DEVELOPING THE NEXT GENERATION OF FOREST ECOSYSTEM MODELS

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ABSTRACT.—Forest ecology and management are model-rich areas for research. Models are often cast as either empirical or mechanistic. With evolving climate change, hybrid models gain new relevance because of their ability to integrate existing mechanistic knowledge with empiricism based on causal thinking. The utility of hybrid platforms results in the combination of mensurational and physiological outputs and model routines. We present model precepts for constructing a hybrid model able to accommodate climate change and schematic examples of hybrid submodules for biomass to dimension conversion, light interception, photosynthesis, and soil water.

Forest growth and change models have a long and rich history of development. For example, Kickert and others (1999) discussed approximately 125 predictive models of all types in the context of global climate change. The Register of Ecological Models, a Web-based meta-database maintained at the University of Kassel, Germany (http://eco.wiz.uni-kassel.de/ecobas.html), indexes 632 models, both empirical and mechanistic, used in forestry, agroforestry, and agriculture. Similarly, Leary (1989) discussed nine unique frameworks used to model the growth of a single tree species, red pine (*Pinus resinosa)*, in the Great Lakes region of the United States. The development of modeling frameworks in forestry has been encouraged by the need to combine complex biological information (Johnsen and others 2001), particularly in the context of evolving climate change (Goudriaan and others 1999). A steady increase in computing power and software has supported this trend by providing the tools for sophisticated model construction. Furthermore, the investment in modeling efforts underscores the importance of numerical, predicative models as tools to evaluate the effect of anthropogenic climate change on forest ecosystems (Friend and others 1997).

Despite this proliferation of models, climate change is not adequately accommodated in the current generation of forest growth simulators. Shortcomings concern model construction (Clark and others 2001) and climate change response potential (Schwalm and Ek 2001). Similarly, the dichotomy of empirical versus mechanistic models is also a shortcoming. The former issue is treated in Kickert and others (1999), Kley and others (1999), and Schwalm and Ek (2001). This paper concentrates on model design that bridges the gap between empirical and mechanistic methods in the context of individual tree level models. Specifically, the paper has the following objectives: (i) to establish the relevance of a hybrid modeling philosophy, (ii) to offer design precepts that allow the construction of an individual tree growth simulator responsive to the boundary conditions that define anthropogenic climate change, and (iii) to present a schematic discussion of hybrid submodules to demonstrate the utility of the approach.

THE RELEVANCE OF A HYBRID MODEL

Before design precepts are discussed in general, the relevance of a modeling framework based on both empirical and mechanistic methods, a hybrid model, must be established. The concept includes not only improving the utility of empirical models, but also improving primarily mechanistic models (Mäkelä and others 2000). Ultimately, this relevance is grounded in improved model flexibility and utility and the inability of solely empirical frameworks to accommodate climate change.

Climate Change

Solely empirical frameworks are incapable of accommodating climate change. By definition, climate change encompasses a

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change in boundary conditions that govern tree growth (sensu Kellomäki and Väisänen 1997). Mechanistic models use parameters with biological interpretability, and models are driven by the very boundary conditions that climate change will modify. On the other hand, empirical models use coefficients as generated by some notion of statistical fit devoid of causal thinking. Consequently, such parameters encapsulate the effect of past climate on tree growth without any formal link to climatological variables (Korzukhin and others 1996, Mäkelä and others 2000). Thus, the climatic information embedded in a calibration data set used to generate coefficients (e.g., Forest Vegetation Simulator: Van Dyck 2001) has become outdated and obsolete and cannot be expected to accurately predict climate change.

Changing Currencies

Assuming that the ecological and physiological interdependencies between tree growth and tree environment have been properly specified and parameterized, another failing of the current crop of forest growth models is their inability to interface with operational considerations (cf. Johnsen and others 2001). Mechanistic modeling logic is ultimately in terms of kilograms of dry matter (e.g., C_3 biochemical model of assimilation developed by Farquhar and co-workers [De Pury and Farquhar 1997, Farquhar and others 1980]). Nonetheless, characterizing the structure of a given forest requires more than the amount of biomass in each tree compartment. Forest structure (e.g., diameter class distribution) requires dimension. It follows that a forest growth simulator must offer a means to change from the currency of mechanistic algorithms (kilograms of dry matter) to dimension (feet or meters). Additionally, the overall utility of a modeling framework would be enhanced by provision for mensurational as well as physiological output.

