A Bottom-Up Evolution of Terrestrial Ecosystem Modeling Theory, and Ideas toward Global Vegetation Modeling

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Introduction

A primary purpose of this review is to convey the lessons I have learned in the development of our current forest ecosystem modeling approach, from its origins in 1973 as a single-tree water-balance model to our current regional applications. This is not an exhaustive literature review, but an opportunity for me to share past successes and failures, and ideas on future terrestrial modeling appropriate to earth systems modeling.

My interests in 1973 as a physiological ecologist were to use computer simulation to explore the system significance of the canopy transpiration measurements I was taking in the field, and to understand the importance of stomatal closure in maintaining a tree's water balance under the severely water-limited conditions of western forests. My introduction to mountain climatology in 1977, and remote sensing in 1982, has resulted in our present modeling logic that incorporates ecological, meteorological, and remote sensing theory and measurements into an integrated framework for calculating ecosystem process rates over large areas.

My second intent here is to use this accumulated bottom-up experience to offer ideas of how terrestrial ecosystem modeling can be taken to the global scale, earth systems modeling. I will suggest a logic where rather mechanistic ecosystem models are not themselves operated globally, but are used to "calibrate" much simplified models, primarily driven by remote sensing, that could be implemented in a semiautomated way globally, and in principle could interface with atmospheric general circulation models (GCMs).

At the outset, I acknowledge the leadership of R.E. Dickinson and P.J. Sellers in developing first-generation models of biospheric processes operated within the GCMs. To me, it is not an accident that physical scientists, not biologists, developed the first GCM-connected biospheric models. It seems that most biologists of my generation were trained from the beginning as reductionists, attempting to dissect and understand what they observed. The fundamental unit of biology is the individual organism, which automatically defines a very restricted spatial domain of interest, and makes global scaling rather untenable. Finally, much of classical biology was descriptive and revolved around taxonomy, the classification of species (which now total something like 100,000 vascular plants worldwide), and attention was focused on the unique characteristics defining each species. The search for common general principles of biological activity, for simple definition of structural and functional attributes of organisms, and for intraorganismal activity (i.e., ecosystem activity) has been a rather recent emphasis of "ecosystem analysis" or systems ecology, a branch of biology that still is in its infancy.

Current Problems of Global Biosphere Models

I believe that the GCMs with integrated biospheric models, such as the biosphere-atmosphere transfer scheme (BATS; Dickinson et al., 1986; Wilson et al., 1987) and the simple biosphere model (SiB; Sellers et al., 1986), are the best point of departure for future earth system models. I will not discuss some other biologically based global models, particularly the global carbon models (Emanuel et al., 1984), because they do not incorporate a direct interface with global atmospheric and hydrospheric models, which is essential. It seems to me that the core deficiencies of BATS and SiB are in two areas. First, the original BATS and SiB treated only energy, water, and momentum variables of the land surface because those are the core flux variables active in the GCMs, so their purpose was to provide surface boundary conditions for the climate models, not represent complete biospheric systems. Ideally a general earth system model will also want a rather sophisticated carbon cycle (including methane and nonmethane hydrocarbons, or NMHCs), nitrogen, phosphorus, sulfur, and possibly other elemental cycles. Additionally, some level of surface disturbance–biome replacement and succession must be treated.

Second, current GCMs define the landscape at a scale that is coarse ($\approx$20,000 km^2) and rather static over time. The spatial coarseness means that a cell that actually incorporates a wide variety of biomes and mesoclimates is aggregated to a single defined

surface type and activity. It also stretches the measurement and modeling capabilities of ecology beyond the size that we have ever worked with before. Without seasonal dynamics in the GCM surface parameterizations linked to the climate simulations, the feedback ability for the surface biological responses to influence the atmosphere is lost, and the ability to realistically model events like the 1988 drought of North America is also lost.

Lessons from the Regional Ecosystem Simulation System

Defining Key Processes, Variables, and Classifications

To begin the evolution of "point-scale" ecological models to GCM scales, my colleagues and I have developed a Regional Ecosystem Simulation System (RESSys) over the last six years (Figure 1). RESSys has three core models, which use four additional core data sets. A topographic model from Band (1986) inputs digital elevation data and outputs effectively a terrain map. This provides a template for the definition of the rest of the system, which can be defined to differing levels of topographic complexity and spatial resolution. Hence, it allows us to zoom in on a small 10-km² watershed or pan out to a whole 10,000-km² region. A mountain climatological model uses this topographic file to extrapolate point-measured meteorological data across the region two-dimensionally for slope, aspect, and elevation. The output file of this model generates the input file of daily meteorological conditions, across the landscape for Forest-BGC (Forest Biogeochemical Cycle), the ecosystem process model. Forest-BGC then simulates the ecosystem processes of importance, which are then mapped back to the region on the topographic template. TOPMODEL then allows topographically defined hydrologic routing. A new project, HYBRID, is connecting the carbon balance of Forest-BGC with the population succession dynamics of a FORET-type model (Shugart, 1984) to give the most realistic forest stand simulator possible.

