

2002

Modeling canopy structure effects on loblolly pine growth

Mauricio Jerez Rico

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_dissertations

Recommended Citation

Jerez Rico, Mauricio, "Modeling canopy structure effects on loblolly pine growth" (2002). *LSU Doctoral Dissertations*. 837.

https://digitalcommons.lsu.edu/gradschool_dissertations/837

This Dissertation is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Doctoral Dissertations by an authorized graduate school editor of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.

MODELING CANOPY STRUCTURE EFFECTS ON LOBLOLLY PINE GROWTH

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The School of Forestry, Wildlife, and Fisheries

by

Mauricio Jerez Rico

B.S., Universidad de Los Andes, Venezuela, 1987

M.S., Universidad de Los Andes, 1992

May 2002

ACKNOWLEDGMENTS

This research would not have been possible without the assistance and cooperation of many individuals and institutions. I thank my advisor Dr. Thomas J. Dean who guided me through this difficult endeavor and showed me new paths to carry out research in Forestry. I am indebted to Dr. Quang V. Cao who helped me many times in the analysis of data and gave me very useful advice, to Dr. Jim L. Chambers who provided support in the physiological aspects of this work, and to Drs. Bill Platt and Gordon Holcomb for their advice and useful comments.

I extend my thanks for their help and friendship to Patricia Young, Karen Vellupillai, and Shufang Yu from the Ecophysiology Lab; Mary Bowen and Dr. Mike Stine from the Genetics Lab, and to Jesús Franco, Ziyin Wang, Dennis Tucker, Minyi Zhou, Chris Dicus, and Jamie Schexnayder from the Forest Productivity and Silviculture labs.

I express my gratitude to the people of Mississippi State University: Ross Hosea, Jessica Smith, Emily Loden, and Katie Fairly for their cooperation during field work, and specially to Dr. Scott Roberts for his support and useful comments. Thanks to Dr. Barry Moser and Yukun Ren from the Department of Experimental Statistics of LSU and Argenis Mora from the School of Forestry of Universidad de los Andes by their statistical advice. Special thanks to Dr. Larry Vincent for encouraging me to accomplish this goal and to AnaYajaira Moret de Peña for her help and support.

Financial aid was generously provided by several organizations. I am very grateful to Universidad de Los Andes and Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICIT) from Venezuela, and to Fulbright-LASPAU from the United States Information Agency (USIA). These institutions gave me the possibility to come to the United

States and provided the funding for my studies. I also want to thank the School of Forestry, Wildlife, and Fisheries and the International Services Office by their support along these years, and to the Graduate School for the tuition waivers awarded. A NASA Grant (NAG 13-99018) provided funds for field and lab work. The Southern Experimental Station of the USDA Forest Service generously provided the long-term data used in this study.

I dedicate this Dissertation to my mother Maria Concepción, who always supported me during the most difficult times and to my son Mauricio David who motivated me to complete this work.

TABLE OF CONTENTS

| | |
|---|-----|
| ACKNOWLEDGMENTS..... | ii |
| LIST OF TABLES..... | vi |
| LIST OF FIGURES..... | vii |
| ABSTRACT..... | ix |
| CHAPTER 1. INTRODUCTION..... | 1 |
| CHAPTER 2. MODELING THE VERTICAL DISTRIBUTION OF FOLIAGE AREA FOR YOUNG LOBLOLLY PINE PLANTATIONS WITH THE JOHNSON'S S _B DISTRIBUTION..... | 5 |
| 2.1. INTRODUCTION..... | 5 |
| 2.2. MATERIALS AND METHODS..... | 7 |
| 2.2.1. Data..... | 7 |
| 2.2.2. Model development..... | 9 |
| 2.2.3. Model evaluation..... | 15 |
| 2.3. RESULTS AND DISCUSSION..... | 17 |
| 2.3.1. Prediction of percentiles from tree dimensions..... | 17 |
| 2.3.2. Comparisons of parameters..... | 19 |
| 2.3.3. Model evaluation..... | 21 |
| 2.4. CONCLUSIONS..... | 24 |
| 2.5. SUMMARY..... | 26 |
| CHAPTER 3 A PRELIMINARY STAND GROWTH MODEL DRIVEN BY CANOPY DYNAMICS FOR UNTHINNED LOBLOLLY PINE STANDS..... | 28 |
| 3.1. INTRODUCTION..... | 28 |
| 3.2. THE MODEL..... | 29 |
| 3.2.1. Philosophy and basic premises..... | 29 |
| 3.2.2. Model construction..... | 32 |
| 3.2.3. Data..... | 38 |
| 3.3. MODEL ANALYSIS..... | 39 |
| 3.3.1. Simulation of yield and growth..... | 39 |
| 3.3.2. Size-density and leaf area relationships..... | 43 |
| 3.4. DISCUSSION..... | 48 |
| 3.5. SUMMARY AND CONCLUSIONS..... | 51 |
| CHAPTER 4. PATTERNS OF BRANCH PERMEABILITY WITH CROWN DEPTH AMONG LOBLOLLY PINE FAMILIES DIFFERING IN GROWTH RATE AND CROWN SIZE..... | 53 |
| 4.1. INTRODUCTION..... | 53 |
| 4.2. MATERIALS AND METHODS..... | 54 |
| 4.2.1. Permeability measurements..... | 56 |

| | |
|---|----|
| 4.2.2. Statistical analysis..... | 58 |
| 4.3. RESULTS AND DISCUSSION..... | 59 |
| 4.3.1. Top stem permeability..... | 59 |
| 4.3.2. Branch permeability..... | 60 |
| 4.4. SUMMARY AND CONCLUSIONS..... | 67 |
| CHAPTER 5. SUMMARY AND CONCLUSIONS..... | 70 |
| LITERATURE CITED..... | 73 |
| VITA..... | 79 |

LIST OF TABLES

| | |
|--|----|
| 2.1. Mean values of stem diameter, total height (H_T), crown length (C_L), and total leaf area (A_L) for the loblolly pine trees sampled in the destructive harvest..... | 8 |
| 2.2. Statistics from the regression model, $A_T = 1/H_{MC} (D/a)^b$ to predict total leaf area for the various categories of destructively sampled loblolly pine trees. In the equation A_T is total leaf area, D is stem diameter (DBH or root collar diameter), and H_{MC} is height to the crown midpoint..... | 16 |
| 2.3. Mean values and standard deviations of parameter estimates for the S_B distribution that describes the vertical distribution of leaf area for individual loblolly pine trees. The parameters γ and δ were obtained for each tree by using equations 2.4 and 2.5 in the text, respectively..... | 20 |
| 2.4. Average values of mean deviations (MD), mean absolute deviations (MAD), and fit index (FI) for various groups of loblolly pine relative cumulative leaf area ($RCLA$) and absolute cumulative leaf area (CLA , m^2)..... | 22 |
| 3.1. Summary statistics for the fit and validation data sets from loblolly pine stands..... | 40 |
| 3.2. Parameter estimates for the components of the model..... | 41 |
| 4.1. Results for the mixed covariance analysis for the natural logarithm of branch permeability ($m^2 \times 10^{-12}$) of loblolly pine families assuming different intercepts and a common slope for combinations of growth rate and crown size. Relative crown depth is treated as a covariate. Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA..... | 63 |
| 4.2. Mean values and results of the t-test ($\alpha = 0.1$) for mean differences of crown dimensions and foliage variables in loblolly pine families differing in crown size. In parenthesis are standard errors. Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA..... | 66 |
| 4.3. Results for the analysis of the final mixed covariance model for current foliage--total foliage area ratio in loblolly pine families differing in crown size. Levels for contrasts at selected crown depths are denoted by CS_L (large-crown size) and CS_S (small-crown size). Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA..... | 68 |

LIST OF FIGURES

| | |
|---|----|
| 2.1. Analogy between foliage distribution and a probability distribution function. The bars in (a) and the step line in (b) represent the observed leaf area distribution. The curves represent the probability density function (<i>pdf</i>) in (a) and the cumulative distribution function (<i>cdf</i>) in (b) of the probability distribution..... | 10 |
| 2.2. Observed (●) and predicted (○) average leaf area (m^2) as a function of relative crown depth for loblolly pine. Predicted leaf area was obtained from the S_B fitted with predicted percentiles from crown dimensions. (a) 15-year-old large-crown trees from Starr Forest in MS; (b) 15-year-old small-crown trees from Starr Forest in MS; (c) 12-year-old trees from Lee Forest in LA; (d) unfertilized 4-year-old trees from Fred, TX; (e) fertilized 4-year-old trees from Fred, TX..... | 23 |
| 2.3. Boxplots of the residuals (observed - predicted) of the fit of the S_B to the leaf area distribution of loblolly pine trees of various age classes and treatments for the total leaf area distribution by classes 0.1 intervals of relative crown depth for loblolly pine trees. Edges of the box indicate the 25 and 75 sample percentiles of the data. Lines include the 10 and 90 percentiles. The center drawn line is the 50 percentile. Individual points are extreme values. (a) 15-year-old large-crown trees from Starr Forest in MS; (b) 15-year-old small-crown trees from Starr Forest in MS; (c) 12-year-old trees from Lee Forest in LA; (d) unfertilized 4-year-old trees from Fred, TX; (e) fertilized 4-year-old trees from Fred, TX..... | 25 |
| 3.1. Schematic representation of the basic components of the model and their interactions. Boxes indicate state variables and valves represent the processes affecting the state variables..... | 30 |
| 3.2. Flow diagram of model implementation. Equation numbers (in parenthesis) for computing the attributes are included..... | 33 |
| 3.3. Simulated outputs for selected variables representing growth and yield for a stand with surviving density of 2500 trees/ha and site index of 20 at base age 25 years. (a) Dominant height (H_D), average height (H_T), and height to the crown base (H_B) versus age. (b) Tree density (N) versus age. (c) Mean quadratic diameter (Q) and maximum quadratic diameter (Q_{max}) versus age. (d) Leaf area index (LAI) and basal area (BA) versus age. (e) Current annual increment (CAI) and mean annual increment (MAI) in volume versus age. (f) Mean tree volume (V) and total stand volume (V_t)..... | 42 |
| 3.4. Simulated growth age and size-density relationships. (a) Current annual increment versus age; (b) stand density index vs. age; (c) Current annual increment vs. stand density index; (d) quadratic mean diameter vs. stand density. Surviving densities at the beginning of the simulations are: 1200 (.....), 1800 (— · —), and 3600 trees/ha (— · —). SI = site index (m) at base age 25..... | 44 |

| | |
|--|----|
| 3.5. Relations of leaf area index with current annual increment and growth efficiency for combinations of surviving density and site index. (a) Leaf area index versus age. (b) Current annual increment versus leaf area index. (c) Growth efficiency versus age. (d) Growth efficiency versus leaf area index. Surviving densities at the beginning of the simulations are 1200 (.....), 1800 (— · —), and 3600 trees/ha (— .. —). SI = site index (m) at base age 25..... | 46 |
| 4.1. Mean values of hydraulic permeability at the top of stem of loblolly pine families differing in crown size. Sample size is 17 and 28 for large and small-crown size families respectively. P is the p-value for the effect of crown size using the model represented by eq. 4.2. Error bars are standard errors. Data are from a progeny trial established in 1985 on the John Starr Memorial Forest near Starkville, MS, USA..... | 61 |
| 4.2. Branch permeability as a function of relative crown depth (RCD) and crown size (CS). Regression lines were obtained from the model $Ln(k) = -0.374 + 0.2859 \times D - 0.45701 \times RCD$, where D=0 for small-crown families and D=1 for large crown families. Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA..... | 64 |

ABSTRACT

This study examined several aspects of canopy structure and their influence on growth of loblolly pine (*Pinus taeda* L.) plantations. Foliage distribution, crown hydraulic architecture, and the effect of chronological changes in canopy structure on stand development were explored as possible components of a future process-based model intended for management purposes.

A model based on the Johnson's S_B distribution was developed to predict leaf area distribution of loblolly pine trees. This is a preliminary step for building a submodel capable of simulating chronological changes in canopy structure and stand growth. The model accurately predicted the cumulative distribution of leaf area in the crown. It has the potential to be included in forest growth models where an accurate description of leaf area distribution is needed.

A novel process-related, non-carbon-based growth model for predicting the growth of closed, unthinned, loblolly pine stands was developed. Its ability to represent the dynamics of the canopy and stand growth was evaluated. Overall, model predictions were in agreement with reported observations or proposed theories in relation to stand growth, size-density relations, and relationships between canopy dynamics and stand growth.

Modeling the hydraulic architecture of the crown is important because it controls crown recession. Patterns in branch permeability with crown depth and permeability at the top of the main stem were analyzed for loblolly pine trees from families selected for differences in growth rate and crown size. The results showed that branch permeability decreased significantly from the top to the bottom of the crown and that genetic-based differences might exist in patterns of stem and branch permeability.

The study showed the potential of using a process approach to develop a forest growth model and utilizing mechanistic and empirical elements in the construction of the simulator. In addition, the integration and synthesis of information coming from diverse sources in the model allow the possibility of detecting deficiencies in the understanding of key processes and provide a guide for formulating hypotheses and planning experiments to fill the gaps in knowledge of the processes regulating stand development.

CHAPTER 1

INTRODUCTION

From a forest management perspective, it is important to understand how natural and induced factors affect present and future forest productivity. Forest models, which are based on biologically sound principles can help achieve that understanding and at the same time produce accurate predictions of future growth and yield of forests under varying silvicultural practices and environmental conditions. Models are tools that help solve problems by providing a simplified representation of a real system and simulating its behavior under a specified set of conditions (Korzukhin et al. 1996). Particularly, forest process-based models are tools that attempt to synthesize our knowledge and understanding of physiological and ecological mechanisms affecting forest growth into predictive algorithms (Johnsen et al. 2001). However, the complexity of these models, poor understanding of some key processes, and lack of data have hindered their acceptance as management tools. Therefore, it has been thought that empirical models are more suitable for the task (Mäkelä et al. 2000). Progress was made toward the application of process-based models as predictive tools in forest management after recognition that both empirical and process based models are part of a continuum from purely empirical to purely process-based models and that the most efficient way to develop predictive forest models is to use the best features in both methodologies. One approach is to conceive the model in terms of the biological processes involved. Then, model construction would proceed using mechanistic processes when they are well understood and empirical relationships when there is not a reasonable theory to describe a process or data for supporting it (Korzukhin et al. 1996; Mäkelä et al. 2000; Johnsen et al. 2001). Examples of this approach are “hybrid models”, in which mechanistic-based elements are blended with

statistical approaches. These models usually represent biological processes in a simplified way, have reduced data requirements, and can be applied across different forests and stand conditions (Johnsen et al. 2001).

This study explores the feasibility of developing a hybrid growth model for loblolly pine (*Pinus taeda* L.) plantations using biological hypotheses that explain the relationship between canopy dynamics and stand development. Some important processes affecting this relationship were examined, modeled, and used as a basis for producing a preliminary process-related model with mechanistic and empirical components.

Canopy dynamics is important in understanding mechanisms regulating forest production (Waring et al. 1981; Kuulivainen 1991). The canopy is the place where important physiological processes such as photosynthesis, respiration, and transpiration occur, and it affects primary production, particularly wood production, as the stem is the main component of the supportive and transport structures of the tree. Therefore, incorporating elements of canopy dynamics is essential for the development of efficient process-related forest growth models. Modeling the leaf area distribution is an essential step for constructing process-based models with research and predictive purposes.

Light penetration and interception by forest canopies are intricately tied to the spatial distribution of foliage and its supporting structures. Quantification of the vertical foliage distribution serves the purposes of characterizing the initial state of the canopy and measuring the change in distribution as a response to natural or induced factors. In this study, a model for predicting leaf area distribution of loblolly pine trees from tree dimensions was developed as a preliminary step for building a submodel capable of simulating chronological changes in canopy structure and stand growth with time under various stand conditions.

Canopy structure and size-density relationships in a stand are strongly interrelated. A feedback mechanism by which stand growth and yield can be predicted consists on modeling dynamic process by which canopy structure (mainly leaf area and its distribution) regulates stem growth and size, which affects the size-density relationships of the stand, which in turn, determines future changes in canopy structure. A process-related, non-carbon based model for unthinned loblolly pine stands was developed based on this mechanism.

An essential aspect in the construction of a canopy dynamics model driven by physiological processes is to predict changes in height to the base of the live crown. Prevalent theories attribute crown recession to insufficient levels of light received by the lower branches. It is hypothesized that in lower crown positions the carbon fixed by branches is not enough to compensate the cost of respiration and maintenance of living structures, much less to produce new leaves (Waring et al. 1981; Sampson and Smith 1993). More recently, hypotheses that incorporate components of hydraulic architecture on processes of height growth and crown recession are gaining acceptability. For example, Protz et al. (2000) proposed that the process that drives crown recession is related with reduced permeability of lower branches as consequence of the effect of reduced light levels in xylem development. Therefore, variations in hydraulic permeability of branches may be a critical factor regulating the process of crown recession, and could constitute the basis for the development of process-based submodels that replace the traditional empirical models used for describing this process.

There were three main objectives in this study. (1) I developed a mathematical model based on a probability function to predict the leaf area distribution of loblolly pine trees growing under various stand conditions as a component for a process-related model. (2) I developed a novel process-related, non-carbon-based growth model for predicting the growth

of closed, unthinned, loblolly pine stands. (3) I examined some elements of the hydraulic architecture of the crowns of loblolly pine, particularly the patterns of branch permeability and their association with foliage structure, as an initial step for integrating hydraulic and mechanical relationships within a canopy dynamics model.

CHAPTER 2

MODELING THE VERTICAL DISTRIBUTION OF FOLIAGE AREA FOR YOUNG LOBLOLLY PINE PLANTATIONS WITH THE JOHNSON'S S_B DISTRIBUTION

2.1. INTRODUCTION

Models that simulate growth and yield of forest stands can benefit from the quantitative description of vertical leaf area distribution. The spatial distribution of foliage and its supporting structures determine the pattern of light attenuation and the distribution of photosynthesis, transpiration, and nutrient cycling (Massman 1982). In addition, stem geometry is strongly affected by the distribution of foliage (Larson 1963; Dean and Long 1986; West et al. 1989). Because silvicultural practices are known to alter foliage distribution, changes in radial increments along the stem might be modeled based on the effect of these treatments on leaf area distribution (West et al. 1989).

Vertical foliage distribution can be included into a growth and yield model. This can be accomplished using a mathematical submodel that is able to generate a smooth curve and captures realistically the properties of the observed foliage distribution and their dynamics under varying conditions. To be of practical use, this model will need as input, information on properties of the foliage distribution (e.g., mean, variance, percentiles) that can be easily obtained using nondestructive techniques. Several nondestructive methods are based on developing equations to predict the properties of the foliage distribution based on attributes of the tree (e.g., diameter at breast height, total height, crown ratio) that can be measured easily on the ground or with remote sensing techniques. Then, the predicted properties of the observed distribution can be used as input to calculate the parameters of an appropriate mathematical function that will produce a smooth curve resembling the observed foliage

distribution for trees with varying characteristics. Statistical probability distributions are mathematical functions that are suitable for such purpose.

