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Evaluating Models of Climate and Forest Vegetation

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Introduction

Understanding how the biosphere may respond to increasing trace gas concentrations in the atmosphere requires models that contain vegetation responses to regional climate. Most of the processes ecologists study in forests, including trophic interactions, nutrient cycling, and disturbance regimes, and vital components of the world economy, such as forest products and agriculture, will be influenced in potentially unexpected ways by changing climate. These vegetation changes affect climate in turn through changing C, N, and S pools; trace gases; albedo; and water balance. The complexity of the indirect interactions among variables that depend on climate, together with the range of different space/time scales that best describe these processes, make the problems of modeling and prediction enormously difficult. These problems of predicting vegetation response to climate warming and potential ways of testing model predictions are the subjects of this chapter.

Before evaluating predictions about vegetation, it is important to consider that "vegetation" encompasses many variables. These include a variety of state variables (e.g., leaf area, density, standing crop, basal area, litter), which can be measured at any given instant, and rates (e.g., growth, thinning, net primary production, decomposition), which can be estimated from repeated measurements. Because these variables are typically considered at different scales of space and time, models differ in how they treat these variables. For example, leaf area is a boundary condition in Running and Coughlan's (1988) model, while it is a prediction of gap models (Botkin et al., 1972; Shugart, 1984). In Clark's (1990a) model, leaf production is dynamic, but, as in Running and Coughlan's (1988) model, individual trees are ignored. Gap models (Botkin et al., 1972; Shugart, 1984; Pastor and Post, 1986) consider every tree larger than a particular diameter. Treatment of such variables differs, because each model is designed for a different purpose. Consequently, each of these approaches has its strengths and weaknesses.

The variables contained in models and the selection of boundary conditions are influenced by the complexity of the process, which is largely determined by the number of ways in which different processes are related. These vegetation variables depend on climate directly and on other factors that also depend on climate. Temperature, for example, has direct effects on rates of photosynthesis and respiration. It also influences the microbially mediated mineralization of N, and hence the accumulation of organic matter in the forest floor; the probability of fire at several time scales; soil moisture storage; and the growth rates of all other plants within a stand that compete for light, water, and N. Temperature effects on these other variables that influence growth rate complicate the response of vegetation to temperature. Similarly, although physiology of seedlings responds to CO_2 concentration (Norby et al., 1986a), it is difficult to extrapolate these results to landscapes of trees of different ages. Increased water use efficiencies of individual trees at elevated CO_2 concentrations are expected to have many indirect effects on stand dynamics (e.g., Jarvis and McNaughton, 1986; Eamus and Jarvis, 1989; Graham et al., in press). Associated changes in litter quality and thus N cycling, for example, could have complex and protracted influences on vegetation composition (Norby et al., 1986a, 1986b). The composite effect of climate on vegetation therefore includes effects on many state variables and fluxes by many indirect and correlated pathways.

This complexity of the climate's control over so many important processes represents perhaps the greatest challenge for prediction of how a change in one or several climate variables in the future may influence vegetation. This complexity may be so severe as to frustrate efforts to predict even what might be the sign of a given response. The fact that increasing temperatures might decrease growth of moisture-limited plants while increasing growth of plants not limited by moisture is one of the simplest such examples—temperature variability potentially has opposing consequences as a result of the indirect effects on moisture availability. In this case, knowledge of the sign of direct and indirect effects is not sufficient for predicting the sign of the composite effect. Either direct or indirect pathways may prevail, depending on the many indirect linkages and correlated causes, functional forms of each dependency, and initial conditions. Nonlinearities in these dependencies result in variable sensitivities of predictions to parameter values. This complexity makes it important to test model output under a range of environmental settings, to test a range of predictions, and to explore sensitivities to the variability in parameter values that may exist in the real world.

