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TERRESTRIAL ECOSYSTEMS AND CLIMATIC CHANGE[*]

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ABSTRACT

The structure and function of terrestrial ecosystems depend on climate, and in turn, ecosystems influence atmospheric composition and climate. A comprehensive, global model of terrestrial ecosystem dynamics is needed. A hierarchical approach appears advisable given currently available concepts, data, and formalisms. The organization of models can be based on the temporal scales involved. A rapidly responding model describes the processes associated with photosynthesis, including carbon, moisture, and heat exchange with the atmosphere. An intermediate model handles subannual variations that are closely associated with allocation and seasonal changes in productivity and decomposition. A slow response model describes plant growth and succession with associated element cycling over decades and centuries. These three levels of terrestrial models are linked through common specifications of environmental conditions and constrain each other.

INTRODUCTION

Climatic change caused by increasing greenhouse gas concentrations may alter earth's vegetation and the turnover of dead organic matter on land. The dependence of plant cell processes and microbial activity on light, temperature, moisture, and nutrients is the basis for this, but with time the consequences extend to variations in ecosystem attributes including species composition, biomass, and leaf profiles, and to continental distributions of vegetation zones or biomes (Larcher 1975, Walter 1979, Woodward 1987).

But land systems partially shape climatic change as they respond to it. Terrestrial ecosystems influence climate by exchanging moisture and heat with the atmosphere, and they form land boundary conditions for albedo and roughness. Furthermore, climatic perturbations can alter terrestrial carbon and nitrogen cycles, leading to further shifts in atmospheric greenhouse gas concentrations.

The human habitat will vary tremendously if these tightly coupled transients in the global biogeochemical cycles and in climate unfold as most analyses indicate they will. In many regions, people will manage ecosystems to meet human objectives in the face of global change. But a large part of the earth's landscape will respond without intervention, and a clear understanding of these natural responses forms the basis for successful ecosystem management where humans do choose to control the landscape.

Terrestrial ecosystems and the global systems they interact with are intricate and tightly coupled. Observational studies are often impractical because of the time scales involved (decades to centuries), the vast extent and spatial heterogeneity of earth systems, and because small but critical perturbations to natural levels are causing global change. Furthermore, many mechanistically important variables cannot be measured directly. Mathematical models are an important means of contending with these limitations of direct studies—they are unsurpassed for synthesizing and integrating diverse concepts and data.

Atmospheric general circulation models and models of the global carbon cycle assume that the major features of vegetation and soils are fixed—maps of biome or vegetation and soil type distributions prescribe these characteristics. But several studies suggest that terrestrial ecosystem responses to climatic change can violate static vegetation and soil assumptions (Emanuel *et al.* 1985a, b, Solomon 1986, Pastor and Post 1988, Prentice and Fung 1990, Schimel *et al.* 1990). While major shifts in the locations of biomes such as grasslands and forests may eventually occur, more subtle variations in the biomass or leaf area of ecosystems may be influencing global climate and element cycling already.

A comprehensive, global model of terrestrial ecosystems is needed in climate and element cycling studies. This need has been apparent for some time, but only recently have the necessary concepts, data, and formalisms for such a model become available. In what follows, we describe some approaches to the development of a global ecosystem model with particular attention to the difficulties associated with the range of scales involved and data limitations that require empirical substitutes for more formal relationships.

TERRESTRIAL ECOSYSTEM RESPONSES TO CLIMATIC CHANGE

Terrestrial ecosystems participate in climate and in the biogeochemical cycles at several scales. The metabolic processes that are responsible for the growth and maintenance of plants and soil microbes move carbon and water through rapid circuits in plants and soil and exchange heat and moisture with the atmosphere. But plants establish a parallel circuit by incorporating some of the carbon they fix by photosynthesis into their tissue, delaying its return to the atmosphere until it is oxidized by decomposition or fire. This slower carbon loop, which is matched by cycles of the nutrients required by plants and decomposers, affects trends in atmospheric CO_2 and CH_4 concentrations and imposes a seasonal cycle on those trends. Furthermore, the structure of terrestrial ecosystems, built by this slower responding carbon machinery, supports the surface roughness and albedo boundary conditions of the climate system.

