COMMENTARY / COMMENTARIE

How forest models are connected to reality: evaluation criteria for their use in decision support

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Abstract: Choice of a model for exploring forest management options depends on the decision space defined by the actions, indicators, ecosystem scope, and cybernetic context of the decisions. To be useful in a particular decision context, candidate models must include all relevant hypotheses of effects of the actions on the indicators in a spatial and temporal structure appropriate for the particular decision. The architecture of a suitable model is implied or constrained by these components of the decision space. A set of attributes for assessing a model's suitability for decision support is proposed. In addition to a firm foundation in science, decision support models should provide predictions with quantified bias and precision, and without artifacts that influence choice of management alternatives. Descriptions of information flow across levels of integration within and between models and between models and field observations should be included in model descriptions. Schematic diagrams of these flows illustrate several broad classes of how modelling systems may be linked to reality to improve their utility.

Résumé : Le choix d'un modèle pour examiner différentes options d'aménagement forestier dépend de l'espace des décisions telle que définie par les actions, les indicateurs, l'ampleur de l'écosystème et le contexte cybernétique des décisions. Pour être utiles dans un contexte décisionnel particulier, les modèles susceptibles d'être choisis doivent inclure toutes les hypothèses pertinentes concernant les effets des actions sur les indicateurs dans une structure spatiale et temporelle appropriée pour ce cas particulier. L'architecture d'un modèle approprié est déterminée ou limitée par ces composantes de l'espace des décisions. Un ensemble de caractéristiques pour évaluer la pertinence d'un modèle d'aide à la décision est proposé. En plus de posséder de solides fondements scientifiques, les modèles d'aide à la décision devraient fournir des prédictions dont le biais et la précision sont quantifiés et qui sont dépourvues d'artéfacts qui influencent le choix des options d'aménagement. La description des modèles devrait inclure la description du flux de l'information entre les divers niveaux d'intégration dans et entre les modèles ainsi qu'entre les modèles et les observations de terrain. Des diagrammes schématiques de ces flux illustrent plusieurs grandes catégories de liens potentiels entre les systèmes de modélisation et la réalité qui sont susceptibles d'améliorer leur utilité.

[Traduit par la Rédaction]

Introduction

Choice of a model for exploring options for managing forested ecosystems depends on the decision space as defined by the set of management actions under consideration, the ecological bounds of the system to be affected, the cybernetic context of the decision, and the indicators of the consequent effects that are meaningful to the decision-maker. Within the framework set by the decision space, the candidate model must contain all of the relevant knowledge of effects in a structure appropriate for the particular decision, in short, how it is linked to the real world. There is inevitably a shortfall between the ideal linkages from a scientific view and the linkages that are feasible in a given decision-making context. Thus, architecture of the ideal model for a particular management analysis is implied (or constrained) by the interactions among these sets of connections.

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My objectives in this paper are threefold. First, I define attributes of the decision space in which the model is to be used. Second, I examine model linkages to the environment and to the system being managed as a protocol for documenting existing models to better inform their selection for decision support. Finally, I examine how these linkages may be strengthened to improve the predictive capabilities of the modelling system and thereby its usefulness for informing management decisions. Categorizing a model's linkages to reality suggests an alternative title for this paper: "An anatomy of empiricism".

Model attributes critical to decision support

Of the many (infinite) ways a model might be designed, which attributes are critical to its usefulness to inform a de-

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cision? Critical, in my view, are appropriate links to the decision space, firm foundation in science, known accuracy and precision, and freedom from artifacts.

Links to decision space

That different models are needed to support different decisions is a widely repeated mantra. Criteria for choice, however, are seldom explicitly stated because the structure of the decision-supporting analysis is not explicitly stated. The decision space of a management or policy analysis is defined by four kinds of information. The first three of these bounds are based on Holling's (1978) comprehensive discussion of these concepts.

The first bound is the set of management actions being proposed. Defining this set is the joint responsibility of the decision-makers and subject-matter specialists. A valuable contribution of the latter is formulating innovative actions that address the problems motivating the analysis. Their role, however, is not the same as the role of decision-maker, no matter how "expert" they may be.

The second bound is the list of attributes (indicators) that rank one alternative relative to another. This list must be provided by the decision-makers and their clientele well in advance of the analysis itself. Each indicator must be defined in terms of its spatial and temporal resolution. Inventory procedures to initiate the model must be compatible with the definitions and specifications of these indicators.

The third bound is the ecological extent of the population to be affected by the decision and the initial states of its indicators.

A fourth attribute of the decision, its cybernetic context, specifies how information from the real world feeds back into the analysis of subsequent decisions. Is the decision of long-lasting consequence, or can it be revised as reality unfolds? For example, a harvest scheduling analysis may "program" harvest for a very long time span. But the processes of inventory, monitoring, and analysis will be repeated at shorter intervals so that feedback effects can be recognized and incorporated into revised plans.

Taken together, these "lists" imply the properties required of the estimates, i.e., permissible bias, stochasticity, and smoothness of predictions. They do not directly define the architecture of the best model to inform the decision.

Foundation in science

First, and foremost, to be useful in the particular decision context, model architecture must provide a comfortable "home" for the scientific hypotheses defining how the particular actions affect the selected indicators. Supplying these hypotheses of effect is the proper role of subject matter specialists (scientists). These hypotheses of effect define the architecture of the model. A decision is "science based" to the extent that all relevant and acceptable hypotheses of effect have been used to display the consequences of the management actions. Hypotheses of effect may be true, but irrelevant. Their inclusion in the model may have little effect on how the indicators respond to the proposed actions. Verifying that relevant hypotheses of effect have not been ignored is a crucial role for scientists in the decision process. That is very different from having scientists make the decision!

Development of a dynamic model of forested ecosystems depends on three broad scientific domains: ecophysiology, statistical inference (including sampling and estimation), and biomathematics (Blake et al. 1990; Sharpe 1990). All three of these scientific domains involve transforming information from the real world into predictions about future states of nature. Slighting any of the three can vitiate a model for use in decision support.

Models with a strong basis in scientific knowledge of the processes represented should behave more realistically, particularly in the extremes, than models having a structure determined by statistical analysis that has not been guided by the same scientific knowledge. It is this lack of scientific context that defines an empirical model rather than its basis in real world data. The differences in behavior are attributable to a strong bias toward parsimony among statistical analysts, while specialists in the particular scientific field have a bias toward ever-greater complexity. Extreme outcomes of the modelled processes are seldom represented in observational data so that the model complexity needed for a full description of the process may fail to pass significance tests. The result is not that the model must necessarily be a tradeoff between statistical precision and biological integrity, but rather, the model represents a judgement call on whether the additional complexity represents firmly founded relations in the relevant science or whether the relations are still hypothetical. This distinction is crucial if the intended use of the model is to support decisions. Its complexity need be no greater than that essential to represent the effects of proposed actions.

Level of organization

Allen and Starr (1982) used level of organization to literally define the "organs" for which the processes are represented and observed. For each level of organization, there is a corresponding set of featured processes within a hierarchical sequence of processes. For example, if the leaves are the organs, then the appropriate processes may be photosynthesis and respiration. In contrast, in a pipe theory model, the featured organs are the population of pipes, modelled by rates of birth, increase in length, and mortality (transition to heartwood). If the level of organization is a tree, the processes being modelled are regeneration, accretion, and mortality. These processes are the aggregation of the leaf-level processes of photosynthesis, respiration, and within-tree allocation of their net productivity, which, in turn, may be guided by a pipe theory submodel. One defining attribute of so-called process modelling is that inference proceeds from lower levels in which the system is observable only in highly instrumented situations to higher levels of organization for which the required indicators are defined (Blake et al. 1990).