Agreement on the key processes required for a global terrestrial ecosystem model will be important when defining the essential classification logic for global partitioning. From the origins as a water balance model, Forest-BGC emphasizes canopy gas exchange processes and system water storages in snow and soil. Currently in RESSys we require definition of only leaf area index (LAI) and soil water holding capacity (SWC) of the landscape, with defaults for all other parameters. The Forest-BGC model was specifically designed to be sensitive to the parameterization of canopy processes by LAI and soil processes by SWC. These choices of one key vegetation and
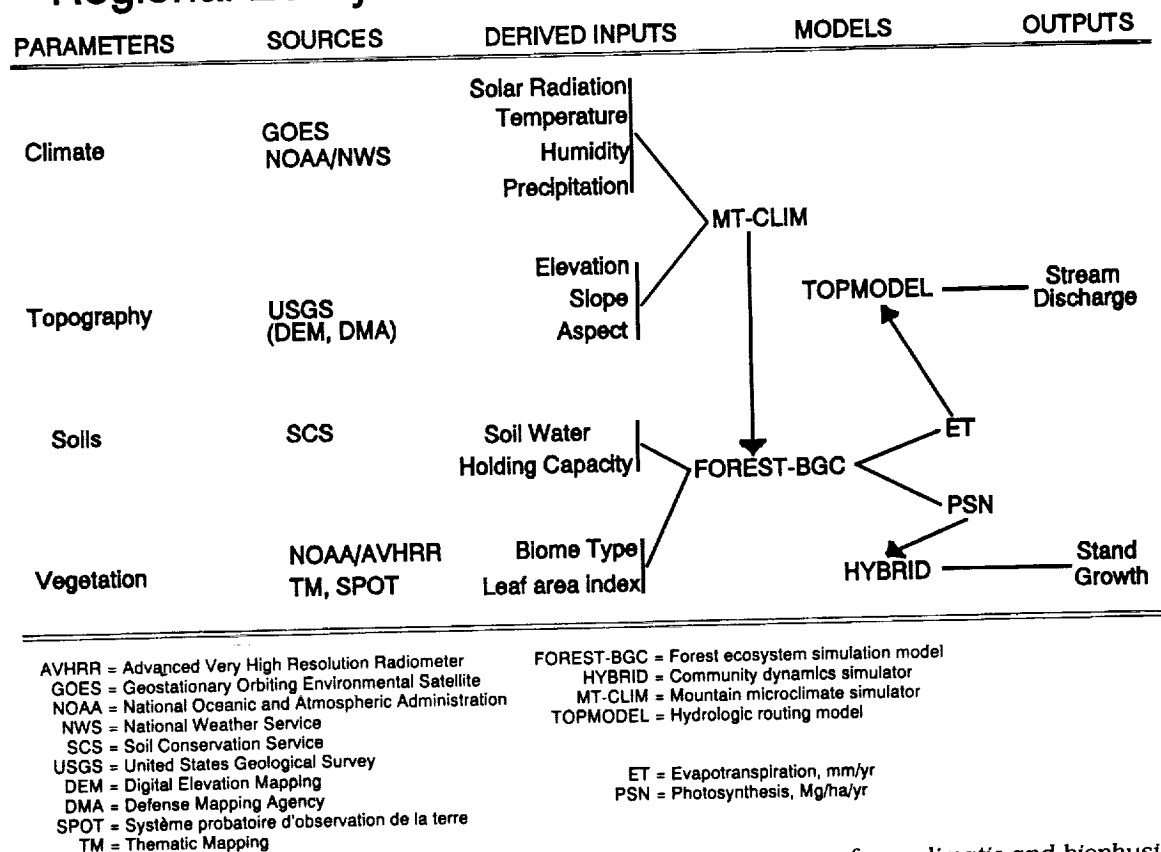
Regional Ecosystem Simulation System (RESSys)

PARAMETERS	SOURCES	DERIVED INPUTS	MODELS	OUTPUTS

Solar Radiation
Temperature
Humidity
Precipitation

Climate — GOES NOAA/NWS

MT-CLIM

Elevation
Slope
Aspect

Topography — USGS (DEM, DMA)

TOPMODEL ——— Stream Discharge

Soils — SCS

Soil Water Holding Capacity

FOREST-BGC

ET

PSN

Vegetation — NOAA/AVHRR TM, SPOT

Biome Type
Leaf area index

HYBRID ——— Stand Growth

AVHRR = Advanced Very High Resolution Radiometer
GOES = Geostationary Orbiting Environmental Satellite
NOAA = National Oceanic and Atmospheric Administration
NWS = National Weather Service
SCS = Soil Conservation Service
USGS = United States Geological Survey
DEM = Digital Elevation Mapping
DMA = Defense Mapping Agency
SPOT = Système probatoire d'observation de la terre
TM = Thematic Mapping

FOREST-BGC = Forest ecosystem simulation model
HYBRID = Community dynamics simulator
MT-CLIM = Mountain microclimate simulator
TOPMODEL = Hydrologic routing model

ET = Evapotranspiration, mm/yr
PSN = Photosynthesis, Mg/ha/yr

Figure 1. An organizational diagram for RESSys, showing the sources of raw climatic and biophysi-cal data, the derived variables produced, and their incorporation into the topoclimate (MT-CLIM, Running et al., 1987) and ecosystem simulation (Forest-BGC, Running and Coughlan, 1988) models.

one edaphic variable then direct our landscape classification, which otherwise could have near-endless layers of variables (quite fashion-able when showing off geographical information system, or GIS, capabilities). We have recently added total canopy nitrogen as a sim-ilar, simplifying definition of forest nutrient status.

