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Terrestrial biogeochemical cycles: global interactions with the atmosphere and hydrology

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ABSTRACT

Ecosystem scientists have developed a body of theory to predict the behavior of biogeochemical cycles when exchanges with other ecosystems are small or prescribed. Recent environmental changes make it clear that linkages between ecosystems via atmospheric and hydrological transport have large effects on ecosystem dynamics when considered over time periods of a decade to a century, time scales relevant to contemporary humankind. Our ability to predict behavior of ecosystems coupled by transport is limited by our ability (1) to extrapolate biotic function to large spatial scales and (2) to measure and model transport. We review developments in ecosystem theory, remote sensing, and geographic information systems (GIS) that support new efforts in spatial modeling. A paradigm has emerged to predict behavior of ecosystems based on understanding responses to multiple resources (e.g., water, nutrients, light). Several ecosystem models couple primary production to decomposition and nutrient availability using the above paradigm. These models require a fairly small set of environmental variables to simulate spatial and temporal variation in rates of biogeochemical cycling. Simultaneously, techniques for inferring ecosystem behavior from remotely measured canopy light interception are improving our ability to infer plant activity from satellite observations. Efforts have begun to couple models of transport in air and water to models of ecosystem function. Preliminary work indicates that coupling of transport and ecosystem processes alters the behavior of earth system components (hydrology, terrestrial ecosystems, and the atmosphere) from that of an uncoupled mode.

1. Introduction

Conventional use of the term "ecosystem" implies systems where internal interactions are more important than external forcing as controls over system dynamics. Recently, it has become apparent that connections between spatially separate ecosystems are pervasive and important. Ecosystems are connected by hydrology (Peterjohn and Correll, 1984; Costanza et al., 1990; Richey et al., 1990; Vörösmarty et al., 1990), aeolian transport (Gosz and Moore, 1989), and transport by grazers and other organisms (Schimel et al., 1986; Roughgarden et al., 1989). Changes in atmospheric chemistry have made the large-scale linkage of ecosystems dramatically apparent. Changes in atmospheric CO_2 and other greenhouse gases are derived from anthropogenic emissions and altered carbon budgets of ecosystems worldwide (Houghton et al., 1983) and have the potential to impact ecosystems remote from the emission source. Ozone derived from biomass burning in the tropics achieves levels high enough to cause damage to plants over large areas; i.e., areas of burning are "linked" to the unburned areas (Crutzen et al., 1985).

Linkages via the atmosphere often result in rather slow changes, requiring decades to a century or so. For example, the effects of CO_2 either via fertilization or climate change on ecosystems result in slow changes in production and nutrient cycling, compared to localized perturbations such as hurricanes or drought. Similarly, elevated ozone or increased deposition of N have chronic rather

than acute effects (Prinz, 1988). The effects of atmospheric deposition have nonetheless become visible, although symptoms may require decades to be fully manifested. Changes due to biogeochemical linkages of ecosystems are, however, fast relative to many changes in the paleoecological record, some of which spanned 1000–10,000 years (Woods and Davis, 1989). Prediction of future effects of environmental changes requires the ability to understand the behavior of ecosystems at large spatial scales and over long intervals of time.

Traditional ecology and biogeochemistry have neither measured nor predicted the behavior of ecosystems at large scales or over long periods of time, albeit with notable exceptions (Thornthwaite and Mather, 1955; Tucker et al., 1986; Houghton et al., 1983; Roughgarden et al., 1989). Few field studies have had the objective of understanding the behavior of ecosystems at large spatial scales (see Sellers et al., 1988 and Yonker et al., 1988) and most large-scale analyses have relied on data compiled from diverse sources (Meentemeyer, 1988; Vitousek, 1982). Currently, ecosystem models developed for plot studies are being used for spatial analysis at subcontinental scales assuming no interactions via hydrology or the atmosphere (Schimel et al., 1990; Pastor and Post, 1988). Simple models of biophysical interactions have been attached to atmospheric models to allow atmosphere-biosphere interactions, but in these models much of the biology is static (Sellers et al., 1986; Sato et al., 1989).

While great progress has been made in simulating the behavior of ecosystems with prescribed boundary conditions (e.g., material input/output, climate), understanding the behavior of coupled systems is in its infancy. Two problems seem immediately limiting to progress in this area. First, we have limited ability to extrapolate rates of biogeochemical cycling to large and heterogeneous areas (Matson et al., 1989). Second, considerable barriers exist to coupling atmospheric dynamics and hydrological transport models to models of production and biogeochemistry. The two problems are not independent since much variation in rates of biological processes is due to variations in climate and hydrology.

Coupling models of primary production to models of decompostion in soils created new behavior modes in ecosystem models, modes which are central to our current understanding of the effects of climate change (Schimel et al., 1990; Pastor and Post, 1988). It is likely that coupling models of ecosystems to atmospheric and hydrological models will similarly allow new behavior modes in models of the earth system. Increasing the linkage between components may increase the realism of simulations. This may lead to increased predictability if the subsystems act to constrain each other's behavior. Alternatively, mathematical chaos and extreme dependence on initial conditions could occur (Lorenz, 1963; Grebogi et al., 1987). Either outcome from experiments with coupled models would advance our knowledge of the behavior of the biosphere.

2. Objectives

At a meeting in 1986, Bolin challenged the ecological community to predict evapotranspiration and CO_2 exchange for a grid of 200 km^2 resolution as a key step in improving earth system models (Bolin, 1988). Evapotranspiration (ET) is in a sense a simple problem, since it is constrained by the amount of precipitation and the energy available for evaporation. Because of its highly constrained nature, simple models (Thornthwaite and Mather, 1955; Running et al., 1989) have been relatively successful. However, ET rate is dependent upon the activity and amount of vegetation, which are not easy to predict. Vegetation amount is also not readily assessed regionally or globally. Solving the ET problem either for the contemporary world clothed in its actual vegetation cover or for the future under a scenario of altered greenhouse gases will require dynamic ecosystem models responsive to variations in climate and edaphic properties. Solving the ET problem requires the development of earth system models.

Success at modeling the earth system will probably require separation of the above two problems, (1) simulation of the contemporary world and (2) prediction of its future course, as their solutions may have somewhat different requirements. In this paper, we review several studies set in motion since Bolin's articulation of the ET problem and discuss lessons learned in those studies. We emphasize the rapid development of techniques for both spatial extrapolation

of ecosystem behavior and coupling ecosystems via the atmosphere or running water, as well as important unknowns that persist. Advances in the understanding of ecosystem responses to changing resources are basic to solving both of these problems, and modeling of resource limitation and interactions is a continual theme in what follows.

3. Control of ecosystem processes

The phrase "ecosystem process" implies processes that are the collective result of the activity of many species (i.e., primary production, decomposition, carbon storage), processes carried out by a small number of species that affect the entire system (i.e., nitrogen fixation), and processes that involve interactions between the biota and physical forces (e.g., leaching of nitrate, evapotranspiration). Herbivory, invasion, succession, and extinction are also ecosystem processes, involving interactions between species and between the biota and the physical environment. The following discussion focuses on regulation of terrestrial biogeochemical cycles, even though these ecosystem processes (production, decomposition, nutrient cycling) have important and reciprocal interactions with species composition and successional dynamics of ecosystems (Pastor and Post, 1986; Tilman, 1985).