Level of integration

Models of the same level of organization may differ in the temporal and spatial scales at which the "organs" interact. For example, the same models of leaf physiology may be integrated to the stand level as in BGC (Running and Coughlan 1988) or at the tree level in Milner's TreeBGC (Milner et al. 2003). Although both models share the same level of organization and processes, they are scaled differently. The validity of moving between levels of integration depends on whether new processes become operative at the upper level and whether the processes are scale invariant.

Basis for treatment effects

Hypotheses of effect relate ecosystem responses to the actions for particular levels of organization and integration of the processes. However, these levels may not correspond to the levels of integration implied by the indicators specified in the decision space. The model provides the missing connections.

Modellers have used two alternative modelling strategies to represent effects of management activities. The choice depends on whether effects of the particular actions can be retrieved from real world data.

The more challenging alternative is the case in which the hypotheses of effects cannot be observed at the level of organization represented by existing data sets. Then, the model must be designed to integrate the known effects at more detailed levels into estimates of effects at the level of the selected indicator variables. For example, existing stand data sets may not include structures that could be created by proposed silvicultural prescriptions (say "partial retention" or many of the currently popular silvicultural proposals). However, we often have data on individual trees that can be modelled at the tree level of organization. Then, integration of these individual tree predictions by the model produces the desired stand-level information. Or consider the "action" of increasing carbon dioxide in the atmosphere. For some time, cells or seedlings were the only level of organization for which hypotheses of effect were known. Then, models were developed to integrate effects up to the tree level of organization and thence to stand (and world) levels of integration. In the ideal world, we would have both detailed studies of the processes under controlled conditions and field experiments similar to the carbon dioxide enrichment plots in loblolly pine (LaDoau and Clark 2001), but replicated in time and in different ecosystems.

In the easier alternative, the proposed actions and the state variables inherent in the hypotheses of effect have been directly observed in existing data sets, or can be quickly collected. The essential prerequisite is that all relevant hypotheses of effect can be tested with the data. Response surfaces of the processes represented in these data will provide accurate representation of the expected outcomes if the sample data have been collected with procedures supporting valid sampling inferences. Then, use of the model is primarily interpolative among the driving variables. It is essentially an inference tool to extend the sample-based information to estimate how population totals would change under proposed management scenarios (collections of actions).

Temporal structure

Farnham et al. (1986) characterized models as having either yield architecture or growth architecture. The dichotomy depends on whether the models use the integrated or differential representation of processes. Yield architecture uses age as an argument in functions estimating increments or state variables characterizing the vegetation. On the other hand, growth architecture uses initial boundary conditions and differential or finite difference equations to generate the vegetation trajectory through time.

Yield architecture generally produces models with stable, predictable behavior. However, its trajectories are so firmly predetermined that introducing effects of intervening treatment tends to be cumbersome and difficult to justify from a biological process point of view. However, Snowdon (2002) and Pienaar and Rheney (1995) provided examples of yield model structures that permit intervention.

Growth architecture can more easily accommodate physiologically detailed submodels because the developmental process of most vegetation is controlled by rates of production and transport rather than by effects of aging per se. Growth architecture has a risk, however. Estimating development of an individual by the simultaneous application of independently developed submodels may result in biological monstrosities. For example, in the aspen model of Sievänen et al. (1988), some combinations of parameters could produce trees of large diameter having negligible biomass. They demonstrated that strict numerical optimization of parameter estimates must be subservient to overall model behavior.

Growth architecture, in addition to the above considerations, requires time steps that are appropriate for the resolution of the process relations and for the mathematical method of integration being used by the model. If change is expressed as differential equations, then size of the time step must be small enough for the numerical integration method to produce adequate accuracy. If change is estimated by finite difference equations, then time steps must conform to the implicit time interval of the functions used to estimate increment. Cao (2000) developed methods of parameter estimation that permit calibration of tree accretion and mortality models with annual time steps using data from longer periods of varying length. However, in his protocol, all interacting models must be calibrated simultaneously.

Temporal resolution of the model is critical when its use in decision support requires linking separate models of ecosystem components. Again, mixtures and gradations are the rule. Linkages between models can be complicated, if not proscribed, by incompatible temporal span and resolution. For example, Elliot and Hall's (1997) variant of the WEPP watershed erosion model was sensitive to the first several months and years after disturbance of the vegetation, whereas candidate vegetation models used yield architecture to initiate a new stand as it would exist no fewer than 3 years after disturbance (Elliot and Hall 1997).

Stochasticity

All processes can be considered as the sum of two components: one deterministic and the other stochastic. Knowledge of the deterministic component is embodied in the model's functional relations. The stochastic component represents influences beyond our present predictive capability (or deliberately omitted from the model). Inclusion of the stochastic component is important in growth architecture models because many processes operate as deviation amplifiers. Simply put, the big get bigger faster. Any process for which the trend with time is monotonically increasing and concave upward will amplify positive deviations from the average increment more than negative deviations. Therefore, models of increments that are to be executed iteratively must include effects of random variation. Otherwise, the mean and distribution of the final indicators will be biased.

Provides appropriate resolution of predictions with quantified accuracy

An oft-repeated criterion for the choice of a model is that broad policy decisions should be based on models that produce correspondingly approximate (low resolution) estimates of effects. I wish I could find the factual basis for this mantra, for I believe it to be wrong. Most decisions in ecosystem management are nested in the sense that the broad policy decisions inevitably are followed by more localized decisions about more detailed prescriptions. Also, from the biological view, the outcomes of many processes are controlled by extremes of the driving variables rather than by variation near their means. Low-resolution models usually represent mean effects, thereby masking variation significant for planning purposes. For example, if volume of timber removed and sediment production are positively correlated, a strategic plan might reduce the intended cut to reduce the sediment to an acceptable level. More effective planning would use information on size and location of areas where the two effects are less positively correlated so that the sediment target could be achieved with a higher cut.

Contradictions between the models supporting different levels of analysis can create chaos in management and (especially) in fostering acceptance of the analyses by interested parties — managers and their publics. Reviewers of broad, policy-setting plans inevitably ask for more detail about specific locales to interpret what the policy means "on the ground". A brute force solution is to use the more detailed model for both levels. A more sophisticated solution is to use metamodelling (Stage et al. 1995; Urban et al. 1999) or sampling inference (Moeur and Stage 1995).

Certain applications, such as harvest scheduling and inventory updating, need unbiased estimates of current increment. Other decisions such as choosing silvicultural systems are based on gaming, optimization, or economic analysis to find a suite of activities that meets the goals of management. For these decisions, the need for unbiasedness shifts to the differences between alternatives.