Probability functions are very appropriate to describe the vertical distribution of leaf area. These functions can take a broad range of shapes and its parameters can be related to easily measured variables. Several probability functions have been used to model vertical foliage distributions, e.g., the normal (Kinnerson and Fritschen 1971), the beta (Maguire and Bennett 1996), and the Weibull distributions (e.g., Gillespie et al. 1994; Baldwin et al. 1997; Xu and Harrington 1998). The normal distribution has been used frequently (e.g., Stephens 1969), but it is a symmetric distribution and has infinite tails. The Weibull distribution has been widely used because of its flexibility, but this distribution has an infinite right tail and must be truncated to fit foliage distributions (Maguire and Bennett 1996). The beta is very flexible and has definite end-points at both sides of the distribution; thus, it may be more suitable than a Weibull distribution for fitting foliage distributions (Maguire and Bennett 1996). A probability function that rarely has been used to fit foliage distributions is the Johnson's S_B (Johnson 1949a). Like the beta, the S_B has definite end-points, but is slightly more flexible. In addition, fractions of leaf area within specific intervals of crown depth can be obtained easily with simple tabulated values of the standard normal distribution. Finally, several methodologies are available to predict the parameters of the S_B indirectly from tree attributes. The main objectives of this study were (1) to examine the ability of the S_B distribution to describe the leaf area distribution of loblolly pine trees and (2) use the S_B distribution as a model for predicting the projected leaf area distribution of loblolly pine trees of various age classes and treatments by using easily measured tree dimensions as predictor variables.

2.2. MATERIALS AND METHODS

2.2.1. Data

Measurements of projected foliage area (m^2) of individual trees came from three separate studies carried out in plots from long-term trials established to investigate the effects of genetic families and silvicultural practices on the growth of loblolly pine plantations. The data came from 52, 15-year-old trees destructively sampled in August 1999 from a trial established at the John Starr Memorial Forest near Starkville, MS. The trial consisted of eight open-pollinated families from North Carolina selected for differences in growth rate and crown size. Trees were planted at 3 x 1.5 m spacing. A second set of 24, 12-year-old trees came from a destructive harvest carried out in December 1993 on a spacing trial (1.2×1.2 m and 2.4×2.4 m) established at Lee Memorial Forest in southeast Louisiana. Finally, 43, 4-year-old trees were destructively sampled in August 1998 from a long-term research study near Fred, TX where factorial combinations of harvest impact, site preparation, and fertilization were applied to plots. Site and climate characteristics for these sites are described elsewhere (Roberts et al. 2002; Dicus 2000; Carter et al. 2002).

Mean and standard deviations for selected tree characteristics, including leaf area per tree are shown in Table 2.1. Trees from Fred, TX and the Starr Forest were sampled during peak leaf area in late summer. Trees from Lee Forest were sampled in winter and represent minimum leaf area. Border, forked, and damaged trees were discarded from the analysis.

All destructive harvests and leaf area measurements were carried out using the following methodology. After felling, stems were divided into 1-meter sections (0.5 m for trees from Fred, TX). Within the crown, branches were removed from each section and

Table 2.1. Mean values of stem diameter, total height (H_T), crown length (C_L), and total leaf area (A_L) for the loblolly pine trees sampled in the destructive harvest.

| Group [*] | n [†] | Stem diameter (cm) [§] | | H_T (m) | | C_L (m) | | A_L (m ²) | |
|--------------------|----------------|------------------------------------|-----------------|--------------|------|--------------|------|----------------------------|-----------------|
| | | Mean | SD [‡] | Mean | SD | Mean | SD | Mean | SD [§] |
| 1 | 23 | 18.25 | 3.71 | 15.97 | 1.84 | 6.08 | 1.16 | 23.76 | 12.41 |
| 2 | 29 | 18.66 | 2.81 | 17.10 | 1.02 | 6.10 | 1.35 | 26.99 | 12.47 |
| 3 | 24 | 11.38 | 2.71 | 11.70 | 1.09 | 5.04 | 1.35 | 8.39 | 5.46 |
| 4 | 18 | 3.44 | 1.83 | 3.23 | 0.75 | 2.54 | 0.63 | 5.76 | 5.30 |
| 5 | 25 | 4.62 | 2.27 | 3.55 | 0.96 | 2.93 | 0.96 | 7.95 | 7.18 |

* Groups: (1) 15-year-old large-crown trees from Starr Forest in MS; (2) 15-year-old small-crown trees from Starr Forest in MS; (3) 12-year-old trees from Lee Forest in LA; (4) unfertilized 4-year-old trees from Fred, TX; (5) fertilized 4-year-old trees from Fred, TX.

[†] Sample size.

[§] DBH for groups 1, 2, and 3; root collar diameter for groups 4 and 5.

[‡] Standard deviation.

separated into current-year foliage and twigs, previous year's foliage and twigs, and nonfoliated live branches. Each component was weighed fresh, and a subsample was removed for determination of moisture content and proportions of foliage and branch mass within each component. Approximately 20 needle fascicles were collected from each age class of foliage within each section, stored on ice, and returned to the lab for specific leaf area (SLA) determination. Total projected leaf area was determined for each section. Section totals were summed for total crown leaf area. Live crown length was converted to relative crown depth. Relative cumulative leaf area is the leaf area from the tip of the crown to a given crown depth divided by the total leaf area of the crown. This allowed for comparisons of the shape of the distribution among trees of varying sizes and from different stands.

2.2.2. Model development

Vertical foliage distribution can be represented in a growth and yield model by characterizing the dynamics of foliage distribution with a set of equations. Several statistical probability distributions are suitable for this purpose. A probability distribution function may be defined by its probability density function (*pdf*), $f(x, \theta)$, where x is a random variable and θ is a set of parameters that define the shape of the distribution. The cumulative distribution function (*cdf*), $F(x; \theta)$, $0 \leq F(x; \theta) \leq 1$, is the result of integrating the *pdf*. If crown depth is considered as the random variable x , then leaf area distribution may be expressed in terms of a probability function by setting the *pdf* equal to the distribution of fractions of leaf area at given intervals of the crown depth. Then, the curve formed by accumulating the amounts of foliage from the tip to the base of the crown would be analogous to the *cdf* of a probability distribution (Figure 2.1). The values of θ determine the possible shapes that a probability function can assume. By estimating the set of parameters of $F(x; \theta)$ in terms of empirical

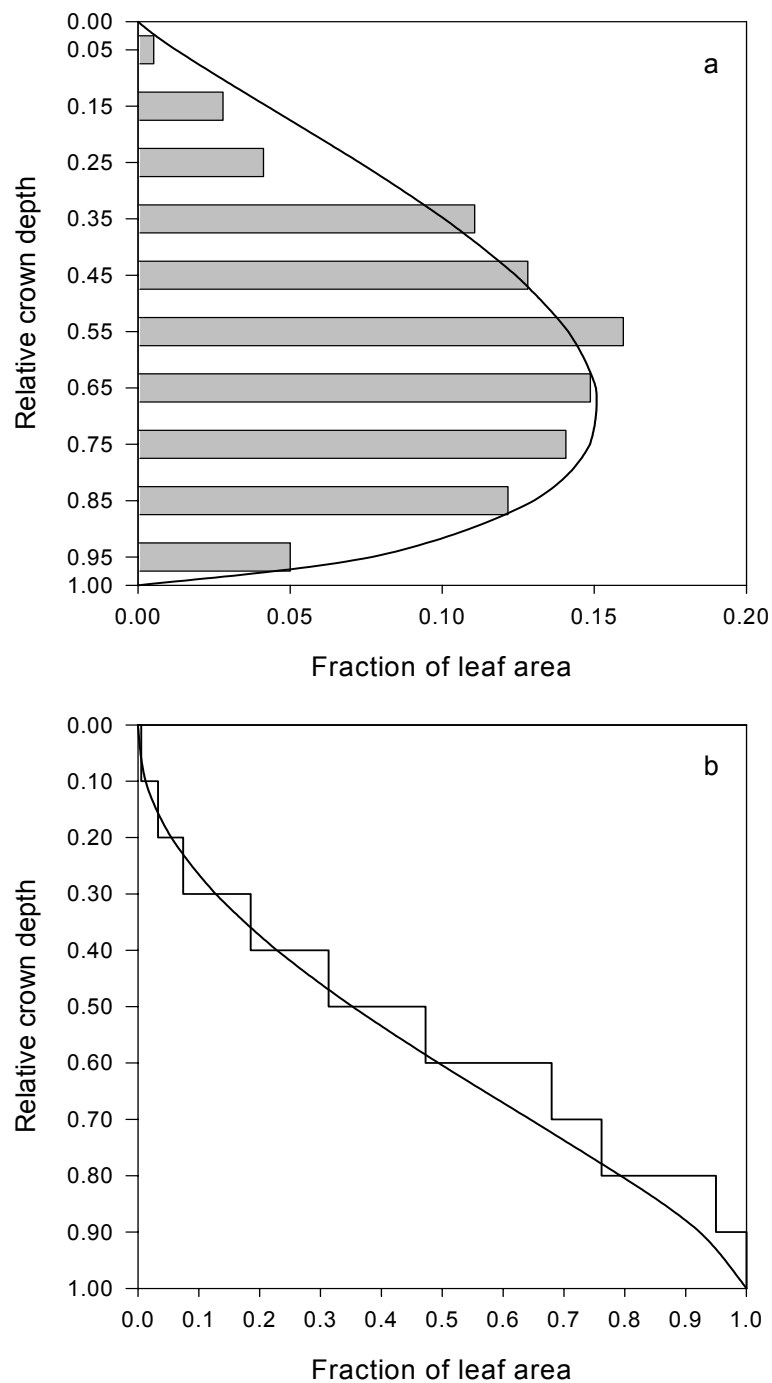


Figure 2.1. Analogy between foliage distribution and a probability distribution function. The bars in (a) and the step line in (b) represent the observed leaf area distribution. The curves represent the probability density function (pdf) in (a) and the cumulative distribution function (cdf) in (b) of the probability distribution.

observations of the leaf area distribution, it is possible to calculate the cumulative or density values of the function at any point along the range of crown depths and to produce a smooth curve that closely resembles the observed leaf distribution.

The practical utility of modeling leaf area distribution using probability functions depends on the ability to predict the parameters of the distributions from tree dimensions or stand variables (Kershaw and Maguire 1996). The *percentile prediction* method consists of developing equations for predicting the location of the leaf area percentiles along the crown from tree variables based on a sample of trees. The predictive equations are then used to calculate the parameters of a probability function and produce a smooth curve resembling the actual leaf area distribution of trees (Knoebel and Burkhardt 1991). One advantage of this method is that the location of leaf area percentiles may be related to the status of the tree within the stand and provide a biological basis for the predicted distribution (Maguire and Bennett 1996).

The model was developed using the Knoebel and Burkhardt (1991) two-percentile method to fit the S_B function to the observed foliage distribution of each destructively sampled tree. Then, predictive equations were developed to estimate the location of the leaf area percentiles of the sampled trees as a function of various tree dimensions. For each tree, the predicted percentiles were used to calculate the parameters of the S_B distribution and generate a smooth curve resembling the actual foliage distribution. In addition, an adequate predictive equation to estimate total leaf area from tree dimensions was used. The final model was evaluated by comparing the predicted leaf area distributions with the observed leaf area distribution of the sampled trees.

2.2.2.1. The S_B probability distribution and curve fitting

The Johnson's S_B distribution (Johnson, 1949a) belongs to a family of distributions based on transformations of a random variable, x , to a standard normal variable, z , as follows:

$$(2.1) \quad z_x = \gamma + \delta \ln\left(\frac{x - \varepsilon}{\varepsilon + \lambda - x}\right),$$

where ε , λ , γ , and δ are parameters and $\varepsilon \leq x \leq \varepsilon + \lambda$, $\delta > 0$, $-\infty \leq \gamma \leq \infty$, $-\infty < \varepsilon < \infty$, $\lambda > 0$. The parameter ε is the lower limit of the range and λ is the range of the distribution, and γ and δ are parameters controlling the shape of the distribution (Johnson 1949a). The cumulative distribution function of the S_B can be expressed as

$$(2.2) \quad F(x, \varepsilon, \lambda, \gamma, \delta) = \Phi(z_x),$$

where $(0 \leq F(x, \varepsilon, \lambda, \gamma, \delta) \leq 1)$, and $\Phi(z_x)$ can be solved for any value of x by use of the standard normal distribution. In this study, x is defined as relative crown depth ($0 < x < 1$). This sets ε and λ to 0 and 1, respectively, reducing the cumulative distribution function to

$$(2.3) \quad F(x, \gamma, \delta) = \Phi\left[\gamma + \delta \ln\left(\frac{x}{1-x}\right)\right].$$

Equation 2.3 can be used to calculate the cumulative fraction of leaf area at any relative crown depth. The shape parameters γ and δ were calculated using the two-percentile method with the following formulae (Knoebel and Burkhart 1991)

$$(2.4) \quad \delta = \frac{z_{xp}}{\ln\left(\frac{x_p}{1-x_p}\right) - \ln\left(\frac{x_{50}}{1-x_{50}}\right)}$$

and

$$(2.5) \quad \gamma = -\delta \ln\left(\frac{x_{50}}{1-x_{50}}\right),$$

where, z_{xp} is the standard normal value corresponding to the x_p cumulative percentile, and x_{50} and x_p are the relative crown depth points where the 50th and p^{th} percentiles of cumulative leaf area occur. In their work, Knoebel and Burkhardt (1991) chose the 50th and 95th percentiles to fit diameter distributions. The 50th percentile should be used because it is necessary to derive the parameter equations (Knoebel and Burkhardt 1991).

The parameter γ is associated with the skewness (i.e., degree of asymmetry) and δ with the kurtosis (i.e., degree of peakedness) of the distribution (Siekierski 1992). The parameter γ takes a value of zero when the distribution is symmetric, is positive when the distribution is skewed positively (upward), and negative when the distribution is negatively (downward) skewed. The larger is the value of δ , the larger the kurtosis or peakedness of the distribution.

2.2.2.2. Percentile prediction from tree dimensions

A series of linear and nonlinear models were screened to develop equations for predicting the location of various percentiles of leaf area (5th, 10th, ..., 95th) from ground accessible tree dimensions. Candidate dimensions were determined from correlation analysis. Prediction models were selected according to statistical and biological criteria. The statistical quality of the model was assessed with the adjusted coefficient of determination (adj-R^2) and the square root of the mean square error (Draper and Smith 1981). Predictor variables included stem diameter (D) at breast height or at the root collar, depending on tree size, and vertical crown dimensions. Vertical crown dimensions included total height (H_T); height to base of the live crown (H_B); crown length ($C_L = H_T - H_B$); crown ratio ($CR = C_L/H_T$); height to crown midpoint ($H_{MC} = H_B + (H_T - H_B)/2$); and relative height (H_{REL}). Relative height was defined as total tree height divided by the average height of dominants and codominants in the

stand. This value is an indicator of the competitive status of a tree within the stand (Maguire and Bennett 1996). Crown ratio and height to the crown midpoint are related to tree size and crown position within the stand. Combinations of D and vertical crown dimensions such as D^2H_T and D/H_T were also analyzed. The effect of age, fertilization, spacing, and genetic differences was assessed with indicator variables. Residuals were checked for normality, homogenous variance, autocorrelation, and multicollinearity. A value of $\alpha = 0.05$ was set to test the hypothesis that regression coefficients did not differ from zero. The coefficients of linear models and nonlinear models were obtained through ordinary linear and nonlinear least squares algorithms included in SAS (Statistical Analysis System v. 8.1, Cary, NC). The final equation set showed correlations among the residuals, thus the coefficients were reestimated using seemingly unrelated regression following the recommendations of Borders (1989).

2.2.2.3. Prediction of total leaf area

An equation for estimating total leaf area is critical in modeling leaf area distributions. Although the shape of the distribution might be recovered accurately, errors in total leaf area amplify prediction errors in the distribution model. Because the precision of leaf area models vary according to stand characteristics (Whitehead 1978), the data were stratified according to the following criteria: (1) 15-year-old trees from families selected for large crowns, (2) 15-year-old trees from families selected for small crowns, sampled in summer (3) 12-year-old trees sampled in winter, (4) 4-year-old unfertilized trees, and (5) 4-year-old fertilized trees sampled in summer. Groups (1) and (2) were distinguished according to previously observed differences in the allometric relationships between leaf area and tree dimensions (Roberts et al. 2002). Groups (4) and (5) were distinguished according to large differences in the average amount of leaf area.

The chosen model to predict total leaf area (A_T , m²) was the following nonlinear equation derived from the uniform-stress model (Dean and Long 1986),

$$(2.6) \quad A_T = \frac{1}{H_{MC}} \cdot \left(\frac{D}{a} \right)^b,$$

where D is stem diameter (DBH or root collar diameter), H_{MC} as defined in 2.2.2.2, and a and b are parameters to be estimated. This model showed the lowest bias across ages and stand conditions among a variety of available models derived from tree dimensions. The statistics of the fitted model for each group are shown in Table 2.2.

2.2.3. Model evaluation

In this study, all data were used in model construction to obtain the best possible estimates of the prediction error. Given the small sample size, no much gain in reliability would be obtained by splitting the data in fit and validation data sets (Roecker 1991). The ability of the models to predict leaf area distribution was evaluated by comparing the observed cumulative distribution against the predicted cumulative distribution for each tree using residual-based statistics. These statistics include the mean deviations (MD) for detecting bias, its complementary measure, the mean of absolute deviations (MAD) and the fit index (FI) for measuring model precision. The MD is computed as

$$(2.7) \quad MD = \frac{1}{n} \sum_{i=1}^n (y_i - \hat{y}_i),$$

where y_i and \hat{y}_i are the observed and predicted value of cumulative leaf area at relative crown depth i , respectively; and n is the number of values calculated for each tree. Models with low bias will have values of MD close to zero, and the sign of MD indicates whether the bias is positive or negative. The value of MD can be misleading when large positive and

Table 2.2. Statistics from the regression model, $A_T = 1/H_{MC} (D/a)^b$ to predict total leaf area for the various categories of destructively sampled loblolly pine trees. In the equation A_T is total leaf area, D is stem diameter (DBH or root collar diameter), and H_{MC} is height to the crown midpoint.

| Group* | n [†] | Coefficients [§] | | Sy.x | Adjusted-R ² |
|--------|----------------|---------------------------|----------|-------|-------------------------|
| | | <i>a</i> | <i>b</i> | | |
| 1 | 23 | 16.58842 [†] | 2.336520 | 7.00 | 0.70 |
| 2 | 29 | 26.47313 | 2.970365 | 5.75 | 0.79 |
| 3 | 24 | 25.98581 | 2.795451 | 3.84 | 0.87 |
| 4 | 18 | 14.68500 | 2.399037 | 1.30 | 0.95 |
| 5 | 25 | 19.96653 | 2.615111 | 16.32 | 0.62 |

* Groups: (1) 15-year-old large-crown trees from Starr Forest, MS; (2) 15-year-old small-crown trees, from Starr Forest, MS; (3) 12-year-old trees from Lee Forest, LA; (4) unfertilized 4-year-old trees, Fred, TX; (5) 4-year-old trees, fertilized, Fred, TX.

[†] Sample size.

[§] All coefficients significant with $P < 0.05$.

negative biases sum to zero. The value of MAD measures the true magnitude of the bias. The value of MAD is computed as

$$(2.8) \quad MAD = \frac{1}{n} \sum_{i=1}^n |y_i - \hat{y}_i|.$$

The fit index (FI) measures the precision of the model being analogous to the R^2 (Kvålseth 1985), but it varies between $-\infty$ and 1, with 1 indicating a perfect fit. The value of FI is computed as

$$(2.9) \quad FI = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2},$$

where \bar{y} is the mean of the observed leaf area for each tree. Mayer and Butler (1993) discussed the interpretation of these statistics in detail. The bias and precision of the models of absolute leaf area were analyzed with more detail for each group by comparing differences between the observed and predicted fractions of leaf area and amounts of leaf area (m^2) at 10 percent intervals of crown depth.

