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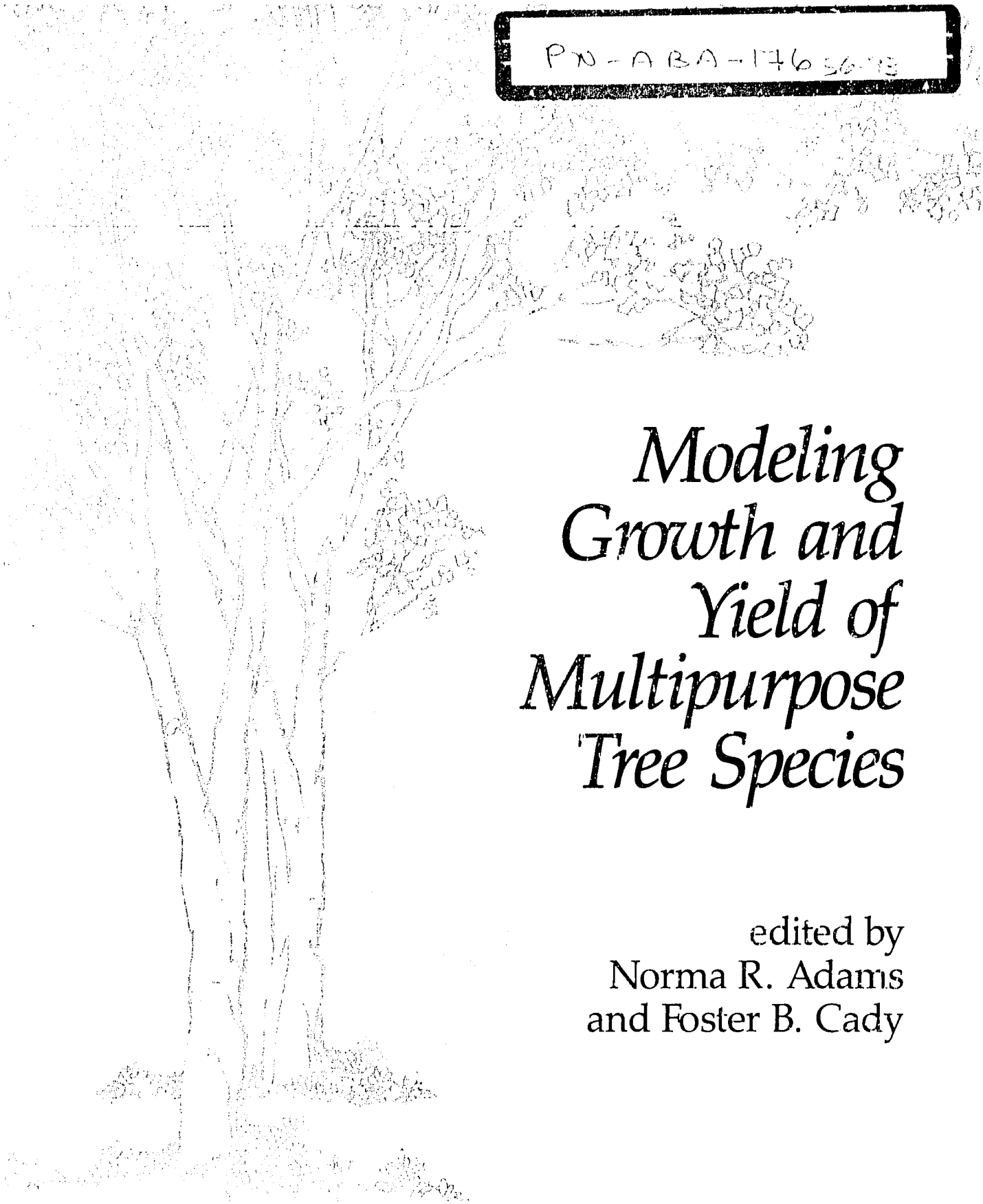

Modeling Growth and Yield of Multipurpose Tree Species

edited by
Norma R. Adams
and Foster B. Cady

Multipurpose Tree Species Network Technical Series, Vol. 1

Multipurpose Tree Species Network Technical Series

This series of publications includes technical papers produced or supported by the Forestry/Fuelwood Research and Development (F/FRED) Project. Volumes in this series are available for distribution to F/FRED network members and other selected individuals and institutions.

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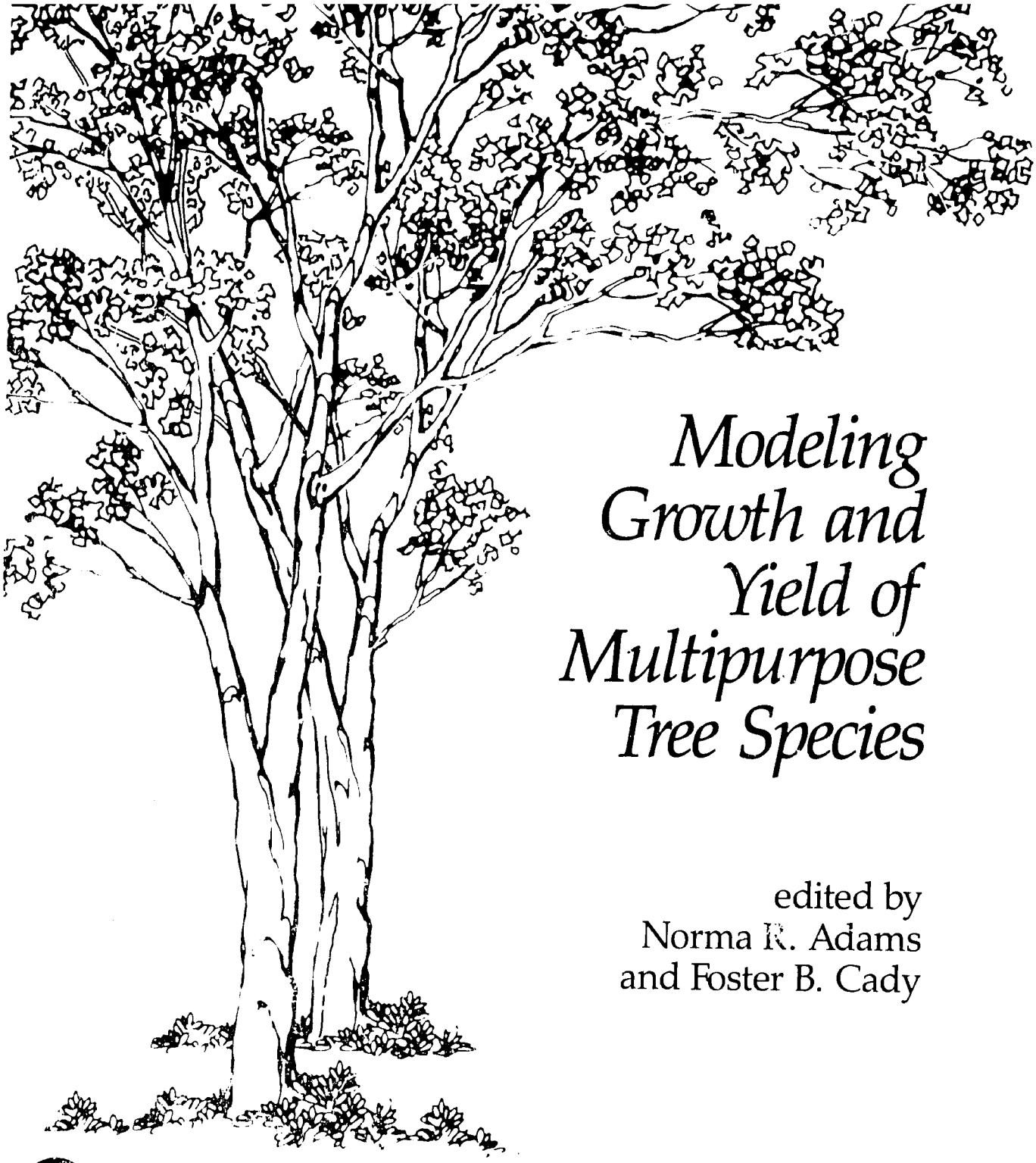

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Winrock International Institute for Agricultural Development

financed by the U.S. Agency for International Development

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Foreword

The United States Agency for International Development (AID) launched the Forestry/Fuelwood Research and Development (F/FRED) Project in 1985 as part of its efforts to prevent further deforestation and to meet the critical needs of small farmers in developing countries for fuelwood and other tree products. Later that same year, AID contracted Winrock International to develop a network of Asian scientists to strengthen research on short-rotation, multipurpose tree species (MPTS).

The development of a related global management information system is helping scientists manage information about MPTS and their potential for producing fuel, fodder, and other tree products. Developed by the University of Hawaii under the F/FRED Project, the Information and Decision Support System (IADSS) consists of relational databases and decision support programs that store, organize, and analyze information on MPTS experiments, literature, and specialists. By simulating complex biological and socioeconomic processes that determine tree production, IADSS serves as an important predictive tool for comparing management systems and assessing trade-offs between productivity and site sustainability. The F/FRED Global Research Team in Hawaii is developing environment models focused on interactions of experiment species, treatments, and environmental factors and simulation models from which scientists can reliably estimate tree performance over a wide range of conditions.

The F/FRED staff is pleased to present the five papers included in this volume, which provide valuable background to those interested in the concepts and practices of modeling growth and yield of multipurpose trees.

Thomas C. Niblock
F/FRED Project Director

Preface

In developing countries, the demand for fuelwood and other tree products, combined with using marginal lands for agricultural production, has increased small farmers' interest in growing and using multipurpose tree species (MPTS). These fast-growing trees, which can provide fuel, food, fodder, and income, also control erosion, serve as living fences, and restore degraded lands.

Modeling can provide scientists a tool to make sound recommendations to small farmers concerning which species to grow in specific areas. By integrating tree-environment interactions in a biologically realistic way, a model can predict the effects of both natural and manmade environmental changes on tree growth. Once a model is proven valid, it can serve as a predictive tool to match species to sites and assess trade-offs between management practices.

Modeling Growth and Yield of Multipurpose Tree Species has been compiled to outline a history of yield models, present the various approaches to modeling tree growth and yield, and assess their appropriateness for modeling growth of MPTS. This volume begins with an overview of the information required for MPTS yield prediction. Rose presents the uses and limitations of traditional yield tables, which may include various management regimes, but are site specific. Scientists need to understand the effects of site quality on production to extend results beyond trial sites. Rose stresses the need for coordinated experiments in different environments using the same measurement standards. From these results, minimum data sets can be established for environmental and simulation modeling.

Next, Harrington reviews the simulation models of tree and stand growth. Before a model is designed to predict MPTS yield, scientists need to assess the strengths and weaknesses of past approaches. An approach for modeling MPTS can then be outlined, identifying the proper level of resolution and the processes to be included based on available data.

Because no physiological time is defined for harvesting MPTS, designing a model to predict MPTS yield is complex. Riha stresses the importance of understanding how to evaluate yield in short-rotation systems when trying to assess effects of management practices. She outlines the management goals of short-rotation systems and the resulting implications for modeling yield. In another paper, Riha discusses the effects of drought stress on MPTS yield and proposes an approach for simulating effects of various durations of drought on biomass production of these species.

Modeling is an essential aid to management decisions, but reliable data are critical to any successful modeling exercise. Blake argues that scientists must understand both the biological and physical processes that affect tree growth and the management systems applied to produce reliable models. At the same time, knowing which data are needed for a particular modeling goal results in more efficient experimentation. Following experimentation, models can be improved based on experiment results. Therefore, linking experimentation and modeling avoids producing unreliable predictive models.

This series of papers covers a wide range of topics to be considered when designing a tree growth model for MPTS. We hope such an overview helps anyone interested in designing or using a computer simulation model to predict biomass yield of these important tropical trees.

Norma R. Adams
Project Editor
Foster B. Cady
F/FRED Research and Development Director

Overview of Yield Prediction for Multipurpose Tree Species

Dietmar W. Rose

University of Minnesota

Generation and successful transfer of data to improve management of multipurpose tree species (MPTS) production systems are the major goals of establishing an MPTS information and decision support system. Databases are useful if they directly support decision making. Field data must either provide the information needed to make decisions or the variables for developing models to support them. Data are transformed into decision-making outputs using scientific methods and models, e.g., simulation, statistics, and economics. Scientists must understand the relation between key dependent and independent variables before setting up experiments. Once understood, they must create a minimum data set of variables for field observation and measurement.

The development and validation of MPTS growth and yield models require more information than any single organization can collect. It is therefore necessary for scientists to pool data from many sources in accordance with data collection standards (Rose and Cady 1987). Coordinated MPTS field experiments avoid duplicated effort and cover the widest possible range of species, sites, and management treatments. This coordination requires establishing measurement standards; minimum data sets for modeling; and efficient data storage, organization, and retrieval.

Growth and Yield Modeling

Growth and yield models are needed to describe the interaction of stand management and environment. Coordinated experiments provide scientists an opportunity to develop such models, whose usefulness extends beyond experiment sites. These environmental models, which relate growth and yield to soil, site, and climate factors, represent a major advance over models developed for temperate forests.

MPTS growth and yield models are used primarily to:

- o match species and sites for survival and performance,
- o quantify the trade-offs between management systems,
- o help transfer technology beyond experiment sites, and
- o facilitate economic analysis of MPTS production systems.

Site Description

Any modeling effort of a biological production system requires an environmentally or geographically based reference system. Without such a system, performance data of specific plant production systems cannot be compared or transferred between locations. An environmental database relates forestry, agriculture, and agroforestry data to a common environmental basis of information. Historically, environmental systems development has depended on relations between climate and vegetation. Because vegetation integrates climatic effects, similar climates can be expected to support similar vegetation. Several environmental models that integrate climate conditions with existing vegetation patterns exist, e.g., Koppen and Holdridge systems. McFadden (1984) discusses several of these models.

Soil Taxonomy, a soil classification system developed by the U.S. Soil Conservation Service, provides a common language for communicating soil and climate information to scientists worldwide. Soil scientists recognize that interactions between soil characteristics, crop requirements, and management practices can be integrated effectively

to help transfer knowledge, especially when *Soil Taxonomy* is included in the equation.

As with most taxonomic systems, *Soil Taxonomy* has many categories and sub-categories. Because its names (*taxa*) are universal, this nomenclature provides a uniform basis for communicating information about soils and their management. Of the six major soil categories, soil family is the one that relates soil properties to management and manipulation for specific uses. It also includes most of the information needed to transfer agrotechnology among similarly classified soils. Cagauan, Tsuji, and Ikawa (1982) apply it to agroforestry and fuelwood production. They present information on procedures used to match tree requirements with environment conditions in new sites and use a case history as an example.

Based on experience with agronomic crops (Silva 1985), propagation and cultural technology associated with MPTS can be transferred more easily within than across the soil family category of *Soil Taxonomy*. Mathematical models describe the relation between soil, climate, and management variables and forestry or agricultural crop yields. Such models may be used to analyze, expand, and transfer MPTS technology.

Minimum Data Sets

To accelerate the development of predictive models for the major outputs of MPTS systems, standardized methodology for experimentation, including a minimum set of measurement variables, is needed. Scientists can coordinate their experiments to cover a wide range of sites, including extreme ones for which information is typically scarce. This coordination ensures that research will focus on the most important species and management approaches.

The two types of site variables collected are:

- o characteristics of climate, soil, and physiography and
- o plot measurements, including height and diameter of main stems and branches, crown, and component biomass weight.

The complex specifications of a minimum data set for agroforestry systems result from the numerous combinations and products of trees, crops, and animals that make replicated trials unlikely. To coordinate such experiments, network participants might concentrate initially on more widely accepted and sometimes simpler agroforestry systems. The Central American Fuelwood Project (Rose and Salazar 1983, Salazar and Rose 1984) has worked successfully with living fences, windbreaks, and individual trees in pasture.

Historical Overview

Historically, yield tables have served as foresters' most valuable tool to calculate allowable cuts and to regulate forests. They are the basis for determining rotation age and predicting yield at specified ages. Yield tables describe stand yield as a function of age and certain site characterizations. Site index is used to describe site quality and is based on the relation of dominant and co-dominant tree heights at a specific base age. If the base age is 50 years, for example, a site index of 65 indicates that dominant and co-dominant trees reached 65 feet height at age 50.

The development of yield tables originated in Germany during the timber famine of the 18th century. Normal yield tables represented fully stocked stands according to a subjective estimate of full stocking and stands that were not subjected to any stand treatment, such as thinning. Their development was based on continuous observation of individual stands over a full rotation. Such time-series data required enormous inputs of time and labor for measurement, especially in view of the long rotation periods for temperate forests. Despite the considerable inputs to develop these tools, they were limited. Since most tables were developed for specific locales, they could not be applied elsewhere. Normal or full stocking could not be defined objectively and stands typically were under some form of management. Utilization standards began to change as tree parts were used increasingly for industry.