Historically, analytical methods for comparing management alternatives have assumed predictions to be deterministic. The accuracy of the estimates has seldom entered analyses in other than a pass–fail mode. A much-used alibi was that planners and managers were uncomfortable with interval estimates. Consequently, early forest growth models represented only the deterministic component. Later, however, models including both the deterministic and stochastic components were developed (e.g., Hatch 1971; Stage 1973; Monserud 1975; Daniels and Burkhart 1975) or the stochastic behavior of the model predictions was modelled explicitly (Stage and Renner 1988; Hamilton 1991). The modellers should break this vicious circle. Indeed, lack of accuracy data for estimates of stand structure was a major point of criticism directed at the California spotted owl draft environmental impact statement.[1]

Accuracy required for a specific decision depends on the costs of improving accuracy in relation to the costs of a wrong decision. (Hamilton 1979). Newberry and Stage (1988) have discussed more details on desirable statistical properties of models of forest dynamics and recurring management decisions.

Absence of artifacts

In the most general sense, models are used in decision support to rank alternatives. Therefore, these ranks must not depend on artifacts produced by the model. In particular, the model structure should not produce artificial discontinuities in what should be smoothly changing state variables. Unfortunately, modellers who use broad classes to represent attributes that are essentially continuous variates often overlook this requirement. For example, the discrete fire behavior fuel models of Anderson (1982), when embedded in a dynamic model for silvicultural gaming, would lead one to create stand structures right at the more favorable side of the discontinuity between fuel models (classes). At that point, the model is most biased so that the expected advantages will not be realized.

Links to real world: environment

Model connections to the environment may be set either at inventory time, or they may interact dynamically with estimates of how factors are expected to change through time. The first class I would call models with a static environment and the second class models with a dynamic environment.

Factors of the environment

Ford and Fraser (1968) have grouped environmental factors affecting growth according to their mode of influence as follows.

(1) Those actually used in the growth process, i.e., photosynthetically active radiation, carbon dioxide, oxygen, water, or nutrients, which can be considered as pools in the environment from which plants draw. How these dynamically changing pools are allocated to individuals in the model depends on the level of organization at which processes are represented and on the resolution at which competition for these pools is modelled.
(2) Those not actually used, but which influence rates, i.e., air or soil temperature, humidity or wind.
(3) Those that operate in the regulation of meristem activity, e.g., day length, temperature, and spectral properties of light.

One class of models requires direct measurement of these factors (driving variables). Often, more easily obtainable surrogates represent the factors, such as latitude for day length, or elevation and aspect for radiation, temperature, and precipitation.

Providing site-specific input of factors affecting growth poses a major impediment to their direct use as driving variables. When the decision space requires site-specific predictions, the input of the growth factors is usually derived as estimates from another model. These estimates add a source of uncertainty that decreases the apparent advantages of the more detailed model architecture.

Another class uses the phytometric approach. Observations on existing vegetation define the integrated effects of

[1] USDA Forest Service, Pacific Southwest Region. 1996. Revised draft environmental impact statement. Managing California spotted owl habitat in the Sierra Nevada National Forests of California. An ecosystem approach.

the factors. For example, the concept of site index uses height of dominant trees as the phytometer. Classifying sites into habitat types as defined by potential vegetation is a phytometric approach at a broader level of organization. In the Rocky Mountains of the western United States, we have found that habitat type, used in conjunction with slope, aspect, elevation, and geographic location, not only indicates conifer productivity but is also crucial to predicting the composition of understory vegetation (Ferguson et al. 1986; Stage 1989). Although readily recognized in the field by observers capable of identifying some 30–40 indicator species, occurrences of habitat types have not been readily predictable from direct measurement of site factors such as precipitation, potential evapotranspiration, soil, and parent material properties. This difficulty suggests that the usefulness of models using biophysical site factors as input to predict occurrence of particular species may be similarly limited.

Of course, when the intended use of the model is to forecast future patterns of vegetation in response to changes in site factors, e.g., global warming or regional cooling, a dynamic-environment model is essential (Neilson and Drapek 1998; Bonan et al. 2003). Again, the design of a management decision model must depend on the alternatives to be evaluated.

Spatial resolution

Models that have no explicit representation of spatial relations are termed point models. Point models represent an average over some neighborhood defined by a limit of within-neighborhood variability. By analogy with terms in geographic information systems, the alternative can be called a polygon model. Polygon models are spatially explicit to some defined level of precision of tree locations within a polygon. Locating sampling points within polygons may bridge the two alternatives.

Representation of trees in spatial relationship to each other has been motivated by the need to represent competition for light, moisture, and nutrients at a finer scale than the stand average. Whether this level of detail adds resolution to the analysis is still in question, although in my opinion, it does in ecosystems that are primarily light limited, although I also believe that exact X,Y coordinates are more precise than the trees' actual occupation of space. In contrast, processes of water uptake in moisture-limited ecosystems permit trees in the same neighborhood, but not physically occupying the same space, to compete for water and nutrients (e.g., Bormann 1957; Wu et al. 1985). Furthermore, some processes such as contagion and diffusion affecting individual trees may act over greater distances than included in most stand models. Analytical integration of spatially structured processes awaits further developments in ecological field theory (Wu et al. 1985; Clark 1990).

In addition, linkage to models of other ecosystem processes, such as a detailed fire spread model, may require spatial distribution of fuels from the vegetation model.

Links to the managed ecosystem (state variables)

Support for use of a model in decision analysis rests in three classes of data. I believe all of these classes must be available without regard for the level of organization of the modelling system. However, the chains of inference between these data and the model will differ, depending on the model's level of organization. The validity of inferences about management effects depends on both the sampling designs (or lack thereof) underlying data collection and the truth of the hypotheses of effect embodied in the model. Hence, model architecture also depends on the kinds of data available from the real world. Model calibration (tuning, to be pejorative) is most likely to produce a well-behaved prediction if the state variables for its level of organization can be directly observed in the field of application. There is, however, a very real risk that statistical zealots will overfit data from case studies and destroy the generality of the model.

The three classes of field data, differing in the methods used to select sample units and in their role in the modelling–decision support system, are as follows.

(1) Inventory data: a random sample of the target population that includes estimates of recent changes (e.g., some inventories).
(2) Treatment effects: a random sample of areas that have received treatments not represented adequately in the population sample, preferably measured to the same standards as (1).
(3) Field laboratories: sites intensively instrumented, with data recorded over periods spanning a substantial range of temporal variation in environmental conditions and stand development.

Inventory data

Models used in decision support have much more stringent requirements for linking to the real world through objective inventory techniques than do models for representing scientific understanding (Landsberg 1981). And even for the latter, the problems of spatial and temporal scaling are substantial (Ehleringer and Field 1992). Whether a model properly represents an effect of management activities can depend on the match between the model structure and the inventory procedures used to initialize its execution. A model calibrated with true values of driving variables will produce biased estimates of effects if there is sampling variation in the initialization of those variables. For example, consider a tree-level, distance-dependent model of the processes of accretion and mortality. The driving variables of the model (e.g., competition, stand density, etc.) are subject to sampling error related to the size of the plot and the sizes of the trees (Schreuder and Williams 1995). This error introduces bias into the parameter estimates. While the plot area is fixed at inventory time, sampling error changes during the projected time because the trees grow larger in relation to plot area. This change introduces bias into the estimates, and the smaller the plot, the larger the bias (Stage and Wykoff 1998).

Often overlooked in the planning process is the need for model-based estimates of state of the ecosystem at inventory time to be in accord with the actual inventory estimates. Discrepancies between these two descriptions of the same world have been the basis for challenging operating plans, at least of some national forests in the United States. Years ago, Bruce (1977) discussed the "fall-down" between modelled yield and the actual yield "over-hill-and-dale". Now, we worry about how much of net primary productivity goes to feed insects and mycorrhizae and to produce seed or defensive chemicals, terpenes, etc. An effective decision support system must include the wherewithal to objectively estimate fall-down. To estimate this fall-down requires data from the real world combined with knowledge of whether differences may be attributable to unique conditions during the period of record.