2.3. RESULTS AND DISCUSSION

2.3.1. Prediction of percentiles from tree dimensions

In addition to the 50th percentile, the 15th percentile was chosen to estimate the parameters of the S_B because its location in the crown was better correlated with tree dimensions than any other percentile of the distribution. Nonlinear models including crown ratio and height to the crown midpoint were the best predictors of x_{15} and x_{50} . An indicator variable (I) distinguishing the 4-year old trees from the 12 -15-year-old trees increased considerably the adjusted- R^2 for all models. The final set of equations for x_{15} and x_{50}

with their coefficients reestimated using seemingly unrelated regression was

$$(2.10) \quad x_{15} = \exp(-2.87162 + 1.11342 \cdot CR + 0.103323 \cdot H_{MC} + 0.806217 \cdot I),$$

$$(\text{Adjusted-}R^2 = 0.35, \text{Sy.x} = 0.080, n = 119)$$

and

$$(2.11) \quad x_{50} = \exp(-1.37013 + 0.569773 \cdot CR + 0.046272 \cdot H_{MC} + 0.346872 \cdot I),$$

$$(\text{Adjusted-}R^2 = 0.24, \text{Sy.x} = 0.008, n = 119).$$

Although this study did not cover a full range of ages, the results indicate that the relationship between the location of the leaf percentiles and tree dimensions is affected by the stage of stand development. The relationship was weaker for 4-year old trees than for older groups, probably due to low levels of intertree competition, as canopy closure had not occurred. Brix (1981) found that variation in the foliage distribution of Douglas fir was a response to light availability along the crown profile. Possibly the relation between tree dimensions and properties of the leaf area distribution is stronger during the interval between canopy closure and self-thinning.

With the exception of the Lee Memorial Forest trees, which were measured in winter, the average location of the selected leaf area percentiles was similar for all stands. The location of the 50th percentile provides useful information about the symmetry of the distribution. The relative crown depth for the mean of the 50th percentile ranged from 0.56 to 0.60 for trees measured in summer when leaf area peaked, indicating a downward skewed distribution. The average location of x_{50} for the Lee Forest group did not differ significantly ($P < 0.05$) from 0.5 of relative crown depth, but it differed significantly from the other groups which had x_{50} located significantly below the center of the crown. More uniform distributions for the Lee Forest group might be the result of lower amounts of leaf area at the bottom of the

crown caused by the shedding of previous year needles. Baldwin et al. (1997) found that leaf phenology in loblolly pine affected considerably the predictions of foliage weight, surface area, and their vertical distribution. The effect of genetics on the location of this percentile was also analyzed by comparing the means of the individual families from Starr Forest, but although the average location of x_{50} ranged from 0.51 to 0.62 of relative crown depth, no significant differences were found.

Apparently, a downward skewed leaf area distribution is advantageous at different stages of stand growth. A nonuniform crown structure reduces the vertical gradient of light attenuation within the tree crown compared with a uniform foliage distribution. Nonuniform distributions allow a better illumination at the lower parts of the crown so that leaves will have higher photosynthetic rates than leaves at the bottom of the crown of trees with a more uniform foliage distribution (Wang et al. 1990).

2.3.2. Comparisons of parameters

Differences in the average values of the parameters γ and δ for each group provide information differences on the leaf area distribution among groups (Table 2.3). The average value of γ ranged from -0.46 to 0.10 , whereas, δ ranged from 0.92 to 1.05 . In all groups, with exception of Lee Forest, the γ parameter was negative indicating that, on average, leaf area is concentrated toward the bottom of the crown. A one-way analysis of variance followed by a protected least significant difference (LSD) test showed that the mean value of γ for the Lee Forest group differed significantly ($P < 0.05$) from the mean value of the other groups. This indicates a concentration of leaf area toward the upper part of the crown in the Lee Forest group, probably due to loss of the previous year's foliage cohort, as measurements were done in winter. A similar test for the means of δ indicated no significant differences between

Table 2.3. Mean values and standard deviations of parameter estimates for the S_B distribution that describes the vertical distribution of leaf area for individual loblolly pine trees. The parameters γ and δ were obtained for each tree by using equations 2.4 and 2.5 in the text, respectively.

| Group* | N [†] | γ | | δ | |
|--------|----------------|----------|------------------|----------|------|
| | | Mean | SD ^{\$} | Mean | SD |
| 1 | 23 | -0.33 | 0.43 | 0.94 | 0.29 |
| 2 | 29 | -0.26 | 0.26 | 0.94 | 0.18 |
| 3 | 24 | 0.10 | 0.42 | 0.92 | 0.24 |
| 4 | 18 | -0.46 | 0.49 | 1.00 | 0.29 |
| 5 | 25 | -0.41 | 0.43 | 1.05 | 0.28 |

* Groups: (1) 15-year-old large-crown trees from Starr Forest in MS; (2) 15-year-old small-crown trees from Starr Forest in MS; (3) 12-year-old trees from Lee Forest in LA; (4) unfertilized 4-year-old trees from Fred, TX; (5) fertilized 4-year-old trees from Fred, TX.

[†] Sample size.

^{\$} Standard deviation.

groups. Thus, the degree of peakedness of the distribution for all groups could be considered similar.

2.3.3. Model evaluation

The percentile-based S_B model predicted well the cumulative distribution of relative leaf area ($RCLA$, Table 2.4) of individual trees within each group. Values of MD and MAD were low for all groups indicating overall low bias. In addition, the FI values were high (≥ 0.95) indicating a high precision in the estimations for all groups. There were no appreciable differences in bias and precision for any group.

The predictions of absolute cumulative leaf area (CLA , m^2) showed increased bias and lower precision with respect to relative leaf area as indicated by the values of MD , MAD , and FI (Table 2.4). Biases for the absolute cumulative leaf area were relatively small for all groups, although no clear patterns were observed. Larger biases and lower precisions in the groups are related to their respective models of total leaf area because bias and precision for the relative cumulative distribution of leaf area were not appreciably different for any group. The FI values for absolute cumulative leaf area were considerably lower for 15-year-old large-crown families and 4-year-old fertilized trees than for the other groups, reflecting the lower precision of the total leaf area models for these former groups.

The predicted average leaf distribution for each group closely resembled the overall shape of the observed distribution when differences between the observed and predicted amounts of leaf area (m^2) at 10 percent intervals of crown depth were compared (Figure 2.2). It can be observed that leaf area tend to be underpredicted at the bottom of the crown for all groups.

Table 2.4. Average values of mean deviations (*MD*), mean absolute deviations (*MAD*), and fit index (*FI*) for various groups of loblolly pine relative cumulative leaf area (*RCLA*) and absolute cumulative leaf area (*CLA*, m²).

| Group [*] | n [†] | <i>RCLA</i> | | | <i>CLA</i> | | |
|--------------------|----------------|-------------|------------|-----------|-------------------------|--------------------------|-----------|
| | | <i>MD</i> | <i>MAD</i> | <i>FI</i> | <i>MD</i> ^{\$} | <i>MAD</i> ^{\$} | <i>FI</i> |
| 1 | 23 | -0.01 | 0.04 | 0.96 | 0.06 | 2.10 | 0.63 |
| 2 | 29 | -0.01 | 0.03 | 0.97 | -0.25 | 1.78 | 0.79 |
| 3 | 24 | 0.00 | 0.04 | 0.95 | -0.24 | 0.93 | 0.81 |
| 4 | 18 | -0.01 | 0.03 | 0.97 | -0.04 | 0.43 | 0.73 |
| 5 | 25 | 0.00 | 0.04 | 0.96 | 0.04 | 1.07 | 0.52 |
| Mean | 119 | 0.00 | 0.04 | 0.96 | -0.10 | 1.31 | 0.71 |

* Groups: (1) 15-year-old large-crown trees from Starr Forest in MS; (2) 15-year-old small-crown trees from Starr Forest in MS; (3) 12-year-old trees from Lee Forest in LA; (4) unfertilized 4-year-old trees from Fred, TX; (5) fertilized 4-year-old trees from Fred, TX.

[†] Sample size.

^{\$} m².

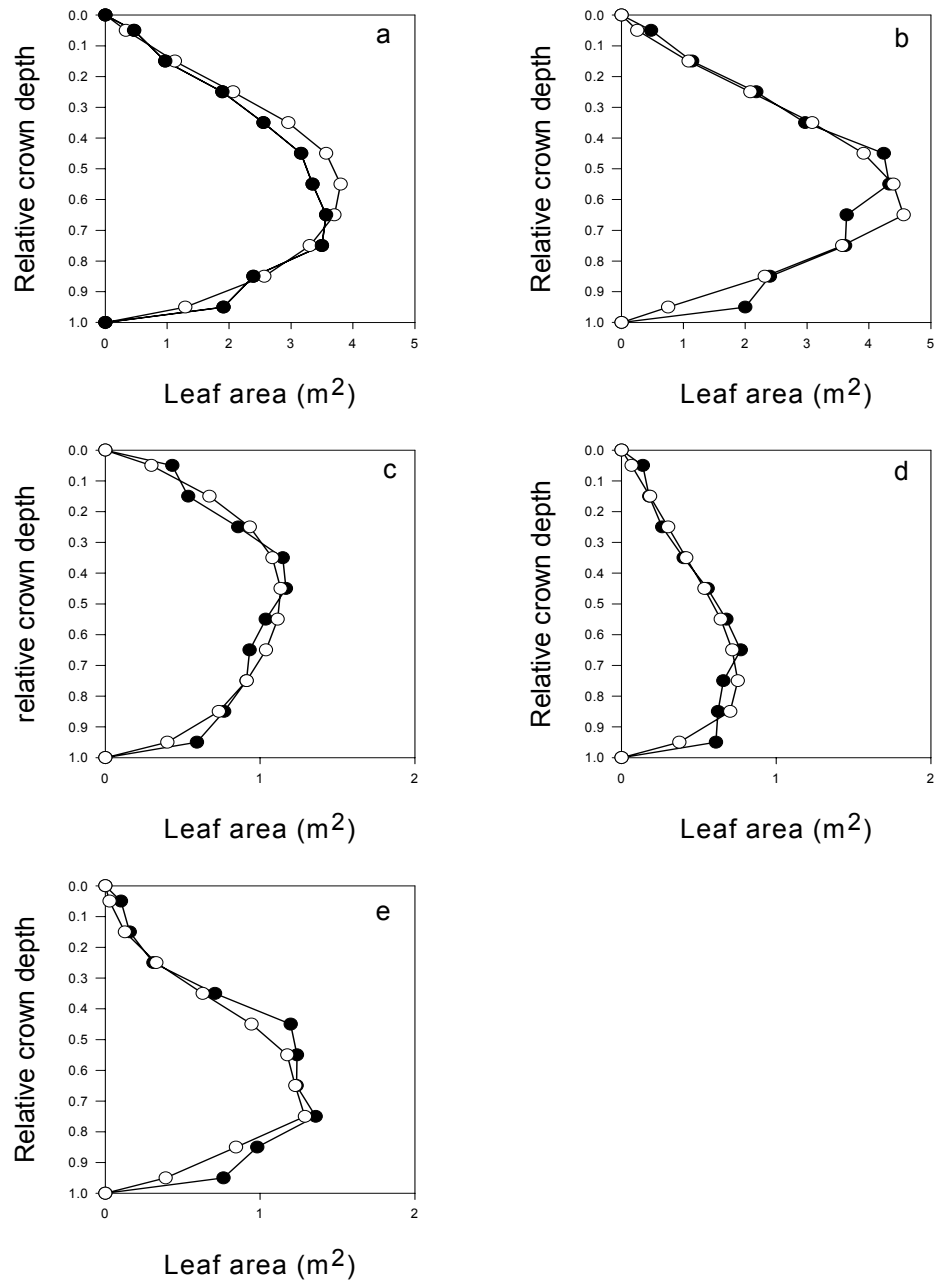


Figure 2.2. Observed (●) and predicted (○) average leaf area (m²) as a function of relative crown depth for loblolly pine. Predicted leaf area was obtained from the S_B fitted with predicted percentiles from crown dimensions. (a) 15-year-old large-crown trees from Starr Forest in MS; (b) 15-year-old small-crown trees from Starr Forest in MS; (c) 12-year-old trees from Lee Forest in LA; (d) unfertilized 4-year-old trees from Fred, TX; (e) fertilized 4-year-old trees from Fred, TX.

Boxplots of residuals show a trend of underpredicting the fractions of leaf area at the bottom of the crown (Figure 2.3). At the central intervals of the crown of 15-year-old, large crown families, negative biases predominated, indicating an overestimation of the fraction of leaf area in those regions of the crown. On the other hand, biases at the center of the crown tended to be slightly positive for the small-crown families and fertilized 4-year-old trees. These biases were usually small, however, residuals were larger for 15-year-old trees, as these trees have larger amounts of leaf area than the other groups. Residuals were larger at the center of the crown because most of the fraction of leaf area exists in this part of the crown. Outliers were associated with trees whose distribution was not correctly described by the distribution model, probably due to large over- or under-estimation of total leaf area. In other cases, some trees showed large fractions of leaf area concentrated in one or two classes of relative crown depth, followed by no leaf area in the adjacent intervals. The resulting shapes of the distribution of these trees could not be accurately described with the distribution function.

2.4. CONCLUSIONS

The results demonstrate that the S_B distribution is a suitable mathematical function for modeling leaf area distributions in loblolly pine. It is flexible enough to represent accurately the range of shapes of leaf area distributions. Furthermore, the parameters of the S_B can be calculated directly by knowing two percentiles of the observed distribution. Also, the S_B can describe the gradual reduction of foliage to zero at the top and bottom of the crown. An additional advantage of the S_B distribution is its potential to describe both the vertical and horizontal distribution of leaf area simultaneously (Johnson 1949b).

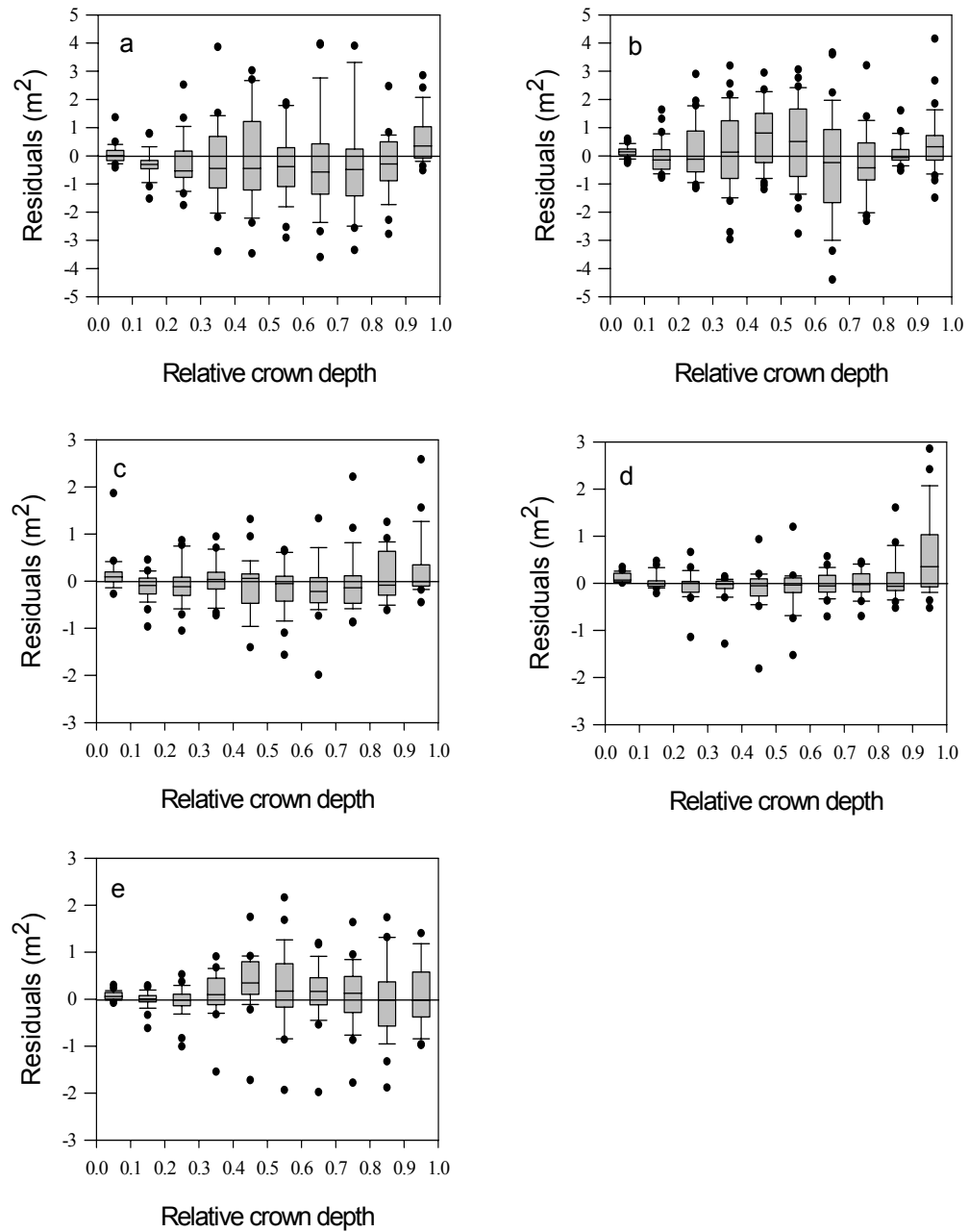


Figure 2.3. Boxplots of the residuals (observed - predicted) of the fit of the S_B to the leaf area distribution of loblolly pine trees of various age classes and treatments for the total leaf area distribution by classes 0.1 intervals of relative crown depth for loblolly pine trees. Edges of the box indicate the 25 and 75 sample percentiles of the data. Lines include the 10 and 90 percentiles. The center drawn line is the 50 percentile. Individual points are extreme values. (a) 15-year-old large-crown trees from Starr Forest in MS; (b) 15-year-old small-crown trees from Starr Forest in MS; (c) 12-year-old trees from Lee Forest in LA; (d) unfertilized 4-year-old trees from Fred, TX; (e) fertilized 4-year-old trees from Fred, TX.

The usefulness of probability functions in modeling the foliage distribution of trees and stands depends on the ability to accurately estimate the parameters of the function from easily obtained variables. Good predictions of relative cumulative leaf area were obtained despite the low precision for predicting the location of the leaf area percentiles along the crown and the amplified error produced by estimations of total leaf area.

The results showed low biases within groups. This suggest that it is possible to predict, with confidence the leaf area distribution of classes of trees by using the S_B distribution if measurements of crown dimensions can be obtained from a large number of trees. Such would be the case if crown dimensions can be acquired using various remote sensing techniques. The methodology used in this study for modeling the leaf area distribution can be used to build a submodel for inclusion in a stand-level or tree-level process model where accurate estimations of leaf area distribution may be necessary to characterize the initial state of the canopy and its changes as the stand develops.

2.5. SUMMARY

A model based on the Johnson's S_B distribution was developed for predicting leaf area distribution of loblolly pine trees from measurements of various tree dimensions. Data came from trees destructively sampled from stands differing in age, silvicultural treatments, and genetics. Equations were developed for predicting the location, in terms of relative crown depth, of the 15th and 50th percentiles of the leaf area distribution of individual trees by using tree dimensions as predictors. The predictions were used as input to estimate the parameters of the S_B distribution. The model predicted well the cumulative fractions of leaf area along the crown, but errors were amplified when transformed to absolute values of leaf area, reducing the apparent precision of the model. The results showed low biases within groups. This

suggest that it is possible to predict, with confidence the leaf area distribution of classes of trees by using the S_B distribution if measurements of crown dimensions can be obtained from a large number of trees. Such would be the case if crown dimensions can be acquired using various remote sensing techniques. The methodology used in this study for modeling the leaf area distribution can be used to build a submodel to integrate in a stand-level or individually-based process model, where accurate estimations of leaf area distribution may be necessary to characterize the initial state of the canopy and its changes as the stand develops.