To overcome the problems of normal yield tables, two other types were developed that are now standard tools for foresters worldwide. The variable-density yield table describes stand yield as a function of age if stand basal area is maintained

at some fixed level over the rotation through thinning. The managed yield table describes stand development for specific management regimes imposed on a stand.

To construct such yield tables, many more plots had to be established. Observing individual plots over full rotations was expensive. Therefore, many tables were constructed from cross-sectional data, i.e., stands representing similar conditions but with different ages used to develop the relation of yield over age. Because these tables were often developed for specific locales, they represented only a small subset of possible management regimes.

Because of these limitations, much effort has focused on the development of more flexible stand-growth and individual tree-growth simulation models for the most important commercial cover types and species. One such model is STEMS (USDA Forest Service 1979). Parameter estimates for the model's potential growth, growth modifier, and mortality components have been derived for the North Central and Northeast U.S. The model is now used routinely by public and private forest managers to simulate management and update permanent inventory plots between samplings

Kimmins (1985) reviewed the major approaches to the scientific investigation of forest yield and growth. The empirical, historical-bioassay approaches described above are becoming less acceptable because of their inability to predict production with changing environment conditions and forest management systems. Newer approaches need to rely on an understanding of the biological and environmental determinants of forest production rather than records of past plant growth. This branch of forest-yield research focuses on organic production and on factors that limit production. As such, research has focused on models of the photosynthesis-respiration carbon balance, the relation between foliar biomass and forest growth, and physiologically-based growth simulation models.

As indicated above, production studies for generating yield tables result in rather inflexible yield predictors, which provide little understanding of whole growth phenomena. The inability to accommodate changes in utilization standards has been pointed out. According to Kimmins (1985), a hybrid approach combines the advantages of bioassays and the production-process approach.

Bioassay models continue their usefulness for predicting yield of short-rotation crops, especially where time required to establish the bioassay is not too long. Parallel to this approach, yield or productivity should be related to either simple or complex environmental gradients or to individual environmental factors, e.g., temperature, precipitation, temperature and precipitation combined, actual evapotranspiration, and vegetation period. This environmental-correlation approach works fairly well for predicting continent-wide patterns of potential productivity, but has not been extensively used at the local level for individual trees or stands to predict spatial variations in productivity or effects of management activities (Kimmins 1985). Within an area of relatively uniform climate, soil moisture and fertility are used increasingly to predict site-yield potential (Kimmins 1985). Other soil, topography, and vegetation parameters should be examined for their potential as yield predictors.

MPTS growth modeling requires new approaches. Yield prediction should be based on general theory or a global model and a procedure to calibrate model parameters based on local growth and yield observations.

Appropriate Model Types

Much of the modeling methodology of temperate forests is applicable to MPTS modeling efforts. An excellent summary of growth modeling methodology is contained in Clutter et al. (1983), which includes estimated volume and weight of individual trees. It describes the most common methods for constructing site index curves and growth and yield models for basal area and volumes of trees and stands. The authors discuss growing stock and stand density measures.

Caution must be used when applying these methods to constructing MPTS growth and yield models. Tree management and modeling problems in the tropics are considerably more complex than those of temperate forests. Tropical forests contain numerous MPTS while temperate forests contain only a few commercial species. Because MPTS

systems produce many outputs that need to be quantified, growth and yield models must be developed for individual components. These components are interdependent (e.g., increased production of one may reduce production of another), requiring the examination of more management regimes. The management treatments may compromise achieving maximum biomass production with reaching defined levels for other outputs.

An advantage of MPTS over temperate species is shorter rotations. This advantage is counteracted by the potential of many MPTS to coppice, which further complicates growth and yield modeling. The quantification of growth and yield of agroforestry systems involving many mixes of tree species, annual crops, and animals is the ultimate challenge to the growth and yield modeler.

MPTS growth and yield modelers can benefit greatly from the global experiences and approaches used for plantation forests of single and mixed species. Measurements should enable modelers to quantify biomass of any tree part in an experiment and to develop functional relations between difficult-to-measure characteristics, like those of tree form or crown, with more easily measured variables, such as dbh and height. Measurements from individual trees should be accessible in the database if development of individual tree-growth models is desired.

For temperate-zone forests, plot data are often lacking for trees less than 10-20 years old. For this reason, few models of the establishment phase exist and relatively little ingrowth modeling has occurred. Models selected to best describe growth and yield of temperate tree species may, therefore, not always be suitable for short-rotation MPTS, for which early growth is greatly significant. Ingrowth should be of less concern in MPTS research because all trees, regardless of size, are included in the measurements.

Forest growth-simulation models based on physiological principles are rare because forests are a perennial crop requiring simulation of the nutrient translocation between growing periods. Light interception by tree canopies is difficult to describe. Generally, the data requirements of these models have ruled out more than modeling of the initial phase or first growing season of individual trees (Promnitz and Rose 1974, Rose and Promnitz 1975).

The development of strictly local yield tables for major species, treatments, and outputs should be discouraged within the MPTS network for Asia. It would require measuring many plots for numerous species managed for different products by region. Measurements of specific locales would lead to duplicated effort among regions and would require unacceptable amounts of time for model development.

A growth and yield simulation model contains various components, including the volume and/or weight of individual stems or trees. Models to quantify yield of wood and other products are likely regression models. Polynomials and nonlinear models are found in the literature (Clutter et al. 1983). Numerous possible model forms have been tested sufficiently for application to MPTS outputs. Prediction of stem volume and weight can be based on known models. Stem content is usually considered a function of tree dbh, some measure of tree height, and an expression of tree form.

What is new for MPTS is the quantification of these outputs via appropriate measurement procedures. The many MPTS, treatments, and outputs make the development of descriptive summary tables and graphs by key environment and management factors the first priority in understanding key relations among factors.

Prediction equations are developed through fairly straightforward application of standard statistical methods, including fitting linear and nonlinear regression equations to tree sample data. Clutter et al. (1983) summarize recommended techniques for fitting volume and weight prediction models to individual trees or plots.

Traditional methods of predicting growth and yield of forest stands are based on the concept that growth and yield are determined largely by the following factors (Clutter et al. 1983):

- stand age or age distribution,
- site quality,

- extent to which site quality is used, and

- applications of cultural treatments,such as thinning, fertilization, or vegetation control.

Site quality is the summary of biotic, edaphic, and climatic conditions that exist at a particular location. In the context of MPTS, site quality is the total production potential of a site for a particular species or group of species. Production potential includes all MPTS products. Clutter et al. (1983) describe the major direct and indirect methods for quantifying site quality.

Among the direct methods, estimation from historical records is of little value for MPTS production systems. There simply are not enough quantified observations of MPTS systems on various sites to estimate site quality. Stand volume and stand height data are two other direct methods for estimating site quality. For even-aged stands, a positive correlation can be observed between stand volume or height growth and site quality. Height growth is often positively correlated with volume growth. Various factors other than site quality, however, can affect the relation between volume or height attained at a given age. This is especially true for volume. Height of larger trees in even-aged stands is less affected by stand density and intermediate cutting (except for thinning from above). Among these confounding factors are stand density, species composition, genetics, and cultural practices. To estimate site quality from volume or height over age, it is therefore necessary to keep these other factors constant across the sites compared.

Most height-based methods use site index curves, which describe the development of height over age. Associated with each curve is a site index number, most frequently based on the height achieved at some reference age. The reference age is typically close to the average rotation age used for managing the species. Clutter et al. (1983) describe models useful for describing the relation between stand height and age.

Important considerations are how to select sample trees and how many to choose. The most common practice is to select samples among the dominant and co-dominant trees in a stand. The number selected for the sample depends on the variability of heights and sampling costs. Two methods for calculating the final site index are available. In one case, equations are fitted to stand average height/age data; in the other case, equations are developed from individual tree height/age data. The appropriate data and equations are needed when estimating site index for a stand using a prediction equation. Clutter et al. (1983) describe techniques for developing site index equations. The guide curve method assumes a family of height/age curves that are anamorphic, i.e., all curves are parallel with equal slopes at each age, but with different intercepts. The difference equation method can be applied with any height/age equation to produce anamorphic or polymorphic curve families. The parameter prediction method of fitting site index curves has been used to fit polymorphic-disjoint site index equations. This method involves three steps:

1. a linear or nonlinear height/age function is fitted to tree or plot data;

2. a site index value is assigned to each tree or plot using the fitted curve; and

3. the parameters of the fitted curves are related to the site indices using linear or nonlinear regression procedures.

Indirect methods for evaluating site quality must be used when the species of interest is not present at the site. Measurements of other site vegetation in the overstory or understory can sometimes be used to evaluate site quality. The best known site-quality system for understory vegetation was developed by Cajander (1926) for the spruce-pine-birch forests of Finland. Other examples of correlating dominant height or other characteristics with understory vegetation exist (Ure 1950). Of special interest are techniques to estimate site quality from topographic, climatic, and edaphic factors. These techniques use regression equations to correlate and predict the relation between soil and other variables and site index, height, and other productivity indicators.

Predicting Current Yield

Predicting current yield differs from predicting future yield. The latter involves a projection of stand density while the former does not. Current yield

predictions are either explicit or implicit. An explicit prediction estimates volume per area directly by solving an equation. Implicit predictions use equations to predict basic stand structure, which is then used to predict yields.

Prediction models for MPTS outputs can be developed for stands or individual trees. Individual tree-based forest-stand growth models represent a powerful approach to predicting forest growth, yield, and response to treatment (Dudek and Ek 1980). Individual distance-independent tree-growth models such as STEMS (USDA Forest Service 1979) represent a useful approach. These models are based on estimates of potential growth of open-grown trees (without competition) and the modification of this growth potential by some modifier function that characterizes competition through descriptors, such as crown ratios, and modeling mortality.

Once calibrated, such a model can handle many spacing patterns or other factors that influence individual tree characteristics. These models are flexible, and require individual tree observations for the range of environments and treatments desired for prediction purposes. Shells of such programs are available on microcomputers and can be modified for MPTS systems. Calibration of model parameters for major environmental zones provide a standard model applicable to whole regions. A modeling methodology still needs to be developed for the modifier function since the current minimum data set does not include characterization of the tree crown. Mortality estimates might be easier to obtain because of the short production periods of MPTS systems.

The STEMS model (both mainframe and microcomputer) is available from the U.S. Forest Service North Central Forest Experiment Station in St. Paul, Minnesota. The microcomputer version is known as TWIGS (The Woodsman Ideal Growth Simulator). The model's structure and the documentation provided by the package make this an excellent choice for MPTS modeling. However, care must be used when adapting these models to MPTS systems since maximum growth without competition is irrelevant. Other modeling methods must be developed.

Individual tree-growth models can complement stand-growth models. Careful use of analysis of variance and multivariate analysis techniques can provide insights into the most important underlying relations and least understood areas to which future experiments and modeling efforts can be directed.

Development and validation of operational simulation models to predict growth and yield of MPTS system components over a wide range of environments and treatments require a range of accumulated data on actual sites and treatments. The current minimum data set offers the potential that such simulation models can be developed. In the development of environmental growth and yield models, climate data play an important role. Long-term historic and experiment weather data make it possible to develop environmental simulation models, which require substantial information. The best hope for obtaining models is that many of the ongoing experiments can be captured in the format of the current minimum data set. Unfortunately, for most ongoing MPTS experiments, on-site weather observations are impossible to obtain. Environmental simulation models are more likely based on historic climate information obtained from the nearest meteorological station.

If only historic climate data from the nearest weather station are used, tree response to climate cannot be modeled as precisely as when actual site data are recorded. If weather station data are used exclusively, scientists might consider fitting functions to describe climate between weather stations via smoothing and other techniques designed to improve the value of climate data where experiments are located far from a weather station or at significantly different elevations.

Expert Systems for MPTS

Rarely do scientists have sufficient data to build a model. Data are often unavailable, unsuitable, or at the wrong level of resolution. Even with careful data collection, scientists inevitably discover that particular information is unavailable. This underscores the need to take maximum advantage of available data and assimilate new data into the model.

This subject area and associated computer software are termed *expert systems*. Expert systems attempt to unify all knowledge about a particular problem or domain. Specialized knowledge acquired by individuals over years of experience can be captured permanently in a computer system. The knowledge base can be expanded to include new information. Successful development of an expert system provides quick and inexpensive access to accumulated knowledge.

The knowledge base contains the facts and heuristics used in a particular subject area and a set of inference procedures, termed *inference engine* (Cooney 1985). A knowledge base is in some ways easier to build than a conventional model (Starfield and Bleloch 1986). It contains lists of decisions, questions and answers, and rules. Both the questions and rules should clearly explain the reasoning behind the knowledge base. The inference engine controls the order in which facts or heuristics are used to solve a particular problem. The knowledge base is specific to each field, but the collection of processing procedures or logical rules used to derive conclusions are transferable to other areas of expertise (Helliwell 1986). Expert systems shells combine the inference engine with a facility for building and managing a knowledge base.

Expert systems are categorized as decision support system software. These programs combine information databases with modeling systems that can project the results of a management action (Rauscher and Cooney 1986). A decision maker generates alternative solutions to a particular problem. The software package helps accumulate the experience or knowledge of the decision maker for specific situations by organizing, storing, retrieving, and analyzing information. In this way, the knowledge base of decision makers is constantly expanding beyond the ability of any one manager to keep abreast of all relevant information. While not capable of independent thought, expert systems structure human knowledge in a manner useful to solving typically unstructured problems (Rauscher and Cooney 1986).

Conclusions

To overcome the enormous obstacles of required time and money to develop predictive models for the numerous MPTS production systems, coordinated experiments and shared research findings are essential. Only by scientists pooling data from well-coordinated experiments can they expect to develop environmental growth and yield models for major MPTS production systems within the next decade.

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Simulation Models of Tree and Stand Growth

Robin A. Harrington

Forestry/Fuelwood Research and Development Project

Modeling productivity of multipurpose tree species provides a framework for integrating and synthesizing knowledge. Models help generate hypotheses on important interactions of multipurpose trees and their environment, including processes that control production. When these processes are integrated in a biologically realistic way, a predictive tool is produced that can:

- o match species and site to optimize total production and biomass allocation,
- o quantify productivity trade-offs between management systems, and
- o transfer this knowledge beyond experiment sites.

Growth model approaches range from leaf-level process models that require numerous species-specific parameters derived empirically to stand-level yield tables that are site-specific and predict yield under prescribed management conditions. Tree growth is considered at the tree or stand level. Individual tree models monitor growth within stands and determine competition among trees, while stand models consider stand-level properties, such as biomass production per unit of land area. Tree models that consider the location of each tree are termed *spatial models* (Shugart 1984). A change in level of resolution from leaf to stand generally reduces the number of required parameters and driving variables and increases the time step (Landsberg 1981).

This paper reviews various approaches used in process-oriented tree growth models. These approaches are evaluated in terms of their appropriateness for modeling multipurpose tree species. An alternative approach is discussed that has particular use in predicting productivity of tree components under different management regimes.

General Model Structure

Tree growth models vary according to which state and driving variables and biological processes are included (Table 1). State variables are the major model compartments. In dynamic simulation models, state variables change over time. Driving variables are the input data that affect the rate at which state variables change. They are external to the system modeled and, although they may change over time, are not affected by state variables (Swartzman and Kaluzny 1987). In process-oriented tree growth models, driving variables affect the rate at which physiological processes occur, which in turn affect the rate at which state variables change. Fig. 1 gives examples of variables and processes that might be included in a simulation growth model.

State and Driving Variables

Biomass components are the major state variables. An important distinction must be made between belowground and aboveground biomass because water uptake and nutrients are a function of root surface area (Atkinson 1980, Larcher 1980). Regrowth of aboveground biomass following cutting is affected by carbohydrate reserves in belowground biomass (Kramer and Kozlowski 1979, Mika 1986). Some models have a single root compartment, while others separate coarse roots from fine (Agren and Axelsson 1980, Cropper and Ewel 1987) or distinguish among primary, secondary, and tap roots (Blake and Hoogenboom 1988). Models that distinguish among root classes usually simulate water uptake and/or transpiration.

Aboveground biomass must be separated into foliage, wood, and fruits to predict multiple product yield. Foliage must be included as a component in a process-based model since carbon gain is based on leaf area available for photosynthesis (Agren

Table 1. General Characteristics and Structure of Tree Growth Models.