A corollary of this results in a model design where typical forest inventory data can be used to initialize a mechanistic model. Typically, field plot data are based on classic mensurational observations concerned with the physical dimension of individual trees rather than kilograms of dry matter. As such, the need for switching between physical dimensions and kilograms of dry matter is omnipresent. Mechanistic models require that a tree be compartmentalized into various component pools of carbon for initialization. However, an accurate determination of plant carbon distribution is impossible without destroying the specimen. This forces the use of allometric relationships (e.g., Ter-Mikaelian and Korzukhin 1997).

Silvicultural Prescriptions

Operational models typically simulate the effects of silvicultural manipulations (e.g., Forest Vegetation Simulator: Van Dyck 2001). However, the current dichotomy between empirical models and mechanistic models is such that the latter rarely provide for silviculture prescriptions. In other words, thinnings are realized by some function of traditional mensurational variables (e.g., diameter at breast height). When a model is designed to be used both in an operational as well as a research context, a net gain results in terms of model utility. The framework is driven by a mechanistic growth engine but is also amenable to the vast amount of thinning algorithms that require dimension.

Knowledge Gaps

To design a model able to accommodate climate change requires that the same model be based on process where possible. However, mechanistic modeling logic is not an end to itself. The inclusion of unified, physiology based formulations is obvious when they exist (e.g., photosynthesis: De Pury and Farquhar 1997, Farquhar and others 1980). In the case of gross and net productivity, carbon allocation and competition, regeneration and mortality (Mäkelä and others 2000 and references within), and stomatal conductance (Campbell and Norman 1998), such unified mathematical treatments do not exist. In the absence of such algorithms, robust and/or climate-driven empirical relationships are required, e.g., stomatal conductance as modeled via reduction factors (Chen and others 1999) or soil water holding capacity as a function of texture (Cosby and others 1984, Kimball and others 1997). This has the advantage of reducing the number of parameters needed for model initialization as well as incorporating existing, albeit descriptive, knowledge of a particular process.

In the end, a hybrid model serves to join mechanistic and empirical philosophies to offset a lack of knowledge of key physiological processes. Simultaneously, the range of applicability of the model itself is enhanced by allowing an interface with silvicultural routines and traditional mensurational output. A reduction in the number of parameters needed is also realized by using empiricism in controlled instances.

DESIGN PRECEPTS

The modeling approach suggested here addresses the lack of an individual tree level model driven by climate and responsive to changing boundary conditions (i.e., climate change). The design philosophy is based on two principles. First, the environmental drivers that influence forest growth in nature must be the same as those that drive model output. As much as possible, the driving variables of the model are climatic (sensu climate change), including ambient concentration of relevant gases (e.g., CO_2 and O_3) (Bossel 1991, 1996). The goal is to obviate, as much as possible, the need for model calibration and to generate model outputs that are devoid of predeter-mined statistical relationships (Friend and others 1997). Second, models should be accessible to both operational forest management professionals and researchers. The net result is a modeling framework that is hybrid in nature. Empirical relationships are used to effect thinnings, produce mensurational output, and initialize the model (i.e., field plot data). Furthermore, physiological processes are replaced with robust, climate-driven empirical relationships where mechanistic algorithms are yet undeveloped or require infeasible parameterizations (Mäkelä and others 2000).

