

Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation

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Summary Recent progress toward the application of process-based models in forest management includes the development of evaluation and parameter estimation methods suitable for models with causal structure, and the accumulation of data that can be used in model evaluation. The current state of the art of process modeling is discussed in the context of forest ecosystem management. We argue that the carbon balance approach is readily applicable for projecting forest yield and productivity, and review several carbon balance models for estimating stand productivity and individual tree growth and competition. We propose that to develop operational models, it is necessary to accept that all models may have both empirical and causal components at the system level. We present examples of hybrid carbon balance models and consider issues that currently require incorporation of empirical information at the system level. We review model calibration and validation methods that take account of the hybrid character of models.

The operational implementation of process-based models to practical forest management is discussed. Methods of decision-making in forest management are gradually moving toward a more general, analytical approach, and it seems likely that models that include some process-oriented components will soon be used in forestry enterprises. This development is likely to run parallel with the further development of ecophysiological based models.

Keywords: carbon allocation, carbon balance, competition, stand productivity, tree growth.

Introduction

Process models and process-based system models are essential scientific tools, providing formalized statements of hypotheses (Landsberg 1986) and a framework that encapsulates disparate pieces of information and knowledge. However,

process-based models are seldom used as practical tools in forest management, and there is a strong view that the conventional statistical approach to growth and yield estimation is superior. Process models are considered to embody too many uncertainties and to require too many poorly known parameters for their projections to be as reliable in practice as those of empirical models (Mohren and Burkhart 1994).

Process-based and empirical models have been regarded as mutually exclusive. However, Korzukhin et al. (1996) recently challenged this view by claiming that neither pure process models nor pure empirical models exist, but that all models can be placed somewhere on a continuum from purely mechanistic to purely statistical.

Currently, there is much interest in the application of process models in forest management. Progress in this area is more a question of incorporating elements of process thinking into management models in order to make better use of empirical observations than of constructing models that are independent of system-level information (Sharpe 1990). Consequently, attention is being paid to the integration of process-based models and information provided by empirical forestry data. Although process-based models have not yet been implemented in operational management systems, many such systems are under development, and experiences of joint work between modelers and forest practitioners have been reported (Sands et al. 2000).

Models in the process-based family that are closest to the operational application stage are the growth and yield models of a single stand. However, there are also models being developed to address larger, regional and successional scale problems, e.g., GIS-based models of stand development in the tropics (Ditzer et al. 2000) or models of regional risk of wind damage (Peltola et al. 2000). At the more detailed level, there is work on stem structure with applications to wood quality (de Reffye et al. 1997, Sievänen et al. 1997, Kellomäki et al.

2000). Acquisition and distribution of photosynthetic products is central to all these models, whether distribution is among trees and species in a stand, or to different structures within a single tree.

The scope of process-based models is rapidly extending beyond that of many mainly empirical models. Examples include the growth of mixed stands (Bartelink 2000) and heterogeneous tropical stands (Ditzer et al. 2000), problems related to the growth and change of stands in a management unit (Valentine et al. 2000), and applications to wood quality (Mäkelä et al. 1997), and regional productivity (Landsberg and Waring 1997, Coops et al. 1998a, 1998b).

Most of the process-based growth and yield models developed toward management applications start with photosynthesis; either treating it as the basic growth process underlying the carbon balance (Bartelink 2000, Ditzer et al. 2000, Lindner 2000, Mäkelä et al. 2000, Raulier et al. 2000, Valentine et al. 2000), or using it as an independent predictor variable (Courbaud 2000, Brunner 2000). Other physiological processes, such as water balance or nutrient cycling, have received less attention in the management context (cf. Ågren 1996, Landsberg and Waring 1997, Sands et al. 2000) although these processes are highly significant for understanding the controls on photosynthesis and the effects of climate change on tree growth (Thornley and Cannell 1996, Kirschbaum 2000, Lindner 2000), as well as in studies considering the variation in productivity between regions (Landsberg and Waring 1997, Coops et al. 1998a, 1998b, Sands et al. 2000).

The objective of the IUFRO meeting “Process-Based Models for Forest Management,” held at Saariselkä, Finland, 1998, was to review the current state of the art in process-based models and to assess their applicability to forest management. The present situation can be summarized by three statements. (1) The carbon balance of trees and forests provides a framework for models intended for management applications. The carbon balance is based on estimates of photosynthetic production, which is used for deriving tree growth. (Modeled photosynthesis can also be used in a more empirical way as an independent variable in statistical growth predictions.) (2) The practical implementation of process models and causal thinking will be accelerated if it becomes generally accepted that empirical models can be improved through the incorporation of causal elements, and causal models can be improved through the incorporation of system-level empirical elements. (3) Incorporating these ideas into operational management systems will require cooperation between forest managers and modelers, with modelers taking the initiative.

We have evaluated these propositions with reference to the papers in this volume, but also taking into account model descriptions published elsewhere. We define process-based models, and consider hybrid models that have both process-based and empirical components. Finally, we describe the prerequisites for implementation of such models in a forest management environment, and give some examples of ongoing work in this area.

Process-based models

Process-based modeling can be defined as a procedure by which the behavior of a system is derived from a set of functional components and their interactions with each other and the system environment, through physical and mechanistic processes occurring over time (Godfrey 1983, Bossel 1994). The functional components are chosen at a specified level of hierarchy, customarily one level below the level of the entire system. The notion of hierarchy is important, because what is understood as mechanistic at one level of system organization may be empirical in another conceptual framework (O’Neill et al. 1986, Sharpe 1990). Consequently, the model system can be regarded as an analog of the real system at a specified level of hierarchy, and the temporal sequence of the interconnected component processes can be taken to embed causality (Hakkala and Ylinen 1978). Hereafter, process-based models will be referred to as PBMs.

The carbon balance

Modeling forest growth in terms of carbon balance involves calculating assimilation of carbon and its distribution at different levels of organization in the stand. The primary effect of environmental factors is on net assimilation rate, either directly, through factors such as light and temperature, or indirectly, for example, through the effects of soil water content on stomatal conductance. Respiration is also directly affected by environmental variables. Tree growth is described as a dynamic process where stand structure affects the distribution of the environmental driving variables in the canopy and between the trees, and this, in turn, affects the amount and distribution of new growth. Stand dynamics—new growth, mortality, and regeneration of trees—result in a new stand structure, implying a new distribution of resources among the trees (Figure 1).