CHAPTER 3

A PRELIMINARY STAND GROWTH MODEL DRIVEN BY CANOPY DYNAMICS FOR UNTHINNED LOBLOLLY PINE STANDS

3.1. INTRODUCTION

Forest process-based models are mathematical tools that attempt to integrate our knowledge and understanding of physiological and ecological mechanisms into predictive algorithms (Johnsen et al. 2001). Until recently, process models were viewed essentially as research tools. Their complexity and data requirements and a poor understanding of key biological processes hinder the applicability of process models to forest management. Thus, empirical models appear superior given their greater simplicity and predictive capabilities (Mäkelä et al. 2000). The realization that all modeling approaches can be placed on a continuum, from purely empirical to purely process-based, has created a pathway towards developing mechanistic models with predictive capabilities (Korzukhin et al. 1996; Mäkelä et al. 2000). An effective approach for building forest models is to envisage them in terms of the biological processes and relationships involved. The actual construction of the model would proceed using mechanistic processes when they are well understood and empirical relationships when there is no a reasonable theory to describe a process or data is not available to quantify the theory (Korzukhin et al. 1996; Mäkelä et al. 2000; Johnsen et al. 2001). The so-called “hybrid models” consist of mechanistic-based elements blended with statistical approaches. Hybrid models may be built either by developing whole models composed of statistical and mechanistic elements (e.g., West 1993; Battaglia et al. 1999) or by coupling empirical growth and yield models with forest process models (e.g., Baldwin et al. 1993, 2001).

From a timber management perspective, it is important to understand how natural and induced changes in canopy structure affect stem growth and quality. Given annual changes in foliage and its vertical distribution, the influence of canopy structure on stem growth and morphology can be modeled based on mechanistic theories such as the uniform-stress hypothesis (Dean and Long 1986, Dean 2001). This hypothesis provides a link between the processes taking place within the canopy and the processes that regulate carbon allocation to the stem.

This work is an initial effort to build a predictive model for unthinned loblolly pine (*Pinus taeda* L.) stands based on biological principles, namely the relationship between canopy dynamics and stem growth. The model relies on empirical surrogates for most processes, but the organization of the model allows future replacement of empirical relationships with process-based routines. The model can be used either as a predictive tool or as a research tool to gain insight in the basic relationships between canopy structure and stand development. The primary objectives of this research are (1) to describe a novel process-related, non-carbon-based growth model for predicting the development of closed, unthinned, loblolly pine stands and (2) to examine the ability of the model to simulate the dynamics of the canopy and stand growth under various combinations of site index and stand density.

3.2. THE MODEL

3.2.1. Philosophy and basic premises

The general concept of the model is based on the relationships between tree size and stand density as controlled by chronological changes in canopy structure as the stand ages during the period of maximum intertree competition (Figure 3.1). The canopy is the principal location where light interception, photosynthesis, respiration, and transpiration occur. The key

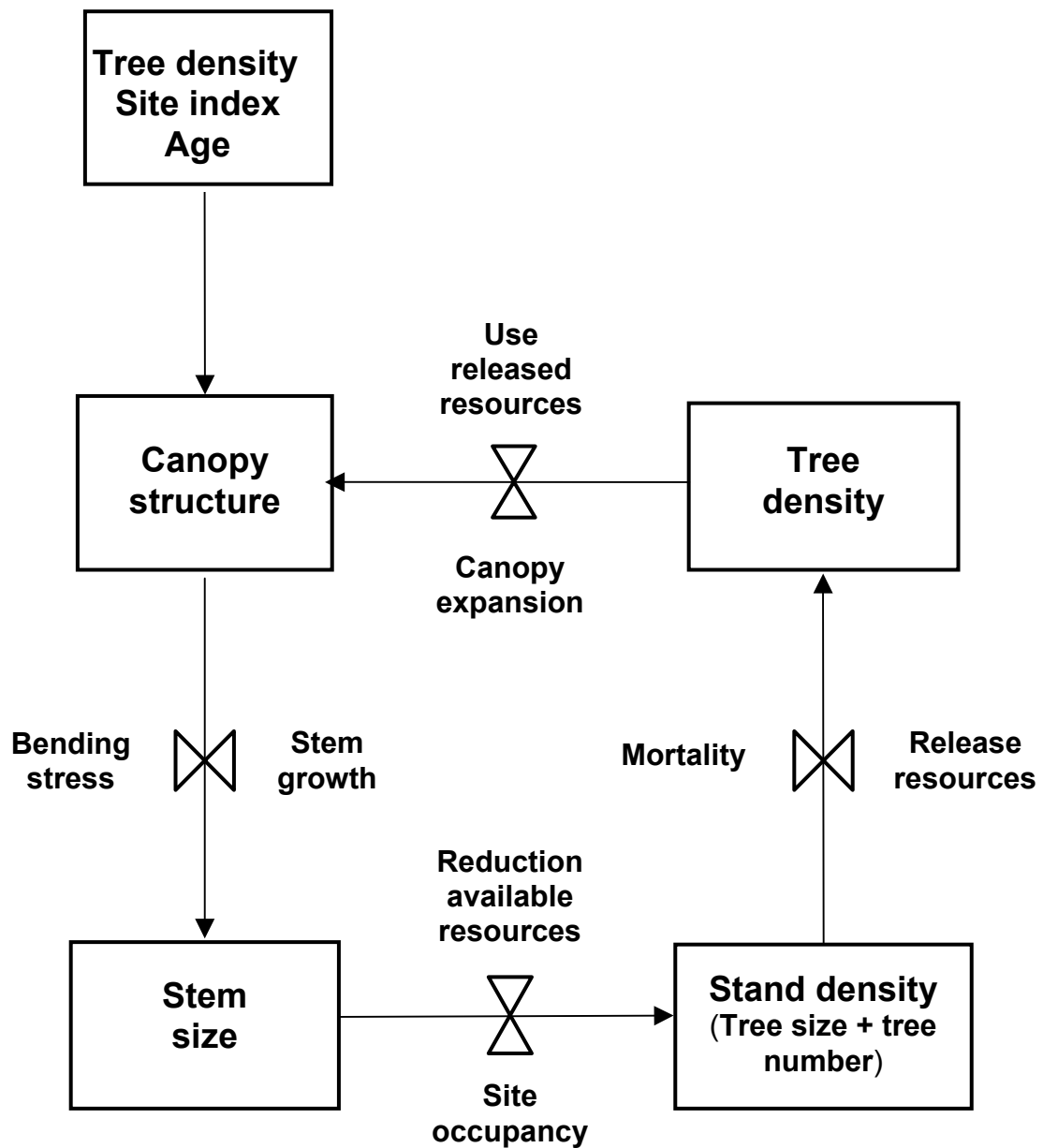


Figure 3.1. Schematic representation of the basic components of the model and their interactions. Boxes indicate state variables and valves represent the processes affecting the state variables.

component of the canopy is the foliage whose amount and distribution affect the rates and efficiencies at which these processes occur. As foliage accumulates, the canopy changes in size and according to the uniform-stress hypothesis these changes determine the rate of stem growth in response to the mechanical requirements imposed on the stem. As trees increase in size, resource use and site occupancy increase producing further changes in canopy structure (e.g., crown recession). At some point, trees must die for others to continue growing. The release of resources that results, allows further accumulation of leaf area among the surviving trees inducing additional increments in stem growth. This process begins after canopy closure and continues until the additional growing space released through mortality is too large to be reclaimed by the surviving trees. At this stage, the relationship between stem growth, mortality, and canopy structure weakens (Dean and Baldwin 1996a).

This conceptual model was used to build a mathematical model for simulating the development of even-aged, monespecific, stands with a surviving density of N trees per hectare at the beginning of the simulation period (initial age t). This is a whole-stand model where the stand canopy is represented by the crown structure of a tree whose diameter at breast height equals the average stand diameter (c.f., Dean and Long 1992). Information referring to the whole stand (e.g., leaf area index) is produced by multiplying the average value by the total number of surviving trees. It was assumed that the environment is constant through the stand development and, therefore, is defined simply by a site index. The foliage accumulates annually and it is distributed along the crown depending on changes in height growth and crown recession. Height growth and crown recession depend on neighbor effects, age, and site index. Changes in crown dimensions and leaf area distribution regulate stem

growth and form according to the uniform-stress hypothesis (Dean and Long 1986). Tree density changes in accordance with observed size-density relations (Cao et al. 2000).

3.2.2. Model construction

The model was programmed in SAS IML language (Statistical Analysis System v. 8.1, Cary, NC). The flow diagram of the model is described in Figure 3.2. The model produces numerical and graphic outputs summarizing the main attributes characterizing stand development.

3.2.2.1. Modeling changes in crown structure of the average tree

I assumed that the tree's crown structure at a given age is completely defined by vertical crown dimensions (total height and height to base of live crown) and the vertical distribution of leaf area. I adopted an empirical approach for accumulating leaf area, since no process-based approach exists for growing leaf area for more than a single year. Changes in crown structure were modeled with empirical equations that predict changes in vertical crown dimensions, total leaf area, and leaf area distribution.

a) Vertical crown dimensions

To define canopy structure, it was necessary to determine the average tree height and the height to the base of the live crown. Average total height of the stand depends on age and site index; however, it is also sensitive to stand density, particularly at high densities, due to the presence of intermediate and suppressed trees. On the other hand, the height of dominants and codominants, or site height, within a stand is highly correlated with age and site index, but is nearly insensitive to changes in stand density. Baldwin and Feduccia (1987) developed the following equation to predict site height

$$(3.1) \quad H_D = SI[b_1(1 - \exp(b_2 \cdot t))]^{b_3},$$

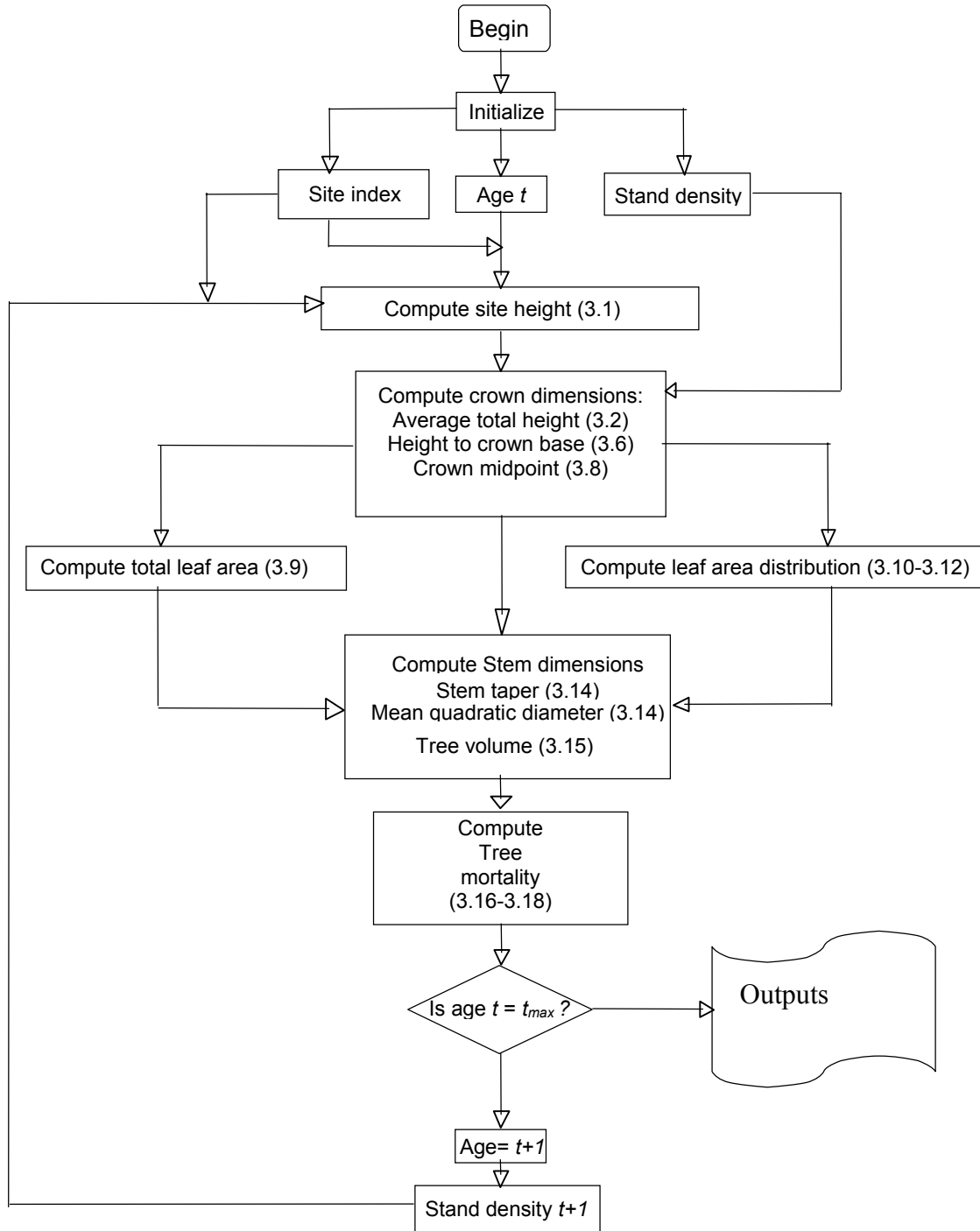


Figure 3.2. Flow diagram of model implementation. Equation numbers (in parenthesis) for computing the attributes are included.

where H_D = height of dominants and codominants (m) , SI = site index (m) at base age 25, t = age (years), and b_1 - b_3 = estimated coefficients. Average total height (H_T) was modeled with the equation

$$(3.2) \quad H_T = b_4 \cdot t^{b_5} H_D^{b_6} N^{b_7}$$

where N = tree density (trees/ha) at age t and b_4 - b_7 = coefficients estimated with nonlinear regression.

Changes in height to the base of the live crown (H_B) were represented using a modified version of the model described by Valentine et al. (1994). Valentine et al. (1994) assumed that average crown length is proportional to mean stand intertree distance (M_{id} , m), and he expressed the relationship in terms of the tangent of an angle θ , i.e.,

$$(3.3) \quad \tan \theta = (H_T - H_B) / M_{id},$$

where $H_T - H_B$ = crown length. Rearranging equation 3.3 to predict H_B results in

$$(3.4) \quad H_B = H_T - \left(\frac{M_{id}}{\tan \theta} \right),$$

and assuming that the space (m^2) occupied by the average tree is $1/N$,

$$(3.5) \quad M_{id} = (10,000/N)^{0.5}.$$

Valentine et al. (1994) determined an average value of 26° for θ in a closed loblolly pine stand. They hypothesized that θ depends on species tolerance and site quality. I found θ to be significantly correlated with age, average height, and site index. Therefore, θ was expressed as a function of these variables according to the following model was used to calculate H_B :

$$(3.6) \quad H_B = H_T - \left(\frac{M_{id}}{\tan(b_8 + b_9 \cdot H_T^{b_{10}} + b_{11} \cdot SI + b_{12} \cdot t)} \right),$$

where the coefficients b_8 - b_{12} were estimated with nonlinear regression.

The average values of total height and base to live crown were used to compute average crown ratio (CR) and average height from the ground to crown midpoint (H_{MC}), i.e.,

$$(3.7) \quad CR = C_L / H_T$$

and

$$(3.8) \quad H_{MC} = H_T - (H_T - H_B) / 2.$$

b) Total leaf area for the average tree

Roberts et al. (2002) suggest that allometric models for calculating leaf area that combine vertical crown dimensions approach the precision of traditional equations based on DBH or sapwood cross-sectional area. Therefore, for this model, projected leaf area per tree (A_L , m²) was derived with following model:

$$(3.9) \quad \log(A_L) = b_{13} + b_{14} \log(H_T) + b_{15} \log(H_{MC}),$$

where the coefficients b_{13} - b_{15} were estimated with linear regression

c) Leaf area distribution

Average leaf area distribution was modeled with a S_B distribution whose parameters were obtained indirectly through the prediction of the location of the 15th and 50th percentiles of leaf area along the crown depth of the average tree. Average crown length is expressed as a fraction of canopy depth with 0 and 1 equal to the top and bottom of the crown, respectively. The cumulative fraction of leaf area (F) from the crown tip to any point x of crown depth was computed as

$$(3.10) \quad F = \Phi \left[\gamma + \delta \cdot \ln \left(\frac{x}{1-x} \right) \right],$$

where x = relative crown depth, Φ is the standard normal distribution, and γ and δ are parameters that control the shape of the distribution. The location of the 15 (x_{15}) and 50 (x_{50})

percentiles of leaf area was predicted from crown dimensions and used to estimate γ and δ with a two-percentile method (Knoebel and Burkhardt 1991). The original equations for x_{15} and x_{50} (Chapter 2) were modified to allow for reasonable extrapolations beyond the range of the original data used for fitting the model. The equations are

$$(3.11) \quad x_{15} = \exp(b_{16} + b_{17}CR^2 + b_{18}H_{MC}^{b_{19}})$$

and

$$(3.12) \quad x_{50} = \exp(b_{20} + b_{21}CR^2 + b_{22}H_{MC}^{b_{23}}),$$

where b_{16} - b_{23} = coefficients estimated simultaneously with seemingly unrelated regression (Borders 1989).

Total cumulative leaf area at any relative crown depth is obtained by multiplying the fraction of cumulative leaf area at that point by total leaf area. Transforming the relative crown depth to absolute values, the height to the tree's center of leaf area (H_{LC}) is calculated as

$$(3.13) \quad H_{LC} = H_B + (1 - C_L)x_{50}$$

3.2.2.2. Prediction of volume and quadratic diameter

According to the uniform stress hypothesis, stems behave as cantilever beams tapered to equalize bending stress across their length (Dean and Long 1986). It is assumed that bending stress is produced mainly by the wind exerting pressure on the crown foliage, which acts like a sail. Bending stress in turn stimulates cambial growth (Telewski and Jaffe 1986, Dean and long 1986). Several experimental and theoretical studies (Dean and Long 1986; West et al. 1989) have provided evidence of a strong relationship between foliage distribution and stem size and taper. Using the predicted crown structure at age t , the uniform-stress model

was used to calculate the stem taper of the average tree using the formula proposed by Dean and Long (1986):

$$(3.14) \quad d_h = b_{24} (A_{L_h} L_h)^{b_{25}}$$

where d_h = diameter (cm) at the stem height h , A_{L_h} = total projected leaf area (m^2) above d_h , and L_h = distance between the physical center of leaf area above d_h and the height at d_h .