In sum, the design philosophy aims to bridge the gap between empirical models and mechanistic models (Korzukhin and others 1996, Mäkelä and others 2000) and to accommodate climate change while requiring only basic meteorological and forest inventory data for initialization. The issue of model resolution or scale, both temporal and spatial, is of prime importance. Its interplay with physiology results in different model formulations of the same underlying process across temporal and spatial gradients (e.g., transpiration: Jarvis and McNaughton 1986, photosynthesis: Chen and others 1999). We assume that the tree is the fundamental unit of prediction with ecophysiological processes, e.g., photosynthesis and transpiration, modeled for a specific tree. In other words, as the simulation progresses, tree-level attributes are updated whereas stand-level attributes emerge (i.e., emergent properties). A daily time step is used to capture seasonal variation in accordance with available meteorological data (Waring and Running 1998) with diurnal variation subsumed into relevant algorithms or accounted for using idealized daily patterns (e.g., the use of sine functions to characterize radiation loads over the course of a day).

MODEL CONSTRUCTION

Constructing a model that incorporates the above specified design philosophy is challenging. Various realizations are possible, depending upon the ultimate use of the model. To illustrate, four submodules will be discussed that incorporate this philosophy: biomass to dimension, light interception, photosynthesis, and hydrology.

Biomass to Dimension

A hybrid model can be thought of as a mechanistic growth engine sandwiched between biomass equations. The modeling framework must provide a means to convert from dimension to dry matter mass. This is typically accomplished using empirical relationships based on tree allometry and the pipe model theory (i.e., physio-allometric relationships: Mäkelä 1997). At the beginning of each simulation, dimension is converted to biomass to initialize various carbon pools as dictated by the model's structure. This includes the conversion of foliage mass to leaf area via specific leaf area values and ultimately leaf area index (Waring and Running 1998). When biomass is to be converted to dimension—for example, in the context of report writing—the same equations are used in reverse, i.e., by switching explanatory and response variables. Statistically speaking, transforming such equations is not without compromise. However, we have been unable to find biomass equations that compute dimension from compartment biomass.

Light Interception

Modeling light interception is a less trivial exercise. Several approaches are seen in forestry modeling. These range from multilayered three dimensional treatments where each tree crown has an idealized geometric shape (e.g., Stand-BGC: Milner and Coble 1995; Hybrid v3.0: Friend and others 1997) to so-called “big leaf” models where the canopy is mathe-matically defined as a single photosynthetic surface (e.g., Biome-BGC: Kimball and others 1997; Forest 5: Robinson 1998). Superimposed on the issue of spatiality is the partitioning of diffuse and direct beam light and their relationships to sunlit and shaded leaf irradiance. The differential response of sunlit and shaded leaves to increased CO_2 (Ågren and others 1991, Campbell and Norman 1998, Goulden and others 1997) highlights the importance of partitioning leaf area as well.

An approach that incorporates the above considerations is based on the relationship between diurnal temperature range and ambient temperature as discovered by Bristow and Campbell (1984) and refined by Thornton and Running (1999). Here, daily total transmittance (T_t) is calculated as a function of common meteorological variables, sun-earth geometry, the solar constant, and rainfall. T_t is then used to attenuate the solar constant through the atmosphere. Radiation is partitioned according to an empirical function of daily total transmittance (Gates 1980, Thornton and others 2000). Irradiance on sunlit and shaded leaves (Norman 1982) is then a function of direct beam versus diffuse light, foliage clumping indices (corrected for crown ratio), zenith angle at solar noon, and leaf area index in both shaded and sunlit. The only parameters required are those concerning foliage clumping indices, and these can be readily gleaned from the literature (e.g., Campbell and Norman 1998, Chen 1996, Chen and others 1997).

Photosynthesis

A natural choice for mechanistic models is the Farquhar C_3 model of biochemical assimilation (De Pury and Farquhar 1997, Farquhar and others 1980). Although Farquhar's model was originally developed for instantaneous net assimilation at the leaf level (Farquhar and others 1980), it has been scaled temporally and with curvature corrections (cf. Kellomäki and Väisänen 1997). Chen and others (1999) integrated Farquhar's original model over a day while incorporating sunlit and shaded components of photosynthesis as specified above. This assumes idealized leaf geometry, diurnal patterns in radiation, temperature, and photosynthesis that enable integration with respect to stomatal conductance. Stomatal conductance is a function of a maximum theoretical value and common meteorological variables embedded in modifiers. Net daily assimilation is then a function of well-defined parameters readily available in the literature, daily temperature, precipitation, stomatal conductance, ambient CO_2 and O_3, and soil water potential. Site nutrient status, via foliar nitrogen, can also be incorporated if desired.