Pastor and Post's (1988) predictions of composition change in Minnesota under doubled CO_2 represent an example from climate change literature of the potential importance of indirect effects of climate on vegetation change (Figure 1). The area considered in this example is predicted to become warmer and drier (Manabe and Wetherald, 1986; Kellogg and Zhao, 1988; Rind, 1988). Sandy soils

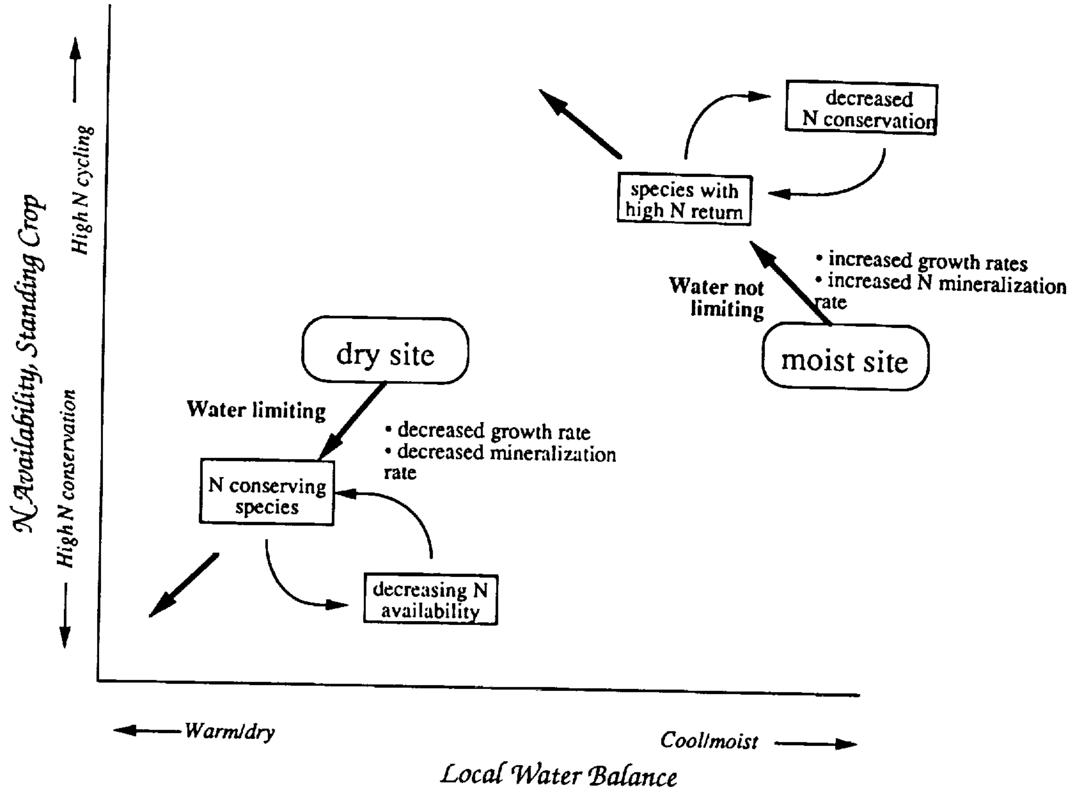

Figure 1. Potential feedback effects of warmer and drier climates on forests suggested by simulation models of Pastor and Post (1988). Sites that initially are rather similar could become increasingly different when subjected to warm/dry conditions as a result of modest initial differences in local water balance. On the moist site, higher temperatures lead to increased mineralization rate, while on the dry site moisture is limiting, and mineralization rate decreases. Subsequent changes in species composition, and thus litter chemistry, provide feedback effects that exaggerate these differences (from Clark, 1991a).

in the region hold little moisture, and the rate of N mineralization is limited by moisture availability; finer-textured soils hold more moisture, and N mineralization rates are higher.

Simulation models predict that future warmer and drier conditions would affect vegetation and nutrient cycling on these different types of Minnesota soils in distinctly different ways. On coarse soils, moisture limitation of N mineralization would become more severe as precipitation decreased and atmospheric demand for soil moisture increased. Decreased mineralization rates would lead to lower N availability and to a shift to species more conservative in their use of N. The change in species composition represents a positive feedback on the nutrient cycle, because N-conservative species return smaller amounts of N to the soil in litterfall. On finer-textured soils that hold more soil moisture, however, the negative effect of drier conditions might be less important than would be the positive effect of higher temperatures. If moisture is not limiting to microbial populations responsible for N mineralization, higher temperatures allow higher mineralization rates. Here again, a positive feedback may come into play, because higher N availability promotes species that cycle larger quantities of N (Chapin, 1980; Vitousek, 1982; Pastor et al., 1984). Mineralization rates increase further with the larger quantities of N returned in litterfall.

Thus, a change to warmer and drier conditions could have opposite effects on different parts of the landscape, and this is indeed what Pastor and Post's (1988) models suggest. In their simulations, similar vegetation types on silty clay loam and on sandy soils changed in opposite directions under warmer conditions. Productivity of dry sites decreased as mixed hardwood and conifer forests shifted to a depauperate oak savanna. On finer soils, stands became *more* productive, as mineralization rates increased and species that cycle larger amounts of N became of increasing importance.