As plants respond to environmental change, competition for light and resources influences reproduction, growth, and mortality to different degrees depending on species characteristics. As a result, the dynamics of species composition, biomass, leaf area, and similar community variables are more complex than the collected responses of individuals that do not interact. Climatic change affects plant productivity immediately, but the immediate responses are modified later by changes in composition and community structure. This adjustment process is similar to secondary succession after disturbances such as fire or harvest.

Natural areas are mosaics of patches that were disturbed at different times by fire, wind, flood, disease, or similar events. Large areas of vegetation reflect disturbance regimes that are part of their normal households—such systems maintain steady state under ordinary local disturbances, but are perturbed by changes in disturbance frequency or intensity. Natural disturbance can quicken the response of vegetated areas to climatic change (Davis and Botkin 1985), and presumably the harvest of wood or crops can have the same effect. Climatic change can alter disturbance regimes, for example warmer or drier conditions can increase fire frequency, causing forests to be replaced by prairie (Grimm 1984).

The abundance of taxa surrounding an area determines the availability of propagules for local recruitment. At this level, climatic change can alter the regional distributions of taxa. Such changes are well documented for the past 20,000 years (Davis 1981, Huntley and Birks 1983, Webb 1986, 1987). Trees migrated with remarkable speed in response to Quaternary changes, but the time needed for large-scale spread and regional population changes may be 1,000 years or more (Davis *et al.* 1986, Bennett 1986, Davis 1987) and can presumably limit the rate of vegetation response to rapid, large climatic changes.

Vegetation and soil are tightly coupled systems Soil water holding capacity and nutrient availability in the soil-water solution influence primary production. Although some aspects of soil formation are slow enough to be considered constant through plant community changes, nutrient turnover depends on litter characteristics so that variations in species composition can affect plant growth and further alter composition (Aber *et al.* 1982, Pastor and Post 1986).

Thus, in the face of climatic change, terrestrial ecosystems have a certain inertia (Smith 1965), comprised of several components: (1) patches of vegetation adjust to climatic change when the available flora is held constant (Type A Responce of Webb 1986), (2) nutrient cycles adjust to changing environmental conditions and vegetation characteristics, (3) the spatial mosaic of vegetation adjusts to climatically induced changes in the frequencies of fire and other natural hazards, and (4) succession further alters ecosystem structure and function as species establish and compete (Type B Response of Webb 1986).

HIERARCHICAL GLOBAL ECOSYSTEM MODELS

Intuitively, we might develop a global model of terrestrial ecosystem dynamics by combining descriptions of each of the physical, chemical, and biological processes involved In such a scheme, longer term changes are derived by integrating rapid responses. But we cannot simply integrate models that describe the rapid processes of CO_2 diffusion, photosynthesis, fluid transport, respiration, and transpiration in cells and leaves in order to estimate productivity of whole plants and ecosystems. The nature of the spatial averaging implied and the selection of parameters and processes to consider is difficult because of nonlinearities and heterogeneity. For example, photosynthesis models traditionally assume uniform biochemical concentrations over an entire plant, a condition rarely found outside of the laboratory. Furthermore, computational error accumulates when small deviations are multiplied by scaling factors or accumulated over long time periods.

To progress in the development of terrestrial ecological models, we choose processes to treat in different models based on the phenomenological scales involved. As is common in the more physically-based sciences, terms in fundamental equations are included or ignored depending on the temporal and spatial scales of interest. We expect the best global ecosystem analysis from a carefully organized suite of models, each describing processes that operate at different rates and with differing degrees of spatial variation. It is useful to organize models at three time scales and relate these in various ways for different kinds of analyses.

The most rapid responses, from minutes to days, involve gas and water vapor exchanges, the biochemical reactions of photosynthesis, and the microbial activity that decomposes dead organic matter. These processes, which are responsible for the rapid circuit of carbon through terrestrial ecosystems, quickly equilibrate to climatic variations and to changes in atmospheric CO_2 concentration.