Net primary production (NPP) and organic matter balance of ecosystems are controlled by the interactive effects of climatic and edaphic properties. Control by the abiotic environment is modulated by the biochemical composition of organic matter produced, herbivory, and disturbance regime (fire, severe storms, etc.). Fig. 1 shows a simplified schematic based on a current ecosystem model (CENTURY). In this formulation, net primary production is determined by water availability (rainfall plus storage) subject to the constraint that plants must maintain critical C:element (N, P, S) ratios. Thus whole plant C:N ratio must not exceed ca. 100, and comparable limits (similar to Redfield ratios; Redfield, 1958) are set for the other elements. Control by light restricts growth as light interception nears 100%. While different schemes are used for production in other models (i.e., West et al., 1981; Pastor and Post, 1986), all embody the same concept: joint regulation by climate and a suite of limiting soil-derived nutrients, with light competition acting as a constraint. This concept is quite different from assumptions underlying many biophysical treatments (reviewed in Schimel et al., 1991).

Soil properties influence primary production through nutrient availability and water holding capacity. The ability of a soil to hold water is related to its structure, texture, and organic matter content. Soil water holding capacity is most strongly controlled by texture or grain size distribution. Fine grained soils hold more water and, hence under a common climate, may support higher NPP than coarse soils. In dry environments, this pattern may reverse, since coarse soils, which allow deeper infiltration, may have lower evaporation and higher transpiration rates than fine soils (Noy-Meir, 1973; Sala et al., 1988).

Nutrients are derived from three sources, mineralization of soil organic matter, the atmosphere, and weathering of soil minerals. Mineralization of nutrients occurs as organic matter is decomposed by microorganisms. A huge literature exists on this subject, covering its biochemistry, microbiology, the role of large organisms (protozoa, microarthropods), and control by the abiotic environment. In its essentials, decomposition is controlled by substrate organic chemistry, nutrient supply, and environmental variables that regulate microbial activity rates. Substrate organic chemistry is generally summarized by "lignin" content. Lignin is a mix of polymers resistant to microbial decomposition. As lignin content increases, decomposition rate decreases. Decomposer organisms require nutrients for growth, which may in part be derived from plant substrate. However, most plant substrates are low in nutrients relative to microbial tissue; plant material C:N ratios are 40–100 compared to 6–12 for most heterotrophs. Thus, nutrients are required from sources in the soil environment and are largely derived from the turnover of soil organic matter (C:N of approximately 10) and of the microbial population itself. Plant material with high lignin or low nutrient content constitutes a sink for nutrients, slowing down nutrient turnover and reducing plant nutrient availability; low lignin or high N material behaves in the opposite fashion. In practice, the organic chemistry of plant litter is often summarized by the lignin:N ratio (Melillo et al., 1984; Parton et al., 1987).

Soil organic matter is central to nutrient cycling

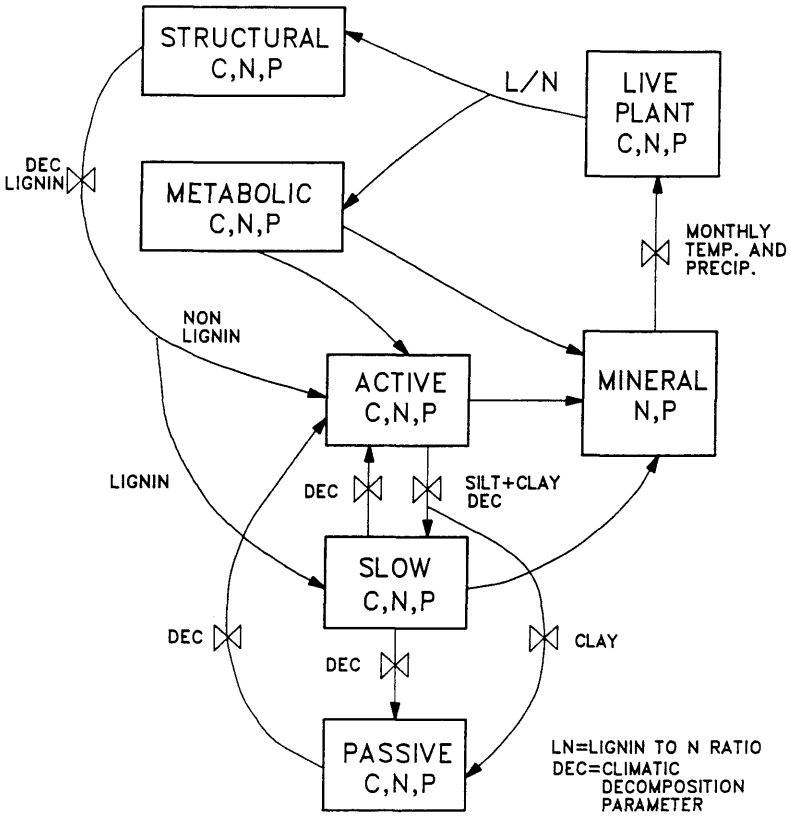

Fig. 1. Schematic of the CENTURY model. Note that flows into soil organic matter are partitioned into 3 pools based on turnover time (Active, Slow, Passive). Nutrient mineralization occurs as plant litter (in the Metabolic Pool) and soil organic matter pools are decomposed. These fluxes are influenced by climate (temperature, precipitation, DEC; DEC = climatic decomposition parameter) and soil texture. Maximum plant production is set by water availability and then constrained by nutrient supply and light limitation (i.e., self-shading).

and organic matter storage. Much of the world's organic carbon is stored in soils (Schlesinger, 1977) and this organic matter reserve is also a major reserve of plant nutrients. Although alternate model formulations for decomposition and soil organic matter formation exist (Fig. 2), all agree that plant debris is progressively decomposed into less labile and more nutrient rich forms (Aber et al., 1978). As the more decomposed forms are reached, decomposition rate slows, but nutrient release per unit carbon respired or metabolized increases. Nutrient mineralization may be dominated by intermediate forms in the decomposition sequence, with small amounts of available N derived directly from either fresh litter or stabilized humus (Parton et al., 1987).

Stabilization of humus appears to be governed largely by the overall decomposition rate (controlled by temperature and moisture) and by the formation of organo-mineral compounds. Organic matter stabilization decreases as mean annual temperature increases (Schimel et al., 1989; Burke et al., 1990), with low soil carbon levels and high mineralization rates in some tropical ecosystems providing an extreme example. Formation of organo-mineral compounds is enhanced by increasing surface activity of soil particles and so increases with increasing clay content (Parton et al., 1987; Sørensen, 1981; Oades et al., 1987). Different types of clay minerals also differentially stabilize organic matter (Strickland et al., 1988). In general, nutrient turnover (nutrient mineralized/