Estimates of b_{24} and b_{25} may vary depending on the season in which leaf area was measured. For loblolly pine stands, these values have been estimated for summer, when leaf area peaks, and winter, when leaf area is at minimum (unpublished data). The values of d_h were calculated at 10 cm intervals to generate stem taper. The predicted diameter at 1.37 m from the ground obtained with equation 3.14 was assumed to represent the quadratic diameter (Q) of the stand (Dean and Baldwin 1996b). Finally, total average tree volume was computed numerically by summing the volume of 10 cm sections of the stem calculated with the Smalian's formula:

$$(3.15) \quad V_s = \frac{\pi \cdot l_s}{8} (d_{1s}^2 + d_{2s}^2),$$

where V_s = volume of section s (m^3); d_{1s} and d_{2s} = diameters at the ends of the section (m); l_s = section length (m). Total volume of the average tree (V) is obtained by summing the volumes of all sections

3.2.2.3. Modeling the link between the size-density relationship and canopy structure

The relationship between tree size and tree density was modeled using a self-thinning curve. Cao et al. (2000) assumed that the relationship between quadratic mean diameter and tree density in tree stands follows a convex curve in a log-log scale as self-thinning proceeds. Based on this assumption, they developed a system of equations to model stand development

based on the reciprocal effects of stand diameter growth and tree mortality through time. In the present model, changes in tree density are predicted using a modified version of the mortality equation of Cao et al. (2000) fitted for densities relevant to loblolly pine management (Cao, personal communication). Future tree density at simulation time $i + I$, N_{i+I} , is given by

$$(3.16) \quad N_{i+1} = N_i - (N_i - N_{m,i+1}) \exp[b_{26}(Q_{m,i} - Q_i)],$$

where Q_i = quadratic mean diameter (cm) at simulation time i ; $Q_{m,i}$ = maximum quadratic stand diameter (cm) at time i ; N_i = stand density at time i , $N_{m,i+1}$ = lower limit for stand survival at time $i+I$ subject to maximum mortality and b_{26} is an estimated coefficient for loblolly pine stands. The value of Q was obtained from equation 3.14, thus it depends on crown structure at time i . The equation for $Q_{m,i}$ produces the self-thinning curve

$$(3.17) \quad Q_{m,i} = b_{27} N_i^{-0.623} [1 - \exp(b_{28} N_i^{b_{29}})],$$

where b_{27} - b_{29} are coefficients estimated with nonlinear regression. The equation for $N_{m,i+1}$ is

$$(3.18) \quad N_{m,i+1} = N_i \left(\frac{t_{i+1}}{t_i} \right)^{b_{30}} \exp[b_{31}(t_{i+1}^{b_{32}} - t_i^{b_{32}})],$$

where t_i = stand age in years at time i , and $t_{i+1} = 1 + t_i$ and b_{30} - b_{32} are estimated coefficients.

3.2.3. Data

Data for developing the empirical relationships and model evaluation came from 278 measurements collected in 114 permanent plots from unthinned loblolly pine plantations located in Louisiana, southeast Texas, and southwest Mississippi. Stand age varied from 10 to 45 years, tree density from 250 to 4500 trees/ha, and site index (base age 25 years) from 12 to 25 m. Each plot was measured two to six times, 5 years apart. The data were randomly divided in to a fit data set for model construction (approximately 50% of the data) and a data

set for validation of the empirical models. Summary statistics for the fit and validation data sets are presented in Table 3.1. Estimates of volume and one-sided leaf area index per plot were available in the data set. These values as calculated by Dean and Baldwin (1996a) were assumed reliable estimations of the true volume and leaf area index and were used to check model behavior. Data for predicting projected leaf area distribution from crown dimensional variables came from two separate studies carried out in Mississippi and Louisiana including 76 destructively sampled loblolly pine trees that were 12-15-year-old (Chapter 2). Some of the empirical models are taken from published sources. These are noted in Table 3.2.

Nonlinear models were fitted using a nonlinear derivative-free algorithm provided by SAS (Statistical Analysis System v. 8.1, Cary, NC). Model coefficients and statistics for precision are shown in Table 3.2. All coefficients were determined to be significantly different from zero using 0.05 as the critical value of α .

3.3. MODEL ANALYSIS

3.3.1. Simulation of yield and growth

Simulations of stand growth and yield variables from age 8 to 45 years for site index of 20 m at base age 25 years and 2500 trees/ha followed typical patterns (Figure 3.3). With respect to crown dimensions, average tree height approached average site height as the stand aged, a consequence of the reduction in stand density and loss of intermediate and suppressed trees (Figure 3.3a). Initially, crowns receded more slowly than the rate of average height growth, producing a increase in crown length. However, crown ratio decreased continuously with stand age (Figure 3.3a). Simulated tree mortality also followed a typical pattern (Figure 3.3b). At early ages, mortality was low due to the small size of the trees and low stand density as indicated by the values of Q and the distance between Q and Q_{max} (Figure 3.3c). Mortality

Table 3.1. Summary statistics for the fit and validation data sets from loblolly pine stands.

| Variable | Fit data set | | | | Validation data set | | | |
|-------------------------------------|--------------|-------|------------------|------------------|---------------------|-------|-------|-------|
| | n* | Mean | Min [†] | Max [§] | n | Mean | Min | Max |
| Age (years) | 138 | 22 | 10 | 45 | 136 | 22.2 | 10 | 45 |
| Tree density (Trees/ha) | 138 | 969 | 249 | 4075 | 136 | 975 | 119 | 4500 |
| Basal area (m ² /ha) | 138 | 31.22 | 7.21 | 48.89 | 136 | 32.08 | 6.57 | 48.69 |
| Quadratic mean diameter (cm) | 138 | 21.59 | 9.33 | 34.30 | 136 | 21.99 | 8.86 | 38.33 |
| Site index (m) at base age 25 years | 138 | 19.09 | 11.89 | 24.20 | 136 | 18.80 | 11.55 | 23.28 |

*Sample size.

[†]Minimum.

[§]Maximum.

Table 3.2. Parameter estimates for the components of the model.

| Submodel | | Equa- tion | Sample size | R ² | Sy.x | Parameter | Estimate | Reference |
|---|-----------------|---------------|----------------|----------------|--------|-----------------|------------|---|
| <u>Site height</u> | | 3.1 | | | | b ₁ | 2.14915 | Baldwin and Feduccia (1987) |
| | | | | | | b ₂ | -0.0025042 | |
| | | | | | | b ₃ | 0.755862 | |
| <u>Average height</u> | | 3.2 | 138 | 0.96 | 0.78 | b ₄ | 1.337744 | New equation from this study |
| | | | | | | b ₅ | 0.083386 | |
| | | | | | | b ₆ | 0.910084 | |
| | | | | | | b ₇ | -0.05036 | |
| <u>Height to crown base</u> | | 3.7 | 138 | 1.01 | 0.93 | b ₈ | 4.268864 | Modified from Valentine et al. (1994) |
| | | | | | | b ₉ | -3.33430 | |
| | | | | | | b ₁₀ | 0.100000 | |
| | | | | | | b ₁₁ | 0.01436 | |
| | | | | | | b ₁₂ | 0.0155652 | |
| <u>Total leaf area</u> | | 3.6 | 138 | 0.77 | 0.253 | b ₁₃ | -2.19715 | Modified from Roberts et al. (2002) |
| | | | | | | b ₁₄ | 7.5437 | |
| | | | | | | b ₁₅ | -5.422006 | |
| <u>Leaf area distri- bution</u> | x ₁₅ | 3.11 | 76 | 0.31 | 0.0083 | b ₁₆ | -3.49992 | New equations from this study |
| | | | | | | b ₁₇ | 1.154893 | |
| | | | | | | b ₁₈ | 1.63746 | |
| | | | | | | b ₁₉ | 0.10000 | |
| | x ₅₀ | 3.12 | 76 | 0.21 | 0.0094 | b ₂₀ | -1.74858 | |
| | | | | | | b ₂₁ | 0.601573 | |
| | | | | | | b ₂₂ | 0.585208 | |
| | | | | | | b ₂₃ | 0.100000 | |
| <u>Uniform- stress model</u> | | 3.14 | | | | b ₂₄ | 3.431 | (Unpublished data) |
| | | | | | | b ₂₅ | 0.309 | |
| <u>Size density relationship</u> | | 3.16 | | | | b ₂₆ | -0.16240 | Cao (personal communication) |
| | | 3.17 | | | | b ₂₇ | 2150.00 | |
| | | | | | | b ₂₈ | -0.05357 | |
| | | | | | | b ₂₉ | 0.52385 | |
| | | 3.18 | | | | b ₃₀ | 0.07124 | |
| | | | | | | b ₃₁ | -0.04380 | |
| | | | | | | b ₃₂ | 1.07124 | |

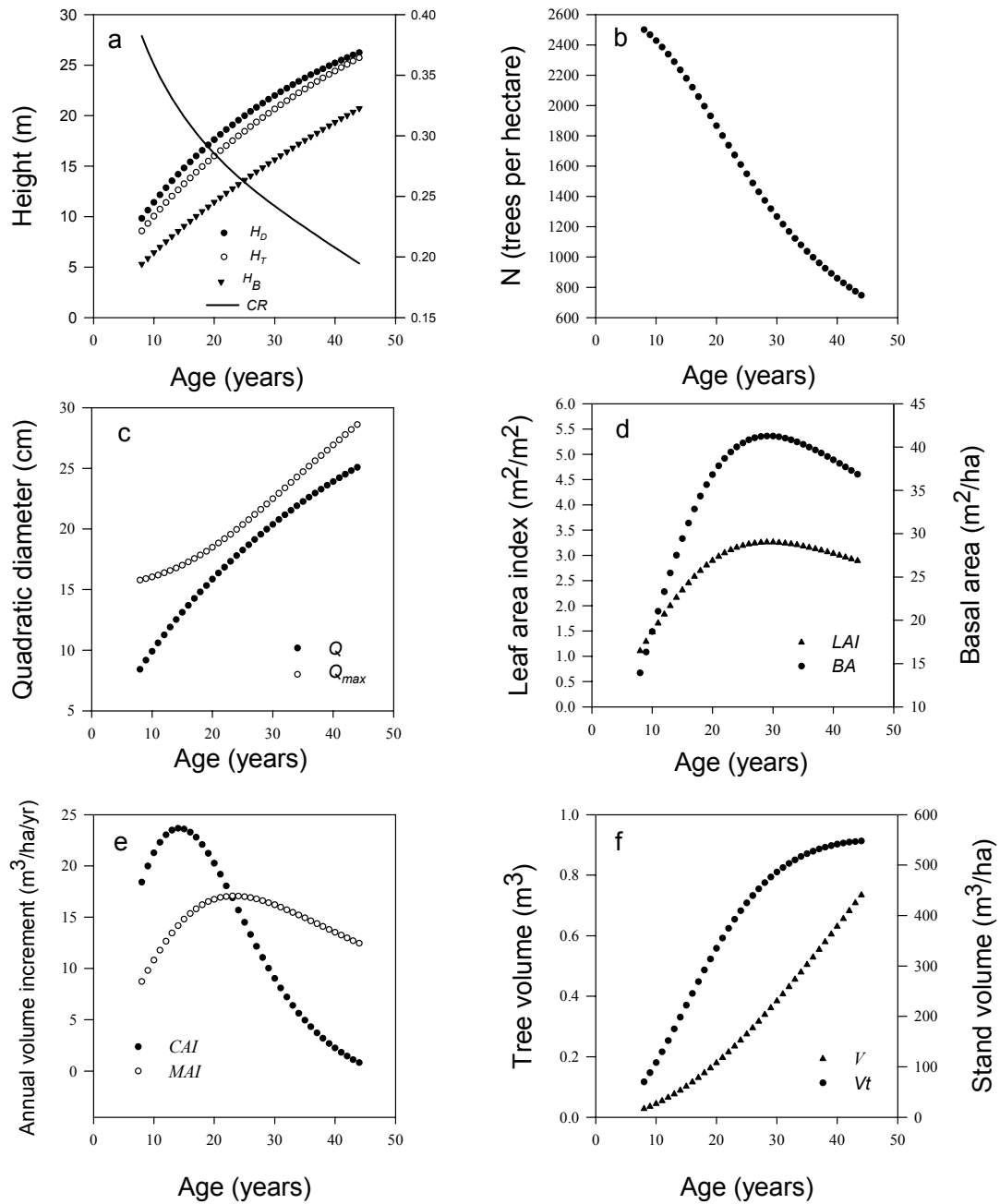


Figure 3.3. Simulated outputs for selected variables representing growth and yield for a stand with surviving density of 2500 trees/ha and site index of 20 at base age 25 years. (a) Dominant height (H_D), average height (H_T), and height to the crown base (H_B) versus age. (b) Tree density (N) versus age. (c) Mean quadratic diameter (Q) and maximum quadratic diameter (Q_{max}) versus age. (d) Leaf area index (LAI) and basal area (BA) versus age. (e) Current annual increment (CAI) and mean annual increment (MAI) in volume versus age. (f) Mean tree volume (V) and total stand volume (V_t).

gradually increased as trees increased in size and Q approached Q_{max} . Mortality rates decreased again when Q began to fall away from Q_{max} , indicating a decline in stand density as the stand aged. Leaf area index increased at early ages, reached a peak, and decreased slowly with age (Figure 3.3d). The pattern of stand basal area growth followed a somewhat similar pattern to LAI (Figure 3.3d). Patterns of LAI agree with results from other researchers (Ford 1982, 1985; Long and Smith 1992). Current annual increment (CAI) and mean annual increment (MAI) also followed typical patterns with CAI peaking early during stand development and then decreasing as the stand ages (Figure 3.3e). Volume per tree exhibited an exponential pattern because of an increase in leaf area per tree and the height of the crown center. Such a pattern is consistent with the delayed culmination of the average individual tree growth compared to the culmination of stand growth (Assmann 1970). Stand volume showed the typical sigmoid pattern. It increased rapidly at early ages, but at older ages tended to reach a plateau because the increases in individual tree growth could not compensate for the reductions in tree density.

3.3.2. Size-density and leaf area relationships

To illustrate the model's ability to simulate the more fundamental relationships of forest production, the model was run for combinations of tree surviving density (1200, 2400, and 3600 tree/ha) and site index (12, 18, and 24 m at base age 25) from 8 to 45 years (Figure 3.4). In general, current annual increment in volume (CAI) increased with site index (Figure 3.4a). For a given site index, the peak of CAI was delayed for lower initial stand densities. However, after peaking, stands with better site index and higher densities showed a substantial decrease in stand increment, reaching quickly null or negative values before stands with lower initial tree density or site index. This pattern has been reported in the literature for

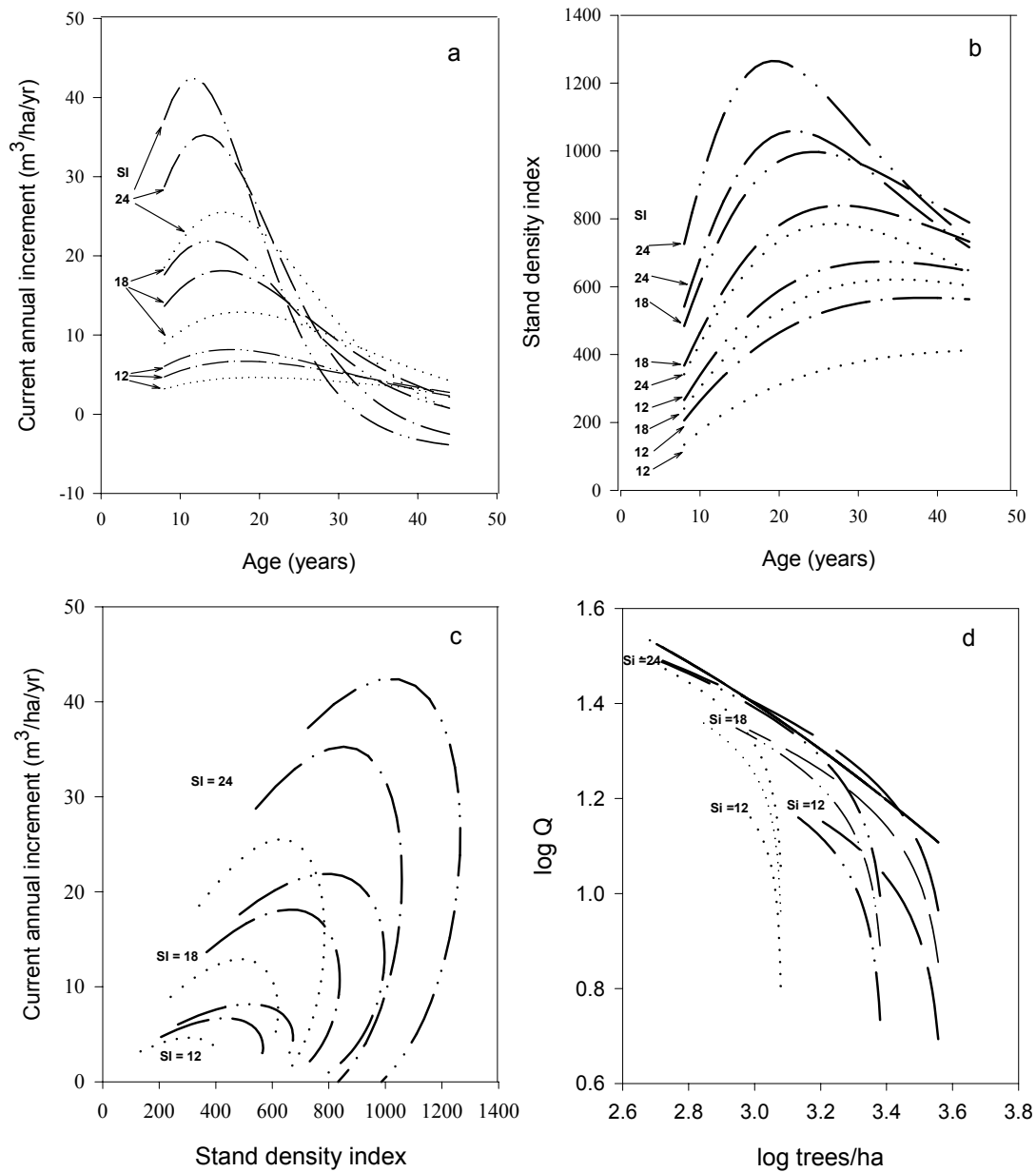


Figure 3.4. Simulated growth age and size-density relationships. (a) Current annual increment versus age; (b) stand density index vs. age; (c) Current annual increment vs. stand density index; (d) quadratic mean diameter vs. stand density. Surviving densities at the beginning of the simulations are: 1200 (.....), 1800 (— · —), and 3600 trees/ha (— · · —). SI = site index (m) at base age 25.

stands with different spacings (Clutter et al. 1983). The faster decrease of *CAI* at higher tree densities and site index appear to be a consequence of faster rates of mortality at early age, which can be not compensated by the increments in tree size at later ages. Patterns of stand density index (*SDI*) are more complex (Figure 3.4b). The *SDI* is larger and peaks earlier for higher tree densities for any site index. However, for a given tree density, stands with higher site index increase faster and peak earlier than for lower site index. Overall, the peaks in *SDI* are delayed as tree density and site index are lower. The maximum stand density index for the best site and highest density combination was slightly over the maximum of 1100 reported for loblolly pine (Reineke 1933). As the stand aged, *SDI* for higher densities decreased faster; whereas, at lower densities and site index, *SDI* tended to reach a peak and remain stable. Differences in *SDI* may be related to a faster mortality that is not compensated by diameter growth. The *CAI* increased with increasing *SDI*, but it decreased rapidly just before peak *SDI* was reached. The form of the relationship between mean quadratic diameter and tree density (Figure 3.4d) shows the typical patterns. Lower tree densities require of larger trees to approach the self-thinning line. For a given density, the stand approaches to the self-thinning line faster for higher site indexes. At the highest combination of site index and tree density ($SI = 24$ m, 3600 trees/ha), the self-thinning curve is slightly surpassed. This could happen because the projected quadratic diameter depends on leaf area and crown dimensions, which are only indirectly constrained by stand density. However, as tree density decreases, these stands depart from the self-thinning curve. For poorer sites, the simulated size-density trajectories tend to approximate to the self-thinning curve slowly, but do not reach it.