Process models based on the carbon balance often deal with particular aspects of this dynamic chain in more detail than others. In models of stand-level productivity, the emphasis is on Box 1 of Figure 1, and its dependence on environmental factors, whereas in models of tree interactions and competition, the emphasis is on Boxes 2 and 3, or the feedback processes in a stand (indicated by the dashed arrows in Figure 1). New models under development consider the allocation of growth within trees (Figure 1, Box 3) at a finer, three-dimensional level. Some of the crucial uncertainties in carbon balance models include total productivity, allocation of carbon, and mortality and regeneration. Note that Figure 1 is conceptual; some models actually compute total production as a sum of individual productions.

Stand-level productivity Models focused on stand-level primary productivity typically use weather data and data on soil structure and chemistry as inputs, and the calculations are usually over one or more growing seasons (McMurtrie et al. 1990, Wang and Jarvis 1990, McMurtrie et al. 1994). Long-term stand-level dynamics are hence irrelevant, and the stand can be specified at a certain stage of development. Because models of this class have tight connections to the basic ecophysiology of trees and forests, they are used primarily to make quantitative

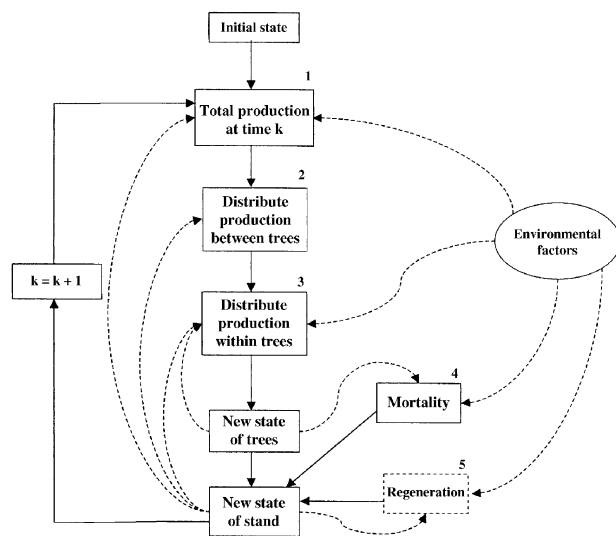


Figure 1. Conceptual structure of an individual-tree based carbon balance model of a forest stand.

predictions of the productivity of different sites and the variation in productivity between years and climates (McMurtrie et al. 1994). Sands et al. (2000) used this approach to produce regional predictions of site productivity in Australia, where empirical information on site productivity is not available for many areas. Similarly, the 3-PG model was used for predictions of site productivity across wide regions (Coops et al. 1998b). Climate change impacts are also often considered at this level (Kirschbaum 2000).

Another type of stand-level model focuses on the long-term dynamics of productivity, concentrating on the effects of different feedback processes (shown by dashed-line arrows in Figure 1) related to carbon allocation (Figure 1, Box 3), interactions between consumption and production, and environmental limitations (McMurtrie and Wolf 1983, Mohren 1987, Valentine 1988). These models consider growth, senescence and mortality as stand average dynamic processes and apply a simplified treatment of the metabolic processes. They are often more theoretically oriented, aiming at developing the general principles of growth modeling. Many models of this type include a nutrient balance, deriving characteristics of stand dynamics from carbon–nitrogen interactions (Ågren 1996, Ågren and Bosatta 1998, Thornley 1991, Thornley and Cannell 1996, Nissinen and Hari 1998).

Dynamics of stand and tree structure In another area of growth and yield modeling, the emphasis has been on interactions between individual trees in stands (Hari et al. 1982, Mäkelä and Hari 1986, Ludlow et al. 1990, Nikinmaa 1992, Sievänen 1993, Ditzer et al. 2000, Bartelink 2000). The origin of this approach is in the JABOWA model (Botkin et al. 1972, Shugart 1984), which, although not in a carbon balance framework, uses competition for light between trees in a forest patch to characterize competition. These models take the annual gross productivity of a stand as given and deal with the way that total carbon is distributed between trees in different local envi-

ronments (Figure 1, Box 2), based on the use of shading models. One of the main responses of trees to competition is an adaptation of carbon allocation to improve survival in a suppressed position. Consequently, this type of modeling has focused on the description of growth allocation in trees differing in size and competitive status (Figure 1, Box 3) (Valentine 1985, Mäkelä 1986, West 1993, Lindner et al. 1997, Deleuze and Houllier 1997, Bartelink 1998).

Because these models describe the interaction and differentiation of trees, they are relevant to such forest management applications as planting and harvesting strategies (Bartelink 1998). The models usually express the state of the stand in terms of traditional forestry variables, such as basal area or dominant height. More recently, this approach has been applied to the analysis of mixed (Bartelink 2000) and heterogeneous (Lindner 2000) stands, as well as tropical forests (Ditzer et al. 2000) and wood quality (Mäkelä et al. 1997). It is not ideal for predicting productivity, but relies on empirical measurements of stand productivity that can be used for model calibration (Sievänen and Burk 1993, Valentine 1997).

Model structure to match the objectives of modeling

Despite their common framework, carbon balance models vary considerably in form, representing those facets of the system considered crucial for the purposes of a particular model: each model is an appropriate simplification of the total picture. The mechanisms invoked to model system behavior must be consistent with the essential features of the system being modeled and the dynamics of those features at the level of concern. The degree of success in simplifying the system and selecting its essential features will be judged by the success of the models in predicting system behavior, as described by relevant empirical data.

Parameter estimation and model evaluation in PBMs

All models share the common need for parameter estimation and evaluation. Because all submodels of a genuine PBM are representations of processes at the same conceptual level of hierarchy, submodels can conveniently be calibrated independently based on measurements designed for the purpose (Sharpe and Rykiel 1991). However, in most practical applications, some submodels, or a subset of submodel parameters, will defy calibration through measurement because of lack of data, problems of scaling up, or poor understanding of processes. In such a case, parameter estimation has to deviate from the strict definition of PBMs, and these submodels or submodel parameters are best estimated using empirical data relating to the whole system (Sievänen and Burk 1993), with the objective of predicting system-level behavior. Robust numerical solution methods are essential (Hornberger and Cosby 1985, Richter and Sondgerath 1990), though less-tested solution techniques are promising (Liepins et al. 1990).