The other control on landscape definition is the topographically induced microclimate variability. Sensitivity of the ecosystem model to climate then helps to define what resolution of elevational and topographic detail need be defined. For example, we have found temperature resolution of ± 1°C and precipitation of ± 2mm to be adequate for driving the ecosystem model.

In simplifying earlier ecosystem models, I eliminated a number of seemingly important details. No internal physiology is represented (of cellular water stress, phloem carbohydrate transport, etc.). No canopy

structure, leaf age class, or leaf angular distribution is defined, only simple LAI. No below-ground details of rooting processes, root water, or nutrient uptake capacity are explicitly defined. Some of these variables are virtually unmeasurable in the field even for small intensive study sites; how would we estimate them at regional or global scales? What we really want is to relate below-ground activity to canopy responses that can be more directly measured.

The following processes are calculated by Forest-BGC:

- Hydrologic:
   precipitation, snow vs. rain partitioning
   snowmelt
   canopy/litter interception and evaporation
   surface runoff vs. soil storage
   transpiration physiological water stress and surface resistance
   subsurface outflow

- Carbon:
   photosynthesis
   maintenance respiration
   growth respiration
   carbon allocation (leaf/stem/root)
   net primary production
   litterfall decomposition (trace gas emissions, CH_4, NMHC)

- Nitrogen:
   mineralization
   allocation (leaf/stem/root/available)

Although the resulting model, neglecting many ecosystem attributes and relating most key variables to LAI and climate, will seem oversimplified to many ecologists, it provides the only means we see to bring ecosystem modeling to regional scales.

I emphasize that an optimal global vegetation classification scheme cannot be devised until a modeling logic has been defined, so that the classification can be based on the variables, such as LAI in our case, that the model has been designed to be particularly sensitive to.

Spatial Scale Definition

GCMs define the land surface in only a spatially coarse (cells of $\approx 20,000$ km^2) and static way. Each cell is defined initially as a single vegetation type, and no dynamic interaction occurs between the resulting climate and surface vegetation definition, a limitation that is particularly unfortunate for long time simulations of 10–100 years. We have found in RESSys development that the limiting fac-

tor is *not* the accuracy of our "point" models, but the accuracy with which we can define key parameters across the landscape. First, one must decide upon the key variables, such as LAI; then one must devise ways to map them across the region. A breakthrough in our regional logic was the demonstration that LAI could be defined by satellite (Peterson et al., 1987).

By far our greatest difficulty in landscape definition has been in soils data. The soil reservoirs of water, carbon, and nitrogen are significant components of the ecosystem cycles, and have fundamentally different (usually 10–100 times slower) time constants than canopy processes. Historically, soil science has emphasized the taxonomic classification of soils into a system that *qualitatively* defines the temperature and moisture conditions of soil development. However, standard soils maps, such as those of the U.S. Soil Conservation Service, do not define soil physical structure, depth, water potential release curves, or chemistry *quantitatively*. At global scales the problem of nonquantitative, spatially coarse soils data is even more acute. We are working on a hydrologic equilibrium theory that integrates climate, LAI, and soil water holding capacity, and allows one to infer the soil characteristics from observable climate and maximum LAI (Nemani and Running, 1989a). For global-scale work, we suspect some type of similar logic will be necessary.

Time Scale Definition

The ecosystem process model Forest-BGC has a dual time resolution. Key hydrologic processes (e.g., interception and evapotranspiration), and carbon process variables (e.g., photosynthesis and maintenance respiration) are calculated daily. The carbon allocation to biomass is calculated annually, as are the litterfall, decomposition, and nitrogen budget processes. We found the dual time step essential for adequately and efficiently simulating these ecosystem processes. The hydrologic partitioning of precipitation into instantaneous interception and evaporation vs. longer-term snow or soil water storage and transpiration or hydrologic outflow proved to be the key process that demands daily timing. Accurate hydrologic partitioning is essential in arid areas for simulating seasonal soil drought and plant water stress, and is essential for producing correct timing on stream discharge hydrographs. In areas of frequent showers, even higher time resolution is useful. However, we have compromised on a daily time step for our models after many years of modeling at hourly time steps (see Knight et al., 1985). Because, on average, diurnal climatology is very predictable, we found that going from hourly to daily meteorological drivers cut the climate files to 1/24 size, yet we could simulate the diurnal conditions well enough

to predict seasonal canopy process rates from a daily model to within 3% of the hourly simulations (Running, 1984). However, given that GCMs require high time resolution, nothing precludes our ecosystem model from matching their time step except computational load.

The carbon growth and decomposition processes and the nitrogen budgets do not require daily time scales. In temperate evergreen ecosystems, yearly calculations match the timing of field measurements, making initial model development and validation convenient. In more seasonal biomes, such as grasslands, the carbon/nitrogen computations need to be done monthly or even weekly to describe certain processes.