At the slow extreme of response times, the life cycles of individual plants and plant community interactions due to shading and competition for nutrients and water determine the dynamics of species composition, biomass, leaf area, and similar community variables over decades and centuries. It is this long-term aspect of vegetation dynamics that can lead to responses that resemble secondary succession.

On intermediate time scales, biotic activity, allocation, system structure, and leaf display change during a year in response to seasonal climate. These intermediate variations are associated with carbon allocation and other processes that are closely correlated with climatic variables.

Models of the rapidly responding components of terrestrial ecosystems assume that the major characteristics of the system remain constant and can be associated with large grid cells, as in atmospheric general circulation models. Inputs at this level include the full suite of climatic drivers as well as summary, static information about the state of vegetation and dead organic matter. Outputs include the heat and moisture balance over the land surface: some models also calculate a net carbon flux into plants.

Seasonal, phenological changes in vegetation are described by models at a second level that are driven by climatic variables summed over time scales of days to weeks (e.g., degreeday sums, photosynthetically active radiation, total precipitation) as well as a productive potential or target structure of the system toward which the vegetation moves in response to climatic drivers. Outputs include seasonal changes in leaf area, leaf nutrient content, and soil water storage. Changes in soil solution chemistry and the soil physical environment at this time scale are appropriate for driving models of trace gas fluxes.

A third class of models represents annual changes in total net primary production and ecosystem structure. Inputs include indices that summarize the effects of climatic conditions on annual plant growth and decomposition (e.g., estimated actual evapotranspiration, annual growing degree-days, drought stress indices). Outputs include total net primary production and its allocation, including total leaf area. Traditionally, total annual nutrient release through decomposition is calculated with an annual time step.

Interactions between time scales occur in two ways: (1) short-term climatic data provide the fundamental forcing functions for all three levels, and (2) the longer-term models determine the surface conditions and vegetation structure used as input to the next, more rapidly responding representation. Thus all three levels are driven by climatic data and constrained by calculated ecosystem structure. A level three model converts annualized indices of climatic conditions and the current ecosystem state into total leaf area and structure for the next year. Given these total values, the second level calculates the phenology of leaf production and loss, and hence the seasonal pattern of ecosystem structure. Using these seasonal patterns, the first level converts climatic data into energy and water balances over very short time steps used in atmospheric models.

Decomposition and nutrient cycling are simulated with a time step of approximately one month. They depend on litter quality and so require input from level three vegetation models that describe plant chemistry dynamics. Rates in the decomposition model are also influenced by temperature and moisture, and so require monthly aggregated climate data. Growth and leaf nitrogen concentration are constrained by nutrient uptake.

It appears that a general structure can be used to represent respiration and carbon storage in both forested and grassland portions of the world. Soil organic matter in forests is dominated by intermediate fractions, with turnover times ranging from about 20 to 100 years, often accumulating in surface horizons. This material may be derived from lignin, which apparently is not microbially reworked to form stable humus. Its accumulation is simply a function of its slow decomposition rate.

PERTINENT TERRESTRIAL MODELS AND ANALYSES

While comprehensive global ecosystem models are just now becoming practical, a number of modeling approaches that comprise their basis have already given important insight into the potential responses of terrestrial ecosystems to global environmental change.

The natural, equilibrium distribution of vegetation is similar to climate. Plant geographers use this correlation to relate vegetation classes to climate (e.g., Holdridge 1947, Box 1981). Woodward (1987) developed an equilibrium model based on the physiological limits of plants, and Bartlein and co-workers (Bartlein *et al.* 1986) related regional abundances of particular taxa to climatic variables by empirical response surfaces.

Sensitivity tests of such equilibrium models suggest bounds on climatic change impacts. Emanuel *et al.* (1985a, b) compared world maps of Holdridge life zones derived from the climate recorded by 7000 meteorological stations and with simulated temperature increases for atmospheric CO_2 concentration twice the reference concentration. Prentice and Fung (1990) consider shifts in the distribution of carbon in the Holdridge framework due to both moisture and temperature change. Lashof (1987) did similar exercises with a vegetation-climate relationship derived from Olson's world map of ecosystem complexes (Olson *et al.* 1983) and meteorological records. Although the transient responses would be complex (Shugart *et al.* 1986, Solomon 1986), such tests indicate the sensitivity of the asymptotic distributions toward which transients eventually converge in the absence of disturbances not included in these equilibrium relationships.