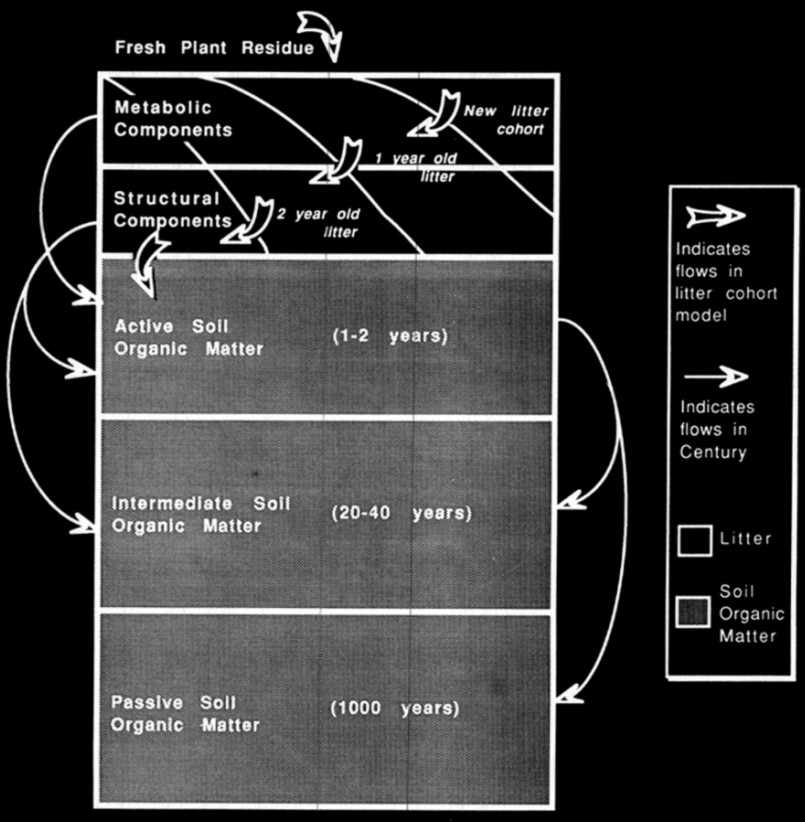

Fig. 2. The two most common schemes for simulating decomposition are the litter cohort model of Aber et al. (1987) and Pastor and Post (1986) and the structural/metabolic scheme used in CENTURY (Parton et al., 1987). The two schemes are not fundamentally different; the litter cohort model can be mapped onto the pools simulated in CENTURY. Time contours indicate the changing composition of litter cohorts in terms of metabolic (protein, soluble carbohydrate) and structural (lignin, lignocellulose) components. Only one or two soil carbon pools are simulated in most litter cohort models; the flow indicated from the last litter cohort into the soil should not be interpreted as a flow into the active fraction but rather as a flow into humus. In the litter cohort model, fresh plant litter flows into the youngest cohort. In CENTURY, the litter flow from dying vegetation is partitioned between structural and metabolic pools depending on the lignin and N contents of the vegetation.

unit organic nutrient) decreases with increasing clay content but absolute mineralization rate may increase, because of larger pool sizes (Schimel et al., 1985; Schimel, 1986).

Nutrient availability and water availability are often correlated within a climatic regime since both are related to soil texture. This is a critical conclusion in understanding the steady state behavior of ecosystems. This correlation could break down under rapid climate change and associated disturbance, and so the interaction between water and nutrient availability must be a focus of intensive research.

In summary, the type of model shown in Fig. 1 and exemplified by CENTURY (Parton et al., 1987) or LINKAGES (Pastor and Post, 1986) include much of what we know about regulation of terrestrial biogeochemical cycles. The models assume that abiotic and biogeochemical factors interactively constrain primary production and carbon storage. Water and N limitations are not independent and so should be correlated at steady state. Both

LINKAGES and CENTURY suggest complex behavior as systems depart from climatic steady state and climatic and biogeochemical constraints become uncoupled (Pastor and Post, 1988; Schimel et al., 1990).

4. Extrapolation

Two basic approaches to extrapolation of biogeochemical cycling have been developed. We refer to these as the "remote sensing" approach and the "geographic" approach. Hybrids exist and will likely become common.

4.1. Remote sensing

The remote sensing approach was pioneered by Fung et al. (1987) and is based on a strong relationship between net primary productivity and annual integrated light interception (Monteith, 1972). The normalized difference vegetation index (NDVI), calculated from the red and near-infrared bands of satellite sensors, is well correlated with intercepted photosynthetically active radiation (IPAR), as is its annual integral with annual net primary production (Sellers, 1985; Running et al., 1989; Goward et al., 1986). The original simple model of Fung et al. (1987) assumed that NPP could be calculated from NDVI using an empirically-derived scaling factor (often referred to as "conversion efficiency") to convert light interception to biomass production (or CO_2 uptake). They calculated respiration from temperature. This simple model adequately mimicked observed global seasonal pattern of atmospheric CO_2 concentrations.

The model of Fung et al. (1987) allowed calculation of a critical flow in terrestrial biogeochemistry but required empirical calculation of biome-specific conversion efficiencies. Their approach suggests an interesting inversion strategy for the CENTURY/LINKAGES class of models. While ecosystem models have not conventionally been parameterized in terms of light interception (in contrast to biophysical models), light interception is related to a number of key ecosystem variables. Sellers (1985) argued that instantaneous NDVI was an estimate of photosynthetic capacity or chlorophyll density. Subsequent research has broadly supported this conclusion. Chlorophyll density and photosynthetic capacity are strongly related to canopy N, and their time series (rather than time integral) may indicate N uptake and dynamics in the canopy (Field and Mooney, 1986; Evans, 1989; Schimel et al., 1991). While NDVI has often been interpreted as leaf area index (LAI, leaf area/ground area) or biomass, more useful interpretations may be in terms of chlorophyll density and, by correlation, N density and photosynthetic capacity. That NDVI predicts LAI or biomass in some cases may reflect constrained ratios of N per unit mass or per LAI within a study region of biome.

Can light interception be used as an input to models of ecosystems? Promising results have been obtained. Running et al. (1989) demonstrated a successful application of such a technique for a model of forest photosynthesis and transpiration. Data from the First International Satellite Land Surface Climate Project Field Experiment (FIFE; Sellers et al., 1988) in a Kansas tallgrass ecosystem show strong relationships between light interception and canopy N mass and N allocation (Schimel et al., 1991).

Long-term success of satellite data-driven models will depend next on development of algorithms to predict above- versus below-ground partitioning of C and N for a given aboveground time series of light interception. Current models assume that allocation above and belowground reflects the relative importance of aboveground (light) and belowground resources (water, nutrients) as factors limiting production (Coughenour, 1985). One simple model assumes that partial derivatives of production with respect to water, N uptake, and light are equal (Field, 1991). Well-constrained solutions to such an algorithm will be difficult if only light interception (NDVI) is available as an input. Such a treatment could better be used in a model where several environmental parameters are used as inputs, with soil moisture or rainfall being most useful, as in a hybrid model including geographic and remotely sensed inputs.

Development of models based on light interception will have to consider canopy structure. It is unlikely that any but the simplest relationships between light interception and ecosystem state or function will be preserved across vegetation physiognomies of diverse architecture and light-harvesting strategies. Canopy structure is intimately involved with light competition, which is a key control over growth in many ecosystems

(Schimel et al., 1991). Much research in physiological ecology has focused on the diverse responses of plants to varying light environments. A few unifying principles have emerged (Field, 1991; Hirose and Werger, 1987), but their application in complex or uneven-aged vegetation is still unclear. Ecosystem models run as inverse models using light interception will have to include a simple representation of canopy structure and radiative transfer.

New innovations in remote sensing may also aid in model inversion (Waring et al., 1987). High spectral resolution spaceborne spectrometers may be able to estimate canopy N, lignin, or other constituents directly (Wessman et al., 1988). These measurements, in combination with estimates of light interception, may sufficiently constrain production and decomposition to allow stable and unique model inversions. For example, forcing an ecosystem model with measured leaf lignin:N ratios would constrain its decomposition submodel. Lignin content of foliage may also be an indicator of nutrient availability, given some evidence suggesting that high lignin content is found on low nutrient sites. Successful use of remote sensing in extrapolation of models of biogeochemistry will require rethinking of traditional modeling approaches. The key will be to use plant physiology as the interface ecosystems between ecosystem properties and remote measurements. Modeling terrestrial ecosystems using satellite inputs will require better understanding of how plant physiology and chemistry reflect the balance between above- and belowground limiting factors.

Remote sensing imposes an awkward combination of temporal and spatial resolutions on the ecosystem modeler. Remote observations are instantaneous measurements, reflecting high frequency changes in vegetation. Prediction of vegetation activity over short intervals is done with highly detailed physiological or biophysical models (i.e., Johnson and Thornley, 1984). On the other hand, remote sensing provides a view of vegetation over a large area. This is traditionally the spatial scale of ecosystem models that have coarse time resolution and limited ability to predict the instantaneous state of vegetation, but that simulate system response to edaphic properties and other factors that drive spatial variability. Most efforts to resolve this problem of scale have used time-integrated remote measurements (e.g., annual $\int$ (NDVI); Goward et al., 1986; Fung et al., 1987). This, however, throws away seasonal information, with potential data on nutrient uptake, herbivory, and other dynamic aspects of ecosystems.

