p_y p_z r_{yz}$ *	*Correlation coefficient* $r_{(FLn,\ NSU)}$ $r_{(FLn,MSUL)}$	$r_{(MSUL,NSU)}$	*Degree of determination* c_{NSU} c_{MSUL}
Cuttings									
	Flush								
	1	NSU	0.99	1.51	0.24	-0.76	**0.92**	**-0.63**	1.13
		MSUL					**-0.28**		-0.14
	2	NSU	0.99	1.34	0.16	-0.51	**0.94**	**-0.55**	1.09
		MSUL					**-0.25**		-0.10
	3	NSU	0.95	1.26	1.12	-1.43	**0.51**	**-0.60**	0.57
		MSUL					**0.40**		0.42
	4	NSU	1.02	0.46	0.92	-0.36	**0.40**	**-0.28**	0.27
		MSUL					**0.76**		0.73
	5	NSU	0.99	0.98	0.98	-0.96	**0.50**	**-0.49**	0.50
		MSUL					**0.50**		0.50
	6	NSU	0.99	0.53	1.36	-0.90	0.12	**-0.53**	0.08
		MSUL					**0.77**		0.90
	7	NSU	1.26	0.62	0.68	-0.04	**0.57**	-0.03	0.45
		MSUL					**0.65**		0.56
Seedlings									
	Flush								
	1	NSU	1.06	1.96	0.34	-1.25	**0.93**	**-0.76**	1.30
		MSUL					-0.47		-0.27
	2	NSU	0.99	1.48	0.13	-0.62	**0.97**	**-0.71**	1.18
		MSUL					-0.51		-0.18
	3	NSU	0.98	1.34	2.31	-2.67	0.01	-0.76	0.01
		MSUL					0.65		0.99
	4	NSU	1.01	0.27	0.43	0.31	**0.82**	0.46	0.43
		MSUL					**0.89**		0.57
	5	NSU	---	---	---	---	---	---	---
		MSUL					---		---
	6	NSU	0.79	0.27	0.40	0.12	0.56	0.18	0.29
		MSUL					0.82		0.52

Note: Path coefficient formula: $p^2_{FLn} = p^2_{NSU} + p^2_{MSUL} + 2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$

*$2p_{NSU}\ p_{MSUL}\ r_{(MSUL,NSU)}$. $c_{NSU} = p_{NSU}\ r_{(FLn,NSU)}$; $c_{MSUL} = p_{MSUL}\ r_{(FLn,MSUL)}$

(---) Could not estimated because at least one of the variance was 0

Numbers in bold are significant ($p<0.05$).

Seedling results have to be viewed with some caution due to the small seedling sample size. Therefore, these results are in agreement with those reported by Bongarten (1986), who concluded that the degree of contribution of *MSUL* and *NSU* to *FLn* depended, among other factors, on the type of the data considered (phenotypic, genetic or

environmental). His results within Douglas-fir and blue spruce provenances were that *MSUL* and *NSU* contributed equally to flush length phenotypic variation. For genetic variation *MSUL* was the primarily component for *FLn* in blue spruce while *NSU* was for environmental. On the other hand Rweyongeza *et al*. (2003) reported that the *NSU* degree of determination was larger than *MSUL* under genetic, phenotypic and environmental analyses. Bridgwater (1990) reported that some loblolly pine families might show superior height increment due to greater number of stem units while other families depend more on the greater elongation of the stem units. Also Kaya (1993) reported for Douglas-fir seedlings that *MSUL* explained nearly two-third of the free growth in an inland population while *NSU* explained coastal population free growth. Bailey and Feret (1982) working with loblolly pine and hybrids from *P. rigida* x taeda result were in agreement to those of this study where *MSUL* was more important for free growth flush length than *NSU* and *NSU* was the dominating factor for fixed growth. Cannell (1978) also reported that *MSUL* tended to be a larger component free growth (summer flushes) than for the first flush.

Least Square Means for Provenance for *FLn, PFL, NSU* and *MSUL*

Significant differences ($p<0.05$) between propagule type were found for all the morphological and growth traits (*FLn*, *NSU*, *MSUL*, *NF* and AHI_{FL}) (Table A-3 in Appendix A).

FL was the only provenance which demonstrated significant differences for *NF* for both propagule types at Site 1. Although, all provenances were significantly different for NF at Site 2, *LG* provenance had the highest *NF*. The Georgia site had higher AHI_{FL} values for all the provenances and propagule types than Site 1. *FL* cuttings were significantly different for AHI_{FL} at Sites 1 and 2 (Figure 3-2).

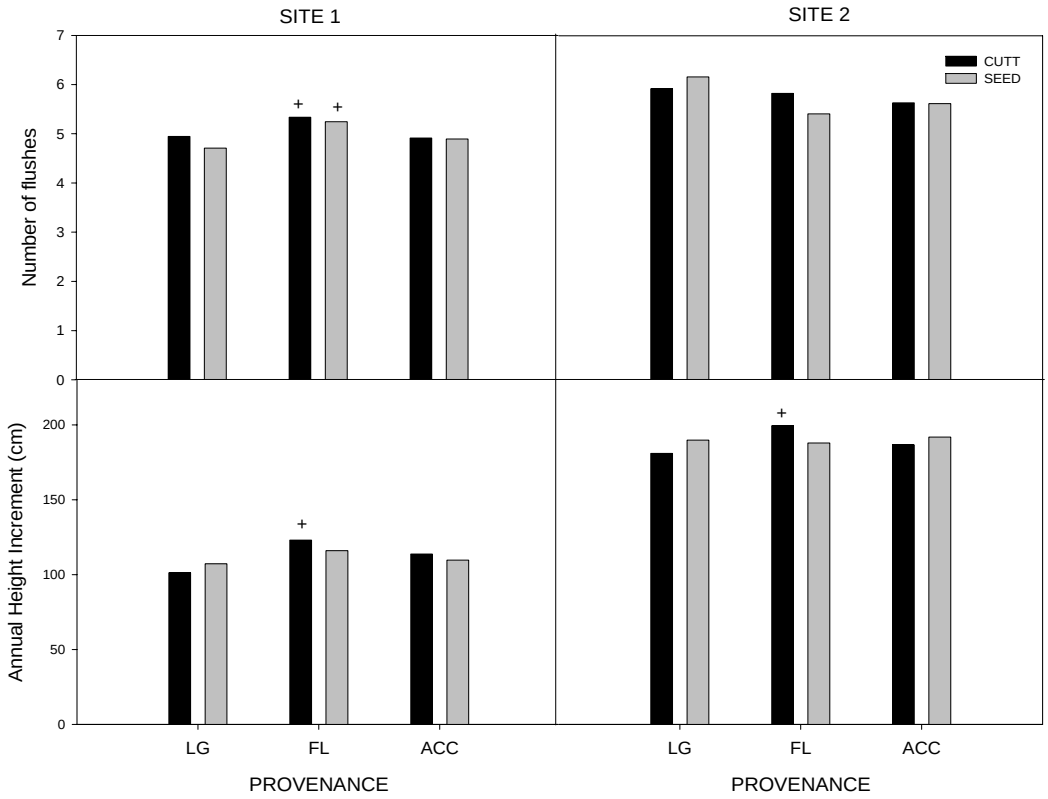

Figure 3-2. Least square means for number of flushes (*NF*) and annual height increment as a summation of flush length (AHI_{FL}) for the 2004 growing season by propagule type at Site 1 (North Central Florida) and Site 2 (Southwest Georgia). (+) indicates significant differences among provenances ($p<0.05$).

Few flushes were coincidently significantly different for provenances for both cuttings and seedlings for the same trait.

Figures 3-3 and 3-4 describe graphically the results from the path analyses for flush length as a product of *MSUL* and *NSU*. After flush 3 *FLn* had the tendency for *MSUL* to be a major contributor while *NSU* is the major importance.

Site 2 seedlings had by far the largest values of *FLn* and *NSU* for flush 1 than cuttings (Figure 3-3 and 3-4).