General Characteristics

Source	Species	Stand/Tree	Time Step
Agren and Axelsson (1980)	*Pinus sylvestris*	T	day
Baumgartner et al. (1986)	*Malus pumila* (golden delicious)	S	day degree
Cropper and Ewel (1987)	*Pinus elliottii*	S	year
Dixon, Luxmoore, and Begovich 1978	*Mixed species*	S	hour
Makela and Hari (1986)	*Pinus sylvestris*	T/S	year
Nilsson and Eckersten (1983)	*Salix* spp.	S	hour
Promnitz and Rose (1974)	*Populus* spp.	S	hour
Seem et al. (1986)	*Malus pumila* (McIntosh)	T	day
Sievanen (1983)	*Salix aquatica*	S	day

State Variables

Source	Biomass				Leaf Area
	Leaf	Fruit	Wood	Root	
Agren and Axelsson (1980)	4		2	2	
Baumgartner et al. (1986)	2	x	x	x	x
Cropper and Ewel (1987)	x		2	2	
Dixon, Luxmoore, and Begovich (1978)	x	x	2	x	x
Makela and Hari (1986)	x		2	x	x
Nilsson and Eckersten (1983)	x		x	x	x
Promnitz and Rose (1974)	x		x	x	x
Seem et al. (1986)	2	x	2	x	
Sievanen (1983)	x		x	x	x

Driving Variables

Source	Radiation*	T-air	Precip.*	Rel. Hum.	Photo-per.	T-soil	Soil† Water	Soil† Nut.
Agren and Axelsson (1980)	x	x		x	x	x	x	x
Baumgartner et al. (1986)	x	x						
Cropper and Ewel (1987)	AET		AET					
Dixon, Luxmoore, and Begovich (1978)	x	x						
Makela and Hari (1986)	x						opt	opt
Nilsson and Eckersten (1983)	x	x			x		opt	opt
Promnitz and Rose (1974)	x	x					opt	opt
Seem et al. (1986)	x	x			x	x	opt	opt
Sievanen (1983)	x	x			x	x	opt	opt

Processes

Source	Ps	Atten.	Rs	Alloc.	Senecs.	Phenol.	Mortal.
Agren and Axelsson (1980)	x		x	x	x		
Baumgartner et al. (1986)	x	x	x	x		x	
Cropper and Ewel (1987)	x			x			
Dixon, Luxmoore, and Begovich (1978)	x	x	x	x		x	x
Makela and Hari (1986)	x	x	x	x	x		
Nilsson and Eckersten (1983)	x	x	x	x			
Promnitz and Rose (1974)	x	x		x			
Seem et al. (1986)	x	x	x	x			
Sievanen (1983)	x	x	x	x			

x = variable or process included in model
*AET = annual evapotranspiration (index of water availability and solar energy)
†opt = optimal (resource does not affect tree growth)

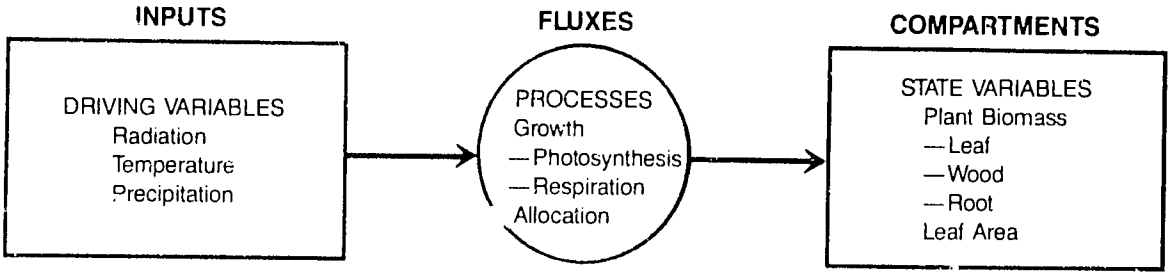

Fig. 1. Simplified overview of simulation model structure.

1981). The foliage compartment may be classified by age to allow photosynthetic rates to vary spatially with leaf age. (Agren and Axelsson 1980, Seem et al. 1986).

Aboveground woody biomass may be further subdivided according to trunk, stems, and branches (Agren and Axelsson 1980, Cropper and Ewel 1987, Makela and Hari 1986). Live biomass may be distinguished from dead standing wood (Dixon, Luxmoore, and Begovich 1978; Arp and McGrath 1987). Classifying woody biomass helps model multipurpose tree growth because fuelwood production (stems and branches) can be estimated separately from pole (trunk) production. In addition, effects of pruning (removal of branches from trunk) can be simulated. Some growth models do not have such woody biomass components. Instead, these models predict growth processes, such as stem elongation and diameter increment (Botkin, Janak, and Wallis 1972; Ek and Monserud 1974; Promnitz 1975). In spatial models of uneven age stands, this approach helps monitor individual tree dimensions to simulate competition.

Tree growth models often include other state variables, such as nutrient and water pools in both plant biomass and soil. Monitoring nutrient content of various biomass components is required to assess fodder quality and to predict effects of fodder and wood removal on nutrient cycling. Fodder digestibility is related to crude protein (and thus nitrogen) content (Torres 1983). Nitrogen mineralization rates are a function of quantity and nutrient content of foliage litter returned to the soil surface (Paster et al. 1984). Foliar nutrient content is important in process models because photosynthetic rates vary with leaf nitrogen content for many species (Field and Mooney 1986). Modeling the changes in soil water content and plant water potential helps predict effects of drought stress on plant water-use and productivity (Landsberg and McMurtrie 1984, Running 1984).

Climate conditions (temperature, precipitation, total radiation, relative humidity, etc.) comprise the major driving variable at all levels of resolution (Landsberg 1981). Other resources required for growth may also function as important driving variables or may modify species response to climatic driving variables. If one or more resources are limiting, growth potential falls below its maximum for a given climate.

Processes

Growth. Modeling may take place at different levels of complexity. Biomass accumulation at the tree or stand level can be modeled as a simple function of one or more driving variables. For example, aboveground annual biomass accumulation in *Eucalyptus globulus* correlates linearly with total annual intercepted radiation (Linder, McMurtrie, and Landsberg 1985). Aboveground production of various temperate tree species correlates with nitrogen availability (Nadelhoffer, Aber, and Melillo 1983, Paster et al. 1984).

Growth may also be modeled as net carbon assimilation integrated over time where total net carbon assimilation by a tree or stand is a function of the instantaneous photosynthetic rate per unit leaf area, total available leaf area, and one or more driving variables. A difficulty of this approach is that instantaneous photosynthetic rates are affected by variable spatial or temporal factors. For example, instantaneous photosynthesis is a

function of light intensity (Larcher 1980), which varies with leaf position in the canopy (Monsi, Uchijima, and Oikawa 1973). Light availability during leaf development can affect the maximum photosynthetic rate attainable by a leaf under optimal conditions (Boardman 1977, Bjorkman 1981). Photosynthetic rate is also a function of leaf age (Chabot and Hicks 1982) and leaf nitrogen content (Field and Mooney 1986). Drought stress reduces photosynthesis through effects of stomatal closure (Kramer and Kozlowski 1979).

A simpler approach is to model growth response to variables individually. In these models, growth (or photosynthesis) is light limited while water and nitrogen availabilities are assumed optimal (Promnitz and Rose 1974, Nilsson and Eckersten 1983, Sievanen 1983). In other models, nutrient effects are important. Increased nitrogen availability promotes growth by increasing total leaf area available for photosynthesis (Arp and McGrath 1987) or by increasing photosynthetic rates (Cropper and Ewel 1987). Photosynthate production has also been modeled as a function of carbohydrate demand (Baumgartner et al. 1986) since photosynthetic rates may be affected by the sinks for carbohydrates (Sweet and Wareing 1966).

Growth may also be modeled to variables indirectly. For example, Nilsson and Eckersten (1983) do not include nitrogen availability as an environmental variable. In their model, willow growth increased with increasing foliar nitrogen content. Another approach used actual annual evapotranspiration as an index of both water availability and solar energy inputs to calculate a climate factor that limits maximum leaf area index (Cropper and Ewel 1987).

Photosynthate not allocated to growth is consumed in respiration. Growth respiration, required to support synthesis of structural components, is proportional to amount of new growth and has been modeled as such (Sievanen 1983, Makela, and Hari 1986). Maintenance respiration, required to support the metabolic process of all living tissue, is proportional to total living biomass and is dependent on temperature (Larcher 1980). A different respiration rate may be calculated for leaves, stems, roots, and fruits (Dixon, Luxmoore, and Begovich 1978), while some models assume that only leaves and roots have maintenance respiration costs (Sievanan 1983). Alternatively, Makela and Hari (1986) assume that most maintenance respiration occurs in large compartments of living woody biomass, and therefore that whole plant respiration is equal to that of woody biomass. Baumgartner et al. (1986) use a maintenance respiration coefficient that is temperature dependent and differs among biomass components. Other models that include temperature effects assume a doubling of respiration rate with a 10-degree increase in temperature (Dixon, Luxmoore, and Begovich 1978; Sievanen 1983).

To determine a canopy's photosynthetic rate from rates of individual leaves, light attenuation through the canopy must be modeled because light intensity, which controls photosynthetic rate, varies with leaf position in the canopy. Approaches to modeling light penetration differ for continuous and noncontinuous canopy systems.

Continuous canopy models include both non-spatial stand-level models of natural forests (mixed species) or plantations (single species) and spatial models of individual tree positions within the total canopy. In these models, light transmission through a continuous canopy follows Beers Law. This approach assumes that a layer of leaves is a uniform absorber of light (Botkin, Janak, and Wallis 1972). In non-spatial models, this approach is used to estimate total light interception by the entire canopy (Sievanen 1983). In spatial models, this method is used to calculate the light available to a particular tree based on the leaf area of all surrounding taller trees (Botkin, Janak, and Wallis 1972; Makela and Hari 1986).

Noncontinuous canopy models are designed for orchard systems in which trees are arranged in rows separated by alleys. A single equation for light interception is inadequate since hedgerows receive light laterally as well as vertically. Jackson (1980a) considers light transmission through a noncontinuous canopy to have two distinct components: (1) light that hits the ground directly between trees and (2) actual transmission through tree canopies. Total transmission is the sum of the two. He uses this approach to model light interception by orchards to predict optimal planting design and management (Jackson 1980b) based on effects of hedgerow shape and spacing

(Jackson and Palmer 1972). This approach is useful for multipurpose tree systems because it differentiates between factors that affect light falling between trees (tree size, shape, and planting geometry) and those that influence actual transmission through the canopy (canopy density and leaf morphology).

Biomass Allocation. Once total biomass accumulation has been estimated, it must be allocated among various plant components. The simplest approach uses partitioning coefficients (McMurtrie and Wolf 1983a, Landsberg and McMurtrie 1985) and/or root:shoot ratios (Nilsson and Eckersten 1983; Linder, Mcmurtrie and Landsberg 1985; McMurtrie et al. 1986) to control the proportion of total photosynthate directed to specific biomass components. Partitioning coefficients are usually multiplied by the total biomass increment. However, allocation may also be a function of the standing biomass of the photosynthetic tissue (Arp and McGrath 1987), site quality (Keyes and Grier 1981), or tree age (Promnitz 1975). Sievanen (1983) uses constant partitioning coefficients, but considers soil water and nitrogen optimal for growth, thereby removing effects of site quality on allocation. Nilsson and Eckersten (1983), who also assume optimal water and nutrient availability, allocate aboveground biomass between leaf and stem using a distribution function (leaf area index/accumulative aboveground biomass), which is controlled by tree age and spacing. Makela and Hari (1986) assume partitioning coefficients independent of tree age or size, but dependent on light availability as it affects partitioning among branches, stems, and needles. Another approach is to transfer carbon from one biomass component to another using transfer coefficients (Cropper and Ewel 1987). This approach simulates the actual path of translocation from leaf to wood to root.

In process-oriented models, allocation may also be controlled by endogenous factors. In one case, growth of individual biomass components is modeled as assimilation of translocated substrate, where the rate of substrate transport is proportional to the substrate gradient between components. Originally developed for vegetative plants (Thornley 1972a), this approach was modified for trees (Dixon, Luxmoore, and Begovich 1978). In other models, allocation is a function of the demand of each component to satisfy respiratory costs and growth (Baumgartner et al. 1986, Seem et al. 1986). If total demand is greater than supply from photosynthesis and reserves, a priority scheme is followed for allocation of dry matter. For example, in an apple tree growth model, priority is fruits > leaves, shoots, wood > roots (Baumgartner et al. 1986).

Growth partitioning between aboveground and belowground biomass is sometimes modeled assuming a balance between the root system, which exploits soil resources, and leaf area, which exploits light. The root system must be large enough to support the demand of aboveground biomass for water and nutrients. In turn, the leaf area must support the carbohydrate demand of the roots.

Partitioning has been modeled by balancing carbohydrate synthesis by the shoot with nitrogen uptake by the roots (Thornley 1972b, Reynolds and Thornley 1982) or by regulating shoot growth based on water uptake by roots (Borchert 1973). In the second approach, when leaf area becomes too great for water uptake to support transpiration, shoot growth is stopped while root growth continues. When leaf area becomes inadequate to support the carbohydrate demand of roots, the shoot growth is initiated again. This results in an oscillation of the root:shoot ratio about the optimum ratio for a site and species.

Competition. Competing for available resources is usually modeled by reducing potential growth under noncompetitive conditions. On an individual tree basis, competition indices assume total competitive ability for all resources represented by an "influence zone" related to tree size. They also assume competition among trees as a function of overlapping influence zones (Daniels 1976). Such an approach also assumes a constant competitive pressure over a defined zone and an absence of competition immediately outside it (Opie 1968). Vandermeer et al. (1984) suggest this assumption may not be valid. They propose a variable competition hypothesis in which competitive pressure is a function of interplant distance.

Different approaches are used when considering competition for specific resources. Light

attenuation reduces amount of light available to leaves in the understory, and therefore reduces growth rate based on leaf position in the canopy. When two distinct canopy layers are considered, such as a tree canopy with a grass understory, canopy interception reduces the light available to the understory (McMurtrie and Wolf 1983b). Within the canopy, light available to an individual tree is a function of leaf areas of the surrounding trees (Botkin, Janak, and Wallis 1972; Makela and Hari 1986). Reduced growth caused by shading can be modeled differently for shade tolerant and intolerant species to predict more realistic competitive interactions (Botkin, Janak, and Wallis 1972).

Some tree growth models use a competition index when considering soil resource competition. The assigned value (0-1) is a function of the intensity of competition (Mcmurtrie and Wolf 1983b), which may be estimated by the basal area of tress on a site (Botkin, Janak, and Wallis 1972).

Competitive interactions for several resources are a function of tree density. Increased tree density results in increased root density on the site but decreased root density per tree (Atkinson 1980). The increase in total root density results in removal of more water and nutrients from the soil. At high densities (111,000 trees/ha), the increased water use of the stand results in water stress (Atkinson 1978). Increased density also results in decreased leaf area per tree, lower light interception, and less growth. Therefore, growth per tree is a function of planting density, which indicates that spacing may be useful in assigning a competition index in multipurpose tree models.

Summary

The variables and processes of tree growth models vary according to particular modeling goals. Photosynthate production and allocation are the two major processes. Models that include photosynthesis require leaf area as a variable and incorporate light attenuation. The most common driving variables are radiation and air temperature, while soil resources (water and nutrients) are often assumed optimal or are ignored. Growth partitioning may be affected by environment, management, or species characteristics in these models. Modeling growth of individual trees within a stand requires that competitive effects be included.

The approaches used in these past modeling efforts have implications for designing a simulation model for multipurpose tree growth. If biological processes are included, ecologically-based parameters should be specific to species rather than sites. Once parameters are estimated, they are valid across sites. The model should also include feedback controls between species and environment because environment is modified by management practices and trees as they grow.

Scientists frequently assume a model that includes more information on biological processes can ensure that species will respond more realistically to environment and management changes. However, more detail increases the amount of data required for parameter estimation and frequently for driving variables. A model for multipurpose trees should include relatively few driving variables because of the lack of detailed climate data available in many developing countries. Also, the physiological data needed for parameter estimation of multipurpose trees is not easily accessible in the tropics. Therefore, a growth model for such species should consist of a relatively simple set of relationships between environmental variables and physiological responses. As long as the environment can be measured and plant parameters estimated, growth can be modeled as a function of that environment (Reed 1980). Such a dynamic model allows for prediction of growth responses to both natural and man-made environmental changes.

Modeling Growth and Partitioning

Variables

The biomass components should allow for yield of multiple products and the modeling of certain biological processes. Leaf biomass is needed to predict fodder or green manure production. Roots are required for uptake of soil resources and to support regrowth after pruning. Separating branches from main stems allows modeling of both fuelwood and pole production. Effect of pruning (removal of branches from the stem) can also be included. If fruits are produced as food or cash

crops, production must also be allocated to this biomass component.

The model should be driven by the minimum amount of climate data available for multipurpose species systems. Easily measured climate inputs are limited to daily maximum and minimum temperatures and total daily precipitation. Temperature can affect growth directly through effects on photosynthesis. Both temperature and precipitation affect growth indirectly by driving soil processes related to water and nutrient availability. Although total daily radiation is an important growth factor, data may not be readily available for these species.

Processes

Growth and Biomass Allocation. Lack of available physiological data for multipurpose trees requires that growth be modeled as a simple function of one or more driving variables. If obtainable, radiation data should be used since growth of many woody species is proportional to total daily radiation. Growth may also be a function of temperature, water, or nutrient availability. Allocation of total growth can be modeled using partitioning coefficients based on field harvests. Since allocation is a function of tree age and resource availability, partitioning coefficients should be modified based on stand development and site conditions.