Model evaluation requires precise specification of the domain in which the model is applicable, as well as a quantitative expression of the desired level of accuracy. Rykiel (1996) emphasized the importance of matching evaluation methods to model type and complexity with due consideration of the nature of available data. When evaluating a PBM of forest

growth it is often difficult to determine whether deviations from predicted performance are caused by variation in the system, by inadequacies of the model, or by incorrect values for sub-model parameters. The large spatial variability in forests can lead to considerable variation in their physical characteristics and growth rates, even for forest stands regarded, for practical purposes, as homogeneous. Corresponding variability in model predictions should not be mistaken for inaccuracy.

Internal evaluation deals with the uncertainty in predictions generated by variability in model inputs, parameters, and submodels. Monte Carlo and so-called error propagation methods can be used to assess internal variability in PBMs (Gertner et al. 1996); the parameter-parameter plots of Sievanen and Burk (1993) are a graphical alternative. External model evaluation focuses on the accuracy of predictions of real system behavior.

We conclude that the variety of PBMs developed from the general principle of the carbon balance demonstrates that models may focus on different parts of the system and still encapsulate some of the essential features of stand development. The different approaches may hence complement rather than contradict each other. All of these models share the problems of parameter estimation caused by lack of precise data and an incomplete understanding of some important processes. A solution to this problem is to wait until basic research has provided the answers. Another solution is discussed in the following section.

Hybrid models

Hybrid models contain both causal and empirical elements at the same hierarchical level. We propose that the implementation of process-based models, and more generally, the causal thinking behind them, would be accelerated if it were accepted that hybrid models could improve on the predictions of both PBMs and empirical models.

Korzukhin et al. (1996) argued that all empirical models have causal elements and all causal models have empirical elements. The need for empirical system-level information in PBMs arises when some parameters cannot be reasonably estimated from their definition, as already noted above. If this is the case, the hybrid character of the models has to be reflected in the methods of parameter estimation and model evaluation, which have usually been defined separately for the two extreme types of model. This has not been fully appreciated until recently (Gertner et al. 1999, Green et al. 1999).

Methods of dealing with the mixed character of PBMs include Monte Carlo methods (Hornberger and Cosby 1985), simultaneous parameter fitting (Sievanen and Burk 1993, Vanclay and Skovsgaard 1997), as well as the more recent Bayesian techniques of parameter estimation (Gertner et al. 1999, Green et al. 2000). The basic idea behind all of these methods is that some of the parameter values can be determined exactly on the basis of *a priori* information, others can be given intervals of likely variation, and some cannot be determined at all on the basis of our current knowledge. Given the initial distributions, the free parts of the parameters are determined by fitting the model output to measurements under

the constraints set by the *a priori* information. These methods apply to any models with hybrid character, whether they are predominantly empirical or process-based.

Empirical components in carbon balance models

In this section we discuss situations where empirical elements and model calibration are required to quantify the carbon balance approach. We also review some of the methods that have been employed by modelers to do this.

Total productivity (Figure 1, Box 1) The gross and net production of a given site are major uncertainties in carbon balance modeling. Growth models usually require estimates of whole-canopy production over periods of weeks, months, or the growing season, but models of photosynthesis and respiration deal with single leaves, shoots or plant parts and operate with time constants of a few seconds or hours. Problems arise in scaling up because the environmental factors vary in space and time, and the response mechanisms are nonlinear. Some of the production and consumption processes are not fully understood. For example, there has been discussion recently of the possible causes of the observed reduction in net growth in larger trees but there is, as yet, no consensus on the mechanism (Yoder et al. 1994, McMurtrie et al. 1995, Gower et al. 1996, Ryan and Yoder 1996).

In scaling up, some growth models rely on summary outputs from detailed models, the parameters of which are determined, at least in theory, from experiments at the subsystem level (Berninger and Nikinmaa 1997, Mäkelä 1997, Valentine et al. 1997, Raulier 2000). Others calculate photosynthetic production from semi-empirical equations for maximum potential productivity and reducing factors determined by the extent to which environmental (including soil) conditions are suboptimal (McMurtrie et al. 1994, Landsberg and Waring 1997, Sands et al. 2000).

Despite the problems and complexities, very simple models that include a description of photosynthesis have been able to capture some of the essential qualitative features of the differences in productivity between both sites and individual trees. When calibrated against growth data, these models have produced fairly accurate estimates of production across individual trees and sites. The simplest models are based on calculations of photosynthesis that are then regressed against growth (Brunner and Nigh 2000, Courbaud 2000). The models of Landsberg and Waring (1997) and Sands et al. (2000) have predicted differences in growth between sites using little system-level input information. In the study by Ditzer et al. (2000), equations that predict net growth, including production, respiration and turnover, were calibrated against diameter growth data from different species. Some modelers have used systematic calibration methods such as the Bayesian technique (Green et al. 2000) to determine ranges of simultaneous variation for all parameters, such that model outputs agree with both measured information and expert opinion. These examples suggest that photosynthesis and respiration models adequately calibrated against growth data can provide a general model of productivity of wide application.

Carbon allocation and competition (Figure 1, Boxes 2–3)

For a long time, allocation of carbon to various components of plants was thought a critical function of process-based models. Although the actual mechanisms have not yet been unraveled (see review by Cannell and Dewar 1994), modelers have been able to describe carbon (NPP) allocation in ways that produce the type of structures, and even the structural variety, found in real forests. The most common procedure starts from measurements of tree structure and forces the allocation of carbon to follow patterns that depend on observed total growth, the relative rates of growth of component parts (Landsberg 1986, Landsberg and Waring 1997), and the relative rates of turnover in different tissues (Mäkelä 1986), leading to tree growth consistent with observed structures. The observed patterns have been expressed as allometric relationships (Landsberg 1986, Sievänen 1993, Landsberg and Waring 1997, Bartelink 1998, Ditzer et al. 2000) or they have been derived from structural–functional theories such as the functional balance or pipe model theories (Valentine 1985, Mäkelä 1986, Mäkelä and Sievänen 1992, Nikinmaa 1992, West 1993, Nikolov and Fox 1994, Bartelink 1998). For tree-level carbon allocation, this method utilizes system-level information for model construction, but in a stand growth model, it can be regarded as an independent submodel based on observed empirical relationships.