At both sites seedlings and cuttings had different patterns for all of the traits analyzed except for MSUL at Site 2. Seedlings trend to have higher values for all the traits from 3 and on while cuttings present lower values after flush 3.

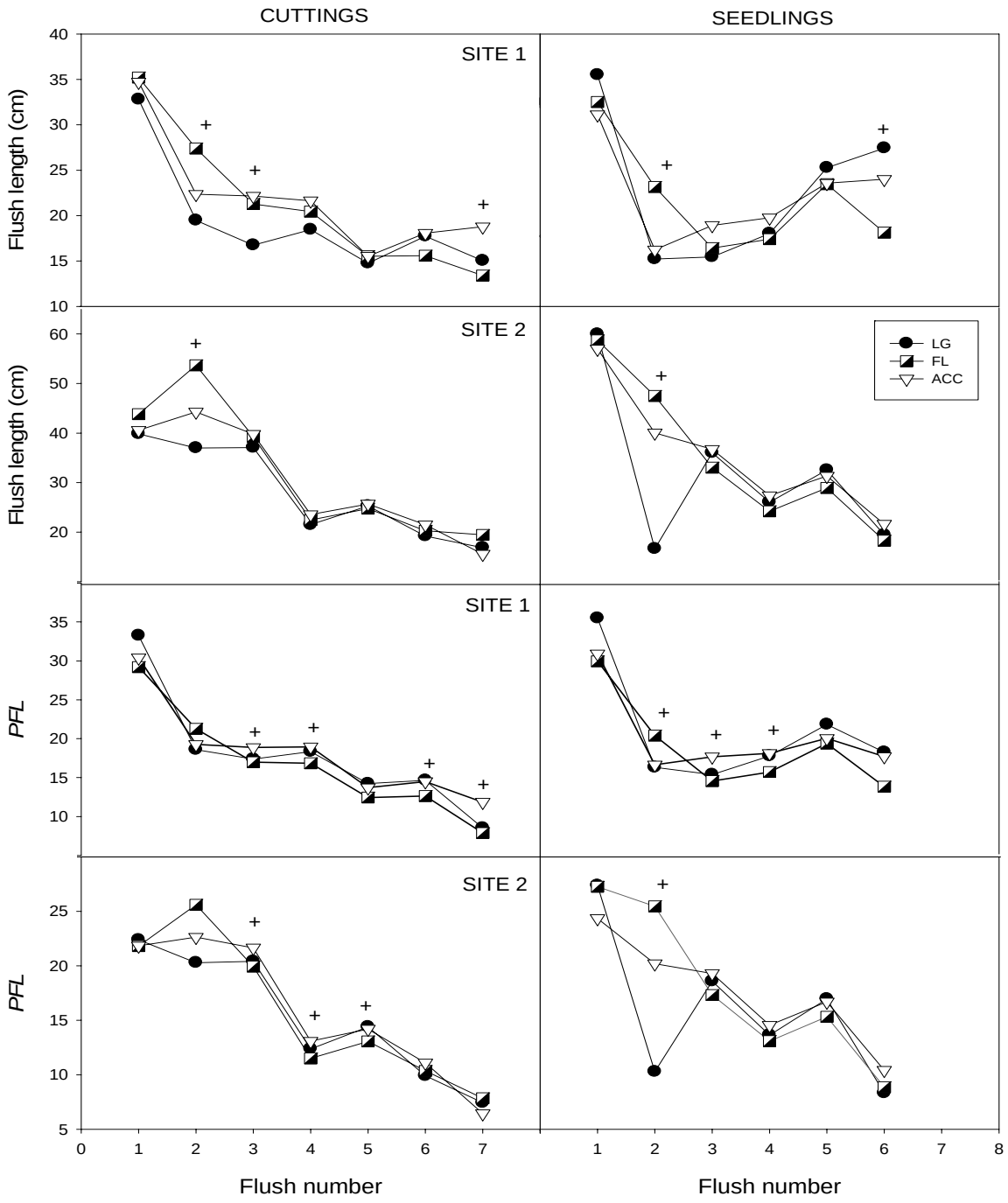

Figure 3-3. Least square means for flush length (*FLn*) and flush length contribution (PFL) by propagule type at Site 1 (North Central Florida) and Site 2 (Southwest Georgia). LG, FL and ACC are Lower Gulf, Florida and Atlantic Coastal Plain provenances, respectively. (+) indicates significant differences between the provenances ($p<0.05$).

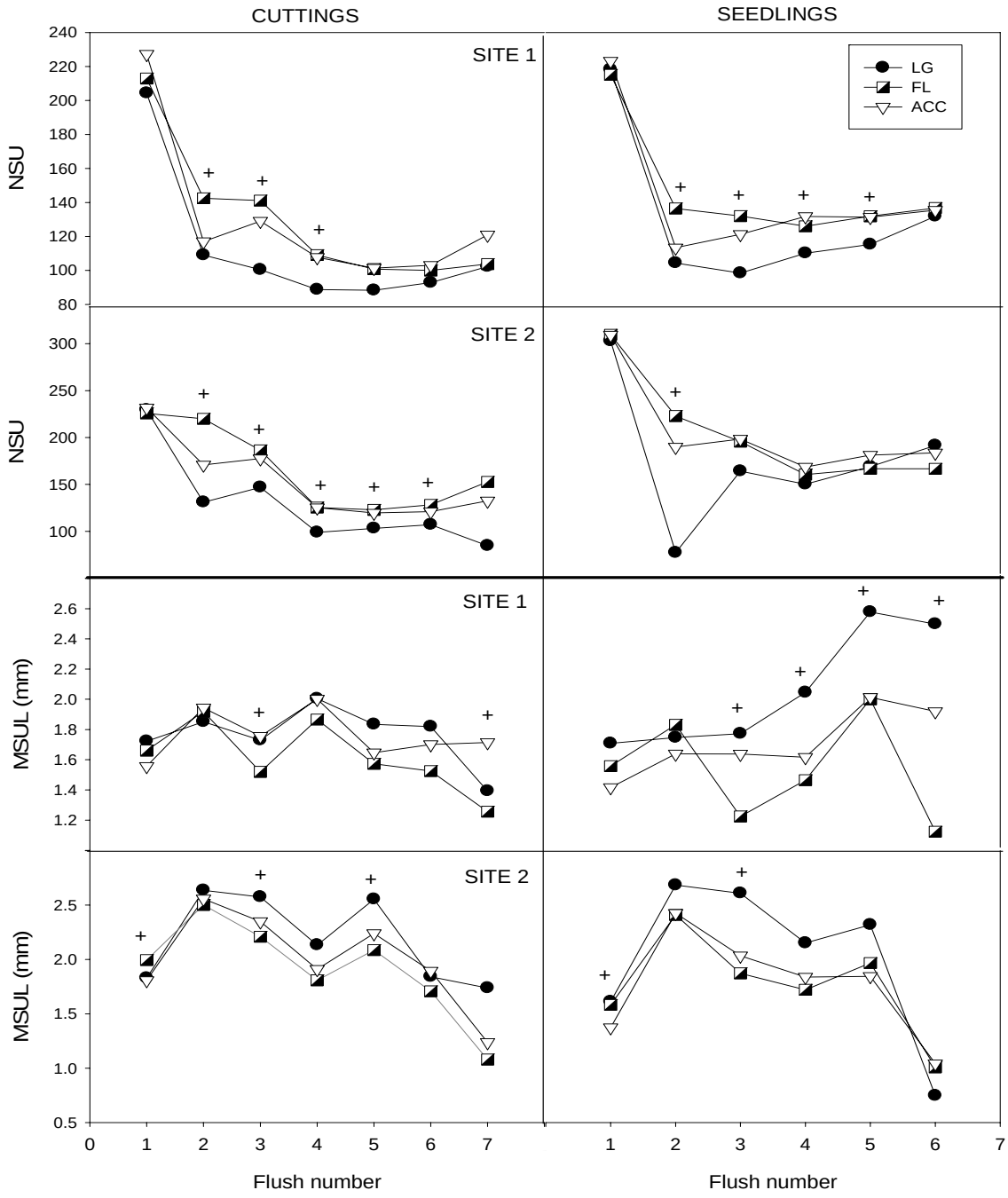

Figure 3-4. Least square means for number of stem units (NSU) and mean stem unit length (MSUL) by propagule type at Site 1 (North Central Florida) and Site 2 (Southwest Georgia). LG, FL and ACC are Lower Gulf, Florida and Atlantic Coastal Plain provenances, respectively. (+) indicates significant differences between the provenances ($p<0.05$).