Another option is to incorporate growth analysis into the tree growth model. Relative growth rate (RGR) measures the growth rate of the whole plant, expressed as biomass produced (g) per unit biomass present (g). RGR consists of net assimilation rate and leaf area ratio. Net assimilation rate measures whole-plant efficiency as an assimilating system. It roughly approximates photosynthesis minus whole plant respiration, and is expressed as the increase in dry matter (g) per unit of leaf area present (m^2). The drawback is that leaf area, which often is not measured in yield studies, is required for an expression of growth efficient. Leaf area ratio (LAR) measures the leaf area present on a plant, expressed as leaf area (m^2) per total weight of plant (g). LAR can be used to assess allocation of total tree biomass between leaf area and standing woody biomass.

Allometry may also be used to partition biomass. Allometric regression equations relate the weight of individual biomass components, such as foliage and wood, to tree dimensions, such as diameter and height. If a growth model predicted aspects of the growth process, such as stem elongation and diameter increment, estimated changes in weight of the various biomass compartments could be monitored over time.

Competition. It has been proposed that a maximum leaf area index (LAImax) for a site-species combination exists (Waring 1983). As actual LAI approaches this maximum throughout stand development, leaf area production is reduced. For example, net leaf area production = coefficient * (LAImax - LAI) (Arp and McGrath 1987). The greater the LAI of the stand, the lower the light availability to each tree. Therefore, this feedback simulates the effect of tree growth on reducing stand light levels, which in turn reduces tree growth. Once LAI = LAImax, net leaf area production is zero. Lost leaf area is replaced but no additional leaf area is accumulated. At this point, leaf area production is equal to leaf area senescence (McMurtrie and Wolf 1983a). This approach can be used to predict effects of light competition without modeling the processes of photosynthesis and light attenuation. Competition for water and nutrients can be modeled using a simple competition index, which is related to tree density or total basal area.

Management

Multipurpose species systems are intensively managed to exploit various tree uses. Growth rates, allocation patterns, and site quality are affected by various management practices. To predict their effects, this feedback link should be incorporated into any multipurpose tree model.

Management effects begin at tree establishment because planting density and geometry affect both the light environment and depletion of soil resources. The more evenly a given LAI is distributed throughout the stand, the greater is light interception (Jackson 1980a). At higher planting densities, a greater soil profile depth is penetrated by roots, so removal of water and nutrients is increased (Atkinson 1978).

Effects of spacing may be further modified by imposing other treatments. The effect of pruning on the light environment depends on which branches are removed. Pruning of outer branches increases light penetration into the interior of the tree canopy, especially important in fruit-bearing trees whose fruit size or quality is increased (Mika 1986). By pruning lower shaded branches, light is intercepted by the rest of the canopy while the respiratory load of the whole tree is reduced (Jackson 1980a). Pruning affects growth and allocation by increasing shoot growth and reducing trunk diameter increment and root growth (Mika 1986). Shoot growth response is a function of the time of pruning and the length of branches removed. To incorporate pruning treatments into a growth model, timing and extent of pruning must be included for control of growth responses.

Conclusions

Environment-plant interactions control production rate and allocation. Management practices can affect growth and allocation directly or indirectly through effects on environment. Understanding feedbacks between trees and environment is vital to predicting growth and allocation on a given site and in predicting response to natural and man-made environmental changes. A model to predict wood and foliage yield of tropical multipurpose trees should first provide a conceptual framework that integrates these feedbacks to assess effects of species, site, planting, design, and management. It should be based on field measurable data appropriate for multipurpose tree systems. Following validation, the model can be used to match physiological species characteristics with physical site factors and to predict the optimal planting design for the desired harvesting regime.

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Understanding Yield in Short Rotations of Multipurpose Tree Species

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Increased demand for fodder, fuelwood, pulp, and lumber has led to intensive cultivation of fast-growing trees in short-rotation systems. Potentially, these systems can produce high biomass yields in shorter time than can more traditional silvicultural systems. To recommend sound silvicultural techniques for short-rotation systems, scientists must understand clearly the effects of management practices on yield. These include initial spacing of trees, pruning, fertilization, and irrigation. Scientists must also know how tree species, site characteristics, and their interactions affect yield.

Defining yields for multipurpose, fast-growing trees is more complex than defining annual crop yields. No physiologically precise time has been determined at which to harvest the various products of multipurpose trees. Furthermore, growth rates change as tree stands age. To evaluate a particular management practice or site productivity, scientists must know how yield changes as a function of stand age and how this relates to time of harvest or rotation length.

This paper briefly summarizes basic concepts related to yield and rotation length in multipurpose tree plantations. Methods used to achieve short rotations are discussed in relation to factors that control stand behavior. Some studies on yield of multipurpose trees in temperate and tropical regions are reviewed and evaluated in the context of achieving maximum yield in short rotations. Finally, yield factors are discussed in relation to modeling yield in short-rotation systems.

Yield and Rotation Length

Wood product yields in tree plantations are commonly expressed as the mean annual increment (MAI). The MAI is total yield per unit ground area divided by the plantation age. Yield can be expressed as mass, volume, or length, depending on the product of interest. The MAI changes as a function of the change in the current annual increment (CAI). The CAI is the increase in yield per unit ground area for a particular year. A hypothetical curve for CAI as a function of stand age, along with the corresponding MAI curve, is presented in Fig. 1.

Characterizing changes in MAI as a function of stand age has long been of interest to foresters (Daniel, Helms, and Baker 1979). Generally, the CAI increases relatively rapidly with stand age and then decreases sharply. The MAI increases and decreases more slowly. The point at which the two curves intersect is the age the stand achieves maximum MAI (Fig. 1). This point, also called the culmination of MAI, is the biological criterion foresters use most frequently to determine rotation length. The most common alternative standard for defining rotation length is the age at which the CAI falls below an acceptable level (defined in physical or economic terms). This age could occur before or after culmination of MAI.

Rotations longer or shorter than the culmination of MAI have several non-yield advantages. Longer rotations are used when yield is less important than quality factors that increase with age. Shorter rotations can ensure frequent and rapid return on investment, reduced period of risk for stand loss, and quick incorporation of yield improvements, such as superior genotypes (Rose et al. 1981). The disadvantages include increased number of plantings and harvests and higher yields of unusable juvenile wood and bark.

The goal of a short-rotation system is to decrease the stand age at which culmination of MAI occurs. This allows for the non-yield advantages of early harvest without sacrificing yield. A short-rotation system, however, does not necessarily

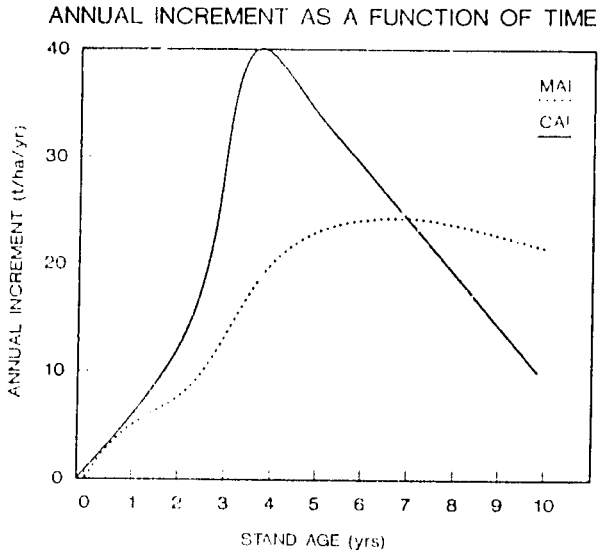

Fig. 1. Hypothetical curve for CAI and MAI for a short rotation.

eliminate the non-yield disadvantages of early harvests. Methods used to decrease the stand age at which culmination of MAI occurs include:

- o planting trees that grow rapidly when young,
- o planting trees densely, and
- o improving site quality.

Since these methods might help increase the value achieved at the culmination of MAI, some scientists have expected short-rotation systems to increase the amount of product harvested from a given site when averaged over long periods of time. Others have argued that short-rotation systems have not evidenced higher production than longer rotation, conventional plantation forests (Cannell and Smith 1980).

Creating Short-Rotation Systems

To achieve maximum MAI at an early stand age, fast-growing tree species can be planted that exhibit rapid height growth when young. Canopies expand quickly, thereby capturing the site and effectively excluding other plants. Additional traits include the relatively early onset of physiological aging and intense interspecific competition with neighboring plants.

A second method used to achieve maximum MAI early is manipulation of planting density. In theory, when plantations have a high tree density, the leaf area index (projected leaf area per unit ground area) quickly reaches an optimum for light interception and therefore for photosynthesis and growth. However, trees in stands with a high planting density may develop canopies whose intense mutual shading decreases growth rates. If this happens before trees have developed a reasonable cambial surface and canopy depth associated with height growth, the stand could stagnate. This implies CAI will not reach its potential maximum, and the stand will not achieve as great a maximum MAI as will stands in which more height growth occurred before intense mutual shading developed (Cannell 1983). On the other hand, trees in stands with low stocking densities take longer to achieve culmination of MAI. Because of incomplete canopy cover, their CAI at an early stand age is low. If an optimal leaf area index for the stand is not achieved before the trees begin to age physiologically, the maximum MAI achieved may be less than for more densely planted trees (Cannell 1983).

A third method used to maximize MAI in a short period is intensive cultivation, including fertilization, irrigation, and weed control. These typical agronomic techniques help avoid reduced yields caused by insufficient nutrients, water stress, and competition from other plants. These management techniques may even be required to establish a specific tree species on a site. For example, fertilization is sometimes required for tree establishment in particular soils, especially those low in phosphorous or lacking specific micronutrients. Some species cannot tolerate long periods of drought, especially when young. Without supplemental water, they could not survive in certain climates. They may need repeated irrigation as the stand ages. Certain tree species in specific environments cannot compete with weeds and may die in the absence of weed control.

In some cases, intensive cultivation practices are used, not only to ensure stand establishment, but also to increase stand growth rate. Management techniques that allow for rapid development of leaf area and early maximum photosynthetic rate per unit leaf area should result in faster culmination of MAI. Whether the maximum MAI achieved during the life of the stand is greater with fertilization and irrigation is questionable.

Early, rapid establishment of the canopy is implicit in all short-rotation methods. However, because most tree species do not behave as crop ideotypes (i.e., plants that establish a canopy in a confined space that do not compete with neighboring plants), too much leaf area in the canopy could cause mutual suppression of growth and lower stand yields. In theory, increased leaf area contributes to increased yield only if the gain in energy captured offsets the cost of creating and maintaining additional leaves and supporting structures. Several authors have attempted to define this optimum leaf area index for a stand of trees (Isebrands and Nelson 1982, Waring 1983, Newton et al. 1986). For agronomic crops, a leaf area index between three and four is generally considered optimal for producing the highest values of crop net photosynthesis (Campbell 1977). For trees, Waring has argued that maximum CAI per unit leaf area occurs at a stand leaf area index of slightly less than four. This implies that the optimum leaf area for maximum stand productivity is greater than four (Newton et al. 1986).

Optimum leaf area occurs at a point at which increasing the amount of leaf area does not offset the decrease in CAI per unit leaf area. Whether the optimal leaf area index of tree stands differs from that of agronomic crops depends on the light compensation points of the leaves and the maintenance respiration rates of leaves and the maintenance respiration rates of leaves and supporting branches. It also may depend on canopy architecture if deep canopies of tree stands with clustered leaves create light interception patterns that differ from those of agronomic crops with similar leaf area indexes. A more complete, mathematical description of the processes that affect optimal leaf area index are presented in the appendix.

Studies on Short Rotations

A short-rotation study using hybrid poplar was conducted over many years in the northern United States. Results from this study show the dependency of MAI on stand age and density (Fig. 2a). Increased planting density decreased the time required to reach maximum MAI, although the more densely planted plots were discontinued (because of small plot size) before it was clear that culmination of MAI had occurred. In the most densely planted treatment (over 100,000 stems ha^{-1}), an MAI of about 10 t ha^{-1} yr^{-1} was achieved by age five. This was similar to the MAI achieved in the least densely planted treatments (approximately 1,700 stems ha^{-1}) at age 10.

Isebrands and Nelson (1982) reported a linear relationship between diameter^2 x height (an estimator of tree volume) and leaf area per tree in four- and five-year-old poplar stands grown at a variety of planting densities. They found that six-year-old stands at a 0.6 x 0.6 m spacing began to deviate from this relationship. These stands had less leaf area for a given d^2h than five-year-old stands at 1.2 x 1.2 m spacing. This led the authors to suggest the point at which volume growth and leaf area begin to diverge from linearity is the biologically optimum age for short-rotation stands. The stand leaf area indexes for the two treatments were 8.8 and 7.6, respectively.

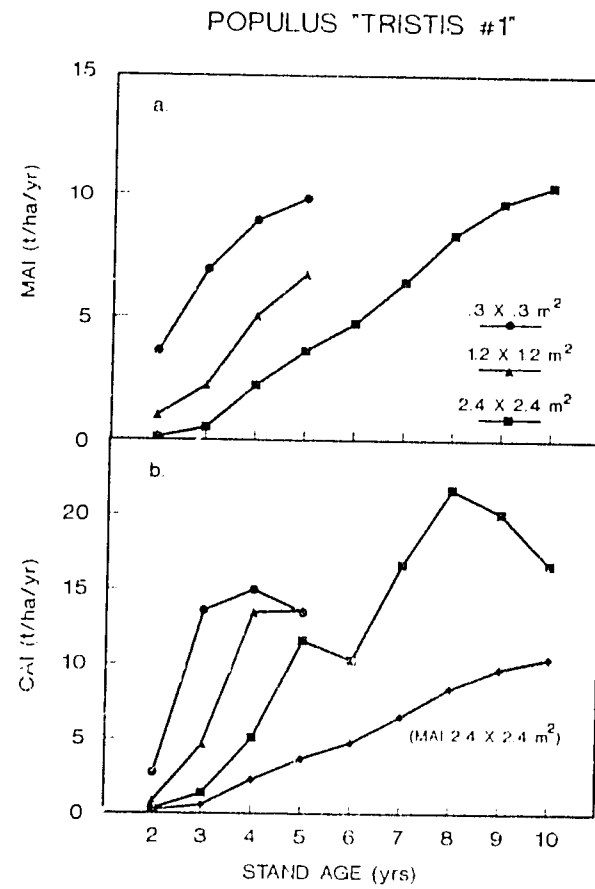

Fig. 2 Change in (a) MAI and (b) CAI for Populus "Tristis #1" density. Source: Savitkovski 1983.

This implies a leaf area index of 8.8 exceeded the optimum leaf area index. Their interpretation is complicated by the relationship between tree biomass (independently measured in these experiments) and leaf area per tree, which followed the same linear regression line for both treatments.

In a study on Sitka spruce, Ford (1982) found a somewhat similar decrease in the proportion of leaf weight to stem size as the stand aged from 16 to 18 years. At the same time, the total leaf area decreased from 10.6 to 7.5. (The projected leaf areas would be approximately 30-50% these values, depending on the shape of the needles.) This coincided with the period in stand development when relative growth rates in basal area for individual trees were no longer similar. The smallest trees began growing slower than other trees, indicating the onset of competition. Ford also found that the loss in basal area suffered by the more slowly growing trees was not entirely compensated for by the larger trees, suggesting maximum CAI had been achieved by age 16.

Although the short-rotation system achieved a high MAI at an early stand age, the question remains whether this is greater than the MAI achieved in more traditional, longer rotation systems. In a review of 11 studies, Cannell and Smith (1980) concluded that maximum MAI of four to five-year-old, short-rotation hardwood systems in the temperate zone is 10-12 t ha^{-1} yr^{-1}. The systems they reviewed were subject to site preparation and weed control, most were fertilized, and some irrigated. From a traditional forestry perspective, these would be considered intensively cultivated sites. Cannell and Smith (1980) cite data that suggest the maximum MAI achieved with the short-rotation, intensively cultivated systems does not differ significantly from the maximum MAI of older (11-26 years) poplar plantations that have been managed traditionally. Also, they suggest the production rate of 10-12 t ha^{-1} yr^{-1} of aboveground biomass may be close to a maximum for temperate region C3 plants.

In Fig. 2b, the MAI and CAI of the 1.2 x 1.2 m poplar experiment are plotted as a function of stand age. The CAI must achieve higher values than 10 t ha^{-1} yr^{-1} for the MAI to average this value. During year eight, the poplar plantation produced 21.7 t ha^{-1}. A CAI value in the temperate zone as high as 26.7 t ha^{-1} yr^{-1} was reported for a 17-year-old spruce stand growing in Scotland (Ford 1982). As illustrated in Fig. 1, the achievement of high maximum MAI is dependent not only on the value of the maximum CAI achieved but also the subsequent rate of CAI decline. Trees that do not compete strongly with other trees at canopy closure may, for this reason, achieve the greatest MAI when grown in stands. Presumably, this relates to the belief that selection of narrowly crowned trees will result in higher stand productivity.