The commonly stated principle relating small space to short time resolution and progressively larger spatial scale to longer time resolution makes a nice graph, but has many exceptions. GCMs define a huge spatial scale at a very fine temporal scale, on the order of 12–30 minutes. For atmospheric dynamics, this is an appropriate space-time definition for the processes being represented. Likewise in ecology, events that are large in spatial scale can occur in a very short time. Ecosystem processes that are driven by meteorological conditions, notably the canopy gas exchange processes, are just as dynamic temporally as climate is. A critical problem of ecological representation, though, is that while a canopy process such as photosynthesis occurs over a large region, the absolute control is still exerted within the physiology of the individual organism. However, this does not argue that we then must represent those individual organisms explicitly.

Many important ecosystem processes are triggered by episodic extreme events. Major freezes can alter regional vegetation cover and activity in one night, and the vegetation may take years to recover. The meteorological conditions that triggered the Yellowstone fires of 1988 were of a short time scale, yet the results will be felt for a century. Both our ecosystem models and our climate models tend to be central tendency simulators, representing mean conditions and mean responses and missing important extreme events.

Standardized Meteorological Data

Ecological modeling has typically been developed around intensive study sites, where a central meteorological station was a first priority. Because one cannot install custom meteorological stations everywhere, the logic of using a routine weather data base with extrapolations was necessary for RESSys. It became clear that daily meteorological data were routinely available from standard sources like the U.S. National Weather Service or the World Meteorological Organization, but hourly, weekly, or any other time were not. Use of

standard available meteorological data became a critical design criterion for RESSys, even if the data were not exactly what was wanted. Part of the purpose of the mountain climate (MT-CLIM; Running et al., 1987) simulator was to calculate humidity and insolation from the daily maximum-minimum temperature and precipitation records that are the standard "weather" data recorded at the greatest number of stations. Humidity and radiation data are available from only about 5% of the reporting weather stations in the U.S.

An alternative to this point meteorological data might be satellite observations that have an areal average of around 100 km². We did not find satellite surface meteorology routinely available, and surface conditions are often obscured by clouds. Areally averaged data would also invert our problem from extrapolation of point data to interpolation of areal averages, problems that both require similar climatology. It should be noted that our mountain climatology out of necessity ignored wind speed and direction, both because of the unpredictability and because forest canopies tend to have high inherent aerodynamic mixing, so exchange processes are not very sensitive to wind. Secondly, our mountain climatology ignores nocturnal, topographically induced cold air drainage.

It appears that the next step of coupling dynamic meteorology to regional-scale ecology should be pursued with mesoscale models run embedded in a GCM (Dickinson et al., 1989). Mesoscale models such as the National Center for Atmospheric Research's MM4 have a spatial resolution much more compatible with RESSys, and variable vegetation dynamics produce important feedbacks to local meteorology (Segal et al., 1988).

Regional Measurements and Validations

For many years the only "ecological" data that could be directly measured at regional scales were occasional land cover classifications from Landsat. Because of the expense and computer requirements needed, these regional maps were produced as one-time static products, much like vegetation maps in atlases. The development of the advanced very high resolution radiometer/normalized difference vegetation index (AVHRR/NDVI) products, produced weekly, began to add some temporal dynamics to our regional view of ecosystems. The observable continental-scale dynamics were dramatic, following the seasonal "green wave" northward in the spring and then back south in the fall (Justice et al., 1985; Goward et al., 1985, 1987). However, the NDVI was still one long step removed from the ecosystem process rates of greatest interest: carbon, water, and nutrient cycling by the surface. More recently, our first- generation RESSys products (Running et al., 1989) have developed the

computational ability to calculate these process rates over progressively larger areas.

We are now finding that there is no established methodology for *validating* these regional ecosystem process maps, particularly from the classical field measurements that ecologists consider "hard" validation. The point samples of 0.1 ha that field ecologists have worked on only represent 0.00001% of the land area of a single GCM cell, and rules for extrapolation are casual. Only remote sensing, a tool foreign to most ecologists, has the capability for repetitive, standardized measurements of regional-scale processes. Yet, with remote sensing we are back to observing optical phenomena, such as the NDVI.

One notable exception is some of the global-scale atmospheric CO_2 concentration analyses (Houghton, 1987; Tans et al., 1990; Fung et al., 1987). These CO_2 data coupled with the seasonal NDVI satellite data are the closest thing to observing a global biospheric "heartbeat" I have yet seen. At a smaller scale, the CO_2 flux measurements taken from aircraft (Wofsy et al., 1988) or micrometeorological tower systems (Baldocchi, 1989) over multiple kilometer scales, if done repetitively, could provide an integrated regional measure of carbon cycle activity. The one other regional-scale data base we have for interpreting ecosystem processes is the hydrologic discharge and balances of gauged watersheds, providing a large spatial measurement of a key ecosystem variable, water cycling. Both these CO_2 and water balance data may provide an integrated spatial measurement for validation, but only at restricted, rather long monthly to yearly time scales. The aircraft and tower flux measurements are the only regional calculations that could provide daily validations.