Provenance demonstrated different shoot elongation patterns. The *FL* provenance had higher growth at the beginning of the growing season while *ACC* and *LG* growth was slightly higher than *FL* seed source after the second flush. Length of the early flushes is what conferred a significant advantage for *FL* cutting over the other seed sources. *LG* provenance had the lowest values for *NSU* and the largest values of *MSUL* at both sites, suggesting that for this provenance *MSUL* was the most important contributor to flush length.

There were no significant differences for provenances for flush 1 for any of the morphological traits analyzed except *MSUL* at Site 2. Values for flush 1 were very similar for the all provenances for all traits.

Phyllostatic Patterns

Phyllostatic patterns demonstrated little genetic variance. Narrow and broad-sense heritability for single site and across-site analyses were extremely low (Appendix C). Similarly, Kremer et al (1989) did not find genetic variability among *P. pinaster, P. banksiana* and*, P. nigra* Arn. ssp. *nigrican* populations or families for phyllostatic traits.

Fibonacci series (3:5:8:13…) were present for 82.5 % of the trees at Site 1 and for 87.9 % of the trees at Site 2. The second most common series was the principal bijugate (4:6:10…) with 12.0% at in Site 1 and 8.3 % at Site 2. First accessory of the monojugate series (4:7:11…) occurred at just 5.5 and 3.2 % at Site 1 and 2, respectively. The principal trijugate series (3:6:9:15…) were present in 0.6 % of the trees at Site 2 and 0% at Site 1 (just 2 trees). At Site 2 one "foxtail" tree had the tetrajugate series (4,8,12…).

The phyllostatic pattern survey for propagule type separately gave similar results as the general, except one for the seedling population at Site 1 (Table 3-17)**.**

Table 3-17. Frequency of phyllostatic series by propagule type in Site 1 (North Central Florida) and 2 (Southwest Georgia)

Pyllostatic series	*Site 1*		*Site 2*	
	Seedlings (%)	*Cuttings (%)*	*Seedlings (%)*	*Cuttings (%)*
Monojugate pattern				
Fibonacci	65.1	86.1	81.0	89.3
First accessory	22.0	9.7	15.1	6.9
Multijugate patterns				
Bijugy	12.9	4.2	2.8	3.2
Trijugy	0.0	0.0	1.1	0.5

These frequencies were comparable to the proportions obtained by Kremer and Roussel (1982); Kremer *et al*. (1989), Zagörska-Marek (1985) and Fady (1990) in *P. pinaster, P. banksiana, P. nigra* Arn. ssp. *nigricans, Abies balsamea,* and *A. cephalonica,* respectively.

CHAPTER 4
CONCLUSIONS

Rooted cuttings differed from seedlings for all phenological and morphological traits that were analyzed in this study. This indicates that regardless of the fact that both propagule types were from the same genetic material the apparent differences in plant architecture and physiological age between them results in different morphological and phenological behavior.

Phenological traits

The results of this study indicated that the average growth rate per day was the most important variable in determining second-year annual height increment. The contribution of growing season duration to second-year annual height increment was negligible. Although significant differences were found among propagule types and seed sources for timing of initiation and cessation these traits were not important contributors to annual height increment. Because average shoot growth rate and growing season duration were low negatively and significantly correlated, growing season duration is a trait that has to be considered because at the same growth rate a longer growing season can result in a difference in height increment. A longer growing season may also adversely affect *FL* material in cooler environment by increasing frost risks.

The narrow and broad-sense heritability estimates for the different dates for height growth increment during the growing season were moderate and decreased from initiation date to cessation date, becoming constant and almost zero for both propagule types after day 268, increment decrease.

Morphological characters

Average flush length was the principal contributor to total annual height while number of flushes had a minor contribution. In our results the most important contribution of number of flushes to total annual height was at Site 2 for seedling material being responsible for 30% of the annual height increment. *NF* and *AvFL* were negatively strongly to moderately and significantly correlated. These results indicate that selecting genetic material for height increment would increase average flush length with minor changes in number of flushes.

NSU was by far the most important phenotypic trait for the length of the three first flushes, and its contribution decreased in subsequent flushes with an increase in the *MSUL* contribution to flush length until reaching to a 1:1 relationship. The genetic contribution of *MSUL* to flush length was relatively larger than the phenotypic contribution becoming more important than *NSU* after flush 3, especially for seedlings.

MSUL and *NSU* were negatively moderately and significantly correlated. The *NSU* and *MSUL* flush length correlations varied greatly depending on the flush and the relationship of *NSU* and *MSUL* to flush length.

Despite *MSUL* and *NSU* being negatively correlated and under low genetic control, both were important determinants of flush lengths and flush length is an important determinant of annual height increment. Thus, both are indirectly important for the maximization of annual height increment. Selection of individuals with high values of *NSU* and *MSUL* would improve annual height growth but comparing heritabilities choosing for height growth directly would be more efficient.

Provenances demonstrated different shoot elongation patterns. *FL* provenance had the highest growth at the beginning of the growing season while *ACC* and *LG* growth was slightly greater than *FL* seed source after the second flush. Length of early flushes appeared to confer a significant advantage for *FL* cutting over the other seed sources.

Phyllostatic patterns had low genetic variability with extremely low narrow and broad-sense heritabilities.

APPENDIX A
DIFFERENCES BETWEEN PROPAGULE TYPES

Table A-1. Significance levels (p-values) between propagule types for annual height increment and phenological traits at Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

Variable	*Significant level between propagule type*
Site 1	
Initiation	<0.000001
Cessation	<0.0000001
Duration	<0.0000001
ASGR	<0.00001
AHI	<0.00001
Site 2	
Cessation	<0.0000001
AHI	<0.000001

ASGR=average shoot growth rate; AHI=annual height increment.

Table A-2. Significance levels (p-values) between propagule types for height increment, average cumulative height increment and average percentage cumulative increment at Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

Variable	*Height increment*	*Average cumulative height increment*	*Average percentage cumulative height increment*
Site 1			
Day			
68	<0.001	<0.001	<0.001
88	<0.001	<0.001	<0.001
141	<0.0001	<0.00001	<0.00001
173	<0.0001	<0.00001	<0.00001
236	<0.00001	<0.00001	<0.0000001
268	<0.001	<0.00001	<0.000000001
278	<0.001	<0.00001	<0.0000000001
299	<0.1	<0.00001	<0.000000001
323	<0.01	<0.00001	
Site 2			
Day			
256	<0.00001	<0.00001	<0.0001
266	<0.0001	<0.0001	<0.0001
273	<0.001	<0.01	<0.000001
294	<0.001	<0.01	<0.00001
321	<0.001	<0.001	<0.00001
349	<0.001	<0.001	<0.00001

Table A-3. Significance levels (p-values) between propagule types for growth and shoot components at Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

Variable by flush N°		*Site 1*	*Site 2*
FLn			
	1	<0.001	<0.0001
	2	<0.01	<0.00001
	3	<0.01	<0.000001
	4	<0.001	<0.00001
	5	<0.001	<0.00001
	6	<0.01	<0.00001
PFL			
	1	<0.001	<0.0001
	2	<0.01	<0.0001
	3	<0.001	<0.000001
	4	<0.001	<0.00001
	5	<0.001	<0.00001
	6	<0.01	<0.00001
NSU			
	1	<0.01	<0.0001
	2	<0.01	<0.0001
	3	<0.001	<0.00001
	4	<0.001	<0.00001
	5	<0.001	<0.00001
	6	<0.01	<0.000001
MSUL			
	1	<0.001	<0.00001
	2	<0.001	<0.000001
	3	<0.01	<0.00001
	4	<0.001	<0.00001
	5	<0.001	<0.00001
	6	<0.001	<0.00001
NF		<0.001	<0.000001
AvFL		<0.001	<0.00001
AHI_{FLn}		<0.001	<0.000001
TH_2		<0.001	<0.000001

Note: *FLn*=flush length; *PFL*=flush contribution to annual height increment in percentage; *NSU*=number of stem units; *MSUL*=mean stem unit length; *NF*= number of flushes; *AvFL*= average flush length; AHI_{FLn}=annual height increment as summation of the flush length; TH_2=second year total height.

