

N94- 30629

209936

P- 22

*Development of Simplified
Ecosystem Models for Applications
in Earth System Studies:
The Century Experience*

*William J. Parton, Dennis S. Ojima,
David S. Schimel, and Timothy G. F. Kittel*

Introduction

During the past decade, a growing need to conduct regional assessments of long-term trends of ecosystem behavior and the technology to meet this need have converged. The Century model is the product of research efforts initially intended to develop a general model of plant-soil ecosystem dynamics for the North American Central Grasslands (Parton et al., 1983, 1987, 1988). This model is now being used to simulate plant production, nutrient cycling, and soil organic matter dynamics for grassland, crop, forest, and shrub ecosystems in various regions of the world, including temperate and tropical ecosystems (Parton et al., 1987; Sanford et al., 1991). This paper will focus on the philosophical approach used to develop the structure of Century. The steps included were model simplification, parameterization, and testing. In addition, we will discuss the importance of acquiring regional data bases for model testing and the present regional applications of Century in the Great Plains, which focus on regional ecosystem dynamics and the effect of altering environmental conditions.

The overall objective of this modeling activity was to develop a generalized ecosystem model that could simulate long-term (50 to 1000 years) changes in plant production, nutrient cycling, and organic matter caused by different management practices under actual or altered climatic conditions. The original goal was to simulate long-term trends of ecosystem processes and components over a large region. However, in recent years we have refined the model in order to simulate year-to-year variability of annual plant production and the seasonal dynamics of plant biomass.

To achieve the overall objective, it was necessary that the input variables be readily available and constitute a minimally sufficient data set to drive ecosystem processes. Given these conditions, the input variables that drive Century are monthly precipitation, average monthly daily maximum and minimum air temperature, soil texture, plant nutrient and lignin content, N inputs, and land management. The model was developed with these input variables specifically in mind, relative to temporal resolution; therefore, parameterizations of processes were made to accommodate these inputs. By achieving these conditions, the model lends itself to regional simulations including a large number of sites and has the potential to be linked to atmospheric mesoscale circulation and general circulation models (GCMs).

The Century model has been used extensively to simulate regional ecosystem dynamics for natural grassland (Parton et al., 1989; Burke et al., 1990) and agroecosystems (Cole et al., 1989) in the North American Central Grassland. The model simulates the spatial variability in the storage and fluxes of C and N within these systems and has recently been used to simulate the response of grasslands to potential climatic change scenarios (Schimel et al., 1990). In this paper we will describe the hierarchical approach used to simulate regional ecosystem dynamics and suggest how this type of model can be linked directly to GCMs.

Philosophical Approach

The philosophy used in developing Century was to use a minimal approach, that is, to use the simplest formulations of essential ecosystem processes. Thus, the model quantifies hypotheses based on our current understanding of these essential processes, which can then be objectively tested against observed data. We used those formulations of biological processes appropriate for the model time step (i.e., monthly) and input driving variables (monthly temperature and precipitation).

Model Description

Century is a general model for plant-soil ecosystems (Figure 1) and has been used to represent grasslands, forests, croplands, and shrublands. The grassland, crop, and forest systems have different plant production submodels that are linked to a common soil organic matter (SOM) submodel. The simplified flow diagram for the model shows that soil organic matter is separated into three fractions (active, slow, and passive) and that plant residue (dead shoots and roots) is split into structural and metabolic components. The