These complex interrelationships present difficulties that are compounded by the need to accommodate vastly different spatial and temporal scales. The climate models are comparatively coarse in space (grid spacing of 1° to 10° latitude by longitude), and they run at rather short time steps (roughly an hour). Many vegetation models have annual time steps on plots with sizes of only fractions of a hectare. One potential approach for integrating such models is to spatially average vegetation parameters to serve as boundary conditions for general circulation models (GCMs) over time and to temporally average climate variables for vegetation models over space. The time-averaged climate output is assumed to apply everywhere in that grid cell, and the spatially averaged vegetation output is assumed constant for many time steps of the climate model. Parameters could also be converted to simple functions of space or time to accommodate topographic complexity or seasonality. Another approach might be to shift the focus of vegetation models to better accommodate the scales of GCMs (Running and Coughlan, 1988). The kinds of GCM output required for biosphere models are discussed in Bretherton et al. (this volume). Below I summarize some important features of models that have been or can be used to explore vegetation responses to climate change. I then suggest some of the ways in which these models can be evaluated.

Types of Models

Several types of models have been used to address forest responses to climate change. A review of these models is beyond the scope of this chapter. Here I simply point out some of the major differences among them and some aspects that will be referenced in the next section on model evaluation.

Models that can be used to predict vegetation response to climate range from simple and highly empirical to rather more mechanistic and complex. Box (1981) applied a simple set of rules that could be used to predict vegetation "life forms" (based on growth form, seasonal habit, and leaf type, size, and structure) on the basis of water-balance variables. Maximum and minimum values of each water-balance variable (monthly totals and means) were identified for locations of each vegetation life form and used to map vegetation types globally. A more recent and independent analysis of the factors regulating vegetation types at subcontinental scales (Neilson et al., 1989) resulted in a set of "rules" that could be applied in a similar on/off fashion for predicting vegetation biomes. Neilson et al. (1989) interpreted empirical relationships between water balance and vegetation cover in terms of life histories of resident plants. They identified combinations of water-balance variables that help to explain distributions at broad scales and ways to link vegetation with macroclimate. The Holdridge life-zone classification scheme used by Emanuel et al. (1985) is a further example in which simple empirical relationships aid identification of the potential effects of climate change on vegetation. All of these studies make use of simple, empirical relationships that can have powerful predictive capabilities, and they can facilitate understanding of mechanisms at broad spatial scales. The most accurate predictions of vegetation responses to climate change might come from applying a simple set of rules regarding vegetation type and water balance.

The principal limitations of such empirical approaches are their inability to handle climate/vegetation relationships that do not currently exist on the globe and their inability to address dynamics. The first limitation is clearly a concern given the past existence of assemblages with no close existing analogs (e.g., Davis, 1981; Webb, 1988). Future climate conditions are also likely to include types of climates that do not now exist, so we cannot hope to confidently predict the assemblages of species that will co-occur in such cases. The second limitation relates to the inherent static nature of such calibration/prediction activities. Results of these models aid understanding of potential patterns, but they do not address the transient aspects of changing climate and tracking vegetation.

Contrasting with this simple approach are forest gap models (Botkin et al., 1972; Shugart and Noble, 1981; Shugart, 1984; Pastor and Post, 1986), which have been used more than other types of models for exploring effects of climate change. These models simulate the growth and development of each tree on a plot the size of one mature individual. Plant recruitment, growth, and mortality depend on resource availabilities, regional climate, and disturbance regimes (Shugart and Noble, 1981). The landscape is assumed to consist of a mosaic of such patches that are independent of one another. Thus, the landscape patterns are summarized from a number of separate runs of the same model, each subject to a different random number sequence, which influences recruitment and mortality processes. As in real forests, recruitment tends to occur most strongly following disturbances, such as the canopy gaps that result from mortality of a large individual. Because plots are independent, gap processes on different plots are out of phase. Recent incorporations of an N cycle (Aber et al., 1982; Pastor and Post, 1986) permit exploration of the role of fertility in the climate response. This class of models is most useful for understanding effects of different equilibrium climates on forest structure. Existing versions of the model would not address protracted transient climate conditions particularly well, because most do not allow for broad spatial processes, such as species migration. The water balances in existing models (e.g., Thornthwaite in Pastor and Post's Linkages model) are semiempirical. The space and time scales used in these models reflect the fact that some of the interesting and important dynamics of forest vegetation are best described at scales much different from those that describe the atmosphere. Resources (light and N) that are the basis for much of the dynamics in these models depend on local neighborhoods measured largely at annual rates (e.g., decomposition and N mineralization), while GCMs have short time steps over large areas.