Results of studies conducted in Hawaii on *Leucaena leucocephala* (Van den Beldt 1983, Pecson 1985), are presented in Fig. 3. As in Fig. 2, MAI is graphed as a function of stand age and density. In these trials, at tree densities of 20,000 (1 x 0.5 m) and 40,000 (1 x 0.25 m) stems ha^{-1}, maximum MAI appears to be achieved by the first or second year. Stands at tree densities of 10,000 stems ha^{-1} (1 x 1 m) appear to reach maximum MAI about a year later.

The data from Waimanalo and Kauai (Figures 3a and 3b, respectively) suggest that maximum MAI achieved is greatest in the 40,000 stems ha^{-1} stands. However, these stands at both sites showed a marked decrease in MAI and CAI the year after achieving the maximum (Fig. 4). Therefore, in the second or third year, the MAI of the 40,000 stems ha^{-1} stands does not differ greatly from that of the 10,000 and 20,000 stem ha^{-1} stands.

If this is not an experimental anomaly, and any yield advantage were to be gained from this high density treatment, the trees would have to be harvested quickly. Perhaps rapid surge, decline, and increase in MAI at this density were caused by the spacing of 0.25 x 1 m. In another study in Chia-Lin, Taiwan (Hu and Kiang 1982), Leucaena was planted at a density of 40,000 stems ha^{-1} using a 0.5 x 0.5 m spacing. The MAI was similar to the 20,000 stems ha^{-1} (1 x 0.5 m) spacing (Fig. 3d).

By the second year at the Waimanalo, Molokai, and Chia-Lin sites (Figures 3a, 3c, and 3d, respectively) and by the third year at the Kauai site (Fig. 3b), the three most densely planted treatments within a site had similar MAI and had all reached or passed culmination of MAI. The MAI

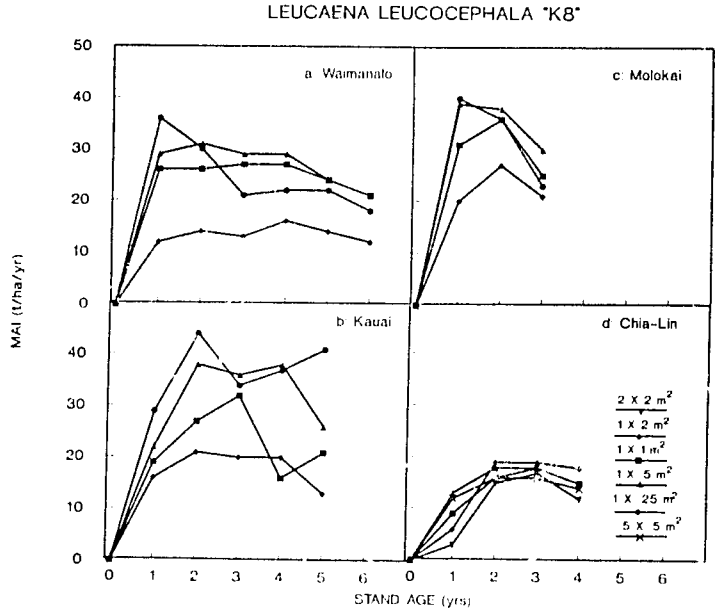

Fig. 3. Change in MAI as a function of stand age and density. Sources: Hu and Kiang 1982, Pecson 1985, and Van den Beldt 1983.

ranged from 32-36 t ha^{-1} yr^{-1} at the Molokai and Kauai sites, 26-31 t ha^{-1} yr^{-1} at Waimanalo, and 16-18 t ha^{-1} yr^{-1} at Chia-Lin. Interestingly, data suggest maximum CAI was achieved within two years by the 10,000 and 20,000 stems ha^{-1} stands at all sites (Fig. 4). However, there were differences in the maximum CAI achieved and the CAI rate of decline. Drought (year 4 at Kauai, year 5 at Waimanalo, and year 3 at Molokai) followed by severe damage caused by the Leucaena psyllid (*Heteropsylla cubana*) contributed to a marked decrease in CAI at the Hawaii sites for all densities (J.L. Brewbaker, private communication).

Although this is a limited data set, it suggests that the time required to reach maximum MAI does not depend highly on the value of the maximum MAI achieved. For example, in the Taiwan study, the value achieved at the culmination of MAI was 16-19 t ha^{-1} yr^{-1}, or half of that achieved at the Molokai and Kauai sites. Yet maximum MAI was achieved at all sites in two to three years of stand growth. This may have been due to a decrease in the maximum potential growth rate after two to four years, regardless of site conditions (Cannell 1983).

Maximum MAI achieved by the 5,000 stems ha^{-1} (1 x 2 m) treatments in Hawaii differed from those at the Taiwan site (Fig. 3). At all three Hawaii sites, the value at culmination of MAI was much lower for this planting density compared to higher planting densities. Maximum MAI were 27 and 21 t ha^{-1} yr^{-1} at the Molokai and Kauai sites, respectively, and 16t ha^{-1} yr^{-1} at the Waimanalo site. Culmination of MAI appeared to occur at the same age it did in the more densely planted stands. The trees may have begun to age physiologically early and consequently reduced their growth rate before capturing the site completely. Alternatively, woody biomass may have been underestimated because it was calculated assuming single stemmed trees. Trees in these least densely planted treatments may have developed multiple stems.

At the Taiwan site, all planting densities achieved a similar maximum MAI, and culmination of MAI occurred at similar ages. However, the MAI values at culmination were not as great as those of the Hawaii plots. Perhaps the trees at the Taiwan site were not growing at their full potential; therefore, high planting densities had little advantage with respect to increasing the maximum value of MAI and reducing the stand age required to achieve it.

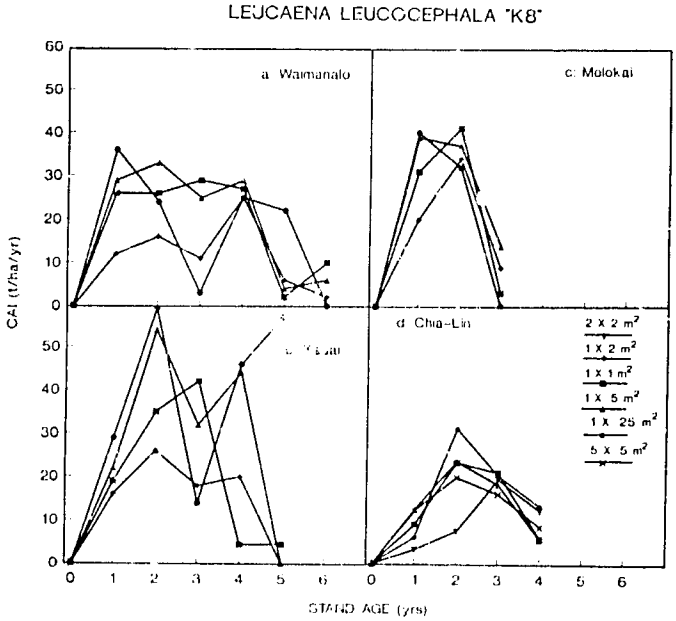

Fig. 4. Change in CAI as a function of stand age and density. Sources: Hu and Kiang 1982, Pecson 1985, and Van den Beldt 1983.

The maximum MAI achieved with Leucaena in some of the Hawaii studies appears close to the maximum for C3 plants in the tropics. Kira (1975) cites values for annual net production of tropical forests ranging from 20-37 t ha^{-1} yr^{-1} with peak values reaching 50 t ha^{-1} yr^{-1} (Cannell 1979).

Implications for Modeling Yield

Both theory (see appendix) and practice indicate a close relationship between the leaf area of a tree and its early growth rate. During initial stand growth, practices that increase the leaf area per unit ground area will increase the tree growth rate per unit area. One simple method to achieve this is to increase planting density. During early stand growth, the relationship between leaf area and growth rate should be independent of planting density. Therefore, stand yield over time should, at an early age, relate directly to planting density.

As the leaf area index increases, the gain in energy captured does not offset the cost of producing and maintaining the canopy. At this point, the CAI begins to decrease.

However, as illustrated in Fig. 1, the MAI does not culminate until CAI has begun to decline. The offset in time depends on the growth patterns of individual trees and the intensity of competition in the stand. This lag between achievement of maximum CAI and culmination of MAI may help explain why tree stands appear to have higher than optimum leaf area indexes associated with high productivity.

Clearly, a model to predict yield of short-rotation, multipurpose tree species should predict the maximum MAI that can be achieved, as well as the age at which it happens. Simulation models are highly suited to this task since they can represent changes in variables, such as yield as a function of time. Such models incorporate the time dependency of functions that affect yield. They can predict early tree growth using initial values for tree size, leaf area, and as a function of species and environment interactions. When the leaf area index of a stand reaches an optimum level or when the trees begin to age physiologically, the relationship between leaf area and tree growth changes, depending on species characteristics and the leaf area index of the canopy.

Growth and competition could be modeled physiologically, using equations like those in the appendix and including temperature, water, and nutrient effects on photosynthesis and photosynthate partitioning. More complex formulations of light penetration through canopies could be used to simulate the effects of increasing canopy density on light interception and photosynthesis. However, it would be difficult to measure all the necessary parameters of such a model. An alternative approach might use equations similar to those in the appendix with parameters derived from whole tree or whole stand performance rather than performance of individual leaves. For example, instead of measuring the relationship between the photosynthetically active radiation (PAR) or temperature and the rate of photosynthesis for individual leaves, measurements are made between light or temperature and leaf or woody biomass growth before the onset of competition or physiological aging.

Based on the previously discussed experiments with Leucaena in the tropics, such relationships would have to be established the first year to ensure competition had not begun. Once an optimal leaf area index had been exceeded, the cost of competition could be simulated as a change in the relationship between leaf area per tree and basal or volume growth as a function of the leaf area of the stand. This is similar to the function presented in the appendix, in which net photosynthesis is dependent on the sunlit leaf area of the canopy as well as the total leaf area.

Conclusions

Maximum yield attained and the time required to achieve it are important factors in short-rotation systems. First, short rotations are advantageous only if trees are harvested at the culmination of MAI. Knowing when maximum MAI will happen and how it varies as a function of different management techniques is essential to taking full advantage of the system. Secondly, although the ideal time to harvest the stand is at the culmination of MAI, manipulations of the canopy, such as pruning, are theoretically advantageous before the culmination of MAI when CAI has reached its maximum. Third, knowing when maximum CAI and MAI are achieved is essential to interpreting results of growth experiments, especially distinguishing clearly between growth relationships at different stages of canopy development.

Acknowledgments

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Appendix

Equations are presented that simulate light interception by the canopy as a function of leaf area index, gross photosynthesis as a function of light level, and net photosynthesis as a function of light intercepted and leaf area index. For a more complete discussion, see Campbell (1977).

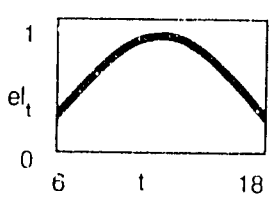
Two examples are given. The first is for a temperate region (latitude = 60 deg.) in June (solar declination angle = 10 deg.). The second is for a tropical region (latitude = 10 deg.) for the same solar declination angle. These are the only variables that are changed in the two examples, except for total growing season, which is assumed to be 130 days in the temperate region and 365 days in the tropical region. The examples are meant to illustrate how leaf area and solar radiation interact in determining maximum productivity.

Example 1: Temperate Region

The sine of the solar elevation angle (el) is calculated as a function of hour of day (t) from latitude and declination angle (in degrees).

rad = 1	
deg = (3.142/180)rad	Terms to convert from degrees to radians
lat = 48 deg	Latitude in degrees
dec = 21.9 deg	Solar declination angle in degrees
noon = 12	Solar noon in hours
t = 6 ... 8	Hours of simulation

$$el_t = \sin(lat)\ \sin(dec) + \cos(lat)\ \cos(dec)\ \cos[15\ deg\ (t - noon)]$$

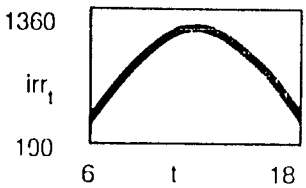


t	el
6	0.277
8	0.588
10	0.815
12	0.898
14	0.815
16	0.588
18	0.277

The sine of the solar elevation angle is 0 at sunrise and sunset and approaches a value of 1.0 at noon.

Irradiance (solar radiation) above atmosphere (irr) is calculated as a function of the sine of the solar elevation angle (el) and the solar constant (1360 W m^{-2}).

$irr_t = el_t \; 1360$



t	irr
6	378
8	799
10	1108
12	1221
14	1108
16	799
18	378

Maximum solar radiation occurs at noon and declines to 0 at sunrise and sunset.

Photosynthetically active radiation (PAR) per unit leaf area is a function of irradiance (irr), canopy leaf orientation (k), and the transmission coefficient of the atmosphere (a). PAR is generally assumed to be 1/2 total irradiance (solar radiation). Since not all solar radiation is transmitted through the atmosphere, the maximum theoretical irradiance is reduced by a transmission coefficient (a). This gives us PAR0, photosynthetically active radiation that could be intercepted by a flat surface.

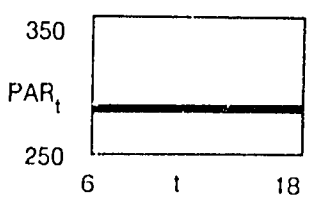
$a = 0.84$

$PAR0_t = a(irr_t/2)$

In reality, plant canopies are not flat surfaces. The amount of radiation intercepted by the canopy when the sun is at a given elevation angle depends on the angles at which the leaves of the canopy are oriented. The equation used here assumes leaves are randomly oriented. For the derivation of this equation and for equations for other leaf orientations, see Campbell (1977).

$k_t = 1/2 \; el_t$

$PAR_t = k_t \; PAR0_t$



t	k	PAR
6	1.804	285.6
8	0.851	285.6
10	0.614	285.6
12	0.557	285.6
14	0.614	285.6
16	0.851	285.6
18	1.804	285.6

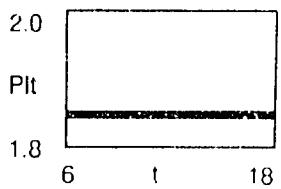
The effect of random leaf orientation is constant radiation interception over the day.

Gross photosynthesis is calculated for a given light level (PAR) as a function of the maximum rate of photosynthesis under optimum light and temperature (Pmlt). The type of equation presented here is commonly used to predict the effect of different light levels on photosynthesis.

Pmlt = 2.5 Maximum rate of photosynthesis (g m^{-2} hr^{-1})

kl = 100 Rate constant for PAR (W m^{-2})

$Pl_t = Pmlt/[1 + (kl/PAR_t)]$



t	Pl
6	1.852
8	1.852
10	1.852
12	1.852
14	1.852
16	1.852
18	1.852

Photosynthesis also does not vary with time of day.

To obtain daily gross photosynthesis (Plsum), hourly photosynthesis values are summed for daylight hours.

$Plsum = Pl_6 + Pl_7 + ... + Pl_{18}$

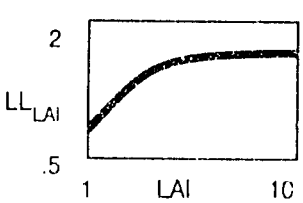
Plsum = 24.072 g m^{-2} day^{-1}

The equations presented here allow us to calculate gross photosynthesis per unit leaf area per day. To calculate net photosynthesis per unit ground area, the sunlit leaf area index of the canopy and the total leaf area index of the canopy must be specified. The sunlit leaf area index (LL) is a function of the leaf area index (LAI). One possible equation to represent this relationship is presented below (see Campbell 1977). The sunlit leaf area depends on the canopy orientation factor, k, which is a function of time of day, as discussed above. The value at 10:00 hours is used.

k = 0.61

LAI = 1 ... 10

$LL_{LAI} = [1 - \exp(-k\ LAI)]/k$



LAI	LL
1	0.749
2	1.155
3	1.376
4	1.496
5	1.562
6	1.597
7	1.616
8	1.627
9	1.633
10	1.636

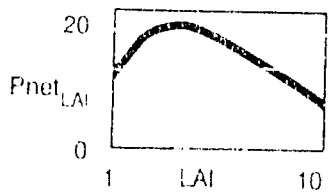
Initially, the sunlit leaf area increases rapidly as total leaf area increases. Then increasing leaf area produces little increase in sunlit leaf area.

Net photosynthesis (Pnet) is gross photosynthesis minus losses due to efficiency and maintenance. Gross photosynthesis per unit leaf area (Plsum) is multiplied by the sunlit leaf area index to give gross photosynthesis per unit ground area. The cost of maintenance increases with increasing leaf area.

eff = .25 Efficiency ratio

mtn = 2.2 Maintenance coefficient

$$Pnet_{LAI} = Plsum\ LL_{LAI} - [eff\ Plsum\ LL_{LAI} + mtn\ LAI]$$



Initially, increasing leaf area index increases Pnet. As LAI increases further, the maintenance cost of more leaves decreases Pnet.