APPENDIX B
SECOND-YEAR PHENOTYPIC, GENETIC AND ENVIRONMENTAL CORRELATIONS BETWEEN FLUSH LENGTHS (*FLN*), NUMBER OF STEM UNITS (*NSU*) AND MEAN STEM UNIT LENGTH (*MSUL*) BY FLUSH

Table B-1. Site 1 (North Central Florida): cuttings genetic, phenotypic and environmental (microsite) correlations between flush length (*FLn*) by flush for 2004 growing season.

FLn-FLn correlations

Flush		1	2	3	4	5	6
2	r_{GCA}	0.63 (0.19)					
	r_{SCA}	---					
	$r_{Clone(fam)}$	0.51 (0.15)					
	$r_{Genetic}$	0.52 (0.11)					
	$r_{Phenotypic}$	0.40 (0.02)					
	$r_{Microsite}$	0.37 (0.03)					
3	r_{GCA}	0.25 (0.26)	0.50 (0.20)				
	r_{SCA}	---	-0.03				
	$r_{Clone(fam)}$	0.07 (0.16)	0.88 (0.20)				
	$r_{Genetic}$	0.12 (0.13)	0.70 (0.12)				
	$r_{Phenotypic}$	0.13 (0.03)	0.20 (0.03)				
	$r_{Microsite}$	0.14 (0.04)	0.05 (0.04)				
4	r_{GCA}	0.10 (0.28)	0.17 (0.26)	0.93 (0.05)			
	r_{SCA}	---	---	---			
	$r_{Clone(fam)}$	-0.06 (0.19)	0.44 (0.20)	0.37 (0.17)			
	$r_{Genetic}$	-0.02 (0.15)	0.31 (0.15)	0.61 (0.10)			
	$r_{Phenotypic}$	0.17 (0.03)	0.12 (0.03)	0.43 (0.02)			
	$r_{Microsite}$	0.21 (0.04)	0.04 (0.04)	0.38 (0.03)			
5	r_{GCA}	-0.12 (0.29)	0.15 (0.27)	0.81 (0.11)	0.83 (0.10)		
	r_{SCA}	---	---	---	---	---	
	$r_{Clone(fam)}$	-0.17 (0.20)	-0.15 (0.20)	0.15 (0.19)	0.68 (0.16)		
	$r_{Genetic}$	-0.15 (0.15)	-0.02 (0.15)	0.45 (0.13)	0.75 (0.10)		
	$r_{Phenotypic}$	0.06 (0.03)	-0.13 (0.04)	0.28 (0.03)	0.48 (0.02)		
	$r_{Microsite}$	0.12 (0.04)	-0.15 (0.04)	0.24 (0.04)	0.42 (0.03)		
6	r_{GCA}	-0.84 (0.24)	-0.61 (0.24)	0.57 (0.25)	0.62 (0.28)	1.00 (0.09)	
	r_{SCA}	---	---	---	---	---	
	$r_{Clone(fam)}$	-0.47 (0.31)	-0.56 (0.28)	0.21 (0.30)	0.90 (0.43)	0.83 (0.48)	
	$r_{Genetic}$	-0.55 (0.23)	-0.55 (0.19)	0.35 (0.20)	0.79 (0.27)	0.91 (0.23)	
	$r_{Phenotypic}$	-0.16 (0.23)	-0.40 (0.06)	0.22 (0.04)	0.16 (0.04)	0.55 (0.03)	
	$r_{Microsite}$	-0.08 (0.06)	-0.39 (0.05)	0.20	0.04 (0.06)	0.47 (0.04)	
7	r_{GCA}	---	---	---	---	---	---
	r_{SCA}	---	---	---	---	---	---
	$r_{Clone(fam)}$	---	---	---	---	---	---
	$r_{Genetic}$	---	---	---	---	---	---
	$r_{Phenotypic}$	---	---	---	---	---	---
	$r_{Microsite}$	-0.01 (0.11)	-0.29 (0.10)	0.09 (0.10)	-0.07 (0.10)	0.18 (0.10)	0.37 (0.09)

Note: (---) Correlation could not be estimated because of variances which were 0.

Table B-2. Site 1 (North Central Florida): cuttings genetic, phenotypic and environmental (microsite) correlations between numbers of stem units (NSU) by flush for 2004 growing season.

NSU-NSU correlations

Flush		1	2	3	4	5	6
2	r_{GCA}	0.30 (0.24)					
	r_{SCA}	---					
	$r_{Clone(fam)}$	0.49 (0.17)					
	$r_{Genetic}$	0.42 (0.13)					
	$r_{Phenotypic}$	0.39 (0.02)					
	$r_{Microsite}$	0.38 (0.03)					
3	r_{GCA}	0.49 (0.18)	0.80 (0.12)				
	r_{SCA}	---	0.73 (0.63)				
	$r_{Clone(fam)}$	0.30 (0.13)	1 (0.14)				
	$r_{Genetic}$	0.38 (0.11)	0.91 (0.08)				
	$r_{Phenotypic}$	0.38 (0.03)	0.45 (0.02)				
	$r_{Microsite}$	0.38 (0.03)	0.29 (0.03)				
4	r_{GCA}	0.55 (019)	---	0.91 (0.07)			
	r_{SCA}	---	---	0.00 (1)			
	$r_{Clone(fam)}$	0.38 (0.20)	0.83 (0.14)	0.82 (0.12)			
	$r_{Genetic}$	0.43 (0.13)	---	0.82 (0.06)			
	$r_{Phenotypic}$	0.29 (0.03)	0.21 (0.02)	1 (0.08)			
	$r_{Microsite}$	0.25 (0.03)	0.06 (0.03)	0.47 (0.03)			
5	r_{GCA}	0.66 (0.17)	0.47 (0.23)	0.84 (0.10)	0.97 (0.04)		
	r_{SCA}	---	---	---	---		
	$r_{Clone(fam)}$	0.38 (0.17)	0.66 (0.19)	0.80 (0.11)	1 (0.17)		
	$r_{Genetic}$	0.48 (0.12)	0.57 (0.13)	0.80 (0.07)	1 (0.08)		
	$r_{Phenotypic}$	0.32 (0.03)	0.19 (0.03)	0.44 (0.03)	0.60 (0.02)		
	$r_{Microsite}$	0.28 (0.04)	0.07 (0.04)	0.30 (0.04)	0.44 (0.03)		
6	r_{GCA}	0.65 (0.22)	---	---	---		
	r_{SCA}	---	---	---	---		
	$r_{Clone(fam)}$	0.54 (0.27)	0.44 (0.32)	0.49 (0.18)	0.95 (0.24)	0.87 (0.16)	
	$r_{Genetic}$	0.57 (0.20)	0.32 (0.10)	0.31 (0.12)	0.70 (0.18)	0.87 (0.17)	
	$r_{Phenotypic}$	0.25 (0.04)	-0.04 (0.03)	0.24 (0.03)	0.38 (0.03)	0.50 (0.03)	
	$r_{Microsite}$	0.17 (0.06)	-0.13 (0.06)	0.22 (0.06)	0.32 (0.05)	0.44 (0.05)	
7	r_{GCA}	---	---	---	---	---	---
	r_{SCA}	---	0.38 (0.43)	0.84 (0.50)	---	---	---
	$r_{Clone(fam)}$	---	---	---	---	---	---
	$r_{Genetic}$	---	0.13 (0.15)	0.20 (0.12)	---	---	---
	$r_{Phenotypic}$	---	-0.01 (0.10)	0.15 (0.08)	---	--	--
	$r_{Microsite}$	0.23 (0.11)	-0.04 (0.12)	0.14 (0.11)	0.26 (0.08)	0.28 (0.10)	0.28 (0.09)

Note: (---) Correlation could not be estimated because of variances which were 0.