A much different approach of Running and Coughlan (1988) uses leaf area as a boundary condition in a model that focuses on energy and water balance. Stands are dynamic only in the sense that there occurs an annual partitioning of dry matter to root and stem, which serves as a basis for net primary production (NPP) calculations. As with many ecological studies, this value is difficult to interpret, because consistently positive NPP implies an infinite standing crop. If an "aggrading forest" is implied, this value is equally difficult to interpret, for NPP changes dramatically with age until some "equilibrium" is achieved, at which point NPP is zero. An annual N cycle is included, but it is highly simplified. There are no individual trees. Because of the focus on water and energy, this model is particularly well suited for application with GCMs: Its use is not closely tied to a particular spatial scale, and it contains much detail on the climate side at the expense of stand dynamics. This model comes closest to GCMs in terms of scale, operating on a short time step over potentially large areas.

Clark's model (1990a) is intermediate between these two approaches in some ways. It uses long-term temperature and precipitation data to reconstruct water balances, which in turn drive leaf and woody detritus production, decomposition, N cycling, and fire probability. It is useful for evaluating responses of these ecosystem-level processes to annual and long-term changes in water balance, but it does not permit exploration of climate effects on stand structure. Because of the annual time step, it cannot now be directly linked to GCMs. Like Running and Coughlan's (1988) model, it is not tied to a particular spatial scale.

Evaluating Models

The problems of scale and complexity that make these models difficult to construct also make them difficult to test. Predictions about processes that operate at scales of subcontinents are not subject to tests that require experimental manipulation. The complexity of the models also means that there can be many routes (many importantly wrong) to a given prediction. Thus, tests of one or several predictions do not constitute strong support for the complete model. On the other hand, a complex model makes many predictions. By employing a range of methods it may be possible to test some predictions that can increase understanding and guide future model development.

Manipulations

Although most models of climate effects on forests are difficult to test using artificial experiments, manipulations can play a role for evaluating submodel predictions. Model predictions of vegetation composition for forests (e.g., Shugart, 1984) and nutrient cycling in grasslands (e.g., Schimel et al., 1990) would require long-term experiments and, in many cases, land areas too large to be manipulated. Submodels dealing with recruitment responses to climate variables, and with N mineralization and immobilization and dry-matter partitioning under different water balances, can be, and in some cases have been, tested with manipulations in the laboratory and field. Many experiments dealing with the soil-plant-atmosphere system are also relevant for understanding climate change effects. Obviously, such studies are the basis for parameterizations of existing models. Pastor and Post (1986) and Running and Coughlan (1988) provide many such comparisons of submodel predictions with empirical data.

One approach to this problem is irrigation experiments. The most profound effects of climate change in many regions may result from altered water balance. Because of the complex ways in which water balance affects ecosystems, the sensitivities of ecosystem-level processes and species composition to water balance are extremely difficult to evaluate. Forecasts of future changes in water balance are tenuous for several reasons (Kellogg and Zhao, 1988; Rind, 1988; Bryson, 1988), but it is possible to explore sensitivity to water balance in several ways (Clark, 1991a). That sensitivity can be assessed by adding water to ecosystems. It is likely that processes will vary in their sensitivities and that indirect interactions among processes could result in unexpected responses. Although species composition and nutrient cycling may have long response times, irrigation for several years might be sufficient to establish whether such processes are sensitive to water balance (Aronsson and Elowson, 1980; White et al., 1988). The potential for manipulation of soil temperature is also being explored within the context of the Long-Term Ecological Research network of the National Science Foundation (W.H. Schlesinger, personal communication). Use of such an approach together with specific submodel tests should provide valuable insights into sensitivity of ecosystems to climate.

Such submodel tests are an important evaluation tool, but they do not test the full model. Submodels could make predictions that match experimental results, while larger models in which they are embedded might incorporate submodel output in ways that produce unrealistic results. Thus, it is important to test performance of submodels, but additional means for assessing predictions of full models are desirable.