The experiment described by Emanuel and co-workers indicates greatest changes at high latitudes where simulated temperature increases are largest and where narrow temperature intervals define Holdridge life zones. Changes are along boundaries and are more extensive than the uncertainty in determining these boundaries within the Holdridge scheme. Such speculations indicate some of the challenges agriculture and forestry may face and bound the broad vegetation changes that might feed back on the global element cycles and climate.

Past vegetation patterns reflected the climates of their time, so static vegetation models can be used to describe past vegetation in terms of reconstructed paleoclimates (Anderson *et al.* 1988). This approach assumes dynamic equilibrium (Webb 1986), which is appropriate on time scales much longer than the vegetation's response time (Prentice 1986a, b). The time scale of interest in studies of human-induced global changes is a few hundred years, comparable with the time needed for replacement of forest types—static models are not sufficient for prediction in this context.

For example, Emanuel and co-workers show conversion of much of today's boreal forest to temperate deciduous forest, but this result does not mean that there is likely to be a gradual, straightforward transition between the two forest types. Higher summer temperatures may at first stimulate the growth of boreal conifers, but higher winter temperatures may be unfavorable for the natural regeneration of some of these taxa at their oceanic limits. Beyond a certain point, increased summer temperature will reduce growth rates again; such a warm climate would probably be suitable for temperate trees, but their recruitment will take time, so production could fall before rising again toward the high level characteristic of temperate forests.

Various vegetation models describe transient responses from different viewpoints. Forest stand growth and succession models (Botkin *et al.* 1972, Ek and Monserud 1981, Shugart 1984) simulate changes based on species attributes and tree interaction assumptions that emphasize competition for light. These models borrow many ideas from forestry models (Munro 1974). Non-woody vegetation dynamics can probably be treated within similar descriptions (Coffin and Lauenroth 1988), and although these models describe small landscape patches, they simulate community phenomena with considerable generality and use factors to describe environmental influences that can be evaluated along gradients or to sample variability within larger landscape units.

The growth equations in these models are based on the following observations (Ek and Monserud 1981):

1. Through time tree dimensions change according to sigmoid growth patterns—change in any one dimension (e.g., height) can be modeled as a sigmoid function (e.g., Richards 1959).
2. Other dimensions (e.g., stem diameter or crown width) are allometrically related to height.
3. Changes in stand density reflect thinning because of competition.
4. The heights of dominant trees of a given age and species are fairly insensitive to changes in stand density and are more closely related to potential site productivity than to other indices (Spurr and Barnes 1980).

Stand models treat a plot of a definite size that is constrained by the assumption that light availability is independent of horizontal position (Shugart and West 1979). Stand size can be constrained further in order to achieve realistic simulations of variations such as gap-phase dynamics, the species replacement sequences initiated by the death of a large tree (Watt 1947, White 1979, Shugart 1984, Smith and Urban 1988). Shugart and West (1977) simulated gap dynamics in an eastern Tennessee temperate forest on a 833 m^2

plot. But in boreal forests, tree crowns are narrow, sun angles are low, and the gap created by the death of a single tree is insignificant. Leemans and Prentice (1987) found that to simulate gap processes, models of these forests must be able to treat 1000 m^2 gaps for establishment of light-demanding species (Whitmore 1982).

Conventionally, leaf area is directly related to stem diameter and considered to be concentrated at the top of the stem, so that the total leaf area of each tree shades all trees below. But some more recent models determine leaf area from sapwood cross-sectional area, allowing for sapwood turnover, and vertically distribute the leaf area of each tree (Leemans and Prentice 1987). A vertical light profile is computed from the Lambert-Beer law, again assuming that shading is horizontally homogeneous.

Trees respond according to their species-specific shade tolerance. Environmental effects enter through factors that multiply growth increment to reflect deviations from best conditions. Usually belowground competition is modeled only in terms of crowding, but some models now include an explicit nitrogen cycle; treating litter production, decomposition, immobilization, mineralization, uptake, and growth response (Pastor and Post 1986).