Carbon allocation patterns change in response to competition. One of the most evident changes is variation in the ratio of height to diameter growth, accompanied by changes in crown rise. Recently, models similar to those based on the functional balance approach have been proposed for these phenomena (Valentine et al. 1994, Mäkelä 1997), but these and other growth models use empirical or hypothetical equations to describe acclimation in response to competition, because it cannot easily be parameterized independently without system-level information (e.g., Lindner 2000). Recent studies (e.g., Mäkelä et al. 2000, Sievänen et al. 2000) show that use of information from empirical measurements of diameter distributions could improve quantitative and qualitative estimates of both individual tree growth and stand growth.

Mortality and regeneration (Figure 1, Boxes 4–5) There is no generally accepted quantitative mechanistic theory of mortality, and this is a case where causal models are not available at the level of hierarchy defined as the basis for the carbon balance model. Empirical models of mortality are often based on relative growth rate and tree size (Belcher et al. 1982, Sievänen 1993). Mortality related to crowding has been described by the so-called $-3/2$ power law of self thinning, which has also been utilized in growth models (e.g., Valentine 1988, Landsberg and Waring 1997). It is important that the parameters of tree mortality are estimated independently and not from stand-level information only, because the same stand development can be consistent with different combinations of growth and mortality.

Regeneration is not often included in stand growth and yield models based on the carbon balance (cf. the gap models, Shugart 1984) but modeling regeneration becomes important if long periods of time and heterogeneous stand structures are considered.

We conclude that the carbon balance framework can readily be applied in forest management, provided that the models are calibrated against whole-system data. Such calibration has recently become more accessible as estimation methods combining physiological and empirical information have been developed. Management applications may serve as tests of the models, pointing out limitations and guiding further ecophysiological research.

Implementation of management applications*Uses of models in forest management*

Decisions about the protection, treatment, and utilization of forest resources in both temporal and spatial contexts are typically based on enterprise (public or private) goals and objectives. Models of various types are used in this arena. These models are increasingly required to cover large areas—diverse parts of regions, countries, and continents. Examples range from inventory updates to physical and economic analysis of site specific treatments or investments, and broad environmental questions.

In recent decades, it has come to be recognized that forests affect atmospheric composition, water resources, and biodiversity. As a result, there has been an increase in analysis and modeling of forest resources conducted by parties outside the forestry enterprise, thereby extending the traditional concept of model use in forest management policy and practice.

Role of process models

Process-based models have been used in projections of climate change and its impacts on forests, with significant implications for forest management (cf. Kirschbaum 2000, Lindner 2000). For example, a clearcut operation was recently carried out in an area of Finnish Lapland where clearcuts had previously not been recommended, because model simulations suggested that climate change would enhance natural regeneration in those areas in the future.

At the operational level, PBMs provide only an incomplete picture. The carbon balance approach applies to projections of stand growth, and can conceivably be applied over wide areas and long time spans if large-scale site data are available and if adequate models of regeneration and mortality are included (e.g., Ditzer et al. 2000). Coops et al. (1998a, 1998b) applied a carbon balance approach to the estimation of NPP, and hence mean annual increments, over very large areas, using satellite measurements to provide information about canopy characteristics such as leaf area index. Key factors affecting the acceptance and usage of models in an operational framework include documentation, coding, ease of calibration and evaluation, completeness, and demonstrations of utility.

Prerequisites for operational process models

Documentation and coding Before a model can become widely used in management, it must be clearly documented and coded in a widely understood language. Documentation should include (1) an explanation of the conceptual basis of the model in lay terms, with enough science to give credibility, (2)

a demonstration of practical application, and (3) clear user instructions.

Calibration and evaluation Models should be calibrated for a range of conditions occurring in the area of application. In temporal terms, the requirement for precision is from the year-long to rotation-length time periods considered in forest management. Conventionally, calibration is done before implementing the model, and the user has only to specify general input conditions, such as location, site type and initial tree stock and condition. Methods of on-line calibration are also being developed. Whichever method is chosen, considerable data and efficient methods of parameter fitting will be required.

External model evaluations will be of greatest relevance and interest to forestry practitioners. Simple criteria expressed in relevant terms, e.g., percent error in predicting future volume per unit area, demonstrated for a broad range of conditions, will be required for a model to be used widely in practice. Graphical presentations of error trends in time and with respect to state variables shed additional light. It has been argued that data for such an exercise must be "independent" of those used for calibration. This presumes the existence of "independent" data, ignores the expense associated with its collection, and misdirects attention away from the more critical need for a rich set of conditions represented in evaluation data. Resampling methods offer an efficient and more effective alternative (Burk 1990).

Completeness A limitation that affects the precision and realism of many models is that they do not cover the full range of forest change. Some of the important aspects that models often lack include regeneration and mortality, effects of weather, disturbance, and site quality.

Regeneration can be ignored for short periods, but over several to many decades, it has to be included unless strict plantation management is the rule. Regeneration models seem a prerequisite for describing uneven-aged forest management options.

Weather is typically not random and its effects cannot necessarily be balanced over any particular time period. If inventory updates are to be improved, the weather for the period, and its effects on growth, must be considered.

It is possible to estimate, or even plan, human disturbance, but natural disturbance, caused by factors such as fires, hurricanes or insect attack, must be estimated. It is vital to include disturbance in models aimed at long-term simulation, or they will overestimate the development of basal area and stocking (Unpublished report, Jaakko Pöyry Consulting, Inc., Tarrytown, NY).

Site quality is a poorly understood and ill defined factor. It depends not only on soil water content and fertility, but also topographic factors such as altitude, slope, and proportion of rocks. We note that site quality could itself be predicted by a growth model that incorporates, or can account for, the influence of these factors.

Demonstration of utility New models must demonstrate their utility if they are to be accepted by forest managers. This means the production of pilot software tools that meet the above requirements and are geared toward common manage-

ment problems. The models should recognize, and account for, the effects of common silvicultural practices that are important for the economics of forest management, such as pruning and thinning. Furthermore, model output should include the most common types of commercial forest product.