Remote sensing has a number of intrinsic limitations. First, the relatively small number of parameters accessible through remote sensing makes it likely that only relatively simple models can be driven by remotely measured inputs. Second, while remote sensing can aid in understanding current variation in ecosystem properties and in detecting change in ecosystems, models driven by remote measurements cannot be used to simulate biospheric response to future change, although they may provide initial conditions. Predictive models must derive input from geographic data bases describing edaphic and other controls. Nonetheless, models driven by remote observations will be essential to describe the current state of the earth, monitor near-term change, and estimate initial conditions for predictive modeling.

4.2. The geographic approach

Driving models of biogeochemistry with spatially explicit information on vegetation type and other ecosystem parameters was pioneered by Houghton et al. (1983) in their analysis of the terrestrial contribution to the atmospheric CO_2 budget. Developments in geographic information system (GIS) software and modeling techniques have allowed increasingly ambitious geographic modeling (Matthews and Fung, 1987; Burke et al., 1990), although global data bases on soils, climate, vegetation, and land management have not kept pace with either GIS or modeling software (Stewart et al., 1989).

The geographic approach defines the land surface as an array of cells with homogeneous properties. These cells may be elements of an uniform grid (e.g., 0.5° latitude × 0.5° longitude) (Gildea et al., 1986) or irregular polygons (Burke et al., 1990). Each cell is associated with tabular data describing salient ecosystem properties. Other data layers contain model output. Choice of properties described for each cell is determined by the parameter structure of the model. In recent regional simulations with CENTURY, Burke et al. (1990) used an irregular grid determined by an

overlay of a climate parameter (potential evapotranspiration/precipitation; PET/P) on a map of soil texture. A common climate time series and soil texture were used within each cell to drive a model run. Similar approaches have been applied in forests (Pastor, personal communication) and in wetlands (Costanza et al., 1990). In future applications, a climate "data layer" will be a simulation of atmospheric motion allowing linkage of cells though matter and energy transfers despite the otherwise intrinsically 1-D nature of the ecosystem model.

Aggregation and interpolation are common problems in developing spatial data bases. Climate data come from point measurements or climate model cell centroids and so must be interpolated to produce spatial surfaces. However, when cells are defined, these surfaces must then be segmented. When multiple data layers are interpolated separately and then overlaid, artificially small cells ("splinters") can emerge that are of a size not warranted given the resolution of the original data. To reduce this problem, Burke et al. (1990) used the annual PET/P index to generate cell boundaries, rather than monthly climate data (i.e., actual CENTURY inputs) which would have required overlaying a dozen climate maps for each parameter. On the other hand, problems also occur when surfaces are segmented into large cells if mapped variables are non-linearly related to responses. In that case, considerable within cell detail must be preserved or cell nonlinear weighted averages must be calculated to avoid such aggregation error in the final estimates. For example, soil texture is non-linearly related to soil carbon storage. Fine textured soils have disproportionately high carbon storage and so must be mapped with care. Soil texture may be averaged within a polygon, but a weighting function for the average must weight fine textured soils more heavily than other types (Burke et al., 1990).

To date, GIS-based simulations have been at regional scales (Gildea et al., 1986; Burke et al., 1990) or have employed very simple models (Esser, 1990). Use of this approach at global scales will require some additional detail. Simulations in temperate ecosystems have assumed minimal effect of clay mineralogy; this will not be true for simulations covering both temperate and tropical ecosystems. Few mapped data on soil P are yet available, yet this will also be required for tropical simulations. Simulation of non-steady state conditions will require information on human land use. Land use data sets remain primitive and have been incorporated into global GIS's at only very coarse resolutions (Matthews 1983, Wilson and Henderson-Sellers 1985). Here remote sensing of initial conditions and rates of change may prove invaluable. Simulation of trace gases (e.g., N_2O, CH_4) will require additional data, especially on hydrology and wetlands. Since significant trace gas production occurs in localized hot-spots where water or organic matter are concentrated, high resolution data or statistical descriptions of topography may be required. The development of models and data bases must proceed hand-in-hand since modeling is limited by the availability of data and data assembly should be guided by model requirements.

5. Coupling between systems

Linkage of ecosystem models to models of transport through either the atmosphere or hydrosphere is in an early stage of development; no linkage involving a model with the complexity of CENTURY or LINKAGES has yet been completed. A number of crucial initial steps have been taken. First, several atmospheric models have shown sensitivity to the inclusion of a model allowing regulation of surface water and energy budgets by vegetation. Inclusion of the Simple Biosphere Model (SiB) in a general circulation model of the atmosphere substantially altered rainfall patterns in midcontinental areas (Sato et al., 1989). The mesoscale atmospheric model RAMS simulated an alteration of winds at the boundary of high and low evapotranspiration areas which differed in vegetation cover (Segal et al., 1988). Another general circulation model of the atmosphere predicted substantial reduction of rainfall over the Amazon basin with vegetation removed (Shukla et al., 1990). These exercises, while preliminary, show striking sensitivity of the atmosphere to the state of the biosphere. Similar examples could be given for the effects of biogenic greenhouse gases on atmospheric heating (Dickinson and Cicerone, 1986).

While much attention has focused on the effect of linkage between ecosystems via atmospheric transport of water or through biogenic greenhouse

gases, mesoscale to global transport of chemicals also results in interactions between spatially separated ecosystems (Melillo and Steudler, 1989). Ecosystem processes are sensitive to levels of nutrient addition (Parton et al., 1987) and to ratios between resources (water:N, N:P), both of which could be altered if transport patterns change (Melillo and Steudler, 1989). We have often thought of atmospheric transport processes affecting ecosystems over very long time spans (Schimel et al., 1985), but recent work on forest decline has made the immediacy of such problems evident (Aber et al., 1989). Our analysis of nutrient storage in the U.S. Central Grasslands (Parton et al., 1987) showed striking correlation between annual rainfall and soil nitrogen. This appears to be due to a correlation between NH_4^+ deposition and precipitation. The source of NH_4^+ is apparently from NH_3 gas evolved from vegetation, soils, and herbivore excreta in other parts of the grassland ecosystem (Schimel et al., 1986). Thus, the nitrogen cycle of the entire region may be spatially integrated over pedogenic time via atmospheric transport of N. We do not know how the regional atmospheric N cycle has changed as a consequence of post-settlement agriculture and grazing management.