Solomon (1986) showed that a stand simulation model treating 76 viable species can generate qualitatively correct forest types across eastern North America. Bonan *et al.* (1990) were able to simulate successional patterns on boreal sites from central Alaska to Newfoundland. These results indicate that a forest stand model can be applied at different locations by specifying values of low level environmental variables: temperature, rainfall, light intensity, soil characteristics, etc. These same variables are modified to analyze environmental change.

Solomon (1986) went on to illustrate responses to climatic changes derived from general circulation model solutions with increased atmospheric CO_2 concentration. He found that changes in composition brought about substantial changes in biomass that could be positive or negative, depending on location. This experiment considered only the effects of increased CO_2 through climatic change. Using reasonable assumptions about the direct effects of CO_2 increase on tree growth, Solomon and West (1986) showed that climatic effects are likely to predominate. Pastor and Post (1988) report model experiments similar to Solomon's but with explicit treatment of nitrogen cycling. They find that effects of climatic change through nitrogen dynamics can be as important as direct effects on plant growth.

These results point to what can be accomplished using stand simulation models to analyze the consequences of environmental change. By developing solutions that sample landscape units or environmental gradients, we can use a collection of these models to analyze the impacts of environmental change on world forests where human intervention can be ignored or perhaps introduced into simulations as are natural disturbances. Other vegetation types can be analyzed when nonwoody plants are incorporated in these or similar models.

Plant growth data requirements for stand model parameter evaluation are not demanding compared to other approaches; however, even these data are not available for some regions, particularly tropical moist forests of South America and Africa. Huston and Smith (1987) demonstrate that stand models that treat functional plant types rather than species can simulate reasonable growth and succession dynamics—these functional types and their parameter values can be derived from theoretical considerations (Smith and Huston 1989). It appears that, where necessary, vegetation can be modeled at this prototypic level until more data are available.

Forest models based on the Botkin formulation are uniquely successful in describing stand dynamics on time scales ranging from decades to centuries. But a model that describes population changes for each species or even plant types, as opposed to treating individuals, may be satisfactory for most continental- to global-scale applications. The computational requirements of population based models can be substantially less than those of models that track individuals.

One possibility is to describe the state of plant communities by the number of individuals of each species or plant type in each of a set of arbitrary width layers dividing space above the landscape unit supporting the vegetation. Again, the patch is sufficiently small so that light extinction can be assumed to be horizontally homogeneous.

Advancement through height layers is a stochastic process. The probability of transfer to higher layers is derived from a mean height increment for the population of each plant type, assumed to be uniformly distributed through each layer. The increment depends on current leaf area and size as well as environmental conditions including available light, air temperature, and soil moisture. The structural emphasis on height and the assumption of homogeneity within height layers for each plant type or species are conducive to incorporating plant types other than trees for which a growth description based on individuals is unnatural.

Parton *et al.* (1987) describe a general model of organic matter turnover in temperate grasslands that can serve as a companion to forest stand models. Competition for light is less important in lower stature ecosystems; however, nutrient cycling, moisture demands, and other belowground processes require careful description in grassland models. The Parton model considers several classes of dead organic matter that differ according to their resistance to further decomposition. Immobilization and mineralization of nitrogen determine its availability for plants. The model is able to simulate broad-scale variations in grasslands with the specification of only four external variables: annual precipitation, temperature, soil texture, and plant lignin content. The nutrient cycling scheme used in the Parton model is consistent with that used by Pastor and Post (1986) in their forest stand model. Thus a uniform description of belowground processes can apparently be worked out for use in both grassland and forest models.

LARGE-SCALE APPLICATIONS

Terrestrial ecosystem models need to be organized for use at several levels of geographic detail and with the rapid and slow modules running in concert or separately. At the most detailed geographic level, underlying data are organized on a grid of land cells, and models are solved for each grid cell or with a sampling strategy. Both data and model solutions are mapped and managed by a geographic information system. The data requirements and implementation logistics are very demanding at this level. In regional studies, data and model results are tabulated against biome or ecosystem extents; while in some applications, it is useful to average or lump data and model results to global scale.