A major discrepancy between the real world and the model output is attributable to net effects of processes not represented in the model and to interactions among modelled processes assumed to be independent. Models may be designed to estimate maximum potential or realizable yield. Unfortunately, some may be hybrids of both, depending on the sources of data used to estimate parameters. For example, I know the height increment component of Prognosis is devoid of top damage, while the diameter increment submodel is calibrated to random inventory data including some damage.

An oft-cited prerequisite for using models for management analysis is to have "done" model validation (Newberry and Stage 1988; Vanclay and Skovsgaard 1997). Unfortunately, the decision space is seldom the same as the space from which the calibration data were drawn, no matter how careful the original sample inferences. Therefore, I believe that managers should maintain a database having an adequate basis for valid inferences about the biases of candidate modelling systems in their particular decision space. Fortunately, the randomization inherent in inventory data can provide this basis for inference.

The first test of a model of the future is whether it can represent the past. The variables in this database would include the indicators deemed appropriate in analysis of similar management decisions. From this database, a model of the discrepancies between the model output and the current real world would be developed that is specific to the decision space of the proposed analysis (e.g., Zumrawi et al. 2002). Sampling intensity for generating this database must give particular attention to its power attributes. Unlike most modelling, the desired outcomes of statistical tests would be to find all variables to have small and nonsignificant effects. By modelling the bias and error properties of candidate models, analysts could establish at least a lower bound for the uncertainties of the proposed analysis. I say lower bound because, by definition, such a database can represent neither new, untried management actions nor environmental conditions that have not occurred previously. This is the real validation data set.

Data on treatment effects

Inventory data seldom include areas that have received the treatments being considered in the current analysis. If they were well represented, the decision would already be "old hat" and not very interesting. Therefore, an additional data set is needed to evaluate performance of the model for the proposed treatments. This information may be sought from research studies of the intended treatments. However, there are serious drawbacks to that source.

Many, perhaps most, of the extant collections of permanent plots lack the requisite randomization validating treatment effects. Attempts to achieve "representativeness" or to provide a uniform test bed for evaluating management actions can introduce subtle sources of bias. For example, the Inland Empire Tree Nutrition Cooperative at the University of Idaho, Moscow, Idaho, has an impressive number of installations of trials of fertilization. As the process of site location progressed, they noted that they were not finding suitable sites on certain types of soil parent material. Indeed, an intensive search for sites to fill the gap also failed. Wherever the targeted parent material was found, the existing stand was so irregular in age and species mixtures that the location was deemed not suitable for the experimental design. Later analysis of other collections of permanent plots verified that the missing soil parent material type was associated with higher mortality rates, hence, the difficulty of finding uniform stands. Although enticing, the use of the Cooperative's data set for model calibration or validation would be ill advised except for representing the specific treatments studied.

Monitoring data obtained from a suitably randomized selection of treated sites are an essential part of the modelling system. Identifying model failures provides guidance for model evolution. Or alternatively, failure of the treatment to produce the expected results may indicate problems in the execution of the intended treatment. In either case, the data should lead to more effective decisions.

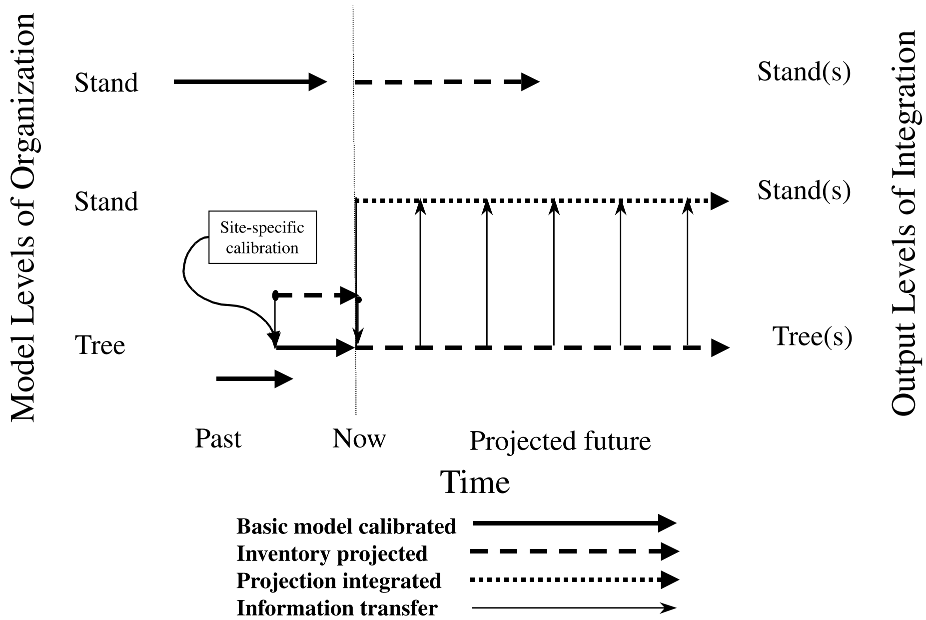
Field laboratories

Models requiring a level of organization that is more detailed than can be observed in routine field sampling still need evaluation at the level of integration specified by the indicators defining the decision space. The requirements for specialized instrumentation to define (and control) the environment and to monitor system responses at the detailed organizational levels preclude randomization as a basis for inference. In its stead, the experimental areas should also include reference areas for which the state variables routinely observed in the inventory are measured at the same spatial resolution.

Inference structures linking models to reality

Let me begin this topic with an illustration from the design of the Prognosis model for stand development as of about 1973. I had recently finished a reconstruction of climatic variation over the past 300+ years as recorded in the growth rings of western white pine (*Pinus monticola* Dougl. ex D. Don), a stint of using the TRAS growth model (Larson and Goforth 1970) to project trends in future inventories and timber supply for the western United States, and an involvement with designing "in-place" inventory procedures for individual-tree prescription in complex stands. From the concatenation of these three efforts, it was clear that growth modelling for both silvicultural decisions and for inventory projection of broad areas should be based on the expectations for individual trees in relation to their environment. Furthermore, effects of the droughts of the 1930s over much of western North America precluded using yield architecture or site index. However, substituting site factors and potential vegetation classes for site index as predictors of productivity

Fig. 1. Two model structures provide stand levels of integration. The upper line represents conventional yield architecture in which the calibration data must span a time interval as long as the maximum period of projection. The lower model representation operates at the tree level of organization using growth architecture with integration to stand-level indicators. Site-specific calibration may improve the accuracy of projections.



left me nervous concerning several questions: how to capture the fact that a particular stand would grow differently if near the ecotone than if in the center of a mapped habitat type and how to capture the effects of long-term trends in weather? My solution for these problems was to program an internal, self-calibration logic that would adjust the accretion submodels to closely match the growth in the immediate past of the inventoried trees. Of course, this facility relied heavily on the ease of measurement of annual rings and whorls for the majority of our species!