Table B-3. Site 1 (North Central Florida): cuttings genetic, phenotypic and environmental (microsite)correlations between mean stem unit length (MSUL) by flush for 2004 growing season.

MSUL-MSUL correlations

Flush		1	2	3	4	5	6
2	r_{GCA}	0.64 (0.18)					
	r_{SCA}	---					
	$r_{Clone(fam)}$	0.34 (0.23)					
	$r_{Genetic}$	0.46 (0.15)					
	$r_{Phenotypic}$	0.24 (0.02)					
	$r_{Microsite}$	0.20 (0.03)					
3	r_{GCA}	0.50 (0.19)	0.61 (0.16)				
	r_{SCA}	---	---				
	$r_{Clone(fam)}$	0.11 (0.16)	0.21 (0.20)				
	$r_{Genetic}$	0.27 (0.13)	0.41 (0.13)				
	$r_{Phenotypic}$	0.13 (0.03)	0.16 (0.03)				
	$r_{Microsite}$	0.89 (0.04)	0.08 (0.04)				
4	r_{GCA}	0.58 (0.18)	0.73 (0.16)	---			
	r_{SCA}	---	0.07 (1)	---			
	$r_{Clone(fam)}$	0.34 (0.18)	0.45 (0.22)	0.88 (0.12)			
	$r_{Genetic}$	0.43 (0.13)	0.54 (0.13)	0.55 (0.08)			
	$r_{Phenotypic}$	0.13 (0.03)	0.24 (0.03)	0.24 (0.02)			
	$r_{Microsite}$	0.45 (0.04)	0.17 (0.03)	0.10 (0.04)			
5	r_{GCA}	0.63 (0.20)	0.57 (0.22)	0.74 (0.11)	0.89 (0.07)		
	r_{SCA}	---	---	---	---		
	$r_{Clone(fam)}$	-0.02 (0.18)	0.18 (0.20)	0.79 (0.14)	0.74 (0.14)		
	$r_{Genetic}$	0.21 (0.14)	0.34 (0.16)	0.77 (0.09)	0.81 (0.09)		
	$r_{Phenotypic}$	0.01 (0.03)	0.02 (0.03)	0.30 (0.03)	0.31 (0.03)		
	$r_{Microsite}$	-0.05 (0.04)	-0.06 (0.04)	0.07 (0.03)	0.10 (0.04)		
6	r_{GCA}	0.34 (0.25)	0.12 (0.30)	0.69 (0.14)	-0.21 (0.17)	0.91 (0.09)	
	r_{SCA}	0.99 (0.00)	---	---	---	0.85 (0.38)	
	$r_{Clone(fam)}$	-0.23 (0.30)	-0.03 (0.32)	0.96 (0.28)	1 (0.40)	0.73 (0.21)	
	$r_{Genetic}$	0.01 (0.20)	0.03 (0.22)	0.83 (0.14)	1 (0.08)	0.81 (0.12)	
	$r_{Phenotypic}$	-0.11 (0.04)	-0.21 (0.04)	0.35 (0.04)	0.35 (0.21)	0.53 (0.03)	
	$r_{Microsite}$	-0.14 (0.06)	-0.27 (0.05)	0.17 (0.05)	-0.21 (0.05)	0.43 (0.05)	
7	r_{GCA}	---	---	---	---	---	---
	r_{SCA}	---	---	---	---	---	---
	$r_{Clone(fam)}$	---	---	---	---	---	---
	$r_{Genetic}$	---	---	---	---	---	---
	$r_{Phenotypic}$	--	--	--	--	--	--
	$r_{Microsite}$	-0.13 (0.10)	-0.14 (0.10)	0.13 (0.10)	0.08 (0.10)	0.24 (0.10)	0.55 (0.07)

Note: (---) Correlation could not be estimated because of variances which were 0.

Table B-4. Site 2 (Southwest Georgia): cuttings genetic, phenotypic and environmental (microsite)correlations between flush length (*FLn*) by flush for 2004 growing season.

FLn-FLn correlations

Flush		1	2	3	4	5	6
2	r_{GCA}	0.44 (0.22)					
	r_{SCA}	---					
	$r_{Clone(fam)}$	0.01 (0.10)					
	$r_{Genetic}$	0.11 (0.09)					
	$r_{Phenotypic}$	0.14 (0.03)					
	$r_{Microsite}$	0.16 (0.04)					
3	r_{GCA}	-0.46 (0.22)	-0.1 (0.25)				
	r_{SCA}	---	---				
	$r_{Clone(fam)}$	-0.17 (0.12)	0.33 (0.11)				
	$r_{Genetic}$	-0.24 (0.10)	0.21 (0.10)				
	$r_{Phenotypic}$	-0.16 (0.03)	-0.03 (0.03)				
	$r_{Microsite}$	-0.14 (0.04)	-0.16 (0.04)				
4	r_{GCA}	-0.39 (0.26)	-0.12 (0.25)	0.83 (0.11)	---		
	r_{SCA}	0.61 (1.1)	---	0.93 (1.4)	---		
	$r_{Clone(fam)}$	-0.15 (0.12)	0.20 (0.10)	0.41 (0.12	---		
	$r_{Genetic}$	-0.18 (0.10)	0.11 (0.10)	0.55 (0.10)	---		
	$r_{Phenotypic}$	-0.12 (0.03)	0.01 (0.03)	0.36 (0.03)	---		
	$r_{Microsite}$	-0.09 (0.04)	-0.05 (0.04)	0.28 (0.03)	---		
5	r_{GCA}	-0.48 (0..21)	-0.08 (0.23)	0.74 (0.14)	0.57 (0.17)		
	r_{SCA}	---	---	---	---		
	$r_{Clone(fam)}$	0.02 (0.13)	-0.05 (0.11)	0.29 (0.14)	0.31 (0.14)	---	
	$r_{Genetic}$	-0.13 (0.11)	-0.06 (0.10)	0.45 (0.11)	0.40 (0.11)	---	
	$r_{Phenotypic}$	-0.12 (0.04)	-0.03 (0.04)	0.27 (0.03)	0.26 (0.03)	---	
	$r_{Microsite}$	-0.12 (0.04)	-0.02 (0.04)	0.20 (0.04)	0.21 (0.04)	---	
6	r_{GCA}	-0.34 (0.27)	-0.53 (0.22)	0.34 (0.27)	0.41 (0.25)	0.40 (0.24)	
	r_{SCA}						
	$r_{Clone(fam)}$	0.24 (0.18)	-0.42 (0.11)	0.26 (0.20)	-0.04 (0.18)	-0.09 (0.19)	
	$r_{Genetic}$	0.09 (0.15)	-0.45 (0.10)	0.28 (0.16)	0.09 (0.14)	0.07 (0.15)	
	$r_{Phenotypic}$	-0.08 (0.05)	-0.44 (0.04)	0.08 (0.04)	0.15 (0.04)	0.00 (0.04)	
	$r_{Microsite}$	-0.15 (0.06)	-0.44 (0.05)	0.01 (0.06)	0.18 (0.06)	-0.03 (0.06)	
7	r_{GCA}	-0.55 (0.44)	-0.17 (0.40)	0.67 (0.31)	0.85 (0.39)	0.35 (0.36)	1 (0.27)
	r_{SCA}	---	---	---	---	---	---
	$r_{Clone(fam)}$	0.87 (0.35)	-0.12 (0.23)	0.32 (0.31)	0.35 (0.31)	-0.08 (0.30)	0.13 (0.30)
	$r_{Genetic}$	0.57 (0.29)	-0.13 (0.20)	0.42 (0.23)	0.45 (0.24)	0.06 (0.23)	0.34 (0.23)
	$r_{Phenotypic}$	-0.19 (0.10)	-0.41 (0.10)	0.18 (0.09)	0.11 (0.08)	-0.03 (0.10)	0.19 (0.09)
	$r_{Microsite}$	-0.7 (0.11)	-0.72 (0.13)	0.03 (0.18)	-0.13 (0.18)	-0.09 (0.17)	0.10 (0.18)

Note: (---) Correlation could not be estimated because of variances which were 0.