Variability along Gradients

Use of spatial gradients as a proxy for response to environmental change through time has long been an invaluable tool and a favorite target for criticism. In the absence of observations over time, analyses of processes along gradients may be the sole opportunity for analyzing a response to environmental change. If we predict that future climates will produce a rising sea level, for example, one source of information on vegetation changes in the coastal zone is the spatial zonation of vegetation types from low to high elevation. Likewise, if the Upper Midwest is predicted to have a climate like that of the Plains States, transitional vegetation might share some characteristics of existing vegetation that lies along a gradient between these two regions.

This method has some obvious shortcomings, but many are not as severe as those of alternatives. Existing patterns result from a possibly long and unknown past. The time scale on which these past influences operate may be vastly different than those that will dictate future climate change. The "transient" patterns may not appear anywhere on the existing landscape, and the existing patterns may themselves be transient and potentially unrelated to the environmental gradient of interest. Cultural practices have been varied and often are difficult to reconstruct. It is generally difficult to establish what lasting effects these practices have had on the modern landscape and how future climate change will interact with land use changes to come.

It is nonetheless important to test model predictions along climatic and soils gradients. Because models for predicting climate effects on forests contain boundary conditions that vary along gradients, an important test of a simulation model is the accuracy and precision with which it can predict vegetation gradients. This ability is a necessary but not sufficient test of such models. Examples of such tests include elevational gradients at Hubbard Brook (Botkin et al., 1972), elevation and fire gradients in Australian eucalypt forests (Shugart and Noble, 1981), and soil-texture variability (Pastor and Post, 1986).

The simpler the model, the easier it may be to test in this manner. The simple and empirical approaches of Box (1981) and Neilson et al. (1989) permit straightforward testing with GCMs. Neilson et al. (1989) evaluated the degree to which GCMs could predict distributions of biomes by comparing model predictions of the relevant water-balance variables with those that best explained vegetation patterns at a continental scale. The many indirect interactions contained in larger models (e.g., Shugart et al., 1986) make it more difficult to identify assumptions responsible for biased predictions.

Forest Reconstructions, Historic Documents, Chronosequences

Vegetation change and chronosequences provide a means for exploring changes over time. Comparisons of such evidence with model results represent one method for evaluating model predictions.

Evidence for actual vegetation changes through time must come from historic documents or from reconstructions from live and dead plant material still present on the site. This stand history is useful for understanding effects of changing climate if some independent record of climate is available for the appropriate spatial and temporal scales. For example, Clark (1990b) compared fire frequencies predicted by models using 20th-century climate data with correlations between 19th-century climate and fire occurrence. In general, however, such information is incomplete, and the data required to understand many processes are not preserved. Historic documents are often "snapshot" views that are difficult to interpret in terms of changes over time. Examples include the original land surveys of the Northeast and Upper Midwest (Grimm, 1984; Seischab, 1990). Forest reconstructions become less detailed as the time before the present increases. The actual evidence for forest changes is limited by mortality and decomposition (forest reconstructions) and incomplete documentation (documents). Although there are many studies of forest history, there are few that consider the effects of changing climate through the past. This is likely to be a focus for future research, and modelers might exploit these results as a basis for testing predictions.

A chronosequence is a series of stands for which different lengths of time have elapsed since the last disturbance occurred, such as fire, logging, or agriculture. Chronosequences have the advantages of containing much information that can be measured directly and offering the opportunity to conduct experiments (e.g., Robertson, 1982). Many processes change with stand age, including nutrient cycling, recruitment, mortality, and species composition, and these changes have been revealed largely through analyses of chronosequences. Unfortunately a "good" chronosequence can be difficult to identify, because the proportion of variance within the series that is due to stand age is generally uncertain. Climate change is a good example of an influence that depends on stand age, and thus its effects on stands within the sequence could depend on time since the last disturbance. This stand age–climate interaction represents a confounding bias. Spatial inhomogeneity is another source of error, as topography and soils are likely to vary within the series. Despite these confounding factors, studies from chronosequences have proved to be among the most useful tools for model development and testing (Shugart, 1984; Pastor and Post, 1986).