LAI	Pnet	LL
1	11.315	0.749
2	16.459	1.155
3	18.249	1.376
4	18.217	1.496
5	17.195	1.562
6	15.635	1.597
7	13.782	1.616
8	11.771	1.627
9	9.674	1.633
10	7.530	1.636

Assuming a growing season of 130 days, a crude estimate of maximum yearly productivity is calculated.

$ha = 1 \times 10^{4}$

$ton = 1 \times 10^{-6}$

season = 130 days

$CAImax = Pnet_3\ \ season\ \ ton/ha$

$CAImax = 23.7\ \ t\ ha^{-1}\ yr^{-1}$

Pnet at a leaf area index of 3 is chosen because this was the highest value obtained.

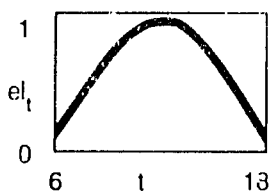
Example 2: Tropical Region

The equations presented above are repeated using a tropical latitude and a year-round growing season.

lat = 10 deg Latitude in degrees

dec = 21.9 deg Solar declination angle in degrees

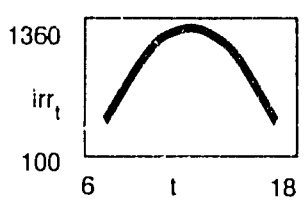
$el_t = \sin(lat)\ \sin(dec) + \cos(lat)\ \cos(dec)\ \cos[15\ deg\ (t - noon)]$



t	el
6	0.065
8	0.522
10	0.856
12	0.979
14	0.856
16	0.522
18	0.065

Day length is shorter compared to temperate region.

$irr_t = el_t\ 1360$



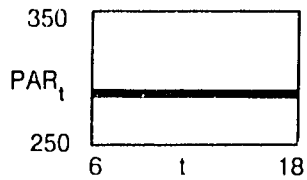
t	irr
6	88
8	709
10	1164
12	1331
14	1164
16	709
18	88

Maximum irradiance is greater than temperate region due to higher elevation angles.

$PAR0_t = a(irr_t/2)$

$k_t = 1/2\ el_t$

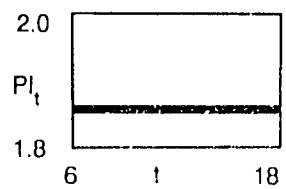
$PAR_t = k_t\ PAR0_t$



t	k	PAR
6	7.740	285.6
8	0.959	285.6
10	0.584	285.6
12	0.511	285.6
14	0.584	285.6
16	0.959	285.6
18	7.740	285.6

As in the temperate zone, the effect of random leaf orientation is constant radiation interception over the day.

$Pl_t = Pmlt/[1 + (kl/PAR_t)]$



t	Pl
6	1.852
8	1.852
10	1.852
12	1.852
14	1.852
16	1.852
18	1.852

Photosynthesis also does not vary with time of day.

$Plsum = Pl_6 + Pl_7 + \ldots + Pl_{18}$

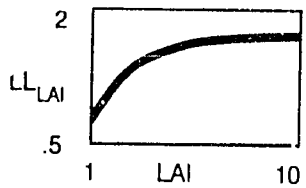
$Plsum = 24.072\ g\ m^{-2}\ day^{-1}$

The daily value for gross photosynthesis per unit leaf area is not different for the temperate region in June and the tropical region. However, the simplifying assumption was made that Pmlt and kl are the same for both regions. The difference in solar elevation angles over the day results in different leaf inclination factors over the day. The value at 10:00 hours is used.

$k = .58$

$LAI = 1 \ldots 10$

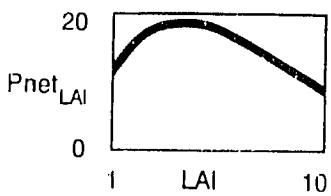
$LL_{LAI} = [1 - \exp(-k\ LAI)]/k$



LAI	LL
1	0.759
2	1.184
3	1.422
4	1.555
5	1.629
6	1.671
7	1.694
8	1.707
9	1.715
10	1.719

Smaller k value means more leaf area sunlit at a given LAI in the tropics compared to temperate zone at this hour.

$Pnet_{LAI} = Plsum\ LL_{LAI} - [eff\ \ Plsum\ \ LL_{LAI} + mtn\ \ LAI]$



LAI	Pnet	LL
1	11.499	0.759
2	16.969	1.184
3	19.064	1.422
4	19.268	1.555
5	18.414	1.629
6	16.968	1.671
7	15.190	1.694
8	13.226	1.707
9	11.159	1.715
10	9.033	1.719

Pnet at an LAI of 4 is greater in the tropics due to greater sunlit leaf area. However, eff and mtn were assumed equal in both regions, which is probably not generally the case.

season = 365 days

$CAImax = Pnet_4\ \ season\ \ ton/ha$

$CAI\ max = 70.3\ t\ ha^{-1}\ yr^{-1}$

In this analysis, the length of the growing season had the greatest effect on increasing productivity in the tropics compared to the temperate region. The difference in solar elevation angles in the two regions can affect the relation between sunlit leaf area and leaf area index. However, this did not greatly alter the leaf area index required to achieve optimum photosynthesis.

Understanding Water Stress and Its Relation to Yield in Short Rotations of Multipurpose Tree Species

Susan J. Riha

Cornell University

Agricultural scientists have long pursued the goal of predicting how much water a certain crop on a given soil requires in a specified period for optimal yield. Their accomplishments have made it feasible to attempt to predict how lack of water affects crop growth. Such predictive capability could greatly benefit many agronomic and forestry projects. Ideally, it could help predict yield and match species to sites. In marginal areas, yield reductions, survivability, and rates and timing of irrigation could be assessed. Scientists could also evaluate and select plants better adapted to low water inputs or extended droughts. The objectives of this paper are to examine how trees respond to lack of water and to discuss how this may relate to growth and yield in tree plantations. Approaches to and the feasibility of predicting yield in short-rotation tree plantations with limited water are also discussed.

Plant Water Use

Water use by plants can be viewed most simply as a problem of supply and demand. A demand for water is set up by the atmosphere and can vary orders of magnitude depending on the time of day, day of the year, and climate. The water supply comes almost entirely from the soil through plant roots. Since most plants have a low water storage capacity, plants can undergo "stress" if demand exceeds supply. Although plant scientists can characterize various plant responses that occur when demand for water exceeds supply (see, e.g., Teskey and Hinckley 1986), no definite physiological criteria exist for plant water stress. Additionally, the connection between the plant's water status and photosynthate production and partitioning is not well understood. An empirical definition of water stress has been used in the past and probably should continue in the near future. Using this approach, if a crop yields less than another grown in the same year and location with optimum irrigation, the non-irrigated crop is said to have been subjected to water stress. In reality, the demand for water could have exceeded its supply even in the irrigated crop.

If plants continue to release water in excess of supply, they quickly lose turgor, wilt, and eventually die. Leaves of some trees may not appear to wilt because of their cuticular coverings, but they undergo the same internal changes in water status as herbaceous plants and grasses. Plants have many available options other than releasing water when faced with excessive demands. These options can be broadly categorized as increasing supply and reducing demand.

Increasing Supply

Water is supplied to plants almost entirely by water flowing through the soil to roots. When demand begins to exceed supply, plants theoretically can obtain more water from the soil, which the roots currently occupy (rooting volume) or grow into new soil, thereby increasing their rooting volume. Getting more water from the current rooting volume appears promising initially because soil can contain as much as 25% water (on a volume basis) when plants are no longer supplied water from the soil. Although a considerable quantity of water remains in the soil, its potential energy is low. Since water flows from the soil to the plant down a potential gradient, the plant water potential must be lower than the soil for water to be supplied to the plant. Scientists have tried to find plants that can lower their water potential when faced with decreasing soil water supplies and perhaps maintain water flow from the soil at lower water contents. The failure to find such plants is a good example of what can happen when an integrated approach is not used. Considering the relation between soil water content and water potential, a large decrease in potential results in little increase in available water once a certain water content has been reached. Therefore, plants would have to lower their water potential

greatly to cause only small amounts of water to flow to roots.

The rate at which water flows through soils also decreases exponentially as a function of decreasing water content. As soil dries, water moves slower. Shortening the distance between any one point in the soil and a root (increasing root density) could decrease the time required for water to move from the bulk soil to roots. This line of reasoning implies that more roots, root hairs, or mycorrhizal mycelium could increase the rate of water supplied to plants. In addition, the total supply of water to roots in the rooting volume might even increase if soil near the roots were to become so dry that water movement in the soil further from roots were greatly slowed. The argument that increasing root density increases the rate of water supply makes sense if the slowest rate and volume of water movement from the soil to the top of the plant is in the soil. Although this was assumed the case for many years, more recent work shows that water moves slowly from the cortex of a root into the root xylem. This rate of movement is of the same magnitude as water movement in a drying soil. At first this may seem self-defeating for the plant and, in fact, scientists have tried to identify plants with high root water conductance. However, low root water conductances could result in a more constant rate and larger volume of water supply because the root will not quickly dry down the soil in its vicinity. In theory, when root water conductance is high, smaller root densities are needed to dry down soil evenly in the vicinity of a root (Riha and Levan 1984).

Soils differ in the amount of water they hold per unit volume at saturation and the water potential at which drainage stops (field capacity). This is a function mainly of soil pore sizes and distribution, but can also be affected by field conditions (such as depth of gravel layer). These same properties affect the rate of infiltration of water into the soil. Soils can also differ in the amount of water they hold per unit volume at field capacity and at a water potential at which most plants permanently wilt. Plants have little short-term effect on these soil properties. Management options for maintaining or increasing favorable pore size distribution include avoiding compaction, adding organic residues to soil, and, in certain cases, tillage. At times, various manufactured organic compounds have been introduced to improve soil water supply, but they are expensive and have never been shown effective in the field.

Plants can also increase their water supply by growing more extensive root systems. Trees are at a particular advantage in this regard because much of their root system is perennial. Their roots can exploit a large soil volume early in the growing or rainy season. Growing a long, horizontal root system may not significantly increase a tree's water supply since the tree may have to compete with other plants for water from a given soil volume. Growing deep roots also does not guarantee that water supply will increase. For many areas of the world, where rainfall does not wet the soil to a significant depth or where soils are shallow, growing deep roots would not be expected to increase water supply unless roots reach a water table or a layer that receives lateral water flow from higher in the landscape. In soils or sediments usually wetted only to a shallow depth, an initial increase in water supply may be achieved when a deep rooted crop uses water held for long periods in soil, rocks, or sediment. Since this supply is not recharged regularly, the water, once used, is unavailable to the crop in succeeding years.

Limiting Demand

During daylight hours, solar radiation arrives at the surface of plant canopies. This radiation can either be absorbed or reflected. Only a small percentage of absorbed radiation is converted into chemical energy. The remaining energy must be reradiated, lost as sensible heat (heat lost from warm objects to cooler surroundings), lost as latent heat (evapotranspiration), or stored. These options, except latent heat loss (energy consumed when water moves from the liquid to gas phase), involve an increase in canopy temperature over air temperature. When plant stomates are open and the aerodynamic resistance to vapor transport at the surface of the canopy is low, a rapid diffusion of water vapor from inside to outside the plant can occur. Under these circumstances, virtually all absorbed solar energy dissipates as latent heat loss.

Plants can, to some degree, limit transpiration by decreasing the amount of radiation they intercept. This can be accomplished by changing the

inclination angles of their leaves relative to the sun. Plants also vary in the absorptivity of their leaf surfaces. However, the major short-term method of limiting demand for water is to close stomates. With this response, more energy dissipates as sensible heat (i.e., leaf temperature increases). The major long-term method of limiting a plant's water demand is for some or all of the leaves to senesce, thereby reducing the radiation absorbed by the canopy.

Scientists have tried to limit demand through management practices, although these are generally practical only for small plants, such as tree seedlings. These include the use of antitranspirants, which supposedly decrease the diffusion of water vapor from the leaf to the air. These have never been greatly successful. Shade cards have given mixed results. The most successful technique is decreasing seedling leaf area on planting, especially with respect to root mass. More research on canopy pruning of trees to decrease demand seems justified. However, as was pointed out in "Understanding Yield in Short Rotations of Multipurpose Tree Species," effectiveness is only likely when the leaf area index is reduced to a level that significantly decreases radiation interception.

Growth in Relation to Supply and Demand

When stomates close and leaves senesce to limit demand in the face of reduced water supply, growth might be less than that of plants where supply is not limited. Stomatal closure has been correlated with various soil, plant, and atmospheric characteristics, although these vary greatly among species. Certainly, stomatal conductance is dependent on light since stomates close in the dark. In some species, increasing the vapor pressure gradient between the leaf and the atmosphere can cause stomates to close. High leaf temperatures and low leaf water potentials can result in stomatal closure. Decreasing soil water potentials may cause stomatal closure, independent of the effect of low water potentials on the supply of water to the plant. High internal CO_2 concentrations inside the leaf can also cause stomates to close. Factors causing leaves subjected to water stress to senesce are less clear. When stomatal closure restricts the diffusion of CO_2 to the site of photosynthesis, plant growth can decrease. This was long considered the primary reason for limited supplies of water reducing plant growth. More recently, however, it has been shown that non-stomatal limitations to photosynthesis are important (Jones 1985, Teskey and Hinckley 1986).

When supply falls below demand, effects other than a change in the rate of photosynthesis, or even net photosynthesis, occur related to plant growth. In trees, water stress is known to affect the number of leaf primordia formed during bud set, as well as the rate of shoot and leaf elongation. It can affect the number of flushes that occur during a growing season and possibly the partitioning of photosynthate between shoots and roots.

Implications for Modeling

Predicting the effects of water stress on stand growth requires both estimating the supply of and demand for water that the stand experiences and knowing the relation between lack of supply relative to demand and tree growth. Estimating the demand for water is probably the simplest part of this task. Estimating the supply of water can be more difficult, depending on the climate, landscape, and soil in which the stand is grown. Although considerable research has focused on plant water relations in general and tree water relations specifically, scientists have not yet achieved a coherent understanding of the physiology of the relation between changing supply and demand for water and growth. Furthermore, much of the current understanding of these relations occurs at the level of individual leaves. Methods to apply this understanding to plant canopies and tree stands are still limited.

A reasonable alternative is to examine the effect of varying water supply on the growth of tree stands. Such information is generally obtained from irrigation experiments. However, few experiments with tree stands use supply of water as a variable and even fewer properly replicated experiments use water supply as an independent variable (Jarvis 1985). In general, the effect of irrigation varies with site, species, years, and with the particular parameter being measured. Although well-designed irrigation experiments could greatly help relate supply and demand for water to stand growth, most forest managers are apparently reticent to establish such experiments because

they cannot envisage the extensive application of this technology (Jarvis 1985). This contrasts with the many field fertilizer experiments that have been established in recent years.

Estimating Demand

Many methods are available for estimating the potential evapotranspiration imposed on a stand of trees. These methods have been thoroughly reviewed (see, e.g., Sharma 1985). In general, their accuracy depends on the frequency and type of environmental data available. On one end of the continuum are methods that use daily, weekly, or monthly air temperature data to estimate potential evapotranspiration. These methods probably work quite well in sunny climates where the air vapor density and temperature change little and not as well in other climates. Other methods measure daily solar radiation or net radiation. In the absence of horizontal transport of energy (advection), incoming solar plus longwave radiation minus outgoing reflected shortwave and emitted longwave radiation (net radiation) set the upper limit to evapotranspiration. Another approach, the combination model or Penman-Monteith equation, implicitly accounts for the dissipation of net radiation as both latent and sensible heat. Proportions depend on environmental conditions and the roughness of the canopy surface. This combination model is used most frequently in scientific studies to estimate potential evapotranspiration from forest canopies. It requires measurements of wind speed and relative humidity, as well as air temperature and net radiation.

No reliable methods exist to estimate advection in the absence of air and canopy surface temperatures even though advection can, in certain environments (including irrigated fields), significantly increase potential evapotranspiration. For non-irrigated multipurpose trees that grow in humid or semi-humid conditions, advection can perhaps be ignored, although it may occur during dry seasons when trees are still transpiring stored soil water.

At best, it is difficult to estimate the distribution of potential evapotranspiration between potential evaporation from soil and potential transpiration from plants under incomplete ground cover. Under well-developed canopies of trees, soil evaporation is generally considered negligible. In the past, this has also been assumed the case under agronomic crops. However, recent work indicates that, in corn and wheat, as much as 30% of potential evapotranspiration can be allocated to the soil surface even when crop leaf area index is high (Norman and Campbell 1983). The assumption that evaporation from the soil surface is negligible could result in overestimates of transpiration.