Table B-5. Site 2 (Southwest Georgia): cuttings genetic, phenotypic and environmental (microsite)correlations between numbers of stem units (NSU) by flush for 2004 growing season

NSU-NSU correlations

Flush		1	2	3	4	5	6
2	r_{GCA}	0.28 (0.24)					
	r_{SCA}	---					
	$r_{Clone(fam)}$	0.04 (0.10)					
	$r_{Genetic}$	0.10 (0.09)					
	$r_{Phenotypic}$	0.23 (0.03)					
	$r_{Microsite}$	0.30 (0.03)					
3	r_{GCA}	0.32 (0.23)	0.34 (0.22)				
	r_{SCA}	---	---				
	$r_{Clone(fam)}$	0.11 (0.12)	0.91 (0.11)				
	$r_{Genetic}$	0.17 (0.11)	0.74 (0.09)				
	$r_{Phenotypic}$	0.16 (0.03)	0.25 (0.03)				
	$r_{Microsite}$	0.16 (0.04)	0.03 (0.04)				
4	r_{GCA}	0.09 (0.30)	0.12 (0.28)	0.76 (0.11)			
	r_{SCA}	---	---	---			
	$r_{Clone(fam)}$	0.11 (0.13)	0.61 (0.11)	0.68 (0.11)			
	$r_{Genetic}$	0.10 (0.12)	0.50 (0.10)	0.70 (0.08)			
	$r_{Phenotypic}$	0.11 (0.03)	0.16 (0.03)	0.43 (0.02)			
	$r_{Microsite}$	0.12 (0.04)	0.02 (0.04)	0.34 (0.03)			
5	r_{GCA}	0.18 (0.30)	0.46 (0.24)	0.85 (0.10)	0.64 (0.23)		
	r_{SCA}	---	---	---	0.85 (0.30)		
	$r_{Clone(fam)}$	0.22 (0.11)	0.68 (0.09)	0.66 (0.11)	0.57 (0.11)		
	$r_{Genetic}$	0.20 (0.10)	0.61 (0.08)	0.75 (0.08)	0.61 (0.09)		
	$r_{Phenotypic}$	0.18 (0.03)	0.34 (0.03)	0.43 (0.03)	0.40 (0.02)		
	$r_{Microsite}$	0.16 (0.04)	0.16 (0.04)	0.30 (0.04)	0.33 (0.04)		
6	r_{GCA}	0.85 (0.54)	0.74 (0.24)	0.96 (0.27)	0.78 (0.40)	0.73 (0.24)	
	r_{SCA}	---	---	---	---	---	
	$r_{Clone(fam)}$	0.44 (0.19)	0.30 (0.16)	0.46 (0.10)	0.46 (0.19)	0.46 (0.20)	
	$r_{Genetic}$	0.48 (0.17)	0.38 (0.14)	0.53 (0.16)	0.47 (0.16)	0.51 (0.16)	
	$r_{Phenotypic}$	0.10 (0.04)	0.24 (0.05)	0.28 (0.04)	0.29 (0.04)	0.41 (0.03)	
	$r_{Microsite}$	-0.03 (0.06)	0.19 (0.06)	0.20 (0.06)	0.24 (0.06)	0.38 (0.05)	
7	r_{GCA}	---	---	---	---	---	---
	r_{SCA}	---	---	---	---	---	---
	$r_{Clone(fam)}$	0.06 (0.20)	0.47 (0.17)	0.26 (0.20)	0.14 (0.18)	0.35 (0.16)	0.44 (0.18)
	$r_{Genetic}$	0.05 (0.16)	0.40 (0.14)	0.20 (0.15)	0.12 (0.15)	0.28 (0.13)	0.43 (0.18)
	$r_{Phenotypic}$	0.03 (0.09)	0.20 (0.08)	0.09 (0.08)	0.08 (0.07)	0.15 (0.07)	0.22 (0.07)
	$r_{Microsite}$	-0.01 (0.24)	-0.20 (0.22)	-0.08 (0.24)	0.13 (0.26)	-0.05 (0.24)	0.13 (0.12)

Note: (---) Correlation could not be estimated because of variances which were 0.

Table B-6. Site 2 (Southwest Georgia): cuttings genetic, phenotypic and environmental (microsite) correlations between mean stem unit length (MSUL) by flush for 2004 growing season.

MSUL-MSUL correlations

Flush		1	2	3	4	5	6
2	r_{GCA}	0.66 (0.14)					
	r_{SCA}	---					
	$r_{Clone(fam)}$	0.49 (0.12)					
	$r_{Genetic}$	0.55 (0.10)					
	$r_{Phenotypic}$	0.36 (0.03)					
	$r_{Microsite}$	0.28 (0.03)					
3	r_{GCA}	0.47 (0.18)	0.85 (0.07)				
	r_{SCA}	---	---				
	$r_{Clone(fam)}$	0.29 (0.12)	0.82 (0.07)				
	$r_{Genetic}$	0.36 (0.10)	0.83 (0.05)				
	$r_{Phenotypic}$	0.20 (0.03)	0.47 (0.03)				
	$r_{Microsite}$	0.12 (0.04)	0.25 (0.03)				
4	r_{GCA}	0.42 (0.20)	0.63 (0.15)	0.85 (0.08)			
	r_{SCA}	---	---	---			
	$r_{Clone(fam)}$	0.37 (0.12)	0.43 (0.09)	0.53 (0.07)			
	$r_{Genetic}$	0.39 (0.10)	0.49 (0.08)	0.63 (0.06)			
	$r_{Phenotypic}$	0.16 (0.03)	0.22 (0.03)	0.39 (0.03)			
	$r_{Microsite}$	0.06 (0.04)	0.05 (0.04)	0.23 (0.03)			
5	r_{GCA}	0.34 (0.21)	0.77 (0.11)	0.84 (0.08)	0.69 (0.13)		
	r_{SCA}	---	---	---	---		
	$r_{Clone(fam)}$	0.21 (0.13)	0.53 (0.10)	0.70 (0.08)	0.47 (0.09)		
	$r_{Genetic}$	0.26 (0.11)	0.61 (0.08)	0.75 (0.06)	0.54 (0.08)		
	$r_{Phenotypic}$	0.14 (0.03)	0.31 (0.03)	0.41 (0.03)	0.28 (0.03)		
	$r_{Microsite}$	0.09 (0.04)	0.14 (0.04)	0.19 (0.04)	0.13 (0.04)		
6	r_{GCA}	0.14 (0.32)	0.68 (0.21)	0.80 (0.17)	0.59 (0.25)	0.59 (0.23)	
	r_{SCA}	---	---	---	---	---	
	$r_{Clone(fam)}$	0.14 (0.15)	0.32 (0.12)	0.44 (0.10)	0.30 (0.11)	0.33 (0.11)	
	$r_{Genetic}$	0.13 (0.13)	0.40 (0.10)	0.51 (0.09)	0.36 (0.10)	0.39 (0.10)	
	$r_{Phenotypic}$	0.04 (0.04)	0.15 (0.04)	0.34 (0.04)	0.20 (0.04)	0.26 (0.04)	
	$r_{Microsite}$	0.00 (0.06)	0.00 (0.06)	0.22 (0.06)	0.11 (0.06)	0.19 (0.06)	
7	r_{GCA}	---	---	---	---	---	---
	r_{SCA}	---	---	---	---	---	---
	$r_{Clone(fam)}$	---	---	---	---	---	---
	$r_{Genetic}$	---	---	---	---	---	---
	$r_{Phenotypic}$	---	---	---	---	---	---
	$r_{Microsite}$	0.00 (0.10)	-0.10 (0.10)	0.22 (0.09)	0.22 (0.09)	0.26 (0.10)	0.28 (0.10)

Note: (---) Correlation could not be estimated because of variances which were 0.