Hydrology similarly affects ecosystems through movement of both water and chemicals. Sophisticated ecosystem models have been coupled to watershed scale models of hydrology (Costanza et al., 1990; Vörösmarty et al., 1989)

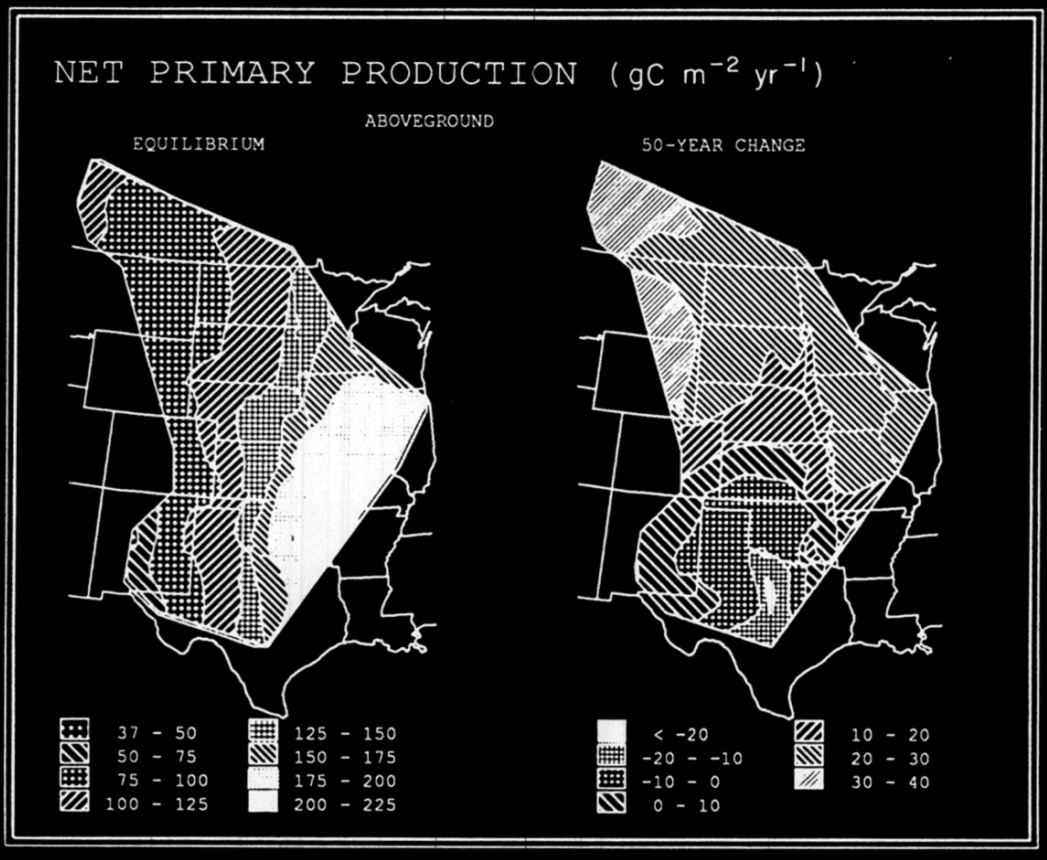

Fig. 3. CENTURY-simulated aboveground net primary production under current climate (right panel) and change in production 50 years after a change to a doubled-CO_2 climate for the North American Central Grasslands (Kittel et al., 1989). Climate forcing functions for the ecosystem model for the doubled-CO_2 climate were derived from the Goddard Institute for Space Studies General Circulation Model (Hansen et al., 1984).

and show strong linkage via water and nutrient flow. Although few models of regional hydrology exist (Band and Wood, 1988), simple hydrological and nutrient models have been coupled for the Mississippi watershed and have produced interesting predictions of effects of land use on nutrient export (Gildea et al., 1986). The use of hydrological models require access to appropriately scaled digital topographic data and algorithms for converting such data into drainage networks (Band, 1986). Such algorithms now exist, and high resolution topographic data are becoming more available.

Given that large changes in hydrology could occur as a result of climatic change, this type of model will be essential for prediction of change. Changes could occur if export of nutrients increased or decreased, impacting downstream environments. A change in export mode from water to wind transport, which could occur with drying of midcontinental areas, would have a major impact on terrestrial, aquatic, and marine systems. Effects due to altered transport of nutrients would occur over time spans longer than those we have been monitoring, but well within a century or so.

Simulation of linkage of ecosystems through either hydrology or the atmosphere will require the sort of geographic representation of the world described in the previous section as an underpinning. Relationships will be modulated by initial conditions at each site. In simulations of the effects of climate change on carbon storage and NPP in the North American Central Grasslands (Schimel et al., 1990; Kittel et al., 1989), we found strong dependency of the response of a cell to GCM-simulated climate change on its initial state. Texture modulated the response, with fine textured soils having smaller responses than coarse. While the simulated change in NPP (Fig. 3) was largely in response to GCM-predicted changes in precipitation, cells on the climatic extremes of the ecosystem (mesic and arid) had larger responses than cells under similar change regimes in the interior. Similarly, one would expect soil properties and initial vegetation to influence runoff of water and export of nutrients, but we did not simulate these fluxes.

Research on the effects of linking element and water budgets of remote ecosystems must consider a range of time scales. For example, current research on coupling atmosphere and biosphere models emphasizes short-term interaction through water and energy fluxes at time scales of one to several years. However, many important interactions are likely to take place at time-scales of decades to a century as steady state biogeochemical or biogeographic relationships become disrupted. This is especially true for geophysical and biological processes linked to the carbon cycle. Analysis of ecosystem change under directional climate changes requires studying biophysical interactions with the atmosphere over time scales of ecosystem change. As time spans increase, inclusion of only the biophysical aspects of vegetation become less and less appropriate and biogeochemical interactions become more important.

6. Validation

Validation of coupled models is extremely difficult. Traditional techniques of experimental manipulation are not generally applicable and many statistical concepts (e.g., replication) are difficult to apply. The time spans over which interactions occur, 10–100 years, result in challenges which highlight the value of long-term data sets. Several approaches to model validation may be adopted. Obviously, component sub-models must be individually tested as well as possible in an uncoupled mode. Study regions must be established where data exist, and these areas then used as benchmarks for model performance. The Amazon and Mississippi basins and the North Sea system are example candidates for monitoring biogeochemical cycles and hydrological transport. These areas are suitable because they are of a size relevant to the globe, have many data, and are of socio-economic importance. Similarly, the North American Central Grasslands and sub-Saharan Africa are suitable study areas for ecosystems linked by atmospheric transport of water vapor, dust, and chemicals. This is an immense enterprise, but individual research groups have undertaken initial stages of such efforts (Burke et al., 1990; Moore and Melillo, personal communication).

At a minimum, regional and global terrestrial ecosystem models should reproduce key features of the geographic distribution and temporal behavior of ecosystem properties. Remote observations will play a key role as one of the few data types that are

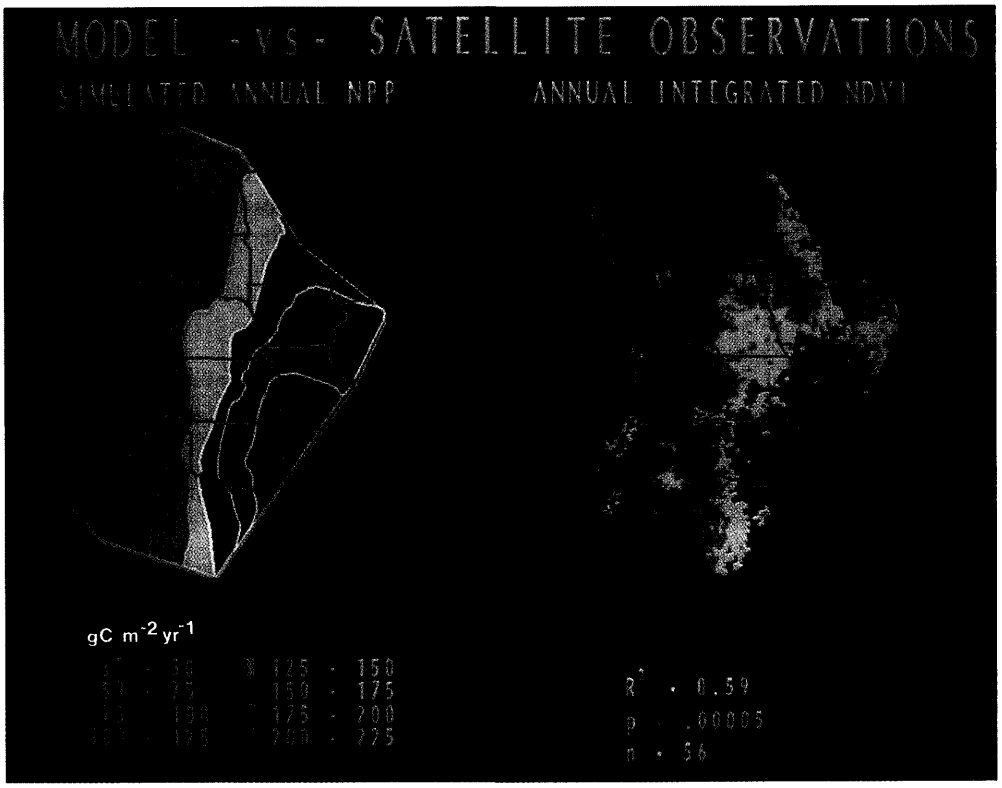

Fig. 4. Comparison of CENTURY-simulated NPP (right panel) and the annual integral of the Normalized Difference Vegetation Index (NDVI), averaged over four years (1983–86), from NOAA AVHRR data. The two fields of data have a correlation of 0.77 (r, $p < 0.0001$). The NDVI color scale was matched to that of NPP using linear regression. The correlation is based on a random sampling of the two data fields, using 56 observations; this was done because the data sets were not gridded identically.