Pollen Analysis

Pollen data provide long records of vegetation change, and pollen grains are sufficiently abundant to permit quantitative analysis. These two attributes of pollen data make them extremely valuable in considering the long-term effects of climate change on vegetation. Pollen grains have been analyzed from sedimentary environments over large geographic areas that have experienced a range of climate changes just since the maximum of the last glaciation (18,000 years before present, or B.P.). Vegetation responses to climate change have been documented in space and time, most fruitfully in recent years with the construction of maps of the pollen data themselves (Webb, 1981), of inferred species migrations (Davis, 1981), of changing community types (Delcourt and Delcourt, 1987), and of rates of change (Jacobson et al., 1987).

There are limitations to the method, which include the facts that pollen data represent a biased record of vegetation and that knowledge of climate changes responsible for past vegetation, and thus pollen, is coarse. The second problem has been addressed by a coordinated effort between climatologists and palynologists through the use of climate/pollen comparisons and GCM predictions of past climate that contain boundary conditions derived from independent evidence. A large data base of fossil pollen from lake and mire sediments (Webb, 1981; Jacobson et al., 1987) has been compared with GCM predictions of climate changes (Kutzbach and Wright, 1985) that have attended past changes in atmospheric CO_2 and aerosols, sizes of ice sheets, amounts and seasonality of solar radiation, and sea surface temperatures (COHMAP, 1988). Comparisons of pollen and other evidence for past species distributions with these climate predictions for past times represents one type of model evaluation.

Overpeck and Bartlein (1989) used modern relationships between surface pollen in lakes and climate variables together with GCM predictions of climate at 18,000 yr B.P. to simulate past pollen distributions. In view of all of the uncertainties associated with the approach, maps of predicted pollen and actual pollen for eastern North America agree reasonably well. This agreement suggests that the GCM captures some of the important features of the climate of 18,000 yr B.P. and that climate/pollen relationships from one time period (i.e., the present) can be cautiously applied to another time period (the past or future). Stand simulations using output from a different GCM produced maps that agreed less well with pollen evidence for forests of 18,000 yr B.P. In such a case it is difficult to determine the degree to which GCM predictions vs. stand simulation predictions might be responsible for unrealistic results. These differences between model predictions and data aid future model development, and they suggest new perspectives for ecologists engaged in attempts to explain past forest changes. Thus, pollen data have already proved a useful tool for model testing, largely because of the broad spatial and temporal domain that can be considered.

Analyzable Models

Development and application of complex simulation models have progressed well ahead of those of the simpler analyzable models that are needed to make simulation models understandable. Despite much debate regarding the relative merits of analytical and numerical models, the topic is so central to the subject of this chapter that some basic points are worth restating. Consider a response variable R that represents some aspect of vegetation. R depends on time t and n factors in the environment, call them c_i:

$$R(t;c) = f(t;c_1,c_2,\ldots,c_n) \qquad (1)$$

Now if these n factors act on R independently, then a linear approximation of this dependency can be written as

$$R(t;c) = \sum_{i=0}^{n} b_i c_i \qquad (2)$$

with slope coefficients b_i, and the effect of any given factor c_i is simply

$$\frac{dR(t;c)}{dc_i} = b_i \qquad (3)$$

Thus we need know only the partial regression coefficient to predict how R might respond to factor i. Sensitivity to c_i is directly related to b_i, thus making the problem rather simple. If the response is importantly nonlinear, then the response to factor i may be more complex than a single coefficient, but it remains a relatively simple and tractable problem.

Now suppose that environmental factors also depend on one another. The effect of c_i on R becomes substantially more complex:

$$\frac{dR(t;c)}{dc_i} = \sum_{j=1}^{n} \frac{\partial R(t;c)}{\partial c_j} \frac{\partial c_j}{\partial c_i} \qquad (4)$$

In order to predict the effect of factor i on R we now need to know the effects of i on all other j factors that affect R. Whereas in the first case the sensitivity of variable R was substantially less complex than that of the full model, now the sensitivity of R to a single variable can and usually will be substantially more complex than is the full model of the process. The predicted response to factor i in the second case is potentially subject to errors contained in every parameter, and those errors are propagated in intractable ways.

In fact, the second model represents a more realistic approach, but it may not be desirable for several reasons. First, complex models cannot be analyzed, and they are notoriously difficult to understand. By analysis, I mean the manipulation of the model to discover its behavior and the contributions of different parameters and variables.