APPENDIX C
SECOND-YEAR GROWING SEASON PHYLLOSTATIC PATTERNS.

Table C-1. Individual tree narrow and broad-sense heritabilities for phyllostatic patterns by propagule type for 2004 growing season in Site 1 (North Central Florida) and Site 2 (Southwest Georgia).

Phyllostatic pattern by flush	*Seedlings*		*Cuttings*	
	h^2	H^2	h^2	H^2
Site 1				
1	0.05 (0.09)	0.05 (0.09)	0.00 (0.00)	0.06 (0.02)
2	0.03 (0.08)	0.03 (0.08)	0.00 (0.00)	0.05 (0.02)
3	0.04 (0.08)	0.04 (0.08)	0.00 (0.00)	0.05 (0.02)
4	0.06 (0.09)	0.06 (0.09)	0.00 (0.00)	0.06 (0.02)
5	0.00 (0.00)	0.24 (0.32)	0.00 (0.00)	0.07 (0.03)
6	0.49 (0.58)	1.00 (1.25)	0.00 (0.02)	0.20 (0.06)
7	---	---	0.27 (0.43)	0.14 (0.21)
Site 2				
1	0.00 (0.00)	0.19 (0.23)	0.00 (0.01)	0.00 (0.01)
2	0.00 (0.00)	0.18 (0.23)	0.00 (0.01)	0.01 (0.04)
3	0.10 (0.10)	0.10 (0.10)	0.01 (0.01)	0.02 (0.04)
4	0.00 (0.00)	0.12 (0.24)	0.00 (0.01)	0.00 (0.01)
5	0.19 (0.18)	0.19 (0.18)	0.01 (0.02)	0.00 (0.01)
6	0.19 (0.77)	1.00 (1.10)	0.00 (0.00)	0.08 (0.10)
7	---	---	0.10 (0.42)	0.05 (0.21)

LIST OF REFERENCES

Allen, H.L., and Wentworth, T.R. 1993. Vegetation control and site preparation affect patterns of shoot elongation for 3-year-old loblolly pine. Can. J. For. Res. **23** (10): 2110-2115.

Allen, R.M., and Scarbrough, N.M. 1970. Morphology and length correlated in terminal flushes of longleaf pine saplings. U.S.D.A. Forest Service Research Paper SO-53 pp.15.

Bailey, D.B., and Feret, P.P. 1982. Short note: shoot elongation in *Pinus rigida* x *taeda hybrids*. Silvae Genet. **31** (5-6): 209-212.

Baltunis, B.S., Huber, D.A., White, T.L., Goldfarb, B., and Stelzer, H.E. 2005. Genetic effects of rooting loblolly pine stem cuttings from a partial diallel mating design. Can. J. For. Res. **35**: 1098-1108.

Bollmann, M.P., and Sweet, G.B. 1977. Bud morphogenesis of *Pinus radiata* in New Zealand. 1. The initiation and extension of the leading shoot of one clone at two sites. N. Z. J. For. Sci. **6**: 376-392.

Bongarten, B. 1986. Relationships between shoot length and shoot length components in Douglas-fir and blue spruce. Can. J. For. Res. **16**: 373-380.

Boyer, W. 1970. Shoot growth patterns of young loblolly pine. For. Sci. **16** (4): 472-482.

Bridgwater, F.E. 1990. Shoot elongation patterns of loblolly pine families selected for contrasting growth potential. For. Sci. **36** (3): 641-656.

Bridgwater, F.E., and McKeand, S.E. 1997. Early family evaluation for growth of loblolly pine. For. Genet. **4** (1): 51-58.

Bridgwater, F.E., Williams, C.G., and Campbell, R.G. 1985. Patterns of leader elongation in loblolly pine families. For. Sci. **31** (4): 933-944.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Volume 1. Conifers. USDA Agriculture Handbook 654. Washington, DC.: 1018-1051.

Cannell, M.G.R. 1978. Components of conifer shoot growth. In: Proceedings of 5th North American Forest Biology Workshop. University of Florida, Gainesville, FL: 313-318.

Cannell, M.G.R., and Johnstone, R.C.B. 1978. Free or lammas growth and progeny performance in *Picea sitchensis*. Silvae Genet. **27**: 248-254.

Cannell, M.G.R., Thompson, S., and Lines, R. 1976. An analysis of inherent differences in shoot growth within some north temperate conifers. Tree Physiol. and yield improvement (Cannell, M.G.R., and Last, F.T., eds): 173-205, Academic Press, New York. 567p.

Cannell, M.G.R., and Willett, S.C. 1976. Shoot growth phenology, dry matter distribution and root: shoot ratios of provenances of *Populus trichocarpa*, *Picea sitchensis* and *Pinus contorta* growing in Scotland. Silvae Genet. **25** (2): 49-59.

Carlson, W.C. 1985. Effects of natural chilling and cold storage on budbreak and root growth potential of loblolly pine (*Pinus taeda* L.). Can. J. Bot. **15**: 651-656.

Critchfield, W.B. 1985. Internode or stem unit: a problem of terminology. For. Sci. **31** (4): 911-912.

DeWald, L., White, T.L., and Duryea, M.L. 1992. Growth and phenology of four contrasting slash pine families in ten nitrogen regimes. Tree Physiol. **11**: 255-269.

Doak, C.C. 1935. Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*. Illinois Biological Monographs, Urbana, IL, University of Illinois **13** (3): 106 p.

Dougherty, P.M., Vose, W. D., and J.M. 1994. Environmental influences on the phenology of pine. Ecol. Bull. **43**: 64-75.

Ekberg, I., Eriksson, G., Namkoong, G., Nilsson, C., and Norell, L. 1994. Genetic correlations for growth rhythm and growth capacity at ages 3-8 years in provenance hybrids of *Picea abies*. Scand. J. Forest Res. **9**: 25-33.

Fady, B. 1990. Variabilite genetic des composant de la croissance en hauteur du sapin de cephalonie (*Abis cephalonica*). Can. J. For. Res. **20** (9): 1453-1460.

Falconer, D.S., and Mackay, T.F.C. 1996. Introduction to quantitative genetics. 4th Edition. Longman Group Ltd., Essex, England. 464 p.

Forest Biology Research Cooperative (FBRC) 2000. Study B: clonal biology and performance of elite genotypes of loblolly and slash pine. FBRC Report # 13. Forest Biology Research Cooperative, Univ. Florida, Gainesville, FL, 31 p.

Forest Biology Research Cooperative (FBRC) 2003. Forest Biology Research Cooperative 7th Annual Report. FBRC Report # 23. Forest Biology Research Cooperative, Univ. of Florida, Gainesville, FL, 100 p.

Ford, E.D. 1980. Impact of environment on the shoot elongation of conifers: short term effects. Control of shoot growth in trees. In: Proceeding of the joint workshop of IUFRO working parties on xylem physiology and shoot growth physiology: July 20-24, Fredericton, New Brunswiick, Canada: 1-7-126.

Fredeen, A.L., Horning, J.A., and Madill, R.W. 2002. Spiral phyllotaxis of needle fascicles on branches and scales on cones in *Pinus contorta* var. latifolia: Are they influenced by wood-grain spiral? Can. J. Bot. **80**: 166-175.

Gilmour, A.R., Gogel, B.J., Cullis, B.R., Welham, S.J., and Thompson, R. 2002. ASReml user guide release 1.0. VSN International Ltd., Hemel Hempstead, HP1 1ES, UK. 267p.

Gómez Cardenas, M., Vargas, Vernandez, J.J., JassoMata, J., Velásquez Martínez, A., and Rodríguez Franco, C. 1998. Patrón de crecimiento anual del brote terminal en árboles jóvenes de *Pinus patula*. Agrociencia. **3** (4): 357-364.