inherently spatial and which increasingly provide high temporal resolution information. Remote observations serve well to estimate relative variation in both spatial and temporal domains. If proportional spatial differences in, say, light interception or canopy N can be established, then ground measurements can tie the relative data to an absolute standard. Fig. 4 shows a spatial comparison of simulated NPP versus the annual integral of NDVI derived from AVHRR.

The good correlation between these two measures, simulated NPP and $\int$ (NDVI), is interesting because, while NDVI is a surrogate for absorption of photosynthetically active radiation, we know that much of the natural and cultivated vegetation in this region is either water or nitrogen limited (Parton et al., 1987). This is indirect support for the hypothesis cited above that water, light, and nutrient limitation should be correlated as a consequence of plant evolutionary strategies (Field, 1991).

Fig. 5 shows a comparison of aboveground plant biomass for a site in the northern shortgrass steppe and the annual integral of NDVI during a climatic anomaly, a drought in 1986, demonstrating the utility of remote sensing in the time domain. It is again interesting that a change in NPP due to water or thermal stress is evident using a remotely sensed measure related to light interception. This result supports the hypothesis that plants adjust canopy light interception (leaf area and N allocation) to balance other limiting factors (Schimel et al., 1991; Field, 1991). This analysis and the previous one (Fig. 4) indicate that important biological dynamics in both time and space are captured by spectral vegetation indices, even though physical interpretation and development of improved indices remain research topics. Improvements in sensors, algorithms, and atmospheric correction techniques should increase the utility of biological remote sensing and its robustness.

The relationships between climate forcing functions, NPP, and light interception are quite linear, and so their spatial extrapolation using optical remote sensing may be fairly straightforward. However, similar relationships between climatic and edaphic controls, biophysical responses, soil carbon storage, and trace gas evolution are nonlinear (Burke et al., 1990); consequently, spatial variation in these processes will be much more difficult to infer from remotely sensed data.

Finally, recent and earlier paleorecords may provide information against which to test models.

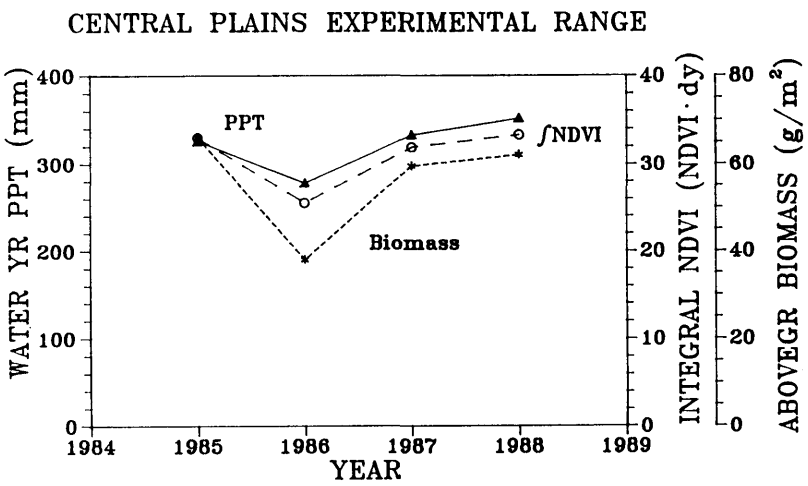

Fig. 5. Comparison of aboveground biomass, precipitation, and the annual integral of NDVI for 1985–1988, showing the effects of a drought in 1986, for the Central Plains Experimental Range in northeastern Colorado. The data sets were highly correlated with each other (NDVI versus rainfall, $r = 0.95$; NDVI versus biomass, $r = 0.99$). The biomass estimates are from stratified sampling of the shortgrass landscape (Lauenroth and Milchunas, personal communication).

This is a critical test, since it compares the model to a real long-term data set. However, this may be problematic since the paleorecord does not always record variables that match those in extant simulation models. In addition, successful comparison of biological data to the paleorecord can be misleading with respect to the task of prediction of future states. Models of ecosystems based on ecosystem response to slowly changing environments may predict key features of the paleorecord but not ecosystem response to the unprecedented rates of change which are occurring as a consequence of human activity.

When seeking to validate models of global change, we should attempt to subject these models to many tests, seeking to determine areas of strength and weakness as well as whether to accept or reject a model in toto.

7. Conclusions

The problem of spatial representation of ecosystem processes in simulation models are being addressed by current research. Pilot efforts using models of gas exchange (water and CO_2) driven by remote observations have been carried out at local and global scales (Running et al., 1989; Fung et al., 1987). A growing body of theory relates light interception by growing vegetation to ecosystem dynamics. Developing technology for better remote estimation of the state and chemistry of vegetation canopies will allow refinement of models driven by light interception. Sophisticated models driven by remote observation should allow timely assessment of ecosystem dynamics worldwide in the Earth Observing System (EOS) era. Simultaneously, models driven by geographic, edaphic, and land use data and climatic data or GCM output are being developed to allow analysis of past long-term changes (i.e., longer than the satellite record) and prediction of future changes. These simulation models rely on mapped data of edaphic and other properties to describe spatial variability in model parameters (i.e., Esser, 1990).

Both classes of models are based on a growing body of theory relating plant (Field and Mooney, 1986; Tilman, 1985) and ecosystem (Pastor and Post, 1986; Melillo et al., 1984; Parton et al., 1987; Schimel et al., 1990, 1991; Eisele et al., 1989) behavior to limitation by multiple resources (water, light, nutrients). While many realizations of the basic theory exist, agreement is growing on a core paradigm. This paradigm suggests a small set of critical environmental variables that must be included in data bases for extrapolative and predictive models. These include climate parameters, soil texture, and phosphorus level. A terrestrial ecosystem model based on these theoretical concepts will, at a minimum, allow consistent exploration of responses of the biota to environmental change. However, there are many probable sources of error. These include ignorance of rates of community and biogeographic response to rapid climate change, of interactions through altered plant architecture, and of ecosystem response to land use change. Better geographic data describing rates of change in the forcing functions, including climate, atmospheric chemistry, and land use, are urgently required.