Examples of management-oriented developments

Process models have not been widely applied in forestry operations. Successful application will require close and ongoing contacts between researchers and practitioners, because the practical problems of model application are often quite different from the problems of model development. Some examples of these efforts are given below.

Projection of regional productivity: 3-PG

The 3-PG model produced by Landsberg and Waring (1997) is being applied in two areas: the first is in Australia which, like Canada and the United States, is in the throes of debate about logging native forests; the second is in South Africa, where proliferation of hardwood and softwood plantations in important water catchments has led to growing concern about the reduction in water yield.

In the Australian case, it is proposed that large plantations could substitute for wood supplies lost by reduction of logging in natural forests. To test this argument, it is necessary to estimate probable growth rates and yields of plantations in areas where plantations have never existed. The 3-PG model has been programmed into a GIS package by a government agency (Bureau of Resource Sciences), with access to country-wide weather and soil data bases, linked to digital elevation maps. The model (called 3-PG (Spatial) in this version) has been calibrated against measurements made on a range of species grown in plantations at various locations. The calibrations allow the model to explore the likely performance of trees in unexploited areas considered suitable for plantations, and to provide information about possible wood supplies from these areas (P. Tickle, Bureau of Resource Sciences, Department of Agriculture, Forestry and Fisheries, Barton ACT, Australia).

The 3-PG model is used in South Africa to analyze the relative economic benefits of water and wood as commodities. The model is being calibrated against available empirical plantation growth data and experimental data on water use. Outputs include water-use efficiency, in terms of wood production per unit of water transpired (report available from P. Dye, ENVIRONMENTEK; Division of Water, Environment and Forestry Technology, CSIR, Pietermaritzburg, South Africa). The relative economic values attributed to given amounts of water or wood are matters for economists and sociologists, who must assess the social and economic impacts of particular policies.

FOREST 5: An individual tree-based model

Researchers at the University of Minnesota are constructing a hybrid approach to modeling forest growth and change. The model FOREST 5 is a rewriting of the individual-based empirical simulator FOREST (Ek and Monserud 1974). It is in-

tended to produce variable outputs suitable for research and forest management applications, and to be applicable at the plot, stand, and landscape levels. FOREST 5 is a modular system comprising both empirical and process-based modules (Robinson 1998). The process-oriented modules were included to provide emergent properties as the outcome of the simulations. FOREST 5 was constructed to make clear the links between tree and landscape models and to compare efficiently the short- and long-term benefits of silvicultural practices, either singly or in combination, for many species and sites simultaneously.

Development of wood quality: PipeQual

Growth models developed at the University of Helsinki (Mäkelä 1997, Mäkelä et al. 2000) are currently being embedded in management applications. A timber quality application (Mäkelä et al. 1997), PipeQual, is under construction in cooperation with VTT Building Technology, with the objective of producing logs with explicit internal structure that can be input to a sawing simulator. The overall objective is to produce models that predict the internal structure and hence timber quality in stands at clearcut. The model will be used to assess the quality distribution of stems from a particular stand, and to plan forest management adjustments to long-term changes in the forestry market.

PipeQual utilizes a process-based approach to growth and consequently to the development of stem form and crown structure, in connection with empirical submodels of branch numbers, locations, and inclinations. The tree growth model is based on an individual-tree carbon-balance model (Mäkelä 1997) in which trees interact through shading and availability of physical space. Extensive empirical work has been carried out to identify and test the model, and to develop parallel empirical models of quality characteristics for the forestry planning simulator, MELA, at Metla, Finland (Siitonen 1995).

Element cycling in terrestrial ecosystems

Ågren and Bosatta (1998) have developed a general framework for analyzing element cycling in terrestrial ecosystems. Based on this framework (plant growth is based on yield tables and soil carbon on a replacement model), a hybrid model has demonstrated that replacement of *Pinus sylvestris* L. with *P. contorta* Dougl. ex Loud. in Scandinavian forests is unlikely to lead to drastic changes in soil carbon and nutrient stores (Ågren and Knecht 2000). However, soils under *P. contorta* will respond less dynamically to environmental changes than soils under *P. sylvestris*.

Increased biomass harvesting, particularly of nitrogen-rich residues, can decrease the long-term productivity of a site (Rolf and Ågren 1999). Because the effects of thinning and nitrogen deposition require long periods to develop, they cannot be separated from variability in short-term field experiments. It is therefore possible to show productivity changes only with this type of model.

Early growth of conifer plantations

Researchers at the Ontario Forest Research Institute (Sault Ste. Marie, Canada) in collaboration with the Canadian Forest

Service, and the University of Maine in Orono are developing a hybrid-type model that uses a carbon balance approach to simulate seedling growth and includes empirical components such as locally developed allometric relationships used to distribute growth among seedling parts, and relationships between maximum seedling growth and site characteristics (e.g., climate, soil bulk density and organic matter).

The model is to be used as a research tool to improve predictions of plantation size structure. A major challenge is to combine the cohort-based approach currently used in the model with a realistic description of seedling size differentiation. An empirical way to "reconstruct" seedling size distribution is to use pre-fitted statistical relationships between distribution parameters and mean seedling size (Knowe and Stein 1995). The model currently explores an alternative approach of Monte Carlo simulations in which certain parameters randomly fluctuate around their mean values, thus mimicking variation in microsite conditions, an approach similar to that discussed by Bonan (1991).

A landscape modeling system

The Silviculture Laboratory at the University of Washington, College of Forest Resources is developing a landscape modeling system in cooperation with the United States Forest Service, Pacific Northwest Research Station (McCarter et al. 1998). Known as the Landscape Management System (LMS), the model uses the hierarchical approach of integrating various stand-level empirical and process-based relationships and models. It links existing growth models (e.g., FVS, Forest Vegetation Simulator) (Donnelly 1996, Teck et al. 1996) with spatial (GIS) and stand inventory data, silvicultural treatment modules, and other tools. It processes the temporal and spatial data and provides output summaries as stand and landscape visualizations (SVS; McGaughey 1997) and charts and tables (UTOOLS; Ager and McGaughey 1997), in terms of stand structures, habitats, hazard risks, timber volume, and financial analyses.