Leaf area index increases at an early age, reaches a peak, and then decreases with stand age (Figure 3.5a). The overall pattern agrees with observations for intermediate

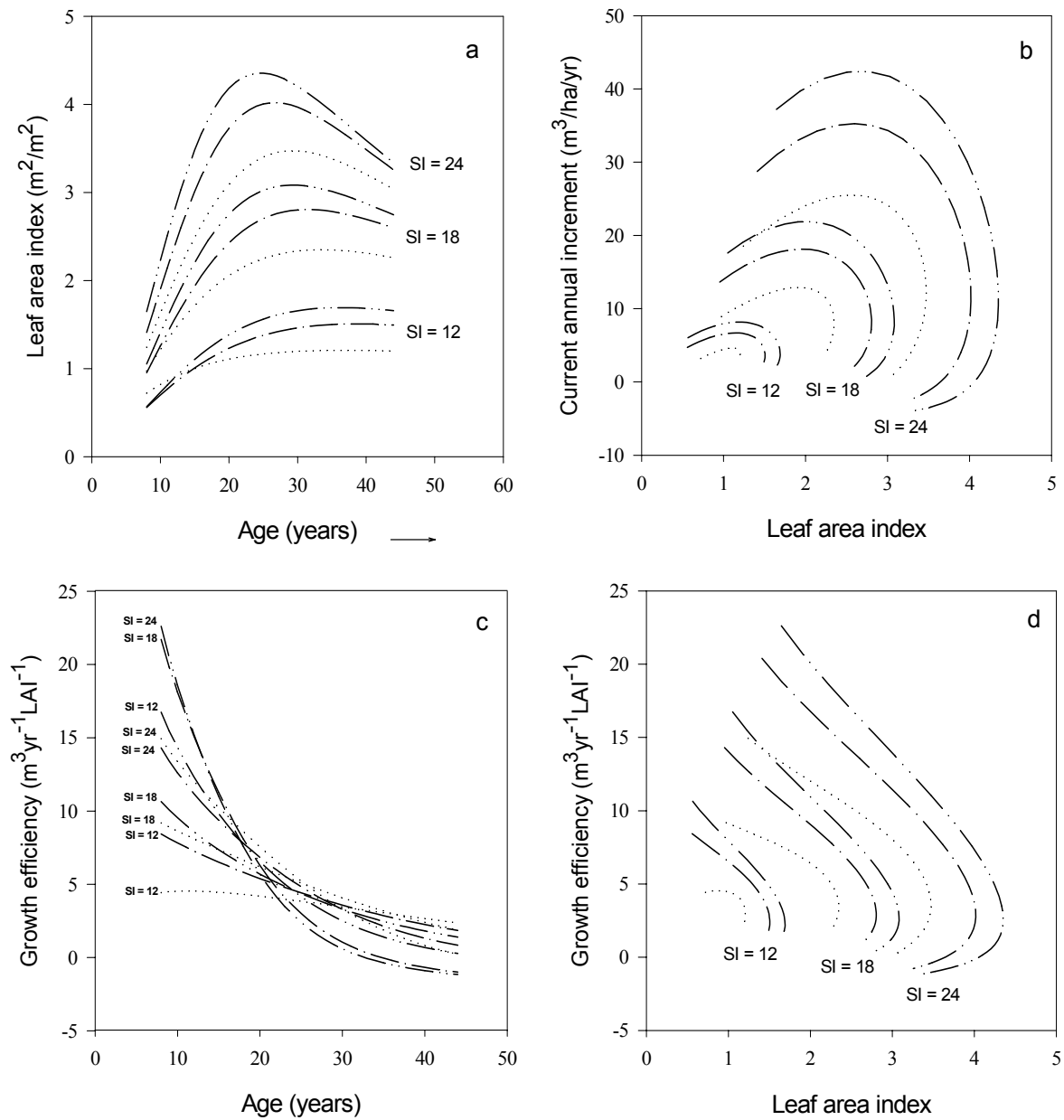


Figure 3.5. Relations of leaf area index with current annual increment and growth efficiency for combinations of surviving density and site index. (a) Leaf area index versus age. (b) Current annual increment versus leaf area index. (c) Growth efficiency versus age. (d) Growth efficiency versus leaf area index. Surviving densities at the beginning of the simulations are 1200 (.....), 1800 (— · —), and 3600 trees/ha (— · · —). SI = site index (m) at base age 25.

densities and site index (e.g., Kuulivainen 1991; Long and Smith 1992). Stands with larger initial tree densities reached a peak sooner than stands with lower densities in agreement with other studies (Turner and Long 1975; Long and Smith 1984). Leaf area index was lower and peaked later for lower site indexes. For poor sites, *LAI* does not decline after reaching a peak, which is consistent with observed behavior in a variety of species (Vose et al. 1994).

The relationship between *CAI* and *LAI* was nonlinear (Figure 3.5b). Several authors have suggested that this relationship should be linear, with *CAI* increasing with increasing *LAI* (e.g., Long and Smith 1990); however, the existence of the relationship in a nonlinear form was suggested by Waring (1983). He stated that in stands with relatively low leaf area, the relationship between leaf area increment and stand productivity should be positive, but at high leaf area, productivity should decrease. The behavior of this model and those produced by another model developed by Shi and Cao (1997) appear to support Waring's hypothesis. Growth efficiency is a measure of how the carbon fixed by the foliage is allocated to stem growth, and its analysis has produced valuable insights in the relationships between canopy dynamics and stand development (e.g., Waring et al. 1980; Waring 1983; Roberts and Long 1992; Gilmore and Seymour 1996). When growth efficiency was plotted against age, it decreased for all combinations of site and stand density. The decrease was steeper for higher tree densities and, the higher the site index, the steeper the decrease for a same tree density (Figure 3.5c). Based on the simulations, growth efficiency decreased with *LAI* for all combinations of site and initial density (Figure 3.5d). Waring et al. (1981) and Oren et al. (1987) reported the same trend. Simulations from a model by Shi and Cao (1997) show growth efficiency decreasing steadily with increasing leaf area index from 5 to 45 years. Low

growth efficiency at high *LAI* has been suggested to be consequence of increasing shading, higher respiration rates, or increased moisture stress (Vose and Allen 1988). The present model showed a continuously decreasing value in growth efficiency, although at a lower rate after leaf area had peaked. Higher initial densities and better sites had larger values of growth efficiency. There is not clear agreement in the literature as how changes in site quality should affect the relationship between growth efficiency and *LAI* (e.g., Brix 1983; Vose and Allen 1988).

3.4. DISCUSSION

Overall, the model predictions appear to be in agreement with reported observations or proposed theories in relation to stand growth, growth and size-density, and growth and leaf area relationships. The model's behavior appeared to be less reliable at extremes of site index, tree density, and age. This is a result of the lack of measurements at the extremes of the site indexes and tree densities, especially at early ages. Some of the empirical equations were used much farther from the range of data used in their construction. For example, the system to predict the leaf area percentiles was fitted using data from trees that were just 12-15-year-old.

Changes in crown structure with time were realistic for all combinations of site index and initial tree density, although some additional runs of the model at very low densities (< 800 trees/ha) were less realistic. The trajectory of the simulated stand is strongly influenced by the crown structure determined at the initial age. The patterns of average height growth appear to be predicted with high precision with the empirical submodel (equation 3.2) at any age. Average height, however, depended on site index through its relationship with site height. Although site index has been assumed invariant with time for most models, under changing environmental conditions and improved silvicultural practices like fertilization, site

index should be considered a variable (e.g., Battaglia et al. 1999). The expression of site index, which is an input for this model, could be replaced with submodels that estimate soil fertility and water availability that would affect site height, average height, and crown recession. If site index does not vary with time and average height can be predicted with high precision, the prediction of height to the crown base is critical for the model. If the initial height to the base of the crown is too low, crown ratios will be unrealistically large and height to the midpoint of the crown very unrealistically low, affecting the estimations of total leaf area and its distribution that are dependent on crown dimensions. The crown rise equation used in this model (equation 3.6) produced realistic predictions of crown length, with the exception of the combination of lowest initial tree density and site index. For this combination, initial predictions of height to the crown base apparently were too low, leading to somewhat large estimations of average leaf area. Unfortunately, no data were available to determine the trends in crown behavior during the period in which crown closure occurs. Crown recession is largely affected by variations in environmental conditions, being very sensitive to light, nutrient, and water limitations. The replacement of empirical models of crown recession with a process-based model is appealing for improving the present model. It appears feasible to develop a process submodel based on recent hypotheses about the relations between crown hydraulic architecture and light limitations at the crown bottom (e.g., Protz et al. 2000).

In this model, leaf area and its distribution determine increases in stem size and growth and control the size-density relationship. Various allometric models were tested previously and incorporated in the model. Some of them were biased and producing underestimations or overestimations of leaf area that led to unrealistic results. For example, in

the cases in which leaf area was underestimated stem growth was very slow, resulting in lower mortality rates which produced unrealistic predictions of stand occupancy at a given stand age. Thus, unbiased and precise estimations of total leaf area or *LAI* are critical for this model. Precise estimations of leaf area or *LAI* for various ages and stand conditions could be obtained from a large number of trees or stands using recent developments in remote sensing techniques (e.g., LIDAR). Also, leaf area estimations could be provided through an available process-based model and its output used as input for this model.

Leaf area distribution affected the model behavior by affecting stem taper and therefore, quadratic diameter. For example, fixing the physical center of leaf area to match with the center of the crown produced large increases in diameter that could not be compensated for by increases in mortality resulting in unrealistically elevated values of the stand density index and quadratic diameters.

The uniform stress hypothesis adequately predicted stem taper and volume based on the crown structure. This equation could be less reliable in open or older stands, where the relationship between stand density and canopy properties appears to be weaker (Dean and Baldwin 1996a). At older ages, the size of the gaps created by fallen trees is larger, and the ability of neighboring trees to close the gap decreases (Zeide 1991). In this case, the relationship between canopy structure and stem growth could be more dependent on environmental factors than on stand density. There are complex models accounting for changes in wind profile acting on the crown and other factors that could produce better predictions of stem growth under such conditions (e.g., West et al. 1989).

The mortality submodel produced realistic results. This model was superior to a model using the Reineke's self-thinning line (Cao 1994) that produced a very fast decline in tree

density at early ages. The mortality submodel is very important because it determines the effect of stand density on crown structure. Although, mortality has a strong stochastic component, using the self-thinning principle as a basis for modeling mortality appears to be appropriate where density-related mortality is more predominant than mortality related to other causes.

The feedbacks of stand development on which this model is based (Figure 3.1) provided an appropriate framework to build a simulation model incorporating mechanistic and empirical elements. In addition, the model produced realistic predictions of the development of closed, unthinned, loblolly pine stands under various combinations of initial tree densities and site index. The model has several advantages such as the possibility of replacing empirical routines with process-based routines (e.g., crown recession), or using outputs from process based models as inputs for the model (e.g., estimations of LAI or site quality). Besides its flexibility, this model can be used as a research tool for proposing hypotheses about the relationships between canopy dynamics and stand development and can guide the planning of experiments for testing them. The effect of silvicultural practices such as thinning could be incorporated in the model with some minor modifications, and the model could be employed to observe the effect of certain management decisions on stand development, thus becoming a management tool as well.

3.5. SUMMARY AND CONCLUSIONS

A novel process-related, non-carbon-based growth model for predicting the growth of closed, unthinned, loblolly pine (*Pinus taeda* L.) stands was developed and its ability to represent the dynamics of the canopy and stand growth was tested. The general concept of the model is based on the relationships between tree size and stand density as controlled by

chronological changes in canopy structure during the period of maximum, intertree competition. Several empirical routines were included when information about a given mechanistic process was not available. Overall, model predictions were in agreement with reported observations or proposed theories in relation to stand growth, size-density relations, and canopy dynamics and stand growth relationships. The model has several advantages such as the ability of replacing empirical routines with process-based routines, or using outputs from process based models as inputs for the model. The model has potential to be used as a research tool for proposing hypotheses about the relationships between canopy dynamics and stand development, and serve as a guide for planning experiments to test such hypothesis. In addition, it has the potential to be used as a management tool.

CHAPTER 4

PATTERNS OF BRANCH PERMEABILITY WITH CROWN DEPTH AMONG LOBLOLLY PINE FAMILIES DIFFERING IN GROWTH RATE AND CROWN SIZE

4.1. INTRODUCTION

Hydraulic permeability, the ability of sapwood to conduct water, is an indicator of water transporting efficiency of stems and branches. Its influence on leaf area--sapwood area relationships in trees is well known (Whitehead et al. 1984; Pothier et al. 1989a,b; Margolis et al. 1995). Hydraulic architecture, the differential patterns of hydraulic efficiency among tree components, in combination with stomatal control, regulate water flux within trees in the face of increasing height, changing water availability, and varying atmospheric conditions (Phillips et al. 2001). Thus, differential patterns of hydraulic permeability among tree parts may be a critical factor limiting tree size and crown dimensions. Protz et al. (2000), for example, found a possible association between reduced branch permeability at the bottom of the crown and branch death in lodgepole pine (*Pinus contorta* Dougl. ex Loud.).

Permeability is affected by stand density (Keane and Weetman 1987), site quality (Pothier et al. 1989a,b), bending stress (Dean 1991; Fredericksen et al. 1994), fertilization (Whitehead et al. 1984; Dean 1991), age (Pothier et al. 1989a,b), and light (Schultz and Matthews 1993; Protz et al. 2000). These factors are known to affect individual tree growth. Several studies have shown faster growth rates to be associated with higher values of permeability in conifers (Booker and Kininmonth 1978; Edwards and Jarvis 1982; Whitehead et al. 1984; Pothier et al. 1989b). However, not all studies have found an effect of growth rate on permeability (e.g., Comstock 1970; Maherali and DeLucia 2000). If growth rate is correlated with permeability, then trees from families or provenances identified as “fast-

growers” might show differing patterns of stem and branch permeability relative to families or provenances considered as “slow-growers”. Conversely, trees from families characterized by having large crowns might also show such differences relative to small crown families.

Differing patterns of stem and branch permeability might have an important effect in how the foliage at a given crown depth responds to environmental stresses such as reduction in light availability and water deficits, thus producing changes in crown structure such as foliage density, crown length, and rates of foliage growth and senescence. Protz et al. (2000), for example, reported that needle mortality rate in lower branches of lodgepole doubled the mortality rate observed in upper whorls. Needle mortality rate was also higher in branches whose permeability had been artificially reduced.

Longitudinal and radial patterns in stem permeability with tree dominance, stand density, and site quality have been analyzed for loblolly pine (Shelburne et al. 1993; Shelburne and Hedden 1996). However, patterns in branch permeability in loblolly pine trees are unknown. The objectives of this study were to (1) identify differences in stem top permeability and patterns of branch permeability with crown depth in specific loblolly pine families selected for differences in growth rate and crown size, and (2) examine if branch permeability shows any association with differences in the foliage structure of these families.

4.2. MATERIALS AND METHODS

The study site is located in Winston County, MS on the John Starr Memorial Forest near Starkville (33° 16'N, 88° 52'W). This is an interior flatwood site underlain with a Glossic Fragiudult soil (Prentiss loam). Average annual temperature at the site is 17.2 °C. Average annual precipitation is 1430 mm. Site index at base age 25 years is approximately 23 m.

Data were collected in August 1999 from a progeny trial planted in July 1985 comprising eight families from eastern North Carolina (Land et al. 1990). These families were chosen based on a 12-year progeny test in North Carolina to represent combinations of fast and slow growth with small and large-crowns (two families of each combination). Trees were selected from a single planting block where families were arranged in row plots 3 meters apart (1.5 m between trees). After discarding border, forked, and broken-top trees, a sample of 47 (five to nine trees per family) was used for the analysis. One of the fast-growth, large-crown families was excluded as all trees belonged to the south border of the plantation. Sample trees represent the range of stem diameters and tree heights present within each family. Diameter at breast height (DBH, 1.37 m) ranged from 11.6 to 25.3 cm. Total height ranged from 10.0 to 18.8 m.

Prior to felling, each tree was measured for DBH, total height, height to base of the live crown and crown width (average of maximum and minimum crown diameters measured from ground level). After felling, the stem was divided into 1-m sections. Within the crown, branches were removed from each section and separated into current-year foliage and twigs, previous year's foliage and twigs, and nonfoliated live branches. Each component was weighed fresh, and a subsample was removed for determination of moisture content and proportions of foliage and branch mass within each component. Approximately 20 needle fascicles were collected from each age class of foliage within each section, stored on ice, and returned to the lab for specific leaf area (SLA) determination.

From each crown section, a representative branch was selected, and a 20-25 cm branch section was taken 5 cm from the branch base. A 20-25 cm section of the main stem was taken at 1-meter from the terminal. Cut samples were sealed immediately in plastic bags, and stored

on ice to prevent drying or contamination. In the laboratory, the branch and stem segments were submerged for five minutes in a solution of 0.5 % of sodium hypochlorite to protect the samples from microbial contamination and then stored at 4°C. Only branches 2-year-old or older were used, as current year branches did not store well.

Biomass subsamples were dried to a constant weight at 80° C. Foliage was separated from twigs to determine foliage mass--wood mass ratios for each component per section. The fresh needle samples were separated from the fascicle sheaths, and projected area was determined with an optical planimeter (LiCor Model 3000). The samples were then dried and weighed to determine SLA (cm²/g). Fresh mass--dry mass ratios, foliage mass--wood mass ratios, and SLA were used to calculate a projected leaf area (LA) for both current-year and previous year's foliage for each 1-meter crown section. Section totals were summed for total crown LA. The relative crown depth of each sampled branch was calculated as the relative position of the midpoint of the section where the branch resided.

4.2.1. Permeability measurements

Permeability was measured according to the technique developed by Booker (1977). An apparatus similar to that described by Sperry et al. (1988) was built using a PVC pipe capped at both ends as water reservoir. The top end was connected with a hose to a source of pressurized air. A five-position manifold was attached at the bottom of the tank. A pressure regulator maintained constant pressure within the system during the measurements, and gauges along the manifold were used to record actual pressure where the branch segment was attached to the outlet. The tank was filled with a solution (pH ≈2) of distilled water and hydrochloric acid (HCL). The HCL was used to minimize microbial growth that could lead to

decline in conductivity (Sperry et al. 1988). The solution was degassed with a 0.22 µm Hellmann filter.

Prior to measurement, both ends of the branch segments were resawn under water. The ends were then carefully shaved with a sharp razor blade to ensure open tracheids. The basal end of the segment was fit with flexible tubing and attached to the apparatus. Samples were perfused following the natural direction of flow. The solution was passed through the sample segments by applying 130 to 175 KPa of pressure. Flux was measured after checking for stable pressure. Flux stabilized usually after 10 minutes. The average of three consecutive flux measurements was used to determine the permeability of the segment. Water passing through the segments was collected in previously weighed glass beakers. Average water temperature varied between 20 and 21 °C. The mass of collected water was measured in a precision balance (Sartorius) and converted to volume using the density of water at the measured temperature. After measurement, total length and two perpendicular measures of diameter under bark were taken at both ends of the sample. Permeability was calculated according to Darcy's law:

$$(4.1) \quad k = \frac{q \times l \times \eta}{A \times \Delta \Psi},$$

where k is permeability (m²), q is the water flux (m³/s), l is the length of the segment (m), A is sapwood cross-sectional area (m²), $\Delta \Psi$ is water potential drop (MPa); and η (MPa × s) is the viscosity of water at ambient temperature (20°C). Sapwood cross-sectional area was assumed as the total cross-sectional area of the segment determined by averaging the diameter under bark at both ends of the segment.