Another potential source of validation for carbon cycle simulations is the variety of crop yield, forest growth, range forage production, etc., standard measurements taken by land management agencies. These again are point samples and not the exact variables needed, but are a huge network of data that could be used for validation of regional primary production simulations.

Applying Ecosystem Modeling Globally

We currently cannot envision taking RESSys-level mechanistic process modeling to the global scale. Alternatively, we see that these ecosystem process models could be used to "calibrate" highly simplified global models in a variety of different biome/climate situations. Many of the following ideas are incorporated in our research plan for the Moderate Resolution Imaging Spectrometer (MODIS), an instrument in the Earth Observing System (EOS) program of the National Aeronautics and Space Administration. EOS is the observational cor-

nerstone of the U.S. Global Change Research Program, and MODIS is the sensor planned for regular global land surface monitoring.

The best current candidate for this global modeling logic is the NDVI, time integrated through the year (annual ΣNDVI). Due to the fact that the NDVI integrates both surface characteristics (vegetation greenness, soil, and LAI) and key meteorological factors such as solar intensity to the surface, the ΣNDVI provides a simple yet surprisingly versatile global measure (Tucker et al., 1985). We tested the correlation between seasonal NDVI and ecosystem process rates for seven locations around North America (Running and Nemani, 1988). For continental-scale dynamics, we found amazingly good correlations between annual ΣNDVI and seasonal photosynthesis, transpiration, and net primary production (r^2 = 0.72–0.87; see Figure 2a). Even weekly ecosystem activity was fairly well described by the seasonal NDVI trace. However, we also found that the NDVI does not change in evergreen forests that are drought or temperature stressed, indicating that the NDVI alone may be able to define structure, but only fortuitously correlates with canopy function (Figure 2b).

We have also found the NDVI to correlate well against LAI of natural forests across Montana (Figure 3a). To provide some satellite-based definition of canopy stress, we combined in a ratio the NDVI and surface temperature, producing an algorithm that represents the partitioning of absorbed solar energy into sensible and latent heat, or Bowen ratio, and mimicking a surface resistance quite well (Figure 3b).

While details of these ideas are available in the references, the general conclusion we have drawn is that the time-integrated NDVI can be a very robust global measure of vegetation activity, if calibrated well to varying conditions and biomes. We are planning to do precisely that for our ten-year MODIS project, as summarized on Figures 4 and 5. We plan to first define a very limited number of biome types based on very simplified structural and functional characteristics. The global vegetation would then be preclassified by these characteristics, illustrating why we feel the model logic must come before the classification scheme. Next we will build a mechanistic ecosystem process model for each of these biomes, designated collectively BIOME-BGC (Running and Hunt, in press), which then would be used to calibrate the simple global NDVI, biome-specific conversion factors, and surface temperature data. After the launch of EOS, this global simulation of biome processes would be done weekly from MODIS data.

Because a prototype of this logic is already fairly complete for western coniferous forests, we feel reasonably confident in this overall idea. However, at this point not all ecosystem processes have
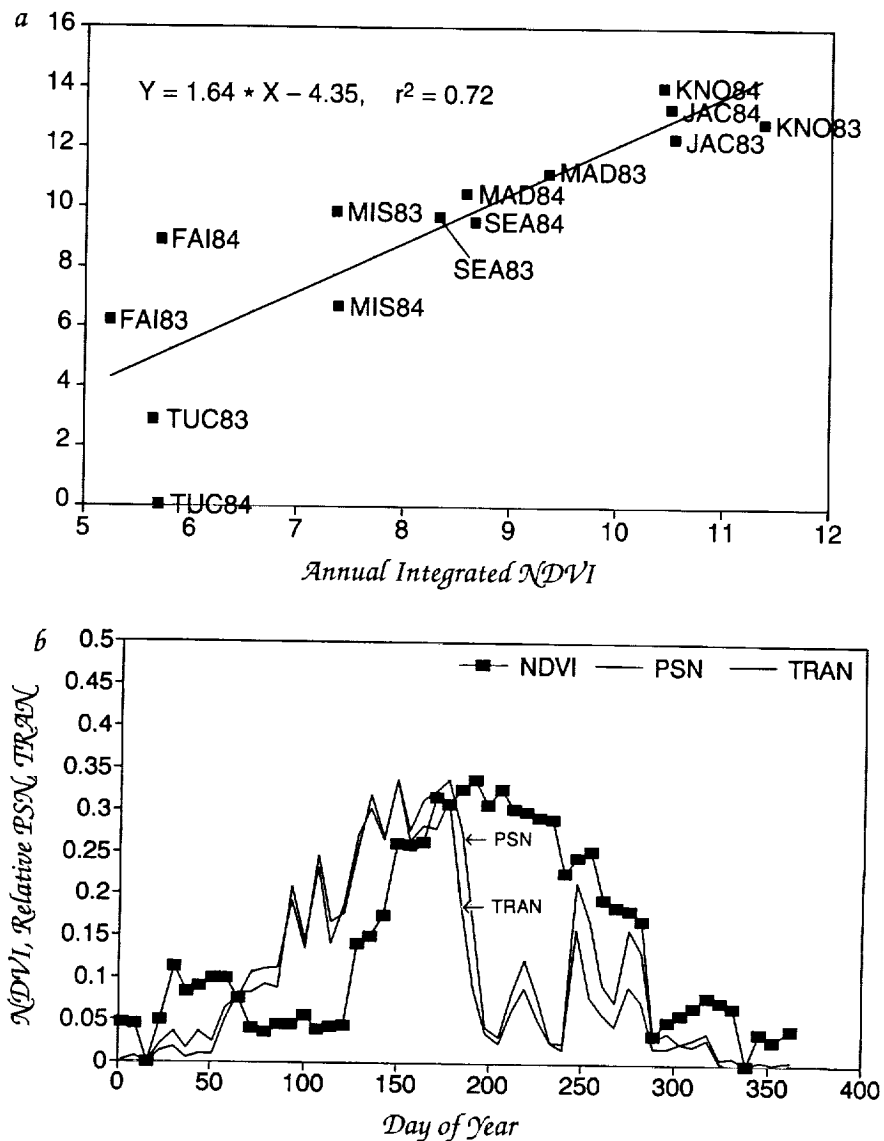
Figure 2. (a) The correlation found between the annual time-integrated NDVI and annual net primary production (NPP) simulated for forests from seven contrasting sites around North America in 1983 and 1984. The sites are Fairbanks, Alaska (FAI); Jacksonville, Florida (JAC); Knoxville, Tennessee (KNO); Madison, Wisconsin (MAD); Missoula, Montana (MIS); Seattle, Washington (SEA); and Tucson, Arizona (TUC). (b) The seasonal trend of weekly composited NDVI compared to scaled weekly photosynthesis (PSN) and transpiration (TRAN) simulated for a cold, dry climate conifer forest in 1984. The absolute units are PSN = 1.78 MG C/ha/week/NDVI and TRAN = 48.1 mm/ha/week/NDVI (reprinted by permission of the publisher from Running and Nemani, 1988; ©1988 by Elsevier Science Publishing Co., Inc.).