Now, shift forward to a 1990 meeting of entomologists, pathologists, and stand modellers sponsored by the Forest Pest Management Branch of the U.S. Forest Service. The workshop objective was to design a model of multiple damaging agents acting in concert. Having produced a growing number of Prognosis extensions for specific pest disturbances (Teck et al. 1996), the workshop participants perceived that to model simultaneous effects of these pests would require a different approach. They concluded that a model of the physiology of individual trees that could indicate “stress” would be required.

As a generalization from these experiences, I propose the following categories to document how models link to the real world and to each other.

Direct experience

Most decisions in forestry relate to actions or environments that are within the scope of our past experience at some level of organization. This perception was the basis for developing yield tables over several centuries. Data from direct experience was the basis for a model in which the level of organization and the level of integration were both the same, usually timber volume per unit area (e.g., upper line in Fig. 1). A limitation of such a model was that the length of the projection could be no greater than the time span of the calibration data. The subject ecosystem was bounded by just the predominant species and two environmental variables, site index and yield class. Environmental effects were integrated over stand lifetimes. The link to time was just advancing age. Thus, I would call the conventional yield table a “direct experience, deterministic, yield architecture point model using phytometric productivity variables: site index and yield class”.

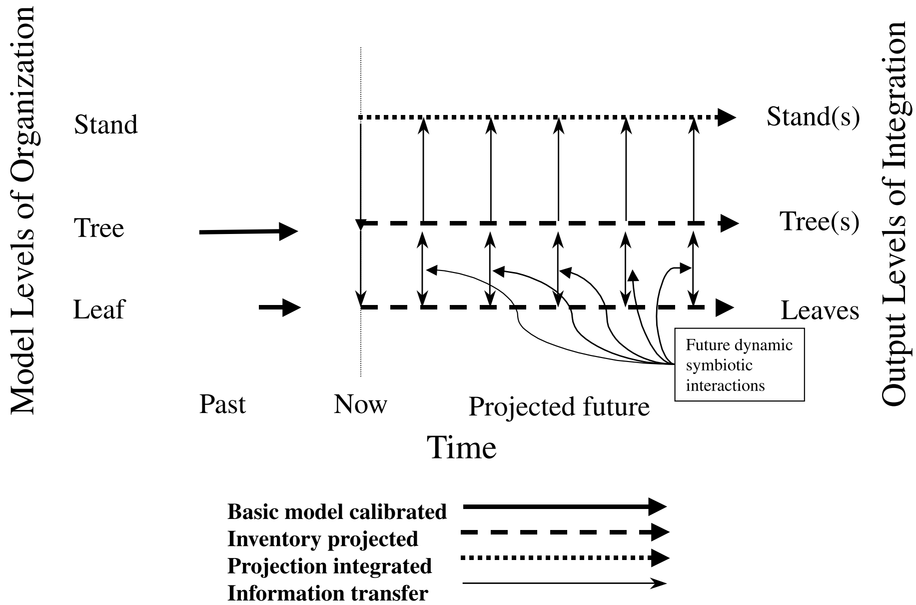
Adding levels of integration

When combinations of species and age-classes were proposed that were not represented by stand data from historical experience, we dropped down an organizational level to trees. At this level, increment data could usually be found for trees growing under diverse relations with their neighbors and in varying age and species mixtures. The mix of ages and species rendered site index a misfit. Consequently, we replaced it with various combinations of potential vegetation, topographic, edaphic, and climatic variables. The choice was dictated by the available data. Munro (1974) aptly classified such a model as an individual-tree stand model, the first part indicating the level of organization and the last part the level of integration.

The lower pair of lines in Fig. 1 represents such a model, operating primarily at the tree level but producing the desired stand-level indicators. Addition of understory vegetation to the mix opened many uses for such models in support of wildlife habitat management decisions and links to models of fire behavior for fuel management decisions.

Although there have been many studies of weather effects on tree increments (e.g., Zahner and Stage 1966; Khatouri and Moore 1993), only a few tree models for decision support use weather variables. The usual rationale is that if we

Fig. 2. Symbiont modelling, combining independent models at two levels of organization, provides a capability for dynamic interaction. Information from the tree-level model is used to initiate the more detailed leaf-level model, assuring a valid link to inventory data and strong integration to stand-level indicators.



must use a "typical" past weather sequence to drive the prediction of the future, there is nothing to be gained over using past experience directly.

Hypotheses of effects of future management and in future environments that are not, and cannot be, represented in past experience such as effects of changing climate have required yet another shift to a more detailed level of organization, the leaf. In this case (Fig. 2), the real world experience is still in the past and often in the laboratory or in highly instrumented field locations such as the Jädraås installation in Sweden used by Troeng and Linder (1982*a*, 1982*b*). Whereas models operating at the tree and stand levels of organization can gain some claim to lack of bias by careful randomization of data collection and use of unbiased estimators in analysis, models at the leaf level are "out on a limb" in this respect. How rates of processes operating at the leaf level may be affected by the complex instrumentation required for observation is not likely to be measurable. Bias in observation of rates of leaf-level processes may be introduced by the complex instrumentation required and by the lack of randomization of sites selected for study.

Models of processes at lower levels of organization often must assume the rates of each process to be independent of other processes operating at that organizational level. Careful representation of scaling relations between levels permits sampling and statistical inference to provide estimates of lower level parameters from data at a higher, field-observable level. For example, in the context of a photosynthesis-based model, Sievänen et al. (1988, 1993) showed the power of statistical analysis to infer process rates and their interactions that are not directly measurable. More recently, Monte Carlo and empirical Bayesian estimation methods have been invoked to combine prior information with particular data sets to estimate distributions of parameters not directly measurable (Mäkelä 1988). Mäkelä and Valentine (2001), however, demonstrated that the same higher level behavior can be obtained from any of three hypothesized alternative relations between lower level models. To resolve such problems of indeterminacy, Reynolds and Ford (1999) described a protocol using multiple criteria to evaluate model behavior.

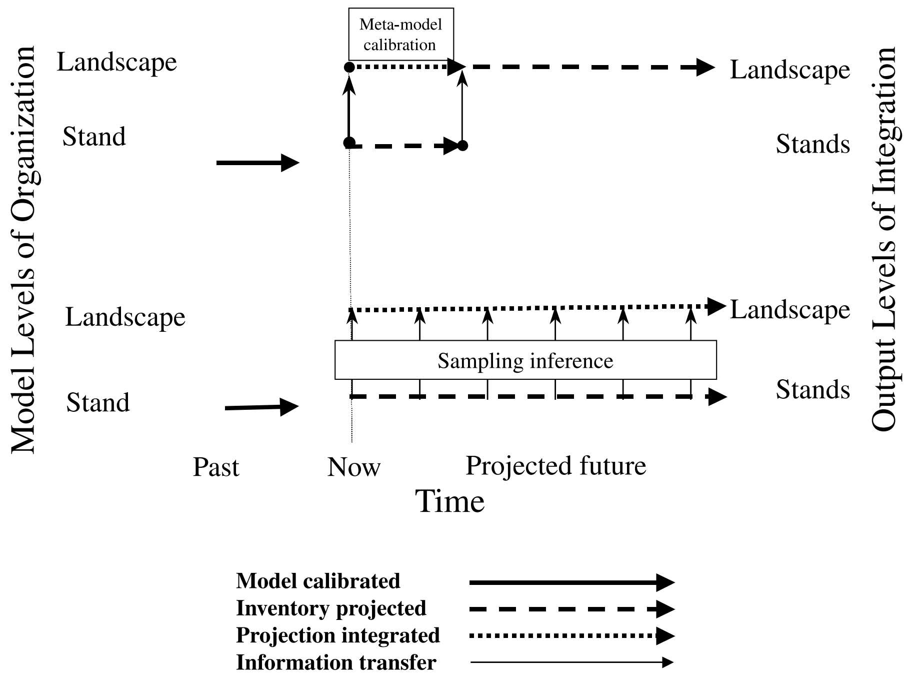
Moving upward in levels of integration has definite risks. Cumulative effects of changes at the lower level may so control processes operating at the lower level that the system changes its overall behavior. The consequence may be that the model will be incapable of representing loss of resilience or other emergent attributes of the system.