Continental-scale simulations can be generated by deriving very large sets of patch model solutions. The region of interest is subdivided. A uniform grid in spherical coordinates is convenient, but arbitrary polygons can be used. Resolutions of about 0.5° are reasonable (Olson *et al.* 1983, Emanuel *et al.* 1985a)—such cells are approximately 50 km on a side at the equator.

A set of patch model solutions is generated for each of these smaller units with appropriately distributed random environmental variables. Disturbance frequency and intensity are also specified—these may depend on environmental characteristics such as temperature or soil moisture as well as the status of vegetation (Kercher and Axelrod 1984). The solution set reflects specified variances in environmental variables, including disturbance frequency and intensity, but is complicated by the stochastic processes simulated by patch models.

For land units small enough to support reasonable resolution, the distributions of basic environmental variables, such as temperature, rainfall, soil type, and soil texture, cannot be derived from currently available observations. Rather the distributions of these variables must be based on geomorphologic features—topography is most important.

There are models for calculating solar intensity at a specified location, elevation, slope, aspect, and time (Swift 1976, Bonan 1988, Kutzbach and Gallimore 1988). Although basic principles are understood for other relations, for example temperature change as a function of elevation, these have not yet been expressed systematically in schemes suitable for global terrestrial ecosystem models. It is important to note that absolute relationships are not required, rather we need to derive the distributions of environmental variables from the underlying variability in topography and other structural characteristics.

Useful simulations of vegetation responses can be derived without considering connections between basic land units. At least three connections, however, are clearly important: hydrologic transport, the dependence of disturbance frequencies on events in adjacent cells as in the spread of fire, and the dependence of seed propagation on the abundances of species in an area and in adjacent areas (Rudis and Ek 1981). The latter two connections can be expressed without adding complex submodels; however, the large-scale hydrologic modeling needed to include the first is only now beginning to be addressed (Eagleson 1986).

Global terrestrial ecosystem models require the same geographic data management and analysis capabilities now being demanded by virtually all fields of environmental science. But some unique features are needed:

1. Values of environmental variables, such as temperature and rainfall, must be estimated for each land unit by interpolating observations that are usually of coarser spatial resolution. In continental-scale applications, interpolation on a sphere is required, and smoothing may be necessary (Renka 1982).

2. Statistical analysis of spatial data on arbitrary landscape units of different resolutions is required both for the organization of solutions by assigning joint distributions to environmental variables and to summarize and interpret model solutions.

3. Collections of solutions must be analyzed to find geographic patterns in variables such as biomass and to map features that reveal the distributions of major vegetation types.

CONCLUSION

Those wishing to study interactions between climate and ecosystems must reconcile the different spatial and temporal scales of atmospheric and ecological processes. The design of atmospheric general circulation models reflects the fast horizontal transport and short memory of the atmosphere—integrations are performed at intervals of less than an hour and at grid points 200 km or more apart. The slowest responding terrestrial ecosystem models are solved on yearly intervals but on patches about 30 m across. These differences reflect the inertia of vegetation and the fine spatial scales at which ecosystem processes act compared to those determining weather.

There are general circulation models that allow a prescribed vegetation, in terms of height, structure, phenology, rooting depth, etc., to interact dynamically with the atmosphere (Dickinson 1984, Sellers *et al.* 1986). Physical vegetation characteristics such as albedo, leaf-area index, and stomatal aperture vary diurnally and seasonally in response to atmospheric variables and in turn affect exchanges of energy, water, and momentum. The task of a global ecosystem model is to simulate the slower processes by which primary ecosystem characteristics—taken as constant in climate models—are transformed through time by changes in climate, including the processes of lateral spread.

We've described the components of a hierarchical scheme for simulating global transient responses of natural terrestrial ecosystems to climatic change. The approach is based on several core descriptions associated with different temporal and spatial scales that in our experience simulate the processes that are responsible for terrestrial responses to environmental changes reasonably well. Substantial data are required to estimate model parameters for world-scale studies, but these needs are realistic.

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