$$NDVI = LN(LAI/1.625) * 0.34$$
$$r^2 = 0.88$$

AVHRR/NDVI (vertical axis)

Leaf Area Index (horizontal axis)

$$R_c = Ln(\sigma/48 + 1) * (-10)$$
$$r^2 = 0.92$$

Canopy Resistance (s/cm) (vertical axis)

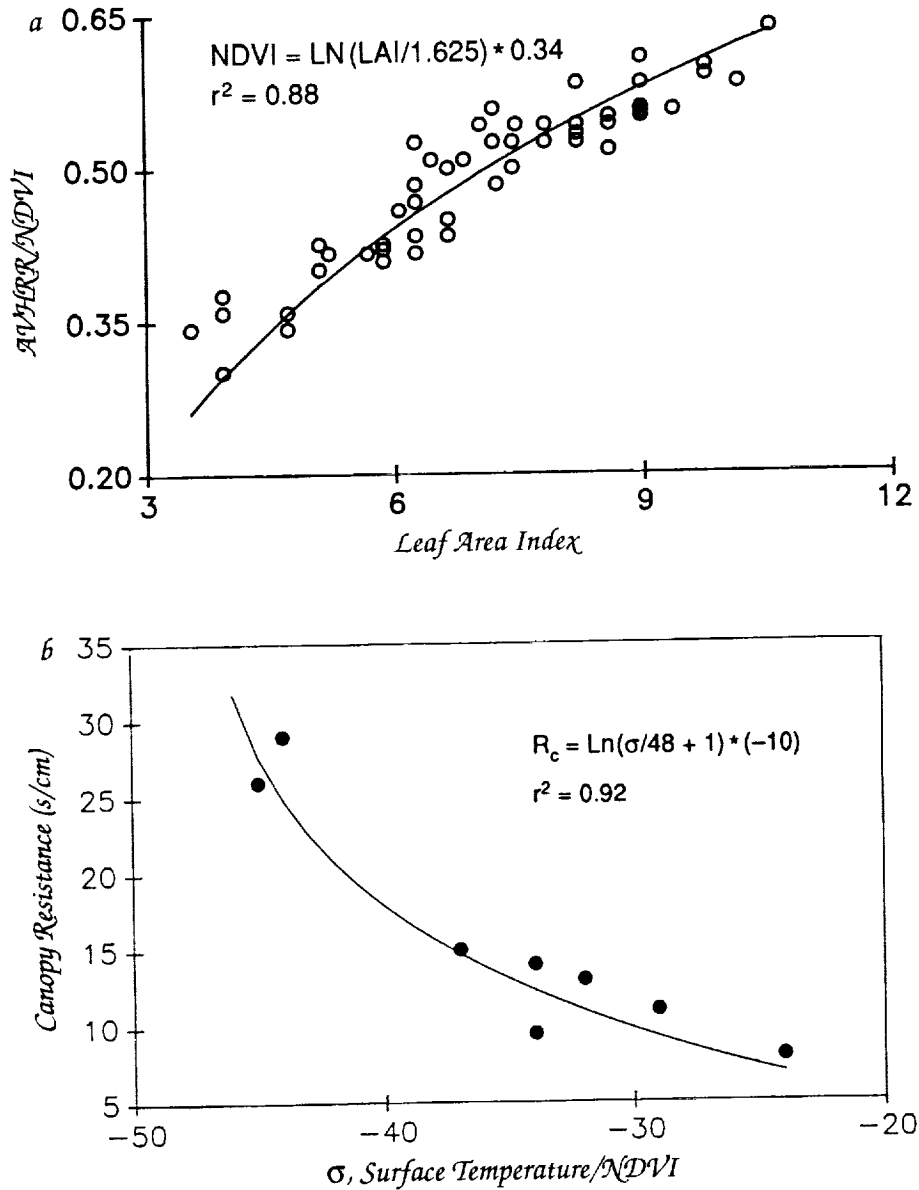σ, *Surface Temperature/NDVI* (horizontal axis)