Site-specific calibration

A basic tenant of forecasting for nonstationary systems is that the immediate past is the best estimate of the immediate future. Periodic inventory data can be used in conjunction with model-based estimates for the same period to scale the immediate future to the past through estimates that differ only in response to changes in driving variables (Stage 1981). Figure 1 illustrates the data flow to introduce greater site specificity into the tree-level projection. Such "self-calibration" is a special case of the more general use of partially specified models (Wood 2001). Furthermore, average values of the calibration factors can be used to localize projections to the particular subpopulation of the ecosystem represented in the original model calibration (Zumrawi et al. 2002).

Total reliance on the sample of current increments would ignore effects of transient factors not represented in the model. In addition, statistical theory holds that performance of sample estimators can be improved by "shrinkage toward the population mean" (James and Stein 1961; Lindley and Smith 1972). Therefore, Prognosis uses multiplicative adjustments to the underlying accretion models that start at an arbitrary half of the indicated adjustments and attenuate ex-

Fig. 3. Data to calibrate models at the landscape level of organization are seldom available, and simple integration of component stand projections may not be computationally feasible. Sampling inference from a designed inventory of sample stands (lower representation) may be used if contagious processes are not hypothesized. Metamodelling (upper representation) permits landscape-level processes to be represented.



ponentially through the course of the subsequent projection (Wykoff et al. 1982).

Metamodelling

Allen and Starr (1982) suggested that, for reasons of practicality, models should not span more than three levels of organization. However, not all decision spaces can be so confined. One approach to the need for modelling landscapes is to capture the essential behavior of lower level models in analytical or tabular forms. These models derived from models are then used to represent the system at a larger scale. In this way, model behavior at the lower level can be used in lieu of data from direct experience to formulate and calibrate the higher level models. For example, Nguyen (1990) constructed a metamodel of Prognosis. The difficulty of that exercise lay in capturing the nuances of species composition and diameter distribution of removals in the partial harvest scenarios. Another option to generate indicators at levels of integration higher than the model's level of organization is to use sampling inference to estimate their distributions (lower representation in Fig. 3). Urban et al. (1999) provided examples of several variants of the metamodelling scheme represented by the upper pair of lines in Fig. 3. Again, the procedures for partially specified models (Wood 2001) seem relevant to their expressed need for systematic approaches to parameterization of the metamodel.

Symbiont modelling

Two models that represent the same system at different levels of organization offer the possibility of being linked to capitalize on their respective strengths. During the early development of Prognosis, we had little experience with tree models. Therefore, I was concerned that long projections summing individual tree estimates would assume away critical information by generating stand variables from a simple aggregation of tree variables. The estimates would ignore effects not represented realistically by the equation forms of the individual tree submodels. Information about these discrepancies should be implicit in stand records of our long-term permanent plots, if only we had enough of them to build a stand-level model for complex forests. Accordingly, I postulated a stand-level model operating in parallel with the individual tree model, with information passing both ways at each time step. Three 10-year periods were postulated as sufficient to estimate first- and second-degree temporal effects, at which point the individual tree model would be shut down and long-range projections produced by the internally recalibrated stand model. Unfortunately, the stand-level model was never built, and the 30-year limit quickly disappeared along with the internal provision for the linked stand model.

The recommendation of the Forest Pest Management Branch workshop lay dormant until 2000 when Kelsey Milner (see Milner et al. 2003) undertook the task of linking his leaf – individual-tree, distance-independent model to the expanded version of the Prognosis model for stand development (Teck et al. 1996). His immediate motivation was to be able to use the highly developed and supported links to inventory methods for initiating the model and representing regeneration and to use the powerful methods for simulating management and controlling model parameters contained in Crookston's (1990) Event Monitor. In the working version (Milner et al. 2003), both sets of models of the accretion and mortality processes are executed in parallel with the capability to interact at arbitrary intervals in the simulation (Fig. 2).

Our present challenge is to develop cross-links at each time step so that a stronger synergism results. It would seem that the strong sampling basis, including the self-calibration capability, of the accretion components in the tree-level model could help overcome the sampling inference deficiencies of the physiological data (Baldwin et al. 2001). Conversely, the indicators of physiological functioning could add resolution to the modelling of pest effects and their interactions with environmental driving variables.

Combination of symbiont modelling with metamodelling would address the problem of cumulative effects operating at landscape and larger scales. The missing landscape-level processes would be added to the metamodel representation of the lower level model to create a model at the landscape level of organization.

Evaluating strength of links to reality

One objective of this discussion of models for use in comparing management alternatives was to search for objective ways to evaluate and improve the strength of potential models or combinations of models for analysis of management alternatives. Accuracy of model forecasts depends on the accuracy of the inventory-based input data, the spatial and temporal variability of the driving environmental variables, as well as on the stochasticity imbedded in the model.

Gregg and Hummel (2002) have provided software to estimate how sampling variation in inventory data propagates through the Forest Vegetation Simulator. Error budgeting addresses the propagation of error attributable to parameter uncertainty within a model and to uncertainty in driving variables (Gertner 1987). Unfortunately, that procedure requires information on the correlation of parameter variation, information seldom available unless the parameters have been simultaneously estimated. Other, also computationally intensive methods to assess uncertainty have been developed (e.g., Green et al. 1999; Guan 2000; Fang et al. 2001).

To scale between levels of organization, Norman (1992) suggested evaluating various scaling schemes against the (more) detailed model. Perhaps symbiont modelling provides an objective and efficient framework for such an evaluation. Coupled with site-specific calibration in highly instrumented installations, the inference process can proceed in both directions.

The preceding analysis methods become very cumbersome when all sources of uncertainty are considered. In final analysis, data obtained from long-term field observation are the standard for assessing model uncertainties. These methods could be combined with analyses of the modelling of spatial and temporal correlations among projection errors (Stage and Renner 1988) to provide error estimates at the ecosystem level.

Summary

That a model used in decision support must span the decision space, in representation of effects of proposed actions on selected indicators, in ecological scope, and with assumptions appropriate to the cybernetic context of the decisions, should be a tautology. Unfortunately, not all model architectures have been designed with these constraints in view. Models used in decision support require a firm foundation in science and should produce predictions with quantified bias and precision and that are free of artifacts that confound choice of management alternatives.

Current classifications of models are not well suited to choosing a model to use in decision analysis. Diversity among extant models is so great that careless classification by a few imprecise adjectives is counterproductive. As a minimum, model descriptions should include the level of organization at which its processes are represented, the level of integration of its indicators of the ecosystem, how the model represents time and space, its links to the environment including the ecosystems represented, and its treatment of stochasticity. Each of these model attributes is needed to evaluate the suitability of a candidate model for decision support. Perhaps with these descriptors tabulated, a classification specialist might find some natural clusters. I doubt it.