Hydrology

Given the heterogeneity of the soil resource, a portable mathematical description of soil hydrology is difficult to realize (Johnsen and others 2001). Mechanistic soil hydrology models typically require detailed knowledge of the pedon and extensive parameterizations, often involving processes seldom measured (e.g., NuCM: EPRI 1993; ACIDIC: Kareinen and others 1998). A mechanistic treatment of water dynamics is often impractical. An approach that dovetails with the above submodules is that used in Biome-BGC (Kimball and others 1997) and Stand-BGC (Milner and Coble 1995). The BGC approach is based on statistical relationships formulated by Cosby and others (1984) with regression equations used to determine soil water potential based on soil texture. All intermediate quantities such as volumetric water at saturation are functions of soil texture as well. Plant available water in totality is a function of soil texture, rooting depth, and precipitation. Total plant available water is abstracted into a water bucket with the amount of water available to a particular tree linked to the ratio of tree leaf area to site total leaf area.

Data Requirements

Based on the schematic discussion of the submodules, the overall data requirements are modest: (i) field plot data: diameter at breast height, total height, crown ratio, and species; (ii) weather station data: daily precipitation and daily temperature, ambient CO_2 and O_3 concentrations; and (iii) other: latitude, Julian day, solar constant, elevation. Alternatively speaking, the result of the aggregation of processes concomitant in the construction of a hybrid model and the application of the design tenants is a series of submodules that require little in the way of initialization.

DISCUSSION

The advantages of hybrid modeling are clear: (i) mensurational and physiological output; (ii) access to empirical treatments of thinning, mortality, and regeneration; (iii) modest data requirements, i.e., model initialization based on typical field plot data; (iv) a decrease in the number of required model parameters; and (v) a means to overcome lack of mechanistic knowledge through empiricism based on causal thinking. Also, using empirical knowledge does not, by definition, prevent a treatment of climate change. In each of the above submodules, all empirical relations use climate-related explanatory variables. This is more than an attempt to maximize some notion of statistical fit; rather it is an attempt to incorporate a degree of causality into such relationships (Korzukhin and others 1996, Mäkelä and others 2000).

Despite these advantages, hybrid modeling endeavors are scant. Friend and others (1997) developed a hybrid model, Hybrid v3.0, for the United Kingdom based on functional groups as the terrestrial component of a whole system hierarchy of models. Milner and others (2002) linked the Forest Vegetation Simulator, Inland Empire version (Wykoff and others 1982), with Stand-BGC (Milner and Coble 1995), an individual tree level version of the BGC logic (Waring and Running 1998) to provide the latter with a mechanistic engine. Similarly, Baldwin and others (1998) linked PTAEDA (Daniels and Burkhart 1975), a distance-dependant growth and yield model, and MAESTRO (Wang and Jarvis 1990), a canopy-level mechanistic treatment of photosynthesis, to better estimate stand carbon gain and to investigate climate change scenarios. Baldwin and others (2001) then combined MAESTRO with an updated version of PTAEDA to predict changes in site quality (i.e., site index) based on physiological (e.g., photosynthesis) and mensurational (e.g., tree per area) variables. Ågren and Bosatta (1988) analyzed nutrient cycling in forested ecosystems using empirical plant growth routines and mechanistic soil carbon algorithms. The individual tree model Forest v5.1, under development at the University of Minnesota, combines the above submodules to predict the tree carbon budget under climate change while allowing for silvicultural manipulation (Robinson 1998).

Viewed in their totality, such modeling endeavors highlight the potential gains from hybrid modeling. As knowledge increases and biologically defensible parameterizations of key physiological processes become a reality, hybrid modeling will likely become less attractive. Nonetheless, the ability of hybrid modeling philosophies to bridge gaps in knowledge and to produce diverse outputs should ensure their use in the foreseeable future.

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