The system allows examination of the effects of diverse stand-level changes over time and across the landscape. By combining stand-level models to examine situations at the landscape level, it helps ensure that the underlying processes are considered, thereby allowing the components of the system to be integrated, checked for consistency, and improved (Wilson and Baker 1999, Wilson et al. 1999).

Conclusions

Recent developments in the application of process-based modeling to the management of forest growth and change have included the development of evaluation and parameter estimation methods suitable for models with causal structure, and the increasing availability of data applicable to the evaluation of such models. We have argued that, for the development of operational models, it is necessary to give up belief in a dichotomy between process and empirical modeling, and accept that all models can have both empirical and causal components at the system level.

It is clear that several questions need further investigation, and that the quantification of models for any particular site cannot easily be carried out without calibration against system-level data. However, even simple models with some process elements related to the carbon balance have turned out to be successful and reasonably general, suggesting that the formulation of growth based on carbon acquisition by trees is an extremely powerful tool in growth models.

Currently, a major obstacle to the application of process-based models is the operational implementation of these models. This is a practical task, rather different from the scientific problems of model development, requiring programming considerations and a thorough understanding of the issues of day-to-day forest management.

We believe that methods of decision-making and analysis in forest management are gradually moving toward a more general, causal-oriented approach. Crucial to this development is mutual appreciation of methods and approaches used by ecophysiological and empirical modelers, and a close interaction between modelers and forestry practitioners. It seems likely that models that include process-oriented components will be used within the next few years in some forestry enterprises. This development is likely to parallel the further development of ecophysiological based models. Furthermore, the aim of producing models of value to managers and decision-makers provides scientists with a valuable guide to research priorities. It also provides a framework for discussion between causal and empirical modelers and forestry practitioners.

References

- Ager, A.A., and R.J. McGaughey. 1997. UTOOLS: Microcomputer software for spatial analysis and landscape visualization. USDA Forest Service, Pacific Northwest Research Station, PNW-GTR-397, Portland, OR.
- Ågren, G.I. 1996. Nitrogen productivity of photosynthesis minus respiration to calculate plant growth. *Oikos* 76:529–535.
- Ågren, G.I. and E. Bosatta. 1998. Theoretical ecosystem ecology—understanding element cycles. Cambridge Univ. Press, 233 p.
- Ågren, G.I. and M.F. Knecht. 2000. Simulation of soil carbon and nutrient development under *Pinus sylvestris* and *Pinus contorta*. *For. Ecol. Manage.* In press.
- Bartelink, H.H. 1998. Simulation of growth and competition in mixed stands of Douglas-fir and beech. Thesis, Landbouwniversiteit, Wageningen, 222 p.
- Bartelink, H.H. 2000. Effects of stand composition and thinning in mixed-species forests: a modeling approach applied to Douglas-fir and beech. *Tree Physiol.* 20:399–406.
- Belcher, D.W., M.R. Holdaway and G.J. Brand. 1982. A description of STEMS, the stand and tree evaluation and modelling system. U.S. Forest Service, GTR-NC-33, 23 p.
- Berninger, F. and E. Nikinmaa. 1997. Differences in pipe model parameters determine differences in growth and affect response of Scots pine to climate change. *Funct. Ecol.* 11:146–156.
- Bonan, G.B. 1991. Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. *Ann. Bot.* 68:341–347.
- Bossel, H. 1994. Modeling and simulation. A.K. Peters Ltd., Wellesley, MA, 484 p.
- Botkin, D.B., J. Janak, and J. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60:849–872.
- Brunner, A. and G. Nigh. 2000. Light absorption and bole volume growth of individual Douglas-fir trees. *Tree Physiol.* 20:323–332.
- Burk, T.E. 1990. Prediction error evaluation: preliminary results. *In Proc. IUFRO Conference Forest Simulation Systems*. Eds. L.C. Wensel and G.S. Biging. Univ. California, Division of Agriculture and Natural Resources Bull. 1927, pp 81–88.
- Cannell, M.G.R. and R.C. Dewar 1994. Carbon allocation in trees: a review of concepts for modelling. *Adv. Ecol. Res.* 25:59–104.
- Coops, N.C., R.H. Waring and J.J. Landsberg. 1998a. The development of a physiological model (3-PGS) to predict forest productivity using satellite data. *In Forest Scenario Modeling for Ecosystem Management at Landscape Level*. Eds. G.-J. Nabuurs, T. Nuutinen, H. Bartelink and M. Korhonen. European Forest Institute, Joensuu, Finland. *EFI Proc.* 19:173–191.
- Coops, N.C., R.H. Waring and J.J. Landsberg. 1998b. Assessing forest productivity in Australia and New Zealand using a physiologically-based model driven with averaged monthly weather data and satellite-derived estimates of canopy photosynthetic capacity. *For. Ecol. Manage.* 104:113–127.
- Courbaud, B. 2000. Comparing light interception with stand basal area for predicting tree growth. *Tree Physiol.* 20:407–414.
- Deleuze, C. and F. Houllier. 1997. A transport model for tree ring width. *Silva Fenn.* 31:239–250.
- de Reffye, P., T. Fourcaud, F. Blaise, D. Barthelemy and F. Houllier. 1997. A functional model of tree growth and tree architecture. *Silva Fenn.* 31:297–311.
- Ditzer, T., R. Glauner, M. Förster, P. Köhler and A. Huth. 2000. The process-based stand growth model FORMIX 3-Q applied in a GIS environment for growth and yield analysis in a tropical rain forest. *Tree Physiol.* 20:367–381.
- Donnelly, D.M. 1996. Pacific Northwest Coast variant of the Forest Vegetation Simulator. Ft. Collins, CO, USDA Forest Service, WO-Forest Management Service Center.
- Ek, A.R. and R.A. Monserud. 1974. FOREST: A computer model for simulating the growth and reproduction of mixed-species forest stands. Report R2635. Madison, WI: School of Natural Resources, College of Agric. and Life Sciences, Univ. Wisconsin-Madison.
- Gertner, G., P. Parysow and B. Guan. 1996. Projection variance partitioning of a conceptual forest growth model with orthogonal polynomials. *For. Sci.* 42:474–486.
- Gertner, G.Z., S. Fang and J.P. Skovsgaard. 1999. A Bayesian approach for estimating the parameters of a forest process model based on long-term growth data. *Ecol. Model.* 119:249–265.
- Godfrey, K. 1983. Compartmental models and their applications. Academic Press, New York, NY, 291 p.
- Gower, S.T., R.E. McMurtrie and D. Murty. 1996. Aboveground net primary production decline with stand age: potential causes. *Trends Ecol. Evol.* 11:378–382.
- Green, E.J., D.W. MacFarlane, H.T. Valentine and W.E. Strawderman. 1999. Assessing uncertainty in a stand growth model by Bayesian synthesis. *For. Sci.* 45:528–538.
- Green, E.J., D.W. McFarlane and H.T. Valentine. 2000. Bayesian synthesis for quantifying uncertainty in predictions from process models. *Tree Physiol.* 20:415–419.
- Hakkala, L. and R. Ylinen. 1978. Introduction to modern systems and control theory. Otakustantamo. Espoo, Finland, 220 p. *In Finnish.*
- Hari, P., S. Kellomäki, A. Mäkelä, P. Ilonen, M. Kanninen, E. Korpilahti and M. Nygren. 1982. Metsikön varhaiskehityksen dynamiikka. Summary: Dynamics of early development of tree stand. *Acta For. Fenn.* 177:1–42.