Figure 3. (a) The relationship between AVHRR/NDVI for September 25, 1985, and an estimated LAI for 53 mature conifer forest stands across Montana (Nemani and Running, 1989a). (b) The relationship between simulated canopy resistance (R_c; from Forest-BGC) and the slope of the surface temperature/NDVI, σ, for eight days during the summer of 1985, for a 20 x 25 km forested area of Montana. We hypothesize that this σ factor approximates a Bowen ratio of latent/sensible heat partitioning at a regional scale (Nemani and Running, 1989b).

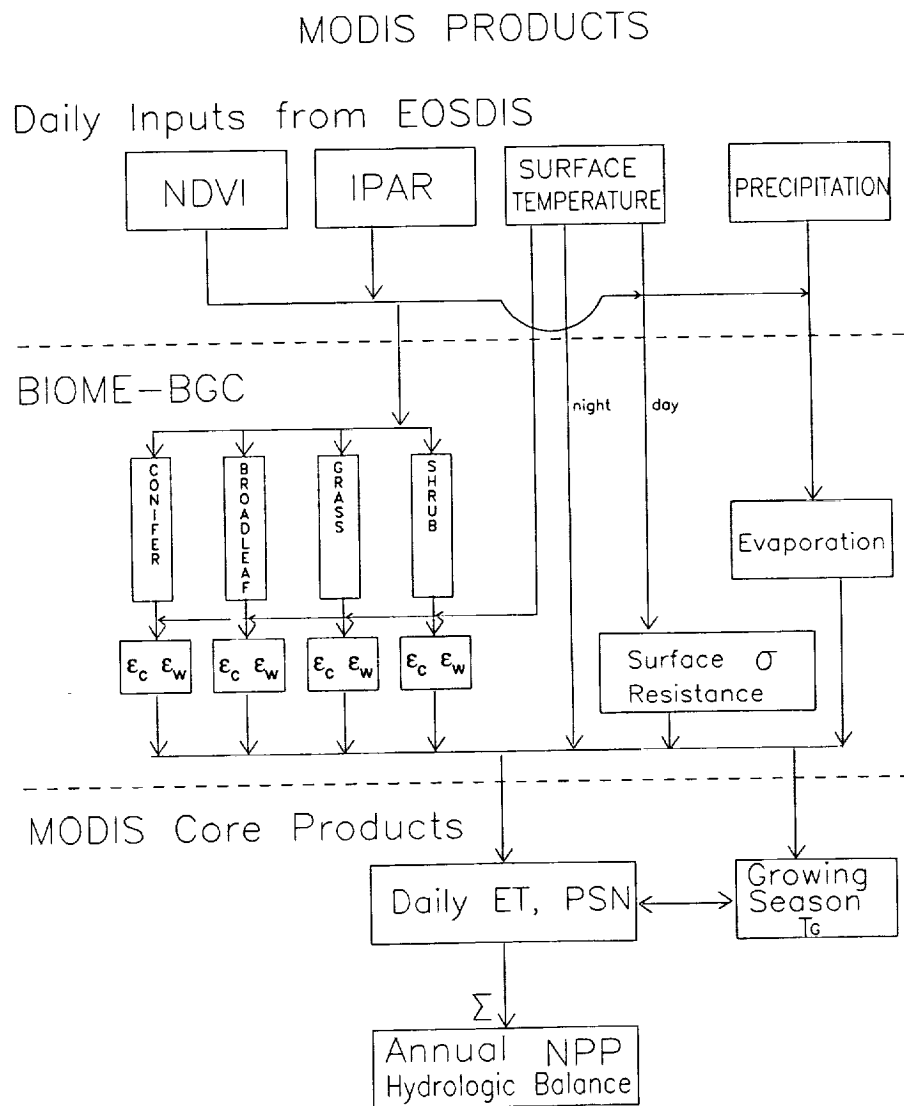## MODIS PRODUCTS

Daily Inputs from EOSDIS

Figure 4. Flowchart of representative biome types we are defining, the input data required for simulating ecosystem processes at local to regional scales, and the output variables required for MODIS algorithm development.
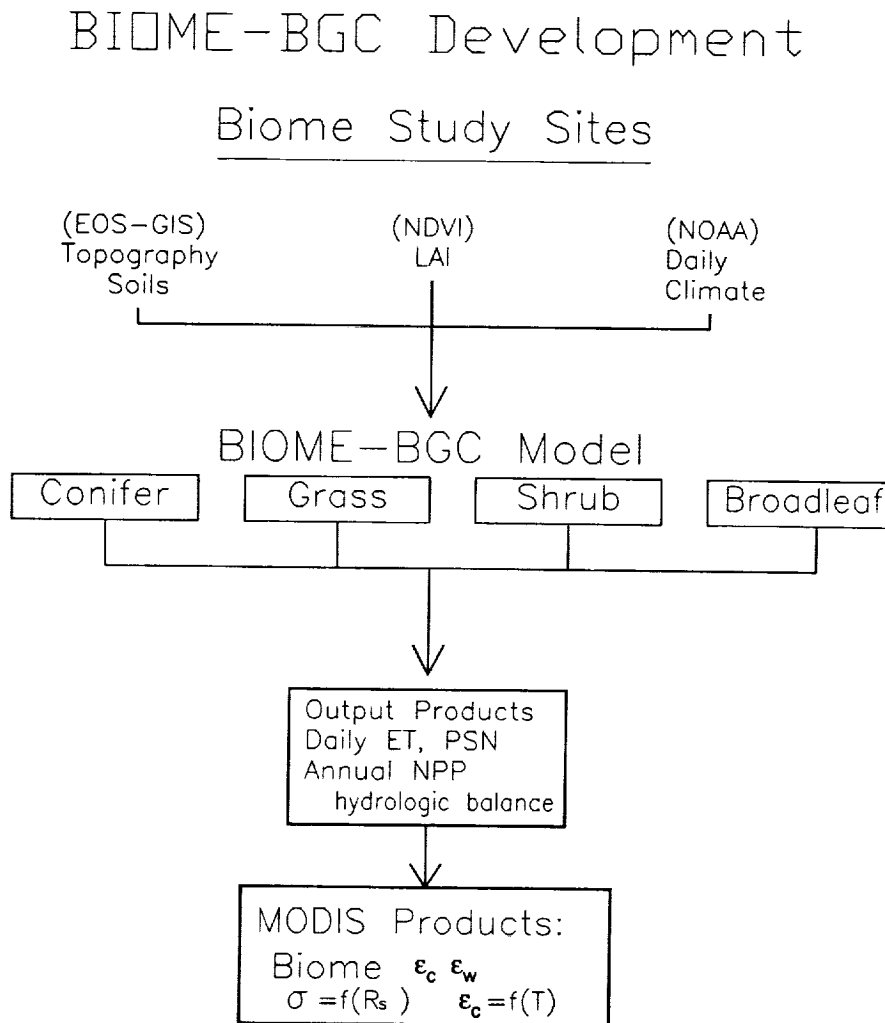
BI⊡ME-BGC Development

Biome Study Sites

(EOS–GIS)	(NDVI)	(NOAA)
Topography	LAI	Daily
Soils		Climate

BIOME-BGC Model

Conifer	Grass	Shrub	Broadleaf

Output Products
Daily ET, PSN
Annual NPP
    hydrologic balance

MODIS Products:

Biome ε_c ε_w

$\sigma = f(R_s)$ $\varepsilon_c = f(T)$

Figure 5. Flowchart of the global-scale inputs from MODIS or other EOS sources, the computational organization, and our planned outputs of MODIS-derived ecosystem process simulations to be executed globally by 1998 as part of EOS.

been tested against NDVI. For example, some of the trace gas and nutrient fluxes may not be correlated with NDVI, which logically can be expected to represent canopy processes best. Hydrologic balances leading to river discharge, ocean coupling, etc., would not be represented here. So, we offer this not as a complete global terrestrial model, but as a dynamic global vegetation model that we know is attainable with current technology.