For example, what is the relative importance of temperature, both direct and indirect, for recruitment of seedlings? Temperature may only influence growth of large trees in the model, but those growth rates influence in several ways the space/time distribution of canopy gaps where recruitment is possible. If a growth effect on soil moisture is also contained in the model, complexity is likely increased by an order of magnitude. This question can be solved explicitly in several simplified models of the shifting mosaic process (Clark, 1991b), but we cannot even write an analytical expression for the process described by gap models. Only a large factorial experiment could be used to address the problem, and we might still have only a vague impression of the effects of many parameters.

Second, a complicated model requires much information that we likely do not have. Nothing is gained by adding relationships that must be parameterized by guesswork. There are situations where a Thornthwaite water balance may be preferable over Penman-Monteith simply because stomatal conductance and wind speed, required by the latter, are unknown. Although Penman-Monteith is more realistic, lack of information can neutralize this advantage. Simple vegetation models (e.g., Box, 1981) may be preferable to gap models in many situations for the same reason.

The inability to conduct comprehensive sensitivity analyses is a drawback that makes this guesswork dangerous. If we could fully analyze the implications of a particular functional form or parameter value, we would know when to be suspicious of uncertain assumptions. But these assumptions are propagated in such intractable ways through complex models that we may never identify the cause for unrealistic predictions. These effects may simply be tuned out during initial model runs, in which case the "mechanistic" interpretation of the model could be wrong. If so, the increased mechanistic detail simply confuses the issue.

The answer is not to focus only on simple models or only on large models with much detail. Results of large numerical models function in many ways like empirical data from observations and experiments: They suggest or support simple models that then can be analyzed. For example, distributions in space and time of leaf area generated by gap models could be analyzed in simpler models with respect to the dominant environmental conditions. The same distributions could be incorporated in GCMs. Summary and derived parameters, such as distributions of fire regimes in different climatic settings (Clark, 1989), can be analyzed, and they can also be incorporated in slightly more complex models that retain the virtue of analyzability. Such models can be used in ways not altogether different from the simple empirical relationships of Box (1981) and

Neilson et al. (1989). Despite the fact that they are less "mechanistic" than the complex gap models, they can often contribute more to understanding simply because they ignore tremendous complexity at lower levels of organization. Seasonality of precipitation in these simple models explains the distribution of a particular vegetation type. The same answer might emerge from a costly and protracted analysis of a more complicated model, but it would be more difficult to identify than it would from a simple empirical approach.

Simple models have long been an important tool in many disciplines, and it is likely that they could contribute much to the understanding of climate effects on forests. A potentially important research step in the future could involve the parameterization of analyzable models from output of less simple simulation models. Much progress has been made toward the construction of numerical models linking vegetation to climate. Simpler analyzable models represent an area for future development.

Conclusions

There are several kinds of models now available for exploring consequences of climate change for vegetation. These models operate at different spatial and temporal scales, and they focus on different aspects of vegetation and climate. The time steps and landscape areas of some are more compatible with GCMs than are those of others. Given the range of scales at which climate affects vegetation, however, this diversity of modeling strategies is to be encouraged and perhaps expanded to include more attention to analyzable models. Thus far, there seems to have been more effort devoted to complex models with much detail. There are a number of reasons that simpler models may be preferable for many problems, including potentially better predictive potential and more understandable results at higher levels of organization.

One of the more pervasive difficulties associated with the assessment of many models is general lack of documentation concerning model tuning. Much effort has been devoted to validation of the models, but these tests are difficult to evaluate and to extrapolate to future, no-analog conditions without knowledge of how models have been tuned to various situations. More effort devoted to documentation of parameter sensitivity and to model tuning would greatly increase the usefulness of the models for individuals not involved with their actual development.

The large-scale and protracted nature of the climate change responses makes many of these models inherently difficult to test. Each of these methods for evaluating model output has some unique advantages and many limitations. The logistical problems of spatially large and long-term manipulations limit the potential for experimental approaches. Many submodel predictions are testable, however, and more emphasis on sensitivity of processes to climate variables would aid understanding of what aspects of ecosystems are likely to be affected first and most dramatically by climate change. Experimental manipulations can aid evaluation of some submodel predictions. Gradients provide opportunities to examine model sensitivity to parameters that vary with soils and/or climate. Evidence for vegetation responses to climate change in the past (e.g., forest reconstructions, historic documents, pollen analysis) has the advantage of allowing examination of long-term changes, but this approach is limited by the availability of independent evidence for vegetation and climate changes for corresponding times and places. Because of the complementary nature of these methods, a combination of approaches provides for the most comprehensive model evaluation.

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