- Hornberger, G.M. and B.J. Cosby. 1985. Selection of parameter values in environmental models using sparse data: a case study. *Appl. Math. Comput.* 17:335–355.
- Kellomäki, S., V.-P. Ikonen, H. Peltola, and T. Kolström. 1999. Modelling the structural growth of Scots pine with implications for wood quality. *Ecol. Model.* In press.
- Kirschbaum, M.U.F. 2000. Forest growth and species distribution in a changing climate. *Tree Physiol.* 20:309–322.
- Knowe, S.A. and W.I. Stein. 1995. Predicting the effects of site preparation and protection on development of young Douglas-fir plantations. *Can. J. For. Res.* 25:1538–1547.
- Korzukhin, M.D., M.T. Ter-Mikaelian and R.G. Wagner. 1996. Process versus empirical models: which approach for forest ecosystem management? *Can. J. For. Res.* 26:879–887
- Landsberg, J.J. 1986. *Physiological ecology of forest production.* Academic Press. New York, NY, 198 p.
- Landsberg, J.J. and R.H. Waring. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *For. Ecol. Manage.* 95:209–228.
- Liepins, G., R. Goeltz, and R. Rush. 1990. Machine learning techniques for natural resource data analysis. *AI Applic.* 4:9–17.
- Lindner, M. 2000. Developing adaptive forest management strategies to cope with change. *Tree Physiol.* 20:299–307.
- Lindner, M., R. Sievänen and H. Pretzsch. 1997. Improving the simulation of stand structure in a forest gap model. *For. Ecol. Manage.* 95:183–195.
- Ludlow, A.R., T.J. Randle and J.C. Grace. 1990. Developing a process-based model for Sitka spruce. *In* *Process Modeling of Forest Growth Responses to Environmental Stress.* Eds. R.K. Dixon, R.S. Meldahl, G.A. Ruark and W.G. Warren. Timber Press Inc. Portland, OR, pp 249–262.
- Mäkelä, A. 1986. Implications of the pipe model theory on dry matter partitioning and height growth in trees. *J. Theor. Biol.* 123:103–120.
- Mäkelä, A. 1997. A carbon balance model of growth and self-pruning in trees based on structural relationships. *For. Sci.* 43:7–24
- Mäkelä, A. and P. Hari. 1986. Stand growth model based on carbon uptake and allocation in individual trees. *Ecol. Model.* 33:205–229.
- Mäkelä, A. and R. Sievänen. 1992. Height growth strategies in open-grown trees. *J. Theor. Biol.* 159:443–467.
- Mäkelä, A., P. Vanninen and V.-P. Ikonen. 1997. An application of process-based modelling to the development of branchiness in Scots pine. *Silva Fenn.* 31:369–380
- Mäkelä, A., R. Sievänen, M. Lindner and P. Lasch. 2000. Application of volume growth and survival graphs in the evaluation of four process-based forest growth models. *Tree Physiol.* 20:347–355.
- McCarter, J.M., J.S. Wilson, P.J. Baker, J.L. Moffett, and C.D. Oliver. 1998. Landscape management through integration of existing tools and emerging technologies. *J. For.* 96:17–23.
- McGaughey, R. 1997. Visualizing forest stand dynamics using the Stand Visualization System. *Proc. Annual Convention, Baltimore, MD. Technical Papers, Bethesda, MD. Am. Congress Surveying Mapping Am. Soc. Photogrammetry Remote Sens.* 4:248–257.
- McMurtrie, R. and L. Wolf. 1983. Above- and below-ground growth of forest stands: a carbon budget model. *Ann. Bot.* 52:437–448.
- McMurtrie, R.E., M.L. Benson, S. Linder, S.W. Running, T. Talsma, W.J.B. Crane and B.J. Myers. 1990. Water/nutrient interactions affecting the productivity of stands of *Pinus radiata*. *For. Ecol. Manage.* 30:381–413.
- McMurtrie, R.E., H.L. Gholz, S. Linder and S.T. Gower. 1994. Climatic factors controlling the productivity of pine stands: a model-based analysis. *Ecol. Bull.* 43:173–188.
- McMurtrie, R.E., S.T. Gower and M.G. Ryan. 1995. Forest productivity: explaining its decline with stand age. *Ecol. Soc. Am. Bull.* 76:152–154.
- Mohren, G.M.J. 1987. Simulation of forest growth, applied to Douglas-fir in the Netherlands. Pudoc, Wageningen, The Netherlands, 83 p.
- Mohren, G.M.J. and H.E. Burkhart. 1994. Contrasts between biologically-based process models and management-oriented growth and yield models. *For. Ecol. Manage.* 69:1–5.
- Nikinmaa, E. 1992. Analyses of the growth of Scots pine; matching structure with function. *Acta For. Fenn.* 235, 68 p.
- Nikolov, N.T. and D.G. Fox. 1994. A coupled carbon-water-energy-vegetation model to assess responses of temperate forest ecosystems to changes in climate and atmospheric CO₂. Part I. Model concept. *Environ. Pollut.* 83:251–262.
- Nissinen, A. and P. Hari. 1998. Effects of nitrogen deposition on tree growth and soil nutrients in boreal Scots pine stands. *Environ. Pollut.* 102:61–68.
- O'Neill, R.V., D.L. DeAngelis, J.B. Waide and T.F.H. Allen. 1986. *A hierarchical concept of ecosystems.* Princeton University Press, Princeton, NJ, 253 p.
- Peltola, H., S. Kellomäki, H. Väisänen and V.-P. Ikonen. 1999. A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce and birch. *Can. J. For. Res.* 29:647–661.
- Raulier, F., P.Y. Bernier and C.-H. Ung. 2000. Modeling the influence of temperature on monthly gross primary productivity of sugar maple stands. *Tree Physiol.* 20:333–345.
- Richter, O. and D. Sondgerath. 1990. *Parameter estimation in ecology: the link between data and models.* Weinheim. Basel, Switzerland, 217 p.
- Robinson, A.P. 1998. *Forest ecosystem dynamics: systematic approach to modelling in a model rich environment.* Ph.D. Thesis, Univ. Minnesota, St. Paul, MN, 235 p.
- Rolf, C. and G.I. Ågren. 1999. A model study of nitrogen limited forest growth. *Ecol. Model.* 118:193–211.
- Ryan, M.G. and B.J. Yoder. 1996. Hydraulic limits to tree height and tree growth. *BioScience* 47:235–242.
- Rykiel, E.J., Jr. 1996. Testing ecological models: the meaning of validation. *Ecol. Model.* 90:229–244.
- Sands, P., M. Battaglia and D. Mummery. 2000. Application of process-based models to forest management: experience with ProMod, a simple plantation productivity model. *Tree Physiol.* 20:383–392.
- Sharpe, P.J.H. 1990. Forest modeling approaches: compromises between generality and precision. *In* *Process Modeling of Forest Growth Responses to Environmental Stress.* Eds. R.K. Dixon, R.S. Meldahl, G.A. Ruark and W.G. Warren. Timber Press Inc., Portland, OR, pp 180–190.
- Sharpe, P.J.H. and E.J. Rykiel, Jr. 1991. Modelling integrated response of plants to multiple stresses. *In* *Response of Plants to Multiple Stresses.* Eds. H.A. Mooney, W.E. Winner and E.J. Pell. Academic Press, New York, pp 205–224.
- Shugart, H.H. 1984. *A theory of forest dynamics.* Springer-Verlag, New York, 278 p.
- Sievänen, R. 1993. A process-based model for the dimensional growth of even-aged stands. *Scand. J. For. Res.* 8:28–48.
- Sievänen, R. and T.E. Burk. 1993. Adjusting a process-based growth model for varying site conditions through parameter estimation. *Can. J. For. Res.* 23:1837–1851.
- Sievänen, R., E. Nikinmaa and J. Perttunen. 1997. Evaluation of importance of sapwood senescence on tree growth using the model LIGNUM. *Silva Fenn.* 31:329–340.