Connection of this modeling to a GCM would require at minimum a weekly redefinition of the surface characteristics of the GCM cells, which in principle should not be difficult. A more dynamic coupling that would allow real-time system feedbacks might require the NDVI model to be run within the atmospheric model so daily fluxes would enter the atmosphere, and responses would influence the vegetation. Then important responses like continental biome shifts resulting from climate change could be explicitly simulated. However, it is difficult to combine real-time global NDVI measurements interfaced to an internally self-sufficient simulation, unless for retrospective testing.

Conclusions

The following issues emerge as important considerations as we further develop earth system models:

- Global land classification logic must be developed in concert with the global modeling. We have found climate, LAI, and soil water capacity to be most fundamental for regional ecosystem definition.

- Vegetation must be defined simply and generically; basic biome types plus LAI seem best from our experience. This definition must then pervade the logic of the biome models.

- In the absence of a GCM with calculated surface meteorology, regional terrestrial models must be designed around a routinely available meteorological data base, which will undoubtedly require both climatological enhancement to fill in missing variables and spatial extrapolation/interpolation to produce a continuous representation of the landscape at scales equivalent to the terrestrial model.

- Any meaningful definition of the physical/chemical nature of the global soils will be a problem.

- Full mechanistic models of biome processes are probably not possible globally, especially at the higher spatial resolution we desire, so the biome models can be used to calibrate simple satellite-driven vegetation models such as weekly ΣNDVI that would then be surface drivers for the GCMs.

Acknowledgments

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