4.2.2. Statistical analysis

The fixed-effects model for a completely randomized design with factorial treatments was used to assess if permeability measured at the top of the stem was significantly different for families selected for differences in growth rate and crown size. The linear model is

$$(4.2) \quad Y_{ijk} = \mu + \alpha_i + \tau_j + (\alpha\tau)_{ij} + \varepsilon_{ijk}, \quad i=1,2 \quad j=1,2 \quad k=1,\dots,9,$$

where Y_{ijk} denotes the permeability of the k^{th} sample, μ denotes the overall mean, α_i denotes the effect of the i^{th} growth rate level (fast, slow), τ_j denotes the effect of the j^{th} crown size level (large, small), and $(\alpha\tau)_{ij}$ denotes the interaction between the i^{th} growth rate and the j^{th} crown size.

The linear model used to analyze differences in branch permeability for levels of growth rate, crown size, and permeability change with relative crown depth is

$$(4.3) \quad Y_{ijkm} = (\mu + \alpha_j + \tau_k + \varphi_{jk}) + (\beta + \delta_j + \rho_k + \phi_{jk})RCD_{m(ijk)} + \gamma_{i(jk)} + \varepsilon_{ijkm},$$

where Y_{ijkm} is the m^{th} value of permeability ($\text{m}^2 \times 10^{-12}$) for the i^{th} tree at the j^{th} growth rate level and k^{th} crown size level for a branch located a given relative crown depth (RCD). The term $\gamma_{i(jk)}$ denotes a random effect included to account for differences among trees (experimental units), and ε_{ijkm} is the error term. The parameter μ is the overall mean intercept, α_j is the effect of growth rate level on the intercept, τ_k is the effect of the crown size level, and φ_{jk} represents the effect of the interaction between growth rate and crown size. The parameter β represents the overall slope with respect to relative crown depth, δ_j is the effect of growth rate level on the slope, ρ_k is the effect of the crown size level, and ϕ_{jk} represents the effect of the interaction between growth rate and crown size on the slope. To determine the appropriate form of the model, the covariance analysis methodology proposed by Littell et al. (1999) was

followed. The Mixed Procedure of SAS (Statistical Analysis System v. 8.1, Cary, NC) was used to carry out the analysis. Patterns in the current leaf area--total leaf area ratio (A_C/A_L) with relative crown depth for levels of growth rate and crown size were examined with the following linear model:

$$(4.4) \quad Y_{ijkm} = (\mu + \alpha_j + \tau_k + \phi_{jk}) + (\beta + \delta_j + \rho_k + \phi_{jk}) \sum_{p=1}^2 RCD^p_{m(ijk)} + \gamma_{i(jk)} + \varepsilon_{ijkm}$$

where all symbols are the same as in equation (4.3) and $\sum RCD^p$ represents a second degree polynomial function.

For all analyses, a significance level of $\alpha = 0.10$ was used. This critical value compensates for the lower statistical power of field studies (Peterman 1990). Residual analyses were carried out to test if the data met the model's assumptions, and appropriate transformations were applied to the data when departures were present.

4.3. RESULTS AND DISCUSSION

4.3.1. Top stem permeability

Values of permeability for main stem samples averaged $2.0 \times 10^{-12} \text{ m}^2$. These values are somewhat lower than those measured in other studies. Shelburne and Hedden (1996) found average values of $4.29 \times 10^{-12} \text{ m}^2$ at the upper part of the main stem of 30-year old loblolly pine trees. Fredericksen et al. (1994) found average values of 2.05×10^{-12} in 30-year old loblolly pine trees artificially bent with pulleys and $2.43 \times 10^{-12} \text{ m}^2$ in stems of trees growing under normal conditions. The lower permeabilities observed in the present study are not extraordinary, as other studies have reported increases in stem permeability with age. For instance, Pothier et al. (1989b) found that permeability increased with age (15 to 35 years) and decreased with height within crowns of jack pine (*Pinus banksiana* Lamb.). For 15-year

old trees, they reported an average permeability of $1.4 \times 10^{-12} \text{ m}^2$ at the base of the upper third of the crown.

Equation (4.2) was fit to the natural logarithm of permeability to correct for observed departures from normality and constant variance when fit to the untransformed data. The analysis of variance of the natural logarithm of permeability indicated, neither significant interaction between crown size and growth rate ($P = 0.823$), nor significant differences for families differing in growth rate ($P = 0.481$). Families differing in crown size, however, differed significantly in permeability ($P = 0.003$). The mean permeability of large-crown families was lower than the permeability of small-crown families (Figure 4.1). Other studies have shown that the strength of apical control is positively related to shoot hydraulic capacity (Sellin 1987; Joyce and Steiner 1995), suggesting a link between stem straightness and sapwood permeability. A study carried out by Land et al. (1990) on these same families at 5-years-old showed that large-crown families tended to have more crooked stems and larger branches than small-crown families. They suggested that this could result from reduced apical control or the large branches increasing the risk of the top breaking out of the trees.

4.3.2. Branch permeability

Branch permeability for the sample averaged 0.74×10^{-12} ranging from 0.12×10^{-12} to 3.5×10^{-12} . Protz et al. (2000) measured permeability values ranging from 0.16×10^{-5} to $0.26 \times 10^{-5} \text{ m}^2$ for lower branches of lodgepole pine trees growing in closed stands. Although I found a significant trend of decreasing permeability with increasing relative crown depth, values for individual branches at similar relative crown depth varied widely. I assumed, initially, that microclimatic conditions within the stand were relatively homogeneous at similar canopy depths; therefore, no information on branch orientation was recorded.

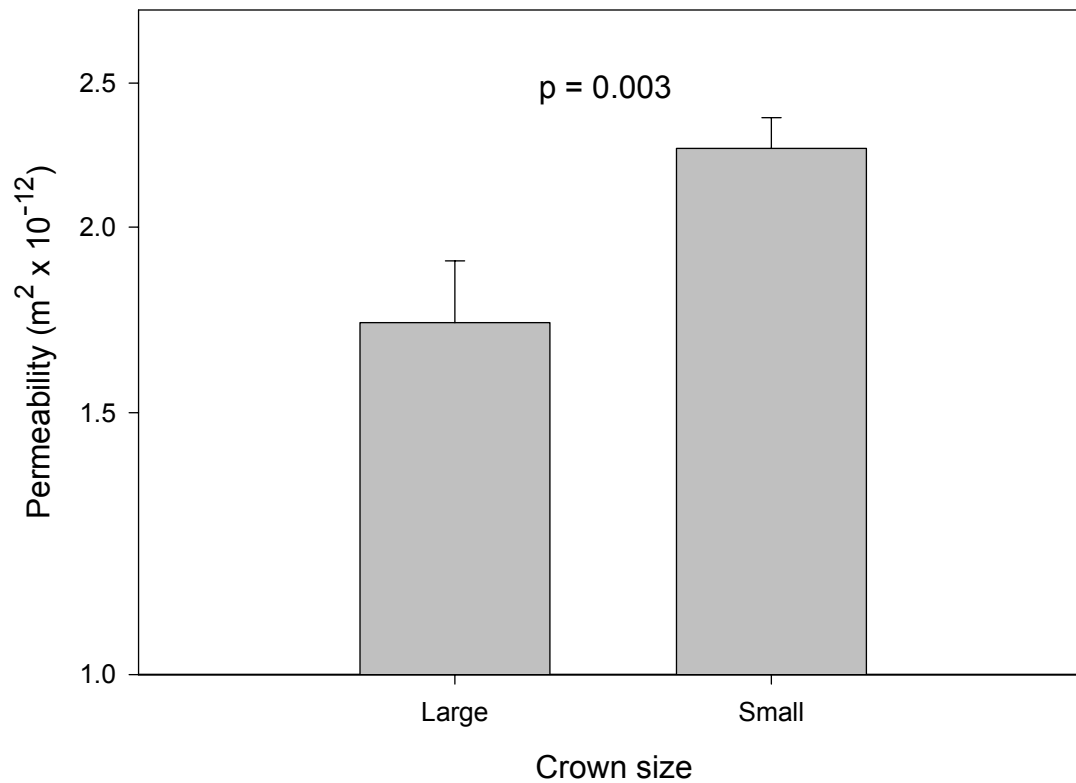


Figure 4.1. Mean values of hydraulic permeability at the top of stem of loblolly pine families differing in crown size. Sample size is 17 and 28 for large and small-crown size families respectively. P is the p-value for the effect of crown size using the model represented by eq. 4.2. Error bars are standard errors. Data are from a progeny trial established in 1985 on the John Starr Memorial Forest near Starkville, MS, USA.

Differences in branch aspect may have considerable effect on branch physiology, however. Working in thinned, loblolly pine plantations, Gravatt (1994) found differences in the morphology and physiology of branches located on the northern and southern aspects of the crown.

Branch permeability was logarithmically transformed to correct for departures from normality and homogeneous variance. Analysis of the full model as illustrated by equation (4.3) indicated that neither families differing in growth rate ($P = 0.178$) nor crown size ($P = 0.226$) differed significantly in the slope between $\ln(k)$ and RCD. Therefore, a reduced model was fit with a common slope (β)

$$(4.5) \quad Y_{ijkm} = (\mu + \alpha_j + \tau_k + \varphi_{jk}) + \beta \cdot RCD_{m(ijk)} + \gamma_{i(jk)} + \varepsilon_{ijkm}.$$

The reduced model had a significant negative slope ($P = 0.003$). The interaction and growth rate terms were not significant (Table 4.1); however, there was a significant, positive effect of the crown size term ($P=0.042$). Thus, parallel lines with common slope but different intercepts describe changes in permeability with relative crown depth for large and small crown families (Figure 4.2).

Despite the large variability, permeability clearly decreased with crown depth. Protz et al. (2000) also reported lower values of branch permeability in the lower portions of crowns in both closed and open stands, the difference being greater in closed stands. Mencuccini and Grace (1996) studied age-related changes of hydraulic conductance in stems and branches of Scots pine, found that for branches of similar size, conductance was consistently lower at the bottom of the crown than at the top of the crown. Protz et al. (2000) suggest that reduced photosynthetic efficiency of branches in the lower crown is a consequence of hydraulic

Table 4.1. Results for the mixed covariance analysis for the natural logarithm of branch permeability ($\text{m}^2 \times 10^{-12}$) of loblolly pine families assuming different intercepts and a common slope for combinations of growth rate and crown size. Relative crown depth is treated as a covariate. Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA.

| Effects | F-value | P-value |
|----------------------|---------|---------|
| Growth rate (GR) | 0.51 | 0.481 |
| Crown size (CS) | 4.41 | 0.042 |
| GR \times CS | 0.05 | 0.823 |
| Relative crown depth | 9.51 | 0.002 |

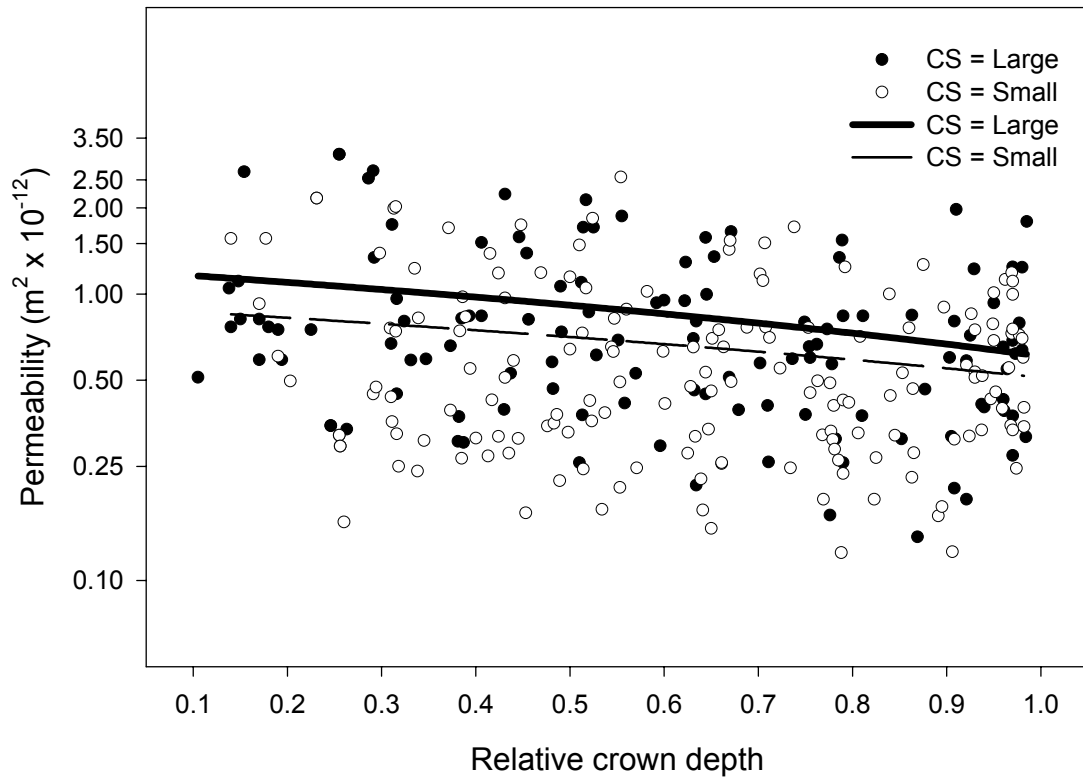


Figure 4.2. Branch permeability as a function of relative crown depth (RCD) and crown size (CS). Regression lines were obtained from the model $\ln(k) = -0.374 + 0.2859 \times D - 0.45701 \times RCD$, where $D=0$ for small-crown families and $D=1$ for large crown families. Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA.

limitations. They found that lower branches showed lower values of permeability and reduced stomatal conductance with respect to upper branches on lodgepole pine trees growing in closed stands. In addition, lower branches were more likely to die than upper branches under drought conditions when branch permeability was artificially reduced by means of drilling holes in the xylem. They suggested that reduced hydraulic permeability was an important factor in causing mortality of shaded branches at the bottom of the crown.

No differences in permeability at the stem or branch level were found for families differing in growth rate. Some studies have found a positive association between growth rate and stem permeability (Whitehead et al. 1984, Pothier et al. 1989a). However, Maherali and DeLucia (2000) reported that ponderosa pine (*Pinus ponderosa* Laws.) trees growing in a desert climate have higher specific conductivities but lower growth rates than trees growing in humid, montane climates, thus the larger specific conductivities observed in desert trees could not be attributed to larger growth rates.

The significantly greater mean branch permeability observed in the large-crown families contrasts with the lower values measured at the top of the main stem relative to the small-crown families. These large-crown families have been identified as “competitor” genotypes that, when growing on wide spacing, may be capable of allocating more photosynthate to lateral branches at the cost of some apical control (Land et al. 1990).

Large-crown and small-crown families did not differ in total foliage amount or crown dimensions (Table 4.2), but they differed significantly in current foliage--total foliage and leaf area--branch mass ratios. A weak but significant correlation was found between branch permeability and current foliage--total foliage ratio ($r = 0.11$, $P = 0.07$) for a given relative crown depth. The covariance model (equation 4.4) describing the relationship between current

Table 4.2. Mean values and results of the t-test ($\alpha = 0.1$) for mean differences of crown dimensions and foliage variables in loblolly pine families differing in crown size. In parenthesis are standard errors. Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA.

| | Crown size | | P-value |
|---|-------------|-------------|---------|
| | Large | Small | |
| Sample size | 18 | 29 | |
| Total height (m) | 16.8 (0.2) | 17.1 (0.2) | 0.462 |
| Height to base of first live branch (m) | 9.3 (0.2) | 9.6 (0.2) | 0.983 |
| Live crown length (m) | 7.7 (0.3) | 7.5 (0.2) | 0.654 |
| Crown ratio | 0.36 (0.1) | 0.36 (0.1) | 0.363 |
| Leaf area (m ²) | 27.7 (10.2) | 28.7 (13.1) | 0.708 |
| Leaf area density (m ² /m ³) | 0.1 (0.02) | 0.12 (0.04) | 0.060 |
| Current foliage area-- total foliage area ratio | 0.67 (0.09) | 0.57 (0.07) | 0.002 |
| Leaf area--branch mass ratio (m ² /kg) | 1.65 (0.51) | 2.16 (0.61) | 0.005 |

and total leaf area showed significant interactions of the crown size term with linear and quadratic terms of relative crown depth (Table 4.3). The relation was further examined with a reduced model including only crown size and using statistical contrasts at fixed 20 % intervals of crown depth. These results show large-crown families having significantly larger amounts of current leaf area relative to total leaf area in the lower two-thirds of the crown relative to small-crown families. Thus, it appears that large-crown families maintain a greater number of active terminal buds lower in the crown than small-crown families.

There were no differences in height to the base of the live crown or crown length between large and small crown families, suggesting, that differences in permeability do not affect rates of crown recession. However, small-crown families did support greater amounts of leaf area per unit of branch mass (Table 4.2) and differed in current foliage--total foliage ratios along the crown, suggesting differences in crown structure.

The observed differences in patterns of stem-top and branch permeability between large and small-crown size families growing in the same environment suggest the presence of a genetic component affecting the hydraulic architecture of loblolly pine trees. The expression of that genetic component on the crown structure of these families may depend, however, on environmental factors.

4.4. SUMMARY AND CONCLUSIONS

Patterns in branch permeability with crown depth and permeability at the top of the main stem were analyzed for loblolly pine (*Pinus taeda* L.) trees from families selected for differences in growth rate (fast, slow) and crown size (large, small). Permeability at the top of the stem averaged $2.0 \times 10^{-12} \text{ m}^2$, being significantly lower for large-crown families than for small-crown families. Average branch permeability was lower ($0.74 \times 10^{-12} \text{ m}^2$) than stem top

Table 4.3. Results for the analysis of the final mixed covariance model for current foliage--total foliage area ratio in loblolly pine families differing in crown size. Levels for contrasts at selected crown depths are denoted by CS_L (large-crown size) and CS_S (small-crown size). Data are from a progeny trial planted in 1985 on the John Starr Memorial Forest near Starkville, MS, USA.

| Effects | F | P-value |
|--------------------------------|--------|---------|
| Crown size (CS) | 4.33 | 0.038 |
| RCD | 101.20 | <.001 |
| RCD \times CS | 7.17 | 0.008 |
| RCD ² | 57.80 | <.001 |
| RCD ² \times CS | 4.67 | 0.031 |
| Contrasts | T | P-value |
| CS_L vs. CS_S at RCD = 0.2 | 0.39 | 0.700 |
| CS_L vs. CS_S at RCD = 0.4 | 2.78 | <.001 |
| CS_L vs. CS_S at RCD = 0.6 | 2.81 | <.001 |
| CS_L vs. CS_S at RCD = 0.8 | 2.79 | <.001 |
| CS_L vs. CS_S at RCD = 1.0 | 2.77 | <.001 |

permeability and decreased significantly with crown depth. Large-crown families had higher branch permeability along the crown than small-crown families. The average permeability in stems and branches did not differ significantly between fast and slow-growth rate families. Large crown families had significantly larger current--total leaf area ratios in the lower two-thirds of the crown. There was a weak but significant association between branch permeability and current--total leaf area ratios for a given relative crown depth. The observed differences in patterns of stem-top and branch permeability between large and small-crown size families growing in the same environment suggest the presence of a genetic component affecting the hydraulic architecture of loblolly pine trees. The expression of that genetic component on the crown structure of these families may depend, however, on environmental factors.