- Sievänen, R., M. Lindner, A. Mäkelä and P. Lasch. 2000. Volume growth and survival graphs: a method for evaluating process-based forest growth models. *Tree Physiol.* 20:357–365.
- Sitonen, M. 1995. The MELA system as a forestry modelling framework. *Lesnictvi-For.* 41:173–178.
- Teck, R., M. Moeur and B. Eav. 1996. Forecasting ecosystems with the Forest Vegetation Simulator. *J. For.* 94:7:7–10.
- Thornley, J.H.M. 1991. A transport-resistance model of forest growth and partitioning. *Ann. Bot.* 68:211–226.
- Thornley, J.H.M. and M.G.R. Cannell. 1996. Temperate forest responses to carbon dioxide, temperature, and nitrogen: a model analysis. *Plant Cell Environ.* 19:1331–1348.
- Valentine, H.T. 1985. Tree-growth models: derivations employing the pipe-model theory. *J. Theor. Biol.* 117:579–585
- Valentine, H.T. 1988. A carbon-balance model of stand growth: a derivation employing pipe-model theory and the self-thinning rule. *Ann. Bot.* 62:389–396
- Valentine, H.T. 1997. Height growth, site index, and carbon metabolism. *Silva Fenn.* 31:251–263.
- Valentine, H.T., T.G. Gregoire, H.E. Burkhart and D.Y. Hollinger. 1997. A stand level model of carbon allocation and growth, calibrated for loblolly pine. *Can. J. For. Res.* 27:817–830.
- Valentine, H.T., A.R. Ludlow and G.M. Furnival. 1994. Modeling crown rise in even-aged stands of Sitka spruce or loblolly pine. *For. Ecol. Manage.* 69:189–197
- Valentine, H.T., D.A. Herman, J.H. Gove, D.Y. Hollinger and D.S. Solomon. 2000. Initializing a model stand for process-based projection. *Tree Physiol.* 20:393–398.
- Vanclay, J.K. and J.P. Skovsgaard. 1997. Evaluating forest growth models. *Ecol. Model.* 98:1–12.
- Wang, Y.-P. and P.G. Jarvis. 1990. Description and validation of an array model—MAESTRO. *Agric. For. Meteorol.* 51:257–280.
- West, P.W. 1993. Model of above-ground assimilate partitioning and growth of individual trees in even-aged forest monoculture. *J. Theor. Biol.* 161:369–394.
- Wilson, J.S., E. Isaac and R.I. Gara. 1999. Impact of mountain pine beetle (*Dendroctonus ponderosae*) infestations on future landscape susceptibility to the western spruce budworm (*Choristoneura occidentalis*) in north central Washington. *J. Appl. Entomol.* In press.
- Wilson, J.S., and P.J. Baker. 1999. Fire hazard modeling on the east slope of the Washington Cascade Range, U.S.A.: a stand-structural approach to managing fire risk on the landscape. *For. Ecol. Manage.* In press.
- Yoder, B.J., M.G. Ryan, R.H. Waring, A.W. Schoettle and M.R. Kaufmann. 1994. Evidence of reduced photosynthetic rates in old trees. *For. Sci.* 40:513–527.