Estimating Supply

Because the water supplied to the plant occurs due to a potential gradient, supply of water cannot exceed demand. However, if water does not move from the soil to the evaporating surfaces of the leaves at a rate equivalent to the potential transpiration rate, supply falls below that of demand. When demand is low, the rate of supply needed to keep up with demand can be comparatively lower. This explains why plants under low net radiation (cloudy, shady, cool environments) require less water and lower rates of water supply than plants under high net radiation. When demand is high, even under well-watered conditions, supply may fall below demand because of the plant's resistance to water flow. Models of water flow in the soil-plant-atmosphere continuum that are potential driven and use hourly time steps can predict this drop in supply relative to demand.

Most models of supply focus more on estimating decrease in water supply that occurs over days and weeks as the soil begins to dry. As the soil dries, water moves slower and the potential energy of the remaining water decreases more rapidly. Two general approaches can be used to predict how this affects the water supplied to plants. One approach assumes that all soil water held between some upper and lower limit is used (Jones and Kiniry 1986). A second approach assumes that water flows according to a potential gradient from the bulk soil to the roots (Riha and Campbell 1985). The length of the pathway for flow depends on root density. The rate of flow depends on the potential gradient and the hydraulic conductivity of the soil. In both cases, the supply of water depends heavily on the water retention properties of the soil and on depth of rooting.

Both approaches need some method of moving precipitation from the soil surface into the soil. In

the first approach, water fills the surface layer of soil to an upper limit and then begins to fill progressively lower layers (Jones and Kiniry 1986). Because water in the upper layers tips over and fills the lower layers, this approach is frequently called the "tipping bucket" method. In the second approach, water moves into and through soil, depending on the potential gradient for flow, soil hydraulic conductivity, and the soil's capacity to store water (Campbell 1985).

In practice, both methods can reasonably predict the movement of water in the soil profile, drainage of water below the root zone, and, under certain circumstances, uptake of water by plants. The problem of both methods is in estimating actual water uptake by plants (actual transpiration) in that plants can dynamically respond to both aboveground and belowground environments. By closing their stomates, they limit actual transpiration below potential transpiration. This, in turn, limits the rate of water supply. Until recently, the effect of the soil environment on stomatal behavior was considered entirely caused by the lowering of soil water potential. This results in a lowering of leaf water potential, which, in turn, causes stomates to shut. Such behavior can be predicted most directly by the second, potential driven approach. More recently, scientists have suggested that other aspects of the soil water environment at fairly high water contents may indirectly affect stomatal behavior. Whether both approaches are equally adaptable to predicting these effects remains to be seen. However, these latter effects are probably less important to trees faced with periods of drought than the lowering soil and leaf water potentials.

With respect to multipurpose tree species, of major interest is the amount of water available to a stand of trees as a dry period begins, the rate at which the stand uses this supply, and the point at which the supply is exhausted. Three issues should be considered when choosing between the two approaches discussed above:

(1) how difficult the soil properties required for input are to measure,

(2) how difficult the equations of each approach are to solve, and

(3) how much computer time is required to solve these series of equations.

The last two issues are becoming less important as numerical techniques are developed and more sophisticated computers are used to solve the equations in the potential driven approach. The precise field measurements of soil properties required for input for either approach is not simple (e.g., to predict soil water content or water supply to plants in a particular experiment). The use of soil survey or other soil data to estimate the soil input parameters in both cases relies on similar information concerning soil texture; soil bulk density; depth of rooting; presence of layers of gravel, pans, etc.; and presence and duration of a water table or of lateral water flow. In the long run, the more direct measurement of the soil properties required for the potential driven model can be more strongly justified than those required for the tipping bucket approach. This is because the input requirements for the potential driven approach can be viewed as general soil properties that describe behavior over a wide range of conditions and are applicable to many problems.

Another input required for estimating water supply is depth of rooting. It could be estimated knowing the rate of precipitation in areas where potential evapotranspiration usually exceeds precipitation or by knowing depth to an impermeable layer or water table.

Predicting Response of Tree Growth to Water Stress

With an incomplete, leaf-scale understanding of water stress and growth and few stand-scale empirical results, what reasonable alternative exists for predicting the effects of limited water supply on stand growth? Jarvis (1985) has proposed that stand growth is directly related to the amount of photosynthetic area maintained by the stand leaf area index and that the major effect of decreasing water supply to a forest stand faced with equivalent demand is to limit the amount of leaf area per unit ground area. Therefore, if the effect of changing supply and demand of water on stand leaf area index can be predicted, the effect on growth can be determined. His arguments were developed using

mainly northern coniferous forests as examples. To apply them to multipurpose tree species grown in the tropics, several points must be considered. First, some of these species are drought deciduous. The balance between supply and demand that causes them to shed their leaves and later regenerate them must be known to estimate the length of time that the canopy actually intercepts radiation. Secondly, development of the leaf area index of the stand over time for short-rotation, multipurpose tree species depends on planting density and other management practices and so is not mainly a function of the environment, as might be the case for Douglas fir or other extensively grown, long-rotation trees. In short rotations, management factors and how they interact with water stress to affect the leaf area of a stand cannot be ignored. Third, the assumptions of Jarvis regarding effect of canopy size on light interception and water loss probably do not apply to short-rotation, multipurpose trees grown in the tropics except when the leaf area index of the stand is much lower than those achieved in coniferous forests of northern temperate regions. For multipurpose trees in the tropics, this would occur early during stand growth after drought causes leaves to senesce and during regrowth of the canopy when the rainy season begins. Last, little experimental evidence currently exists to support or challenge the assumption that, for multipurpose tree species, the effects of water stress on growth per unit leaf area are not significant.

Leucaena Experiments

During the 1940s and 1950s, irrigation experiments were conducted in Hawaii that focused primarily on forage production using *Leucaena leucocephala (L. glauca)*. In one experiment at Waimanalo, researchers found that during the summer dry period, there was a linear response to water applied and yield of "dehydrated" forage (Kinch and Ripperton 1962). With 15-23 cm of applied water, they found an increase in dehydrated forage of approximately 80 kg/ha per cm of water. Although they did not measure leaf area, if one assumes about 1 cm^2 of projected leaf area for every 8 mg of dry leaf weight and that the dry leaf weight equaled 90% of the dehydrated forage weight, then their stands had leaf area indexes in the range of 2.8-4.4. Their experiments support the assumption that, at least at a low leaf area index, decreasing water supply while maintaining equivalent demand decreases stand leaf area. Although woody biomass production was not reported, presumably it also decreased.

In an experiment at Poamoho, Takahashi and Ripperton (1949) found that in a low rainfall period (approximately 7 cm over a four-month period), stem elongation and leaf initiation began to decrease after eight weeks with little or no rain in comparison to irrigated treatments. Green forage yield was only approximately one third that of the irrigated treatments. Again, this indicates that lack of water reduces leaf area in these stands. In this experiment, two irrigation treatments were used: irrigation water applied either weekly or only when stem elongation began to decrease below that of the weekly irrigation treatment. Over the four-month period, this resulted in only three irrigation treatments received. The authors contrasted an irrigation frequency for Leucaena with that for Napier grass. Leucaena required approximately 10 irrigations per year while Napier grass, grown under the same conditions, required 25-30 irrigations per year. The authors assumed this difference was caused by the deep rooting of Leucaena. However, since they could not accurately control or measure the amount of water they applied, it is unclear whether water was available at depth to the trees. Also, they did not report rooting depth. Based on green forage yield during the wet season, they suggest that 1,000 mm of rainfall well distributed throughout the year would produce adequate forage and that 1,300 mm would result in good forage yield.

In a more recent study conducted on Molokai in 1979 (Van den Beldt 1984) in which Leucaena trees were subjected to a nine-month dry season, non-irrigated trees had little foliage during this period. Surprisingly, there was little difference in height and stem diameter growth, and, by inference, in woody biomass yield between the irrigated and non-irrigated treatments. Van den Beldt suggests that the Leucaena subjected to drought stress may have made compensatory growth during the wet season.

Several researchers working with Leucaena have indicated a strong correlation among leaf growth,

solar radiation, and minimum air temperature (Gueverra, Whitney, and Thompson 1978; Ferraris 1979; Denton and Nickell 1985; and Evenson 1985). Minimum nightly air temperatures of 21-23°C appear more conducive to growth than those of 16-20°C. In several of these studies (Gueverra, Whitney, and Thompson 1978; Ferraris 1979; and Evenson 1985) there is a high positive correlation among solar radiation, maximum air temperature, and minimum air temperature. Without independent control of these environmental factors, the importance of each to the growth of Leucaena is difficult to determine. The significance of Leucaena's growth response to changes in its radiative and thermal environments is emphasized by Ferraris (1979). He found that growth (of both leaves and wood) was poorly correlated with rainfall in the relatively moist environment and deep soils of his experimental site. The growth of leaves and wood in the cooler months of his study was only half that which occurred in the warmer months. This suggests that if drought occurs during cooler months, yield reductions in non-irrigated plots compared to irrigated controls may be less than if drought occurs during warmer months. This could be one reason for differences in Leucaena response to irrigation.

Denton and Nickell (1985) found a strong dependence of growth on seasonal rainfall for giant Leucaena stands growing in both fertile and infertile soils in the Philippines. They found that Leucaena growth resumed almost immediately after the onset of the rainy season and growth slowed 60-75 days after the rains ceased. This lag in growth decline was presumably due to the continued supply of stored soil water. There was approximately 20% less growth during the 1983-1984 growing season than in previous years, which farmers attributed to drought stress. Using a non-linear function relating relative growth rate to monthly rainfall, researchers concluded that the reduced growth in 1983-1984 was due to drought stress (Denton and Nickell 1985). Their approach, however, did not explicitly account for the effects of stored soil water.

In summary, the current literature on Leucaena suggests that leaf area is strongly affected by water supply to the trees (Kinch and Ripperton 1962, Takahashi and Ripperton 1949, Van den Beldt 1984). The supply of water is not necessarily well-correlated with water input rates due to the utilization of stored soil water occurring often eight or more weeks following high rates of irrigation or precipitation (Takahashi and Ripperton 1949, Ferraris 1979, Denton and Nickell 1985). Increased growth may (Relwani, Mohatkar, and Nakat 1983; Denton and Nickell 1985) or may not (Van den Beldt 1984) be associated with increased water supply and leaf area. Growth response to water inputs appears to depend on the storage capacity of the soil (Ferraris 1979, Takahashi and Ripperton 1949), solar radiation and air temperature during the dry season (Ferraris 1979; Gueverra, Whitney, and Thompson 1978; Denton and Nickell 1985), and the density of the tree stands (Relwani, Mohatkar, and Nakat 1983). Leucaena stands subjected to drought seem less likely to exhibit reduced growth in relation to irrigated controls if there is a large supply of stored soil water. if they are planted at low densities, and if drought occurs when solar radiation and air temperature are reduced.

Conclusions

A reasonable model linking water supply and demand to multipurpose tree growth would use one of the available methods for estimating potential evapotranspiration on a daily or weekly basis, depending on the climate data available. This amount of water would then be removed from the soil with the constriction that the water potential of the tree roots could not fall below some given potential (generally in the range of -1,500 J/kg). As the soil dries, actual transpiration would fall below potential transpiration, decreasing the rate of tree water uptake. When the rate of actual transpiration would become low and constant (during long low-rainfall periods), the leaf area index of the stand would decrease because of increased leaf senescence with little or no new leaf growth. This, in turn, would restrict woody biomass accretion, which depends on stand leaf area. With the recharge of the soil profile with water (simulated with the potential driven model), leaf growth would resume, thus increasing stand leaf area and woody biomass growth. Using this approach, it is important to understand how decreasing the supply of water to the plant below the potential demand

affects leaf growth and senescence. Also, it is important to determine whether there is a significant effect of lowering water supply in relation to demand on tree growth per unit leaf area.

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Integrating Experimentation and Modeling in Applied Research Management

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Modeling enables scientists to extrapolate a system's behavior, knowing only a defined set of variables and their relation to one another. It plays a formidable role in focusing resources, predicting responses, and communicating an understanding of physical, biological, social, and economic systems. Modeling is an essential tool for regulating management decisions that involve new technologies (Connant and Ashby 1970). The need to build on principles inherent in a basic model is paramount. However, all models are incomplete by definition. Experimentation then becomes the anvil upon which the model of any phenomenon is forged into a form consistent with observations. The challenge is to use experimentation effectively to define the limits of the model's valid domain.

Applied research involving modeling, experimentation, and adaptive probing (Shrank 1983, Walters 1986) can play a central role in developing "controllable" technologies--feasible management activities that can be regulated so that output from production systems remains within a pre-defined limit. For example, while site preparation for tree establishment can often be achieved through slash burning, it is difficult to regulate the impact on air quality, sedimentation, and nutrient loss. Improving control over these factors requires evaluating existing models of basic atmospheric and soil processes through experimentation and understanding the value of information in management decisions (Blake et al. 1988a).

Experimentation in Testing and Database Development

Basic Research

Basic research provides insights into a system's structure by clarifying the causes of observable phenomena. The definition of the system is provided by a body of theory. The role of experimentation is to evaluate whether to reject an hypothesis related to a system's observed behavior.

Experimentation is critical to basic research since conclusions are often affected by assumptions in methods. New experimental methods with separate sets of assumptions designed to test the same hypothesis may lead to different conclusions. Recent research in carbon allocation to forest root systems using improved experiment methods, is significantly changing concepts about the importance of tree root dynamics in productivity (Vogt and Persson 1988).

Applied Research

Applying basic research to technology development, e.g., biotechnology, is fundamental in many organizations. Designing experiments is inherently difficult since the experimenter or organization must clearly understand both basic processes that control the physical or biological phenomenon and the management or social system in which it can potentially function. Because of this constraint, most successful applied research occurs within organizations that have a well-defined goal and employ various experts in marketing, chemistry, physiology, economics, sociology, and quantitative analysis.

In applied research, experimentation is used to determine the functional domain of a technological model, e.g., the relation between tree spacing, biomass, and harvestable product distribution. The important tests relate to the external parameters required to regulate the process effectively, e.g., initial planting arrangement and harvest intervals. The internal conditions are assumed (often erroneously) as correctly defined by a basic model. External conditions include not only physical

characteristics, such as climate or soil for a particular species, but also the overall prescription for a management environment, such as regional markets and economic constraints.

Since some types of information must be common to both biological and management environments, experimentation must be planned carefully to provide relevant information. Researchers frequently use limited databases coupled with numerous modeling techniques to accomplish this task. Applied research is limited to the degree it assumes the system of interest is "knowable" through basic research and that the key relations can be quantified. This means the processes that affect its behavior can be determined through systematic experimentation.

Technology Research

Technology research is often equated with applied research, however, technology research is more narrowly focused. Experimentation in technology research is often limited to evaluating response distribution from an existing or proposed management activity, such as regionwide fertilization, tree improvement, or weed control. There is usually no formal hypothesis to test since no theoretical basis exists to which observations must be compared.

Experimentation aims primarily at creating a database large enough for researchers to use response variations to estimate risks and benefits accurately. The results may be explained in terms of a limited set of variables, such as the rate and timing of a particular chemical, seed source, or number of trees to plant.

This type of experimentation is often preferred by operations personnel because it is linked directly to an existing technology. For example, experiments that demonstrate competitive interactions between trees and herbaceous vegetation mean little to land managers unless control technologies, such as herbicides or tillage practices, can be applied economically. Herbicide study results assume greater value because of apparent direct connections between management actions and productivity. Technology experimentation requires that uniform treatments be relatively inexpensive to apply and responses easy to evaluate. Without well-designed and replicated trials over the population of interest, these kinds of experiments are of limited value.

Often, technological experimentation is not feasible with certain treatments in forestation schemes because of the response time frame. For example, estimating efficacy of various treatments for animal damage control during establishment may be determined effectively in a screening trial; however, the impact of control on yields is difficult to estimate without flexible tree growth models.

Another major constraint is the direct relation of the response model to the specific technology. This has been shown in the case of nitrogen fertilizers in northern Europe (Gustavsen and Lipas 1975). Ammonium nitrate was found to give superior growth responses in Scots pine when compared with urea at the same rate of elemental nitrogen. Finally, identifying response related variables, such as soil chemical properties, is often a matter of educated guesswork, since no theoretical framework exists to predict important factors. Regardless of the limitations, technology experimentation continues to perform an important research function in environments where growth responses are easy to evaluate.

Modeling in Applied Research

Predicting Responses

Predictive modeling is essential in managing technology to meet organizational goals. Without an acceptable model of a system's behavior, management decisions cannot be regulated effectively to meet objectives. For example, a typical forest growth and yield model is designed to predict yields and uncertainty at a specific location under a given set of management inputs, such as spacing, site quality, and fertilization, using information derived from other locations.