It is critical to ask the question "how do connections between ecosystems via the atmosphere or hydrosphere cause behavior that is different from that predicted assuming weak interaction?" It is implicit in much ecological research that ecosystems are more strongly controlled by internal interactions than by coupling to other systems. This is in part a problem of scale; few long-term or large scale studies have been conducted of biogeochemical cycling. The time scale at which biogeochemical coupling between systems is evident, decades to a century or so, is poorly understood. We may know more about process and dynamics over paleoecological time (100–10,000 years) than we do about changes at a time scale of a century or so. Evidence from studies of herbivory (Schimel et al., 1986), atmospheric deposition (Melillo and Steudler, 1989; Aber et al., 1989), population dynamics (Roughgarden, 1989), and land surface climatology (Sato et al., 1989; Dickinson, 1987; Pielke and Avissar, 1990) suggests that the assumption that internal regulation far exceeds external regulation is false over time scales of decades to a century or so. Studying interactions between ecosystems at landscape to global scales will require new measurement approaches for empirical studies and new types of models. More importantly, we need a conceptual framework within which to analyze ecosystems as part of a linked whole (i.e., the biosphere or earth system), rather than as separate entities (grasslands, forests,

wetlands, etc.). While the nature and reality of ecosystems and boundaries between them has been argued ad nauseam, the idea of ecosystems as interacting regions within the biosphere may in fact be a less problematic concept.

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REFERENCES

Aber, J. D., Botkin, D. B. and Melillo, J. M. 1978. Predicting the effects of differing harvest regimes on forest floor dynamics in northern hardwoods. *Can. J. For. Res. 8*, 306–315.

Aber, J. D., Nadelhoffer, J. K., Steudler, P. A. and Melillo, J. M. 1989. Nitrogen saturation in northern forest ecosystems—Hypotheses and implications. *Bioscience 39*, 378–386.

Band, L. 1986. Topographic partitioning of watersheds with digital elevation models. *Water Resour. Res. 22*, 15–24.

Band, L. and Wood, E. F. 1988. Strategies for large scale distributed hydrologic simulation. *Appl. Math. Comput. 27*, 23–37.

Bolin, B. 1988. Linking terrestrial ecosystem process models to climate models. In: *Scales and global change. Spatial and temporal variability in biospheric and geospheric processes* (eds. T. Rosswall, R. G. Woodmansee and P. G. Risser). Chichester: John Wiley & Sons, 109–124.

Burke, I. C., Schimel, D. S., Yonker, C. M., Parton, W. J., Joyce, L. A. and Lauenroth, W. K. 1990. Regional modeling of grassland biogeochemistry using GIS. *Landscape Ecol. 4*, 44–54.

Costanza, R., Sklar, F. H. and White, M. L. 1990. Modeling coastal landscape dynamics. *Bioscience 40*, 91–107.

Coughenour, M. B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. *Ann. Mo. Bot. Gard. 72*, 852–683.

Crutzen, P. J., Delany, A. C., Greenberg, J., Haagenson, P., Heidt, L., Lueb, R., Pollock, W., Seiler, W., Wartburg, A. and Zimmerman, P. 1985. Tropospheric chemical composition measurements in Brazil during the dry season. *J. Atmos. Chem. 2*, 233–256.

Dickinson, R. E. (ed.). 1987. *The geophysiology of Amazonia.* New York: John Wiley and Sons.

Dickinson, R. E. and Cicerone, R. J. 1986. Future global warming from atmospheric trace gases. *Nature 319*, 109–115.

Eisele, K. A., Schimel, D. S., Kapustka, L. A. and Parton, W. J. 1989. Effects of available P and N:P ratios on non-symbiotic dinitrogen fixation in tallgrass prairie soils. *Oecologia 79*, 471–474.

Esser, G. 1990. Modeling global terrestrial sources and sinks of CO_2 with special reference to soil organic matter. In: *Soils and the greenhouse effect* (ed. A. F. Bouwman). Chichester: John Wiley & Sons, 247–262.

Evans, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia 78*, 9–19.

Field, C. B. 1991. Ecological scaling of carbon gain to stress and resource availability. In: *Integrated responses of plants to stress* (eds. H. A. Mooney, W. E. Winner and E. J. Pell). Academic Press, in press.

Field, C. B. and Mooney, H. A. 1986. The photosynthesis-nitrogen relationship in wild plants. In: *On the economy of plant form and function* (ed. T. J. Givinish). Cambridge: Cambridge University Press, 25–55.

Fung, I. Y., Tucker, C. J. and Prentice, K. C. 1987. Application of AVHRR vegetation index to study

atmosphere-biosphere exchange of CO_2. *J. Geophys. Res. 92*, 2999–3016.

Gildea, M. P., Moore, III, B., Vörösmarty, C. J., Bergquist, B., Melillo, J. M., Nadelhoffer, K. and Peterson, B. J. 1986. A global model of nutrient cycling: I. Introduction, model structure and terrestrial mobilization of nutrients. In: *Watershed research perspectives* (ed. D. L. Correll). Washington, DC: Smithsonian Institution Press, 1–31.

Gosz, J. R. and Moore, D. I. 1989. Strontium isotope studies of atmospheric inputs to forested watersheds in New Mexico. *Biogeochemistry 8*, 115–134.

Goward, S. N., Tucker, C. J. and Dye, D. G. 1986. North American vegetation patterns observed with the NOAA-7 Advanced Very High Resolution Radiometer. *Vegetatio 64*, 3–14.

Grebogi, C., Ott, E. and Yorke, J. A. 1987. Chaos, strange attractors, and fractal basin boundaries in nonlinear dynamics. *Science 238*, 632–638.

Hansen, J., Lacis, A., Rind, D., Russell, G., Stone, P., Fung, I., Ruedy, R. and Lerner, J. 1984. Climate sensitivity: Analysis of feedback mechanisms. In: *Climate processes and climate sensitivity* (eds. J. E. Hansen and T. Takahashi). Washington, DC: American Geophysical Union, 130–163.

Hirose, T. and Werger, M. J. A. 1987. Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* (Berlin) *72*, 520–526.

Houghton, R. A., Hobbie, J. E., Melillo, J. M., Moore, III, B., Peterson, B. M., Shaver, G. R. and Woodwell, G. M. 1983. Changes in the carbon content of terrestrial biota and soils between 1860 and 1980. *Ecol. Monogr. 53*, 235–262.

Johnson, I. R. and Thornley, J. H. M. 1984. A model of instantaneous and daily canopy photosynthesis. *J. Theoret. Biol. 107*, 531–545.

Kittel, T. G. F., Schimel, D. S., Parton, W. J. and Galvin, M. O. 1989. Response of biogeochemical dynamics to climate change: Simulation of the North American Central Grasslands. *Bull. Ecol. Soc. Am. 70 (2, Suppl.), 170*. Abstract.

Lorenz, E. N. 1963. Deterministic nonperiodic flow. *J. Atmos. Sci. 20*, 130–141.

Matson, P. A., Vitousek, P. M. and Schimel, D. S. 1989. Regional extrapolation of trace gas flux based on soils and ecosystems. In: *Dahlem workshop on exchange of trace gases between terrestrial ecosystems and the atmosphere* (eds. M. O. Andreae and D. S. Schimel). Berlin: John Wiley & Sons, 97–108.

Matthews, E. 1983. Global vegetation and land use: New high-resolution data bases for climate studies. *J. Clim. Appl. Meteorol. 22*, 474–479.

Matthews, E. and Fung, I. Y. 1987. Methane emission from natural wetlands: Global distribution, area, and environmental characteristics of sources. *Global Biogeochem. Cycles 1*, 61–86.

Meentemeyer, V. 1988. Macroclimate and lignin control of litter decomposition rates. *Ecology 59*, 465–472.

Melillo, J. M., Naiman, R. J., Aber, J. D. and Linkins, A. E. 1984. Factors controlling mass loss and nitrogen dynamics of plant litter decaying in northern streams. *Bull. Mar. Sci. 35*, 341–356.

Melillo, J. M. and Steudler, P. A. 1989. The effect of nitrogen fertilization on the COS and CS_2 emission from temperate forest soils. *J. Atmos. Chem. 9*, 411–418.

Monteith, J. L. 1972. Solar radiation and productivity in tropical ecosystems. *J. Appl. Ecol. 9*, 747–766.

Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annu. Rev. Ecol. Syst. 4*, 23–51.

Oades, J. M., Vasallo, A. M., Waters, A. G. and Wilson, M. A. 1987. Characterization of organic matter in particle size and density fractions from a red-brown earth by solid-state ^{13}C N.M.R. *Aust. J. Soil Res. 25*, 71–82.

Parton, W. J., Schimel, D. S., Cole, C. V. and Ojima, D. S. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Sci. Soc. Am. J. 51*, 1173–1179.

Pastor, J. and Post, W. M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry 2*, 3–27.

Pastor, J. and Post, W. M. 1988. Response of northern forests to CO_2-induced climate change. *Nature 334*, 55–58.

Peterjohn, W. T. and Correll, D. L. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. *Ecology 65*, 1466–1476.

Pielke, R. A. and Avissar, R. 1990. Influence of landscape structure on local and regional climate. *Landscape Ecol. 4*, 133–135.

Prinz, B. 1988. Ozone effects on vegetation. In: *Tropospheric Ozone* (ed. I. S. A. Isaken). Dordrecht, The Netherlands: D. Reidel Publ. Comp., 687–689.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. *Am. Sci. 46*, 205–222.

Richey, J. E., Adams, J. B. and Victoria, R. L. 1990. Synoptic-scale hydrological and biogeochemical cycles in the Amazon River Basin: A modeling and remote sensing perspective. In: *Remote sensing of biosphere functioning* (eds. H. A. Mooney and R. J. Hobbs). Ecol. Study Ser. 79, New York: Springer-Verlag, 249–268.

Roughgarden, J., Gaines, S. and Possingham, H. 1989. Recruitment dynamics in complex life cycles. *Science 241*, 1460–1466.

Running, S. R., Nemani, R. R., Peterson, D. L., Band, L. E., Potts, D. F., Pierce, L. L. and Spanner, M. A. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation. *Ecology 70*, 1090–1101.

Sala, O. E., Parton, W. J., Joyce, L. A. and Lauenroth, W. K. 1988. Primary production of the Central Grassland Region of the United States. *Ecology 69*, 40–45.

Sato, N., Sellers, P. J., Randall, D. A., Schneider, E. K., Shukla, J., Kinter, III, J. L., Hou, Y.-T. and Albertazzi, E. 1989. Effects of implementing the Simple Biosphere

Model in a general circulation model. *J. Atmos. Sci. 46*, 2757–2782.

Schimel, D. S. 1986. Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. *Biogeochemistry 6*, 239–243.

Schimel, D. S., Stillwell, M. A. and Woodmansee, R. G. 1985. Biogeochemistry of C, N and P in a soil catena of the shortgrass steppe. *Ecology 66*, 276–282.

Schimel, D. S., Parton, W. J., Adamsen, F. J., Woodmansee, R. G., Senft, R. L. and Stillwell, M. A. 1986. The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochemistry 2*, 39–52.

Schimel, D. S., Andreae, M. O., Fowler, D., Galbally, I. E., Harriss, R. C., Ojima, D., Rodhe, H., Rosswall, T., Svensson, B. H. and Zavarzin, G. A. 1989. Priorities for an international research program on trace gas exchange. In: *Dahlem workshop on the exchange of trace gases between terrestrial ecosystems and the atmosphere* (eds. M. O. Andreae and D. S. Schimel). Berlin: John Wiley & Sons, 179–183.

Schimel, D. S., Parton, W. J., Kittel, T. G. F., Ojima, D. S. and Cole, C. V. 1990. Grassland biogeochemistry: links to atmospheric processes. *Climatic Change 17*, 13–25.

Schimel, D. S., Kittel, T. G. F., Knapp, A. K., Seastedt, T. R., Parton, W. J. and Brown, V. B. 1991. Physiological interactions along resource gradients in a tallgrass prairie. *Ecology 72*, 670–682.

Schlesinger, W. H. 1977. Carbon balance in terrestrial detritus. *Annu. Rev. Ecol. Syst. 8*, 51–81.

Segal, M., Avissar, R., McCumber, M. C. and Pielke, R. A. 1988. Evaluation of vegetation effects on the generation and modification of mesoscale circulations. *J. Atmos. Sci. 45*, 2268–2392.

Sellers, P. J. 1985. Canopy reflectance, photosynthesis, and transpiration. *Int. J. Remote Sens. 6*, 1335–1372.

Sellers, P. J., Mintz Y., Sud, Y. C. and Dalcher, A. 1986. A simple biosphere (SiB) model for use within general circulation models. *J. Atmos. Sci. 43*, 505–531.

Sellers, P. J., Hall, F. G., Asrar, G., Strebel, D. E. and Murphy, R. E. 1988. The First ISLSCP Field Experiment (FIFE). *Bull. Am. Meteorol. Soc. 69*, 22–27.

Shukla, J., Nobre, C. and Sellers, P. 1990. Amazon deforestation and climate change. *Science 247*, 1322–1325.

Sørensen, L. H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biol. Biochem. 13*, 313–321.

Stewart, J. W. B., Aselmann, I., Bouwman, A. F., Desjardins, R. L., Hicks, B. B., Matson, P. A., Rodhe, H., Schimel, D. S., Svensson, B. H., Wassmann, R., Whiticar, M. J. and Yang, W. 1989. Group Report: Extrapolation of flux measurements to regional and global scales. In: *Dahlem workshop on exchange of trace gases between terrestrial ecosystems and the atmosphere* (eds. M. O. Andreae and D. S. Schimel). Berlin: John Wiley & Sons, 155–174.

Strickland, T. C., Sollins, P., Schimel, D. S. and Kerle, E. A. 1988. Aggregation and aggregate stability in forest and range soils. *Soil Sci. Soc. Am. J. 52*, 829–833.

Thornthwaite, C. W. and Mather, J. R. 1955. *The water balance.* Centerton, NJ: Drexel Institute of Technology.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat. 125*, 827–852.

Tucker, C. J., Fung, I. Y., Keeling, C. D. and Gammon, R. H. 1986. Relationship between atmospheric CO_2 variations and a satellite-derived vegetation index. *Nature 319*, 195–199.

Vitousek, P. M. 1982. Nutrient cycling and nutrient use efficiency. *Am. Nat. 119*, 553–572.

Vörösmarty, C. J., Moore, III, B., Grace, A. L., Gildea, M. P., Melillo, J. M., Peterson, B. J., Rastetter, E. B. and Steudler, P. A. 1989. Continental-scale models of water balance and fluvial transport: An application to South America. *Global Biogeochem. Cycles 3*, 241–265.

Waring, R. H., Aber, J. D., Melillo, J. M. and Moore, I. B. 1987. Precursors of change in terrestrial ecosystems. *Bioscience 36*, 433–438.

Wessman, C. A., Aber, J. P., Peterson, D. L. and Melillo, J. M. 1988. Remote sensing of canopy chemistry and nitrogen cycling in temperate forest ecosystems. *Nature 335*, 154–156.

West, D. C., Shugart, H. H. and Botkin, D. B. (eds.). 1981. *Forest succession: concepts and application.* New York: Springer-Verlag.

Wilson, M. F. and Henderson-Sellers, A. 1985. A global archive of land cover and soils data for use in general circulation climate models. *J. Climatol. 5*, 119–143.

Woods, K. D. and Davis, M. B. 1989. Paleoecology of range limits: Beech in the Upper Peninsula of Michigan. *Ecology 70*, 681–696.

Yonker, C. M., Schimel, D. S., Paroussis, E. and Heil, R. D. 1988. Patterns of organic carbon accumulation in a semiarid shortgrass steppe, Colorado. *Soil Sci. Soc. Am. J. 52*, 478–483.