CHAPTER 5

SUMMARY AND CONCLUSIONS

This study, examined several factors of canopy structure and their influences on the stand development in loblolly pine (*Pinus taeda* L.) plantations from a modeling perspective. Aspects of the canopy such as foliage distribution, crown hydraulic architecture, and the effect of chronological changes in canopy structure on stand development were explored as possible components of a future process-based model intended for management purposes.

The quantitative description of vertical leaf area distribution is an essential component in forest growth models because the spatial distribution of foliage and its supporting structures determine the pattern of light attenuation and the distribution of photosynthesis, transpiration, and nutrient cycling and because strongly influences stem growth and form. A model based on the Johnson's S_B distribution was developed for predicting leaf area distribution of loblolly pine (*Pinus taeda* L.) trees from measurements of various tree dimensions. The model predicted well the cumulative fractions of leaf area along the crown, but errors were amplified when transformed to absolute values of leaf area, reducing the apparent precision of the model. The model has the potential to be included in forest growth models where an accurate description of leaf area distribution is necessary. A modification of this model was implemented in the preliminary model subsequently built.

A novel process-related, non-carbon-based growth model for predicting the growth of closed, unthinned, loblolly pine (*Pinus taeda* L.) stands was developed and its ability to represent the dynamics of the canopy and stand growth was tested. The general concept of the model is based on the relationships between tree size and stand density as controlled by chronological changes in canopy structure during the period of maximum, intertree

competition. Several empirical routines were included when information about a given mechanistic process was not available. Overall, model predictions were in agreement with reported observations or proposed theories in relation to stand growth, size-density relations, and relationships between canopy dynamics and stand growth. The model has several advantages such as the ability of replacing empirical routines with process-based routines or using outputs from process based models as inputs for the model.

A critical component affecting the model behavior was the submodel of crown recession. This component was modeled empirically and had a reasonable performance within certain limits of density and site index, but as any empirically based model it was less satisfactory when simulations were run for stands with characteristics outside the range of conditions used in model construction. Given the large effects that physiology and environment have in the process of crown recession and its influence on canopy structure, it was deemed reasonable to analyze the possibility of replacing the empirical process for a process-based submodel. However, the processes intervening in crown recession are not totally understood, and the effort was dedicated to examine some physiological aspects that could be critical for the development of future models describing this process. Particularly, the hydraulic architecture of loblolly pine crowns is a topic that has been little explored and could have consequences on photosynthetic efficiency observed at the bottom of the crown. In this study, patterns in branch permeability with crown depth and permeability at the top of the main stem were analyzed for loblolly pine (*Pinus taeda* L.) trees from families selected for differences in growth rate (fast, slow) and crown size (large, small). The results showed significant differences between patterns of stem and branch permeability and that genetic differences affect this pattern. In addition, branch permeability decreased significantly from

the top to the bottom of the crown. Although, large crown families had significantly larger current--total leaf area ratios in the lower two-thirds of the crown than small crown families, only a weak but significant association between branch permeability and current--total leaf area ratios was found. These results show that variations in the hydraulic architecture of the crown of loblolly pine trees may be an important factor in regulating the process of crown recession. More research is required, however, before the effect of hydraulic architecture can be used for modeling crown recession, particularly studies that examine the relationships between hydraulic efficiency and light limitations. So far, little research has been done in this respect (e.g., Schultz and Matthews 1993, Protz et al. 2000).

The study showed the potential of using a process approach to conceptualize a forest growth model and utilizing mechanistic and empirical elements in the construction of the simulator. In addition, the integration and synthesis of information coming from diverse sources in the model allows the possibility of detecting deficiencies in the understanding of key processes and provide a guide for formulating hypotheses and planning experiments to fill the gaps in knowledge of the factors regulating stand development.

LITERATURE CITED

- Assmann E (1970) The principles of forest yield study. Pergamon Press, New York.
- Baldwin VC Jr., Burkhardt HE, Dougherty PM, Teskey RO (1993) Using a growth and yield model (PTAEDA2) as a driver for a biological process model (MAESTRO). U.S. For. Serv. South. For Exp. Stn. Res. Pap. SO-276.
- Baldwin VC Jr., Burkhardt HE, Westfall JA, Peterson KD (2001) Linking growth and yield and process models to estimate impact of environmental changes on growth of loblolly pine. For. Sci. 47: 77-82.
- Baldwin VC Jr., Feduccia DP (1987) Loblolly pine growth and yield prediction for managed West Gulf plantations. USDA For. Ser. Res. Pap. SO-236.
- Baldwin VC, Peterson KD, Burkhardt HE, Amateis RL, Dougherty PM (1997) Equations for estimating loblolly pine branch and foliage weight and surface area distributions. Can. J. For. Res. 27: 918-927.
- Battaglia M, Sands PJ, Candy SG (1999) Hybrid growth model to predict height and volume growth in young *Eucalyptus globulus* plantations. For. Ecol. Manage. 120: 193-201.
- Booker RE (1977) Problems in the measurement of longitudinal sapwood permeability and hydraulic conductivity. N.Z.J. For. Sci. 7:297-306.
- Booker RE, Kininmonth IA (1978) Variation in longitudinal permeability of green radiata pine wood. N.Z.J. For. Sci. 8:295-308.
- Borders B (1989) Systems of equations in forest stand modeling. For. Sci. 35: 548-556.
- Brix H (1981) Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. Can. J. For. Res. 11: 502-511.
- Brix H (1983) Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. Can. J. For. Res. 13: 167-175.
- Cao QV (1994) A tree survival equation and diameter growth model for loblolly pine based on the self-thinning rule. J. App. Ecol. 31: 693-698.
- Cao QV, Dean TJ, Baldwin VC Jr. (2000) Modeling the size density relationship in direct-seeded slash pine stands. For. Sci. 46: 317-321.
- Carter MC, Dean TJ, Zhou M, Messina MG, Wang Z (2002) Changes in C, N, and biota following harvesting and regeneration of a loblolly pine (*Pinus taeda* L.) plantation. For. Ecol. Manage. in press.
- Clutter JL, Fortson JC, Pienaar LV, Brister GH, Bailey RL (1983) Timber Management a Quantitative Approach. John Wiley & sons. New York.

- Comstock, GL (1970) Directional permeability of softwoods. *Wood Fiber* 1: 283-289.
- Dean TJ (1991) Effect of growth rate and wind sway on the relation between mechanical and water-flow properties in slash pine seedlings. *Can. J. For. Res.* 21: 1501-1506.
- Dean, TJ (2001) Potential effect of stand structure on belowground allocation. *For. Sci.* 47: 69-76.
- Dean TJ, Baldwin VC Jr. (1996a) Growth in loblolly pine plantations as a function of stand density and canopy properties. *For. Ecol. Manage.* 82: 49-58.
- Dean TJ, Baldwin VC Jr. (1996b) The relationship between Reineke's stand-density index and physical stem mechanics. *For. Ecol. Manage.* 81: 25-34.
- Dean TJ, Long JN (1986) Validity of constant stress and elastic-instability principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Ann. Bot.* 58: 833-840.
- Dean TJ, Long JN (1992) Influence of leaf area and canopy structure on size-density relations in even-aged lodgepole pine stands. *For Ecol. Manage.* 49: 109-117.
- Dicus CA (2000) The Relationship of Biomass Allocation and Nutrient Dynamics in Loblolly and Slash Pine Forests Ph.D. Dissertation. Louisiana State University.
- Draper NR, Smith H (1981) *Applied Regression Analysis*. John Wiley & Sons New, York. pp 7.
- Edwards WRN, Jarvis PG (1982) Relations between water content, potential, and permeability in stems of conifers. *Plant Cell Environ.* 5: 271-277.
- Ford ED (1982) High productivity in a polestage Sitka spruce stand and its relation to canopy structure. *Forestry* 55: 1-17.
- Ford ED (1985) Branching, crown structure and the control of timber Production. In *Attributes of Trees as Crop Plants*, Cannell MGR, Jackson JE (eds.). Inst. Terr. Ecol. Titus Nelson and Sons, Cumbria, UK. pp. 228-252
- Fredericksen TS, Hedden RL, Williams SA (1994) Effect of stem bending on hydraulic conductivity and wood strength of loblolly pine. *Can. J. For. Res.* 24: 442-446.
- Gillespie AR, Allen HL, Vose JM (1994) Amount and vertical distribution of foliage of young loblolly pine trees affected by canopy position and silvicultural treatment. *Can. J. For. Res.* 24: 1337-1344.
- Gilmore DW, Seymour RS (1996) Alternative measures of stem growth efficiency applied to *Abies balsamea* from four canopy positions in central Main, USA. *For. Ecol. Manage.* 84: 209-218.

- Gravatt D (1994) Physiological Variation in Loblolly Pine (*Pinus taeda* L.) as Related to Crown Position and Stand Density. Ph.D. Dissertation. School of Forestry, Wildlife, and Fisheries. Louisiana State University.
- Johnsen K, Samuelson L, Teskey R, McNulty S, Fox T (2001) Process models as tools in forestry and management. *For. Sci.* 47: 2-8.
- Johnson, NL (1949a) Systems of frequency curves generated methods of translation. *Biometrika* 36: 149-176.
- Johnson, NL (1949b) Bivariate distributions based on simple translation systems. *Biometrika* 36: 297-304.
- Joyce BJ, Steiner KC (1995) Systematic variation in xylem hydraulic capacity within the crown of white ash (*Fraxinus americana*). *Tree Physiol.* 15: 649-656.
- Keane MG, Weetman GF (1987) Leaf area-sapwood cross-sectional area relationships in repressed stands of lodgepole pine. *Can. J. For. Res.* 17: 205-209.
- Kershaw JA, Maguire DA (1996) Crown structure in western hemlock, Douglas-fir and grand fir in western Washington: horizontal distribution foliage within branches *Can. J. For. Res.* 26: 128-142.
- Kinnerson RS Jr., Fritschen LJ (1971) Modeling a coniferous canopy. *Agr. Meteorol.* 8: 439-445.
- Knoebel BR, Burkhart, HE (1991) A bivariate distribution approach to modeling forest diameter distributions at two points in time. *Biometrics* 47: 241-253.
- Korzukhin M, Ter-Mikaelian MT, Wagner R (1996) Process versus empirical models: which approach for forest ecosystem management? *Can. J. For. Res.* 26: 879-887.
- Kuulivainen T (1991) Long-term development of needle mass, radiation interception and stemwood production in naturally regenerated *Pinus sylvestris* stands on Empetrum-Vaccinium site type in the northern boreal zone in Finland: and analysis based on a empirical study and simulation. *For. Ecol. Manage.* 46: 103-122.
- Kvålseth TO (1985) Cautionary note about R^2 . *Am. Stat.* 39: 279-285.
- Land SB Jr., Belli KL, Duzan HV (1990) Family, spacing and family-by-spacing effects on loblolly pine during five years after planting. Sixth Biennial Southern Silvicultural Research Conference, Memphis, TN, Oct 30-Nov. 1.
- Larson PR (1963) Stem form development of forest trees. *For. Sci. Monogr.* 5.
- Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1999) SAS system for mixed models. SAS Institute, North Carolina.

- Long JN, Smith FW (1984) Relation between size and density in developing stands: a description and possible mechanisms. *For. Ecol. Manage.* 7: 191-206.
- Long JN, Smith FW (1990) Determinants of stemwood production in *Pinus contorta* var. *latifolia* forests: the influence of site quality and stand structure. *For. Ecol. Manage.* 53: 53-64.
- Long JN, Smith FW (1992) Volume increment in *Pinus contorta* var. *latifolia*: the influence of stand development and crown dynamics. *For. Ecol. Manage.* 53: 53-64.
- Maguire DA, Bennett WS (1996) Patterns in vertical distribution of foliage in young coastal Douglas-fir. *Can. J. For. Res.* 26: 1991-2005.
- Maherali H, DeLucia EH (2000) Xylem conductivity and vulnerability to cavitation of ponderosa pine growing in contrasting climates. *Tree Physiol.* 20: 859-867.
- Mäkelä A, Landsberg J, Ek AR, Burk TE, Ter-Mikaelian M, Ågren GI, Chadwick DO, Puttonen P (2000) Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiol.* 20: 289-298.
- Margolis H, Oren R, Whitehead D, Kauffmann MR (1995) Leaf area dynamics of conifer forests. In: Smith KW, Hinckley TM (eds.) *Ecophysiology of Coniferous Forests*. Academic Press, New York, pp 181-223.
- Massman WT (1982) Foliage distribution in old-growth coniferous tree canopies. *Can. J. For. Res.* 12: 10-17.
- Mayer DG, Butler DG (1993) Statistical validation. *Ecol. Modell.* 68: 21-32.
- Mencuccini M, Grace J (1996) Developmental patterns of aboveground hydraulic conductance in a Scots pine (*Pinus sylvestris* L.) age sequence. *Plant Cell Environ.* 19: 939-948.
- Oren R, Waring RH, Stafford SG, Barrett GW (1987) Twenty four years of ponderosa pine growth in relation to canopy leaf area and understory competition. *For. Sci.* 33: 538-547.
- Peterman RM (1990) The importance of reporting statistical power: the forest decline and acidic deposition example. *Ecology* 71: 2024-2027.
- Phillips N, Bond BJ, Ryan M (2001) Gas exchange and hydraulic properties in the crowns of two tree species in a Panamanian moist forest. *Trees* 15: 123-130.
- Pothier D, Margolis HA, Poliquin J, Waring R (1989a) Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can. For. J. Res.* 19: 1564-1570.

- Pothier D, Margolis HA, Waring RH (1989b) Patterns of change of saturated sapwood permeability and sapwood conductance with stand development. *Can. J. For. Res.* 19: 432-439.
- Protz CG, Sillins U, Liefers VJ (2000) Reduction in branch sapwood hydraulic permeability as a factor limiting survival of lower branches of lodgepole pine. *Can. J. For. Res.* 30: 1088-1095.
- Reineke LH (1933) Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46: 627-638.
- Roberts SD, Dean TJ, Evans DL (2002) Family influences on leaf area estimates derived from crown and tree dimensions in *Pinus taeda*. *For. Ecol. Manage.* in press.
- Roberts SD, Long JN (1992) Production efficiency of *Abies lasiocarpa*: influence of vertical distribution of leaf area. *Can J. For. Res.* 22: 1230-1234.
- Roecker EB (1991) Prediction error and its estimation for subset-selected models. *Technometrics* 33: 459-468.
- Sampson DA, Smith FW (1993) Influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta* var. *latifolia*) forest. *Agric. For. Meteorol.* 64: 63-79.
- Schultz HR, Matthews MA (1993) Xylem development and hydraulic conductance in sun and shade shoots of grapevine (*Vitis vinifera* L.): evidence of how light uncouples water transport capacity from leaf area. *Planta* 190: 393-406.
- Sellin A (1987) Hydraulic conductivity of the water transport system in Norway spruce. *Sov. Plant. Physiol.* 34: 545-553.
- Shelburne VB, Hedden RL (1996) Effect of stem height, dominance class, and site quality on sapwood permeability in loblolly pine (*Pinus taeda* L.). *For. Ecol. Manage.* 83: 163-169.
- Shelburne VB, Hedden RL, Allen R (1993) The effects of site, stand density, and sapwood permeability on the relationship between leaf area and sapwood area in loblolly pine (*Pinus taeda* L.). *For. Ecol. Manage.* 58: 193-209.
- Shi K, Cao QV (1997) Predicted leaf area growth and foliage efficiency of loblolly pine plantations. *For. Ecol. Manage.* 95: 109-115.
- Sikierski K (1992) Comparison and evaluation of three methods of estimation of the Johnson S_B distribution. *Biom. J.* 7: 879-895.
- Sperry JS, Donnelly JR, Tyree MT (1988) A method for measuring hydraulic conductivity and embolism in xylem. *Plant Cell Environ.* 13: 279-287.

- Stephens GR (1969) Productivity of red pine I. Foliage distribution in tree crown and stand canopy. *Agr. Meteorol.* 6: 275-282.
- Telewski FW, Jaffe M (1986) Thigmomorphogenesis: field and laboratory studies of *Abies fraseri* in response to wind or mechanical perturbation. *Physiol. Plant.* 66: 211-218.
- Turner J, Long WN (1975) Accumulation of organic matter in a series of Douglas-fir stands. *Can. J. For. Res.* 5: 681-690.
- Valentine HT, Ludlow AR, Furnival GM (1994) Modeling crown rise in even aged stands of Sitka spruce or loblolly pine. *For. Ecol. Manage.* 69: 189-197.
- Vose MJ, Allen HL (1988) Leaf area, stemwood growth, and nutrition relationships of loblolly pine. *For. Sci.* 34: 547-563.
- Vose MJ, Dougherty PM, Long JN, Smith FW, Gholz HL, Curran PJ (1994) Factors influencing the amount and distribution of leaf area of pine stands. *Ecol. Bull.* 43: 102-114.
- Wang YP, Jarvis PG, Benson ML (1990) Two-dimensional needle-area density distribution within the crowns of *Pinus radiata*. *For. Ecol. Manage.* 32: 217-237.
- Waring RH (1983) Estimating forest growth and efficiency in relation to leaf area. *Adv. Ecol. Res.* 6: 327-354.
- Waring RH, Newman K, Bell J (1981) Efficiency of tree crowns and stemwood production at different canopy leaf densities. *Forestry* 54: 129-137.
- Waring RH, Thies WG, Muscato D (1980) Stem growth per unit of leaf area: a measure of tree vigor. *For. Sci.* 26: 112-117.
- West PW (1993) Model of above-ground assimilate partitioning and growth of individual trees in even-aged monoculture. *J. Theor. Biol.* 161: 369-394.
- West PW, Jactett DR, Sykes SJ (1989) Stresses in, and the shape of, tree stems in forest monoculture. *J. Theor. Biol.* 140: 327-343.
- Whitehead D (1978) The estimation of foliage area from sapwood basal area in Scots pine. *Forestry* 51: 35-47.
- Whitehead D, Edwards WRN, Jarvis PG (1984) Conducting sapwood area, foliage area, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can. J. For. Res.* 14: 940-947.
- Xu M, Harrington TB (1998) Foliage biomass distribution of loblolly pine as affected by tree dominance, crown size, and stand characteristics. *Can. J. For. Res.* 28: 887-89.
- Zeide B (1991) Self-thinning and stand density. *For. Sci.* 37: 517-523.

VITA

Mauricio Jerez Rico was born August 10, 1963, in Madrid (Spain). At four years old, he moved to Mérida, Venezuela, along with his parents. In 1987, he graduated from the School of Forestry at Universidad de Los Andes (Mérida, Venezuela). After graduation he worked as a forester at Caparo Experimental Station (Barinas, Venezuela) from 1988 to 1990. There, he got experience in tropical silviculture and timber management activities. In 1990, he entered to the School of Economics and Social Sciences at Universidad de Los Andes, and earned a master of science in applied statistics in 1992. Since 1993, he is part of the faculty of the Facultad de Ciencias Forestales y Ambientales at Universidad de Los Andes. He has done research on tropical plantation silviculture, forest inventory, biometry, and tree-growth modeling. Jerez came to the United States in August 1997 as a Fulbright Fellow and enrolled in the doctoral program at Louisiana State University under the direction of Dr. Thomas J. Dean. His current research addresses the modeling of canopy structure effects on loblolly pine growth. He is scheduled to complete his doctoral program in May 2002.