In contrast to technology research, a predictive model for applied research is more difficult to develop because of the number and complexity of relationships (Landsberg 1986). Scientists may incorrectly perceive the relation between their own work and the overall organizational objective. For example, increased nitrogen nutrition, through manuring or litter conservation, can be shown to

increase the maximum rate of photosynthesis at light saturation for an individual leaf. However, a model derived from this experiment to estimate the relation between nitrogen nutrition and increased productivity may be erroneous because the scientist failed to consider the effect of nitrogen on leaf area development. The latter may be the main cause of increased plant growth.

In predictive modeling, it is essential to simplify relationships, eliminate non-essential detail, and retain logical structural-functional relationships (Hillel 1987). For example, nutrient and water uptake by roots may be simulated effectively by root-length density functions rather than by considering the complex geometry of flows to individual roots as they grow and branch. The result is a minimum set of equations that adequately simulates the complex system behavior with respect to a chosen set of parameters.

The specification for an efficient model may require a set of parameters different from those perceived as important by the experimenter. Integration can be achieved by using the structural-functional base for a model to communicate the importance of selected relations and parameters. The experiment studies can usually be expanded to include additional valuable measurements, such as leaf area.

Focusing Research Resources

A model's ability to focus resources initially is of substantial value. A strong modeling effort often results in more efficient experimentation. Since applied research requires much integration among diverse areas of expertise, individual efforts must be linked via a framework of preliminary conceptual or theoretical models of the various systems. These can be modified as information is added at successive stages. In this way, maximum efficiency is obtained in terms of usable information per unit of effort.

Objections to the above approach occur because the factors controlling system behavior are incompletely understood. However, applied research uses a portion of the behavior that is partially specified to determine experimentally the external controls needed to exploit it as a technology. Typically, many phenomena, such as regulation of a tree's water balance, are incompletely understood in terms of the basic relations that control moisture uptake and stress resistance. However, a preliminary model of the phenomenon may suffice to identify important experiments. For example, a phenological model of crown and stem growth for a tree species within its natural climatic range may be adequate to design a species provenance trial and to identify important variations in physiological traits that relate significantly to productivity (Blake, Rosero, and Lojan 1976).

As model reliability increases through initial testing and validation, future experimentation can be continually refocused. Reference to the evolution of formal modeling efforts can provide important and succinct documentation on the progress of applied research in meeting organizational goals. A reasonable model structure allows the organization to question alternate hypotheses concerning the sensitivity of the response to specific variables and their critical threshold levels at less cost. By exploring the limits of the domain where model assumptions appear to break down, potentially important relationships can be identified for future experimentation.

This point is clearly illustrated in the current discussions regarding the -3/2 power "rule" relating plant spacing, biomass, and mortality (White 1981). Many tree growth modelers conveniently accept this relationship; however, careful examination of experimental data indicates that variance in model coefficients may result from real differences in species and environmentally dependent processes rather than experimental error (Perry 1984).

Integrating Experimentation and Modeling : Examples

The historical basis for integrated experimentation and modeling in applied forest growth studies is meager (Mitchell 1975). Various explanatory models have been developed for basic research in succession and forest development. Their ability to predict forest growth in managed environments, in a way similar to yield tables, is limited by the long time spans used and oversimplifications and assumptions about physiological and soil processes. The International Biological Program has made significant attempts

to model forest growth (Reichle 1981). A major effort to link modeling and experimentation to predict forest growth evolved from a 1979 conference in Sweden (Linder 1981). Some recent attempts point to a positive outlook (Mohren 1987).

The examples that follow are presented in the context of initiatives to link experimentation and modeling in applied research programs. They have not been developed sufficiently to determine unqualified success or failure. The following analysis expresses the author's views based on publications of and personal communication with individuals involved in various programs.

Regeneration Research in Conifers

Traditionally, regeneration research in conifer species used in commercial softwood management programs has been technologically oriented. Research usually consists of treatments closely linked to alternative management practices, rates of herbicide, planting spacing, mechanical site preparation treatments, lifting and storage of nursery stock, and cultural practices that regulate seedling traits. Successful implementation of treatment results is often limited because seedling, physiological, and environment relations are confounded with management problems. As no sound theoretical models of early growth and development exist, individual experiments must be carried out for 10-15 years to obtain results needed to estimate product yields reliably.

For example, Blake et al. (1987) showed that significant gains in early growth related to initial seedling leaf area (Table 1) were offset substantially by planting density because of stand-level competition at harvest (Table 2). The modeling analysis demonstrated that the most important information needed to infer early gains reliably were an experimentally determined growth convergence rate and biomass distribution at densities below "normal" stocking conditions. While neither topic has attracted much research interest, both are critical in interpreting early plantation treatments.

A recent crop model was modified by Blake and Hoogenboom (1988b) to simulate tree seedling growth and water balance factors during establishment for loblolly pine. The objective was to integrate experimental information on specific physiological processes and evaluate their potential importance in various environments. The model is used for exploratory analysis to increase the efficiency of experiment studies. For example, in the southeastern U.S., a major drought occurred during the winter and spring of 1986. Although rainfall was near normal during the summer and fall, mortality of new plantings was extensive. To evaluate the importance of the winter-spring drought on mortality, simulations were initiated during the longest continuous drought period and compared with the same period in 1985, a near normal rainfall year (Fig. 1).

The simulation results indicate that threshold levels for drought stress-induced mortality did not occur when seedling roots were planted deep and initial soil moisture was near maximum saturation. However, seedlings planted under reduced initial soil moisture content (11% or -0.064 Mpa) died. These results are consistent with observed patterns in the region. Experienced landowners, in contrast to less experienced ones, did not find significant increases in mortality. The former are usually aware of critical planting factors and provide close supervision. The identification of initial soil moisture as a critical planting factor has led to initiating related planned experiments. These studies will determine if vegetation control several months prior to planting can control initial soil moisture content by trapping periodic summer rainfall.

Productivity in Radiata Pine

Radiata pine plantations in Australia, New Zealand, and Chile are important national sources of softwood timber. Because of the range of environments and management inputs, productivity varies greatly. In Australia, traditional growth and yield models provide historical standards for yields on the same or similar sites, but often do not indicate potential yields under newer management regimes (Woods 1976). From the late 1950s-1960s, productivity declines in successive rotations were recognized. This generated research that examined dynamic environmental and growth processes, such as annual variations in climate, mycorrhizae stability, nutrient losses through burning, and competition. Because experimental information on basic biological and environment relations controlling stand productivity lacked an integrated framework, initial research (1970-80) tended to

Table 1. Gain in average usable tree volume in relation to increase in initial leaf area.[a]

	Initial Leaf Area (m^2 per seedling)					
Soil Productivity	.010	.016	.024	.032	.041	.054
	Usable Volume (m^3 per tree)					
High	.76	.80	.83	.86	.88	.91
Average	.47	.55	.64	.72	.76	.79

[a] 35-year-old Douglas fir trees from initial planting of 545 trees per ha.

Table 2. Simulated effects of initial planting density on percentage of maximum usable mean tree volume.[a]

Planting Density (trees/ha)					
250	500	750	1,000	1,250	1,500
% Maximum Increase in Usable Tree Volume[b]					
82	96	84	61	37	15

[a] initial leaf area = 0.54.
[b] decreases are caused by effects of planting density on mortality and mean tree diameter.

concentrate on arbitrary factors. Early research results contributed little until management policy shifted to litter conservation, nitrogen fertilization, and herbicides to control competition. These factors appeared responsible for the recovery in plantation yields and subsequent increased growth.

In the early 1980s, an integrated effort under the Biology of Forest Growth (BFG) Program of the Commonwealth Scientific and Industrial Research Organization (CSIRO) linked experimentation on management practices affecting productivity with basic growth and site processes. The modeling objective was to better understand the interaction between factors that limit productivity, e.g., light, water, nutrients, and to predict their effects under specific regimes (McMurtrie, Landsberg, and Linder 1988).

Of particular importance in Australia is identification of growth conditions that can be experimentally modified to increase water-use efficiency or the amount of growth per unit of water transpired. In New Zealand, a similar approach has been used to explore light environments at various spacing levels to evaluate tree growth under various agroforestry schemes and in response to thinning treatments.

Table 3 summarizes results of experimental measurements and model simulations for the control and irrigated plus fertilized treatment at the BFG site near Canberra, Australia. Experimental data were collected on soil and growth variables to help model the factors responsible for observed growth changes. The BIOMASS model was then used to partition the cause of observed growth responses into several components.

The growth response to irrigation appears to result from modest increases in leaf area coupled with significant extension of active growth. When irrigation is combined with nitrogen fertilization, improved growth results from extended growing period, greater leaf area, and improved photosynthesis. The negative impact of nitrogen fertilization during this period is apparently associated with foliage build-up during a previous wet season (1983-84), which caused rapid moisture depletion during drought cycles (1984-86). By combining experiment treatments with modeling, it is possible to assess the impact of nitrogen fertilization on water-use efficiency. Because of the factors involved, nitrogen does not appear to increase water-use efficiency. The results indicate growth increases may occur at the expense of moisture stored in the soil profile.

Air Pollution Effects on Forest Growth

The impact of air pollution on forest growth cannot be directly measured because treatments cannot be imposed in the same way as, for example, a factorial fertilizer trial. The complexity of the agents and their interaction with specific growth processes make it desirable to evaluate the effects through a dynamic model of stand development. Experimentation is used largely to determine the means by which pollutants interact in the tree-soil-atmosphere system. The relevant stand growth parameters can be assembled, along with the specific pollutant responses, to estimate tree growth.

The integration of experimentation and modeling is a major emphasis of a research program sponsored by the Electric Power Research Institute (Chen and Goldstein 1986). This program identifies modeling, field research, controlled experiments, and data management as essential tasks. Basic research on plant responses to common environmental stress is carried out by the Response of Plants to Integrated Stresses (OPIS) Project, designed to provide experimental data on how plants respond to stress. The results are used to formulate model relationships or algorithms to simulate tree growth. The Integrated Forest Study provides basic information on effects of acidic deposition on changes in forest nutrition. The goal is to predict changes in tree growth resulting from short- and long-term impacts of acid rain on nutrient cycling. The experiment results from various field locations are integrated through a model to predict impacts on growth.

The National Acid Deposition Pollution Assessment Program (NAPAP) of the U.S. Forest Service and the Environmental Protection Agency (EPA) recently initiated a forest growth modeling research effort to complement experiments (Kiester 1988). The modeling is used to explain the behavior of completed experiments on seedlings using various pollution response relations and to predict potential responses of large trees to pollutants. The

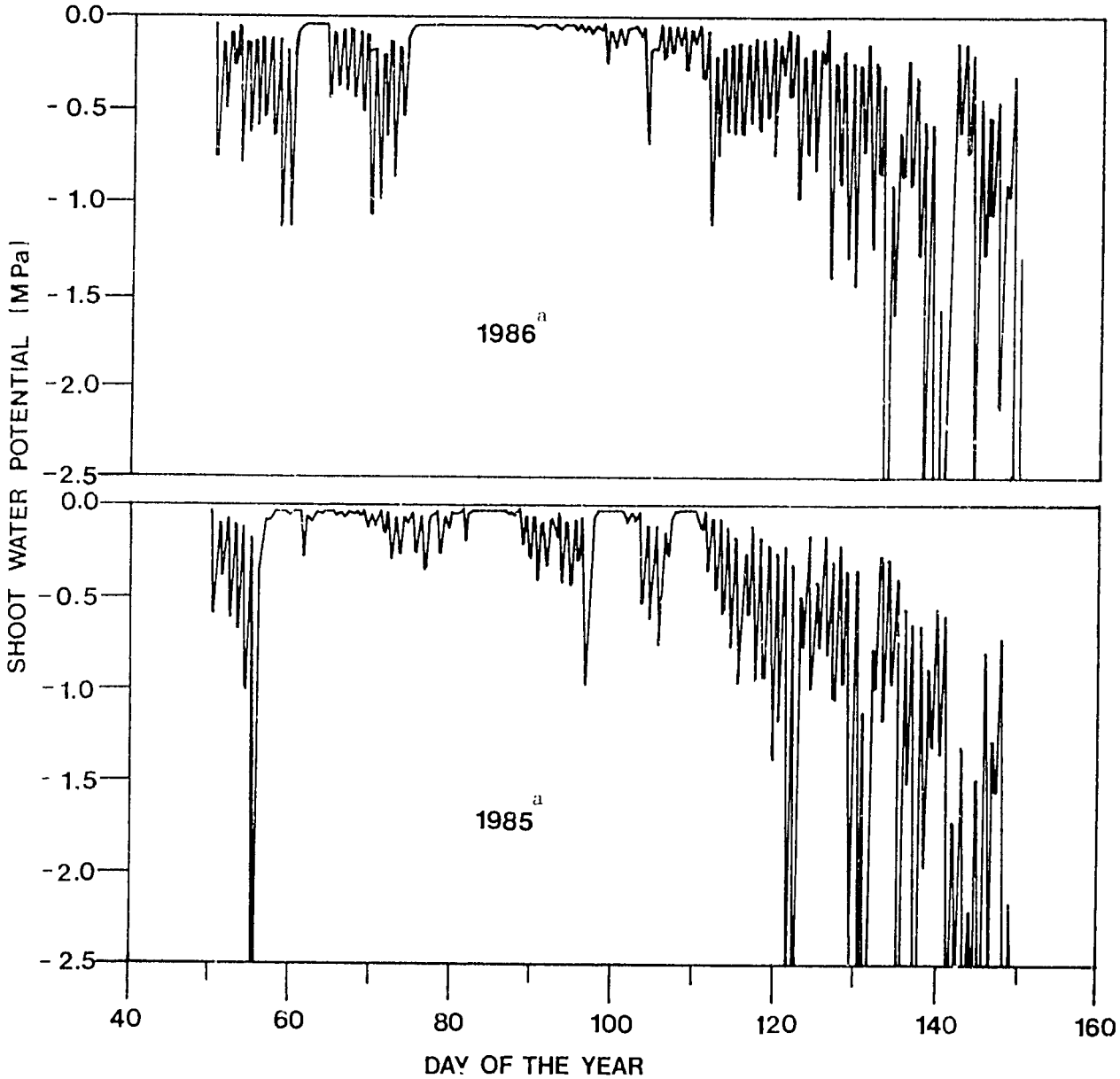

Fig. 1. Effects of annual differences in precipitation, pan evaporation, and temperature on simulated maximum and minimum seedling water potential (Auburn, Alabama). Low stress corresponds closely to periodic rainfall and new root growth.

Table 3. Partitioning of cause of observed growth responses on BFG treatments.[a]

Treatment	Observed Growth (m^3/ha/yr)	Water Relations (% total change)		Nutrition (% total change)		Carbon Allocation
		Ps Rate[b]	Growth[c]	Ps Rate[b]	LA[d]	
Control	19.7	-	-	-	-	-
Fertilization	16.2	-10	-20	10	-90	10
Irrigation	30.8	0	80	-10	30	0
Fertilization + Irrigation	44.0	14	50	15	21	0

[a] Values are based on calculations using data presented at the IUFRO conference, Management of Water and Nutrient Relations to Increase Forest Growth (Canberra, Australia, October 1987).

[b] Ps rate = maximum rate of photosynthesis per unit leaf area.

[c] Growth = extension of active period for photosynthesis, needle elongation, and stem growth.

[d] LA = leaf area.

initial effort is directed at displaying the current level of understanding about tree response to selected pollutant levels since experiment studies are heavily dose-response oriented. In contrast to the Electric Power Research Institute, the NAPAP modeling strategy depends largely on external information on components that control non-pollutant stress effects on growth.

The integration of modeling and experimentation has already contributed to evaluating a major early hypothesis on effects of acid rain on forest growth. Initially, acid rain was thought to reduce soil pH. This would result in release of monomeric aluminum, highly toxic to roots. Simple soil chemical models of aluminum exchange appeared to support this hypothesis (Reuss and Johnson 1986). However, a major weakness was lack of quantitative data on the amount and source of acidic hydrogen ions in forest soils and the kinetics of aluminum ions. Subsequent experiment data on sources of acidity in forest soils indicate that trees contribute the largest amounts through synthesis of organic matter and carbon dioxide release by roots.

Model revision based on the experiment data improved the correspondence with observed soil behavior. The problem of potentially toxic aluminum concentrations based on the soil chemistry model remained until scientists recognized that soil organic matter might be forming complexes with aluminum ions and therefore reducing their concentration in soil solution. This has been confirmed by experiment studies.

Conclusions

Early linking of modeling and experimentation is key to an integrated adaptive research and management program. Failure to link modeling and experimentation early frequently results in inefficient resource allocation and unreliable predictive models. Without acceptable models of a system's behavior, management cannot be effectively controlled through technology.

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The Forestry/Fuelwood Research and Development (F/FRED) Project is designed to help scientists address the needs of small-scale farmers in the developing world for fuelwood and other tree products. It provides a network through which scientists exchange research plans, methods, and results on the production and use of trees that meet the household needs of small farmers. These trees, in project terms, are multipurpose tree species (MPTS).

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