Validity of model-based evaluations of management alternatives rests on the strengths of their inferential links to the real world. Sample inventory data are inferred to the managed population through statistical inference. Hypothesized effects of management actions are imputed to members of the managed population through physiological inferences. If either science is slighted, model predictions are suspect. However, by combining dynamic calibration of model estimates to field data with dynamic interactions between models of the same ecosystem at different levels of organization, the usefulness of the estimates for decision-making may be improved.

Data from a randomized inventory of the target population should be used to construct a model of the bias inherent in the predictions. Variables significant in this model of differences between the model and the real world define the unknowns in the model–ecosystem relations. Understanding the limits of our knowledge may be a deciding factor in the decision process. Continuous updating of this bias model and the insight it provides is the real contribution of ecosystem monitoring to management of forested ecosystems and to the further evolution of modelling systems capturing this new knowledge.

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References

Allen, T.F.H., and Starr, T.B. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Ill.

Anderson, H.E. 1982. Aids to determining fuel models of wildland fire behavior: a user's manual. U.S. For. Serv. Gen. Tech. Rep. INT-122.

Baldwin, V.C., Burkhart, H.E., Westfall, J.A., and Peterson, K.D. 2001. Linking growth and yield and process models to estimate impact of environmental changes on growth of loblolly pine. For. Sci. **47**: 77–82.

Blake, J.I., Somers, G.L., and Ruark, G.A. 1990. Perspectives on process modeling of forest growth responses to environmental stress. *In* Process modeling of forest growth responses to environmental stress. *Edited by* R.K. Dixon, R.S. Meldahl, G.A. Ruark, and W.G. Warren. Timber Press, Portland, Oreg. pp. 9–17.

Bonan, G.B., Levis, S., Sitch, S., Vertenstein, M., and Oleson, K.W. 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamic. Global Change Biol. In press.

Bormann, F.H. 1957. Moisture transfer between plants through intertwined root systems. Plant Physiol. **32**: 48–55.

Bruce, D. 1977. Yield differences between research plots and managed forests. J. For. **75**: 14–17.

Cao, Q.C. 2000. Prediction of annual diameter growth and survival from periodic measurements. For. Sci. **46**: 127–131.

Clark, J.S. 1990. Integration of ecological levels, individual plant growth, population mortality and ecosystem processes. J. Ecol. **78**: 275–299.

Crookston, N.L. 1990. User's guide to the Event Monitor: part of Prognosis model version 6. U.S. For. Serv. Gen. Tech. Rep. INT-275.

Daniels, R.F., and Burkhart, H.E. 1975. Simulation of individual tree growth and stand development in managed loblolly pine plantations. VPI&SU Sch. For. Wildl. Resours. FWS-5-75.

Ehleringer, J.R., and Field, C.B. (*Editors*). 1992. Scaling physiological processes: leaf to globe. Academic Press, San Diego, Calif.

Elliot, W.J., and Hall, D.E. 1997. Water Erosion Prediction Project (WEPP) forest applications. U.S. For. Serv. Gen. Tech. Rep. INT-365.

Fang, S., Gertner, G., and Price, D. 2001. Uncertainty analyses of a process model when vague parameters are estimated with entropy and Bayesian methods. J. For. Res. **6**: 13–19.

Farnham, P., Lembersky, M.R., and Hyink, D.M. 1986. Use and interpretation of forest growth models for decision making. *In* Douglas-fir: stand management for the future. *Edited by* C.D. Oliver, D.P. Hanley, and J.A. Johnson. Institute of Forest Resources, University of Washington, Seattle, Wash. pp. 337–343.

Ferguson, D.E., Stage, A.R., and Boyd, R.J. 1986. Predicting regeneration in the grand fir – cedar – hemlock ecosystem of the northern Rocky Mountains. For. Sci. Monogr. 26.

Ford, E.D., and Fraser, A.I. 1968. The concept of actual and potential production as an aid to forest management. Forestry, **41**: 175–181.

Gertner, G.Z. 1987. Approximating precision in simulation projections: an efficient alternative to Monte Carlo methods. For. Sci. **33**: 230–239.

Green, E.J., MacFarlane, D.W., Valentine, H.T., and Strawderman, W.E. 1999. Assessing uncertainty in a stand growth model by Bayesian synthesis. For. Sci. **45**: 528–538.

Gregg, T.F., and Hummel, S. 2002. Assessing sampling uncertainty in FVS projections using a bootstrap resampling method. *In* Second Forest Vegetation Simulator Conference, 12–14 Feb., 2002, Fort Collins, Colo. *Compiled by* N.L. Crookston and R.N. Havis. U.S. For. Serv. Proc. RMRS-P-25. pp. 164–167.

Guan, B.T. 2000. Effects of correlation among parameters on prediction quality of a process-based forest growth model. For. Sci. **46**: 269–276.

Hamilton, D.A., Jr. 1979. Setting precision for resource inventories: the manager and the mensurationist. J. For. **77**: 667–670.

Hamilton, D.A., Jr. 1991. Implications of random variation in the Stand Prognosis Model. U.S. For. Serv. Res. Note INT-394.

Hatch, C.R. 1971. Simulation of an even-aged red pine stand in northern Minnesota. Ph.D. thesis, University of Minnesota, St. Paul, Minn. [University Microfilm 72-14, 314.]

Holling, C.S. (*Editor*). 1978. Adaptive environmental assessment and management. Wiley IIASA international series on applied systems analysis. John Wiley & Sons, New York.

James, W., and Stein, C. 1961. Estimation with quadratic loss. Proc. 4th Berkeley Symp. Math. Stat. Prob. **1**: 361–379.

Khatouri, M., and Moore, J.A. 1993. Climatic variation affects growth and mortality more in unmanaged ponderosa pine plots compared to managed plots. Internal report, College of Forest, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho.

LaDoau, S.L., and Clark, J.S. 2001. Rising CO_2 levels and the fecundity of forest trees. Science (Washington, D.C.), **292**: 95–98.

Landsberg, J.J. 1981. The number and quality of driving variables needed to model tree growth. Stud. For. Suec. **160**: 43–50.

Larson, R.W., and Goforth, M.H. 1970. TRAS: a computer program for the projection of timber volume. U.S. Dep. Agric. Agric. Handb. 377.

Lindley, D.V., and Smith, A.F.M. 1972. Bayes estimates for the linear model. J. R. Stat. Soc. Ser. B, **34**: 1–41.

Mäkelä, A. 1988. Parameter estimation and testing of a process-based stand growth model using Monte Carlo techniques. *In* Forest Growth Modelling and Prediction: Proceedings of the IUFRO Conference, 23–27 Aug. 1987, Minneapolis, Minn. *Edited by* A.R. Ek, S.R. Shifley, and T.E. Burk. U.S. For. Serv. Gen. Tech. Rep. NC-120. pp. 315–322.

Mäkelä, A., and Valentine, H.T. 2001. The ratio of NPP to GPP: evidence of change over the course of stand development. Tree Physiol. **21**: 1015–1030.

Milner, K., Smith, E.L., and McMahan, D. 2003. FVSBGC, a dual resolution hybrid model with physiological and biometrical growth engines. Can. J. For. Res. **33**. This issue.

Moeur, M., and Stage, A.R. 1995. Most Similar Neighbor: an improved sampling inference procedure for natural resource planning. For. Sci. **41**: 337–359.