Greenwood, M.S. 1980. Reproductive development in loblolly pine: I. The early development of male and female strobili in relation to the long shoot growth behavior. Amer. J. Bot. **67** (10): 1414-1422.

Griffing, C.G., and Elam, W.W. 1971. Height growth patterns of loblolly pine sapling. For. Sci. **17** (1): 52-54.

Guyon, J.P. 1986. Influencie du climat sur l'expression des composantes de la croissance en hauteur chez le pin noir d' Autriche (*Pinus nigra* Arn. ssp *nigricans*). Ann. Sci. Forest. **43** (2): 207-226.

Hanover, J.W. 1963. Geographic variation in ponderosa pine leader growth. For. Sci. **9** (1): 86-95.

Harrington, C.A. 1991. Retrospective shoot growth analysis for three seed sources of loblolly pine. Can. J. For. Res. **21** (3): 306-317.

Isik, F., Isik, K., Yildirim, T., and Li, B. 2002. Annual shoot growth components related to growth of *Pinus brutia*. Tree Physiol. **22**: 51-58.

Isik, F., Li, B., and Frampton, L.J. 2003. Additive, dominance, and epistatic variance estimates from a replicated clonal test of loblolly pine. For. Sci. **49**: 77-88.

Jayawickrama, K.J.S., McKeand, S.E., and Jett, J.B. 1998. Phenological variation in height and diameter growth in provenances and families of loblolly pine. New Forest. **16**: 11-25.

Jean, R.V. 1988. Phyllotatic pattern generation: a conceptual model. Ann. Bot. **61**: 293-303.

Jokela, E.J., and Long, A.J. 2000. Using soils to guide fertilizer recommendations for southern pines. Florida Cooperative Extension Service Circular 1230. 9 p.

Kaya, Z. 1993. Genetic variation in shoot growth components and their correlations in *Pseudotsuga menziesii* var. *menziesii* seedlings. Scand. J. For. Res. **8** (1): 1-7.

Kremer, A. 1985. Component analysis of height growth, compensation between components and seasonal stability of shoot elongation in maritime pine (*Pinus pinaster* Ait.). Crop physiology of forest trees: 203-217.

Kremer, A., and Larson, P.R. 1983. Genetic control of height growth components in jack pine seedlings. For. Sci. **29** (3): 451-464.

Kremer, A., and Lascoux, D.M. 1988. Genetic architecture of height growth in maritime pine (*Pinus pinaster* Ait.). Silvae Genet. **37** (1): 1-8.

Kremer, A., and Roussel, G. 1982. Composantes de la croissance en hauteur chez le pin maritime (*Pinus pinaster* Ait.). Ann. Sci. Forest. **39** (1): 77-97.

Kremer, A., and Xu, L. 1989. Relationship between first-season free growth components and later field height growth in maritime pine (*Pinus pinaster*). Can. J. For. Res. **19**: 690-699.

Kremer, A., Xu, L.A., Guyon, J.P., and Roussel, G. 1989. Genetic, age and ontogenetic variation of phyllotactic arrangements in pine species. Can. J. Bot. **67** (4): 1254-1261.

Lanner, R.M. 1976. Patterns of shoot development in pinus and their relationship to growth potencial. Tree Physiol. and Yield Improvement (Cannell, M.G.R., and Last, F.T., eds): 223-244, Academic Press, New York. 567p.

Li, B., Williams, C., Carlson, W.C., Harrington, C.A., and Lambeth, C.C. 1992. Gain efficiency in short-term testing: experimental results. Can. J. For. Res. **22** (3): 290-297.

Li, P., and Adams, W.T. 1993. Genetic control of bud phenology in pole-size trees and seedlings of coastal Douglas-fir. Can J. Forest Res. 23: 1043-1051.

Lu, P., Joyce, D.G., and R.W. Sinclair. 2003. Effect of selection on shoot elongation rhythm of eastern white pine (*Pinus strobus* L) and its implications to seed transfer in Ontario. Forest Ecology and Management. **182**: 161-173.

Magnussen, S., and Yeatman, C.W. 1989. Height growth components in inter- and intra-provenance jack pine families. Can. J. For. Res. **19**: 962-972.

McCrady, R.L., and Jokela, E.J. 1996. Growth phenology and crown structure of selected loblolly pine families planted at two spacings. For. Sci. **42**: 46-57.

McKeand, S.E., Mullin, T., Byram, T.D., and White, T. 2003. Deployment of genetically improved loblolly and slash pines in the south. J. Forest. **101** (3): 32-37.

Mirov, N.T., Duffield, J.W., and Liddicoet, A.R. 1952. Altitudinal races of *Pinus ponderosa* a 12-year progress report. J. Forest. **50**: 825-831.

Monroe, K.W. 2005. Soil Survey of Randolph County, GA. USDA Natural Resources Conservation Service. 289p. http://www.mo15.nrcs.usda.gov/technical/surveys/georgia/randolph/Randolph.pdf. March, 2006.

Perry, T.O., Wang, C.W., and Schmitt, D. 1966. Height growth for loblolly pine provenances in relation to photoperiod and growing season. Silvae Genet. **15**: 61-100.

Pollard, D., and Logan, K. 1974. The role of summer shoots in the differentiation of provenances of black spruce. Can. J. For. Res. **4**: 308-311.

Readle, E.L. 1990. Soil Survey of Putnam County, FL. USDA Natural Resources Conservation Service. 224p.

Rehfeldt, G.E., and Lester, D.T. 1966. Variation in shoot elongation of *Pinus resinosa* (Ait.). Can. J. Bot. **44**: 1457-1469.

Richards, F.J. 1951. Phyllotaxis: its quantitative expression and relation to growth in the apex. Philo. Trans. R. Soc. London, Ser. B. 235: 509-563.

Rweyongeza, D.M., Yeh, F.C., and Dhir, N.K. 2003. Genetic variation in stem growth components in white spruce seedlings and its implications to retrospective early selection. For. Genet. **10**: 4299-4308.

Smith, C.K., White, T.L., and Hodge, G.R. 1993a. Genetic variation in second-year slash pine shoot traits and their relationship to 5- and 15-year volume in the field. Silvae Genet. **42** (4-5): 266-275.

Smith, C.K., White, T.L., Hodge, G.R., Duryea, M.L., and Long, A.J. 1993b. Genetic variation in first-year slash pine shoot components and their relationship to mature field performance. Can. J. For. Res. **23** (8): 1557-1565.

Surles, S.E. 1993. Early selection for volume growth in slash pine. (Ph. D. dissertation. University of Florida, Gainesville. pp. 81).

Waxler, M.S., and Van Buijtenen, J.P. 1981. Early genetic evaluation of loblolly pine. Can. J. For. Res. **11**: 351-355.

Williams, C.G. 1988. Accelerated short-term genetic testing for loblolly pine families. Can. J. For. Res. **18**: 1085-1089.

Wright, S. 1968. Evolution and the genetics populations. University of Chicago Press, Chicago, IL.

Yamada, Y. 1962. Genotype by environment interaction and genetic correlation of the same trait under different environments. Jpn. J. Genet. **37**: 498-509.

Zagörska-Marek, B. 1985. Phyllotactic patterns and transitions in *Abies balsamea*. Can. J. Bot. **63**: 1844-1854.

Zhang, S.S., Allen, H.L., and Dougherty, P.M. 1997. Shoot and foliage growth phenology of loblolly pine trees as affected by nitrogen fertilization. Can. J. For. Res. **27** (9): 1420-1426

BIOGRAPHICAL SKETCH

Liliana Parisi was born in the town of La Plata in Argentina and grew up in the city of Pergamino, Buenos Aires Province, a region without many trees but where agriculture and cattle are very popular. In 1996, she graduated as an Agricultural Engineer at the Universidad Nacional de La Plata (UNLP) in La Plata, Argentina. Between 1997 and 2003, she worked as a junior researcher at the forestry division of INTA Bella Vista Experimental Station. She enrolled in the School of Forest Research and Conservation master's program in August 2003 at the University of Florida. After her graduation, she will continue her studies at the University of Florida pursuing her PhD degree.