Monserud, R.A. 1975. Methodology for simulating Wisconsin northern hardwood stand dynamics. Ph.D. thesis, University of Wisconsin-Madison, Madison, Wis. [University Microfilm 76-2496.]

Munro, D.D. 1974. Forest growth models — a prognosis. *In* Growth models for tree and stand simulation. *Edited by* J. Fries. Royal College of Forestry, Stockholm. For. Res. Note 30. pp. 7–21.

Neilson, R.P., and Drapek, R.J. 1998. Potentially complex biosphere responses to transient global warming. Global Change Biol. **4**: 505–521.

Newberry, J.D., and Stage, A.R. 1988. Validating forest growth models: procedures defined by resource decisions. *In* Forest Growth Modelling and Prediction: Proceedings of the IUFRO Conference, 23–27 Aug. 1987, Minneapolis, Minn. *Edited by* A.R. Ek, S.R. Shifley, and T.E. Burk. U.S. For. Serv. Gen. Tech. Rep. NC-120. pp. 786–793.

Nguyen, C.T. 1990. A metamodel for the Stand Prognosis Model. Ph.D. dissertation, University of Idaho, Moscow, Idaho.

Norman, J.M. 1992. Scaling processes between leaf and canopy levels. *In* Scaling physiological processes: leaf to globe. *Edited by* J.R. Ehleringer and C.B. Field. Academic Press, San Diego, Calif. pp. 41–76.

Pienaar, L.V., and Rheney, J.W. 1995. Modeling stand level growth and yield response to silvicultural treatments. For. Sci. **41**: 629–638.

Reynolds, J., and Ford, E.D. 1999. Multi-criteria assessment of ecological process models. Ecology, **80**: 538–553.

Running, S.W., and Coughlan, J.C. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. Ecol. Model. **42**: 125–152.

Schreuder, H.T., and Williams, M.S. 1995. Assessing measures of tree competition using fixed-area, variable-radius, and horizontal-line sampling. Can. J. For. Res. **25**: 1578–1582.

Sharpe, P.J.H. 1990. Forest modeling approaches: compromises between generality and precision. *In* Process modeling of forest growth responses to environmental stress. *Edited by* R.K. Dixon, R.S. Meldahl, G.A. Ruark, and W.G. Warren. Timber Press, Portland, Oreg. pp. 180–190.

Sievänen, R., and Burk, T.E. 1993. Adjusting a process-based growth model for varying site conditions through parameter estimates. Can. J. For. Res. **23**: 1837–1851.

Sievänen, R., Burk, T.E., and Ek, A.E. 1988. Parameter estimation in a photosynthesis-based growth model. *In* Forest Growth Modelling and Prediction: Proceedings of the IUFRO Conference, 23–27 Aug. 1987, Minneapolis, Minn. *Edited by* A.R. Ek, S.R. Shifley, and T.E. Burk. U.S. For. Serv. Gen. Tech. Rep. NC-120. pp. 345–352.

Snowdon, P. 2002. Modeling Type 1 and Type 2 growth response in plantations after application of fertilizer or other silvicultural treatments. For. Ecol. Manage. **163**: 229–244.

Stage, A.R. 1973. Prognosis model for stand development. U.S. For. Serv. Res. Pap. INT-137.

Stage, A.R. 1981. Use of self-calibration procedures to adjust general regional yield models to local conditions. *In* Proceedings, XVII IUFRO World Congress, 6–12 Sept. 1981, Kyoto, Japan. S4.01. Mensuration, growth and yield. pp. 365–375.

Stage, A.R. 1989. Utility of vegetation-based land classes for predicting forest regeneration and growth. *In* Proceedings — Land Classification Based on Vegetation: Applications for Resource Management, 17–19 Nov. 1987, Moscow, Idaho. *Compiled by* D.E. Ferguson, P. Morgan, and F.D. Johnson. U.S. For. Serv. Gen. Tech. Rep. INT-257. pp. 180–185.

Stage, A.R., and Renner, D.L. 1988. Comparison of yield-forecasting techniques using long-term stand histories. *In* Forest Growth Modelling and Prediction: Proceedings of the IUFRO Conference, 23–27 Aug. 1987, Minneapolis, Minn. *Edited by* A.R. Ek, S.R. Shifley, and T.E. Burk. U.S. For. Serv. Gen. Tech. Rep. NC-120. pp. 810–817.

Stage, A.R., and Wykoff, W.R. 1998. Adapting distance-independent forest growth models to represent spatial variability: effects of sampling design on model coefficients. For. Sci. **44**: 224–238.

Stage, A.R., Hatch, C.R., Rice, T.M., Renner, D.L., and Korol, J. 1995. Calibrating a forest succession model with a single-tree growth model: an exercise in meta-modelling. *In* Recent Advances in Forest Mensuration and Growth and Yield Research. Proceedings from 3 Sessions of Subject Group S4.01 “Mensuration, growth and yield” at the 20th World Congress of IUFRO, 6–12 Aug. 1995, Tampere, Finland. *Edited by* J.P. Skovsgaard and H.E. Burkhart. Danish Forest and Landscape Research Institute, Hoersholm, Denmark. pp. 194–209.

Teck, R., Moeur, M., and Eav, B. 1996. Forecasting ecosystems with the Forest Vegetation Simulator. J. For. **94**: 7–10.

Troeng, E., and Linder, S. 1982*a*. Gas exchange in a 20-year-old stand of Scots pine. I. Net photosynthesis of current and one-year-old shoots within and between seasons. Physiol. Plant. **54**: 7–14.

Troeng, E., and Linder, S. 1982*b*. Gas exchange in a 20-year-old stand of Scots pine. II. Variation in net photosynthesis and transpiration within and between trees. Physiol. Plant. **54**: 15–23.

Urban, D.L., Acevedo, M.F., and Garman, S.L. 1999. Scaling fine-scale processes to large-scale patterns using models derived from models: meta-models. *In* Spatial modeling of forest landscape change: approaches and applications. *Edited by* D.J. Mladenoff and W.L. Baker. Cambridge University Press, New York. pp. 70–98.

Vanclay, J.K., and Skovsgaard, J.P. 1997. Evaluating forest growth models. Ecol. Model. **98**: 1–12.

Wood, S.N. 2001. Partially specified ecological models. Ecol. Monogr. **71**: 1–25.

Wu, H., Sharpe, P., Walker, J., and Penridge, L. 1985. Ecological field theory: a spatial analysis of resource interference among plants. Ecol. Model. **29**: 215–243.

Wykoff, W.R., Crookston, N.L., and Stage, A.R. 1982. User’s guide to the stand prognosis model. U.S. For. Serv. Gen. Tech. Rep. INT-133.

Zahner, R., and Stage, A.R. 1966. A procedure for calculating daily moisture stress and its utility in regressions of tree growth on weather. Ecology, **47**: 64–74.

Zumrawi, A.-A., Stage, A.R., and Snowdon, B. 2002. Stand-level scaling of a single-tree, distance-independent, diameter-growth model: interim calibration of Prognosis for the southeastern interior of British Columbia. *In* Second Forest Vegetation Simulator Conference, 12–14 Feb. 2002, Fort Collins, Colo. *Compiled by* N.L. Crookston and R.N. Havis. U.S. For. Serv. Proc. RMRS-P-25. pp. 151–157.