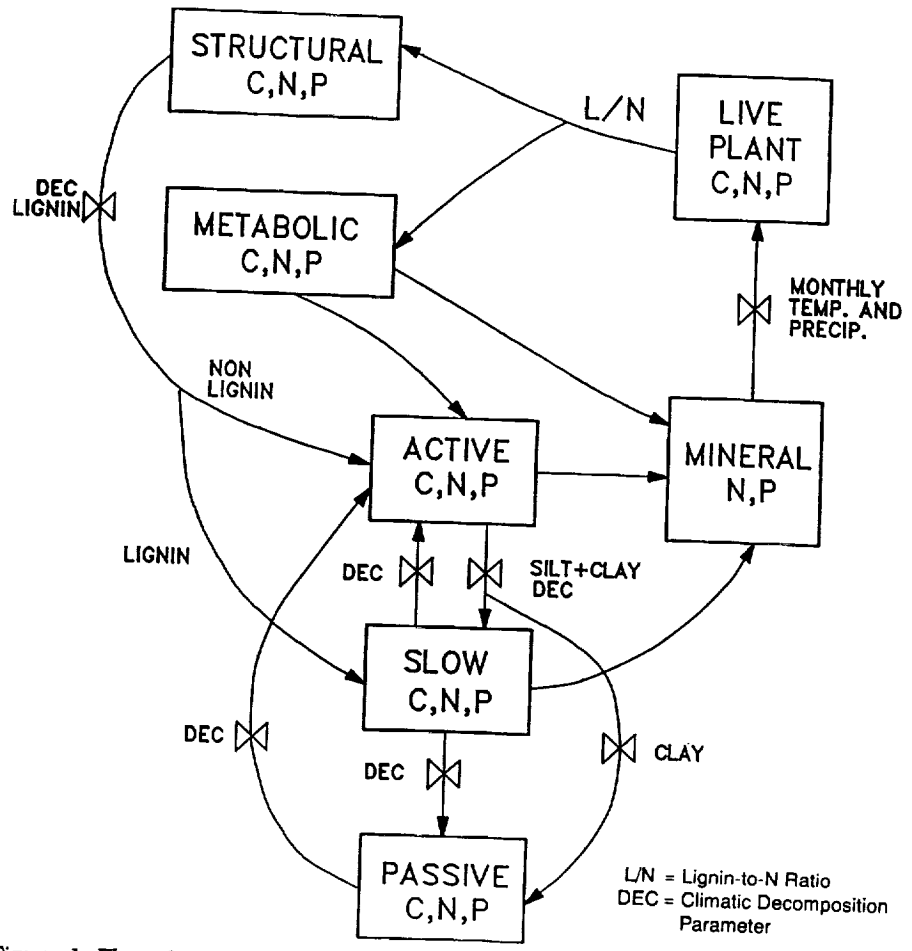


Figure 1. Flow diagram for the Century model.

turnover time of the SOM pools varies according to a soil abiotic decomposition parameter that is a function of monthly precipitation and temperature. Typical values for a temperate grassland site are 2, 20, and 1000 years, respectively, for active, slow, and passive SOM pools. Inputs of C to the soil are derived from plant residue (i.e., dead shoots and roots). The division of residue into structural (slow decomposition) and metabolic (fast decomposition) components is a function of the lignin-to-nitrogen (L:N) ratio of the material (i.e., a higher L:N ratio results in a greater partitioning of material into the structural fraction). The lignin fraction of the plant material does not go through the microbes (active SOM) and is assumed to cycle directly to the slow C pool. Soil texture influences the turnover rate of active SOM (higher rates for sandy soils), the stabilization of active SOM into slow SOM (lower for sandy soils), and the amount of passive SOM that is formed (higher for clay soils).

Plant production submodels simulate the dynamics of grasslands, agricultural crops, and woody (forest and shrubland) systems. The grassland model simulates grass growth and includes the effects of grazing and fire on plant production. The crop growth model simulates production for different crops (e.g., wheat and corn) and can simulate the effects of different fertilization levels, different cultivation practices, and the addition of plant residue on plant production. The forest model (Sanford et al., 1991) simulates forest growth and includes the effects of fire, large-scale disturbances (e.g., hurricanes), tree harvest practices, and fertilization on forest production. All of these plant production models assume that potential plant production is controlled by monthly temperature and precipitation and that plant production rates are decreased from these maximum rates if there are insufficient soil nutrients.

The grass (Figure 2) and crop growth submodels have the same structure and include live shoots and roots and standing dead material. In the grass model, allocation of C to shoots and roots changes as a function of the climate, grazing rate, and fire. The allocation pattern in the crop growth submodel is fixed for a specific crop. The forest growth model also uses a fixed allocation scheme, but in addition simulates the production of live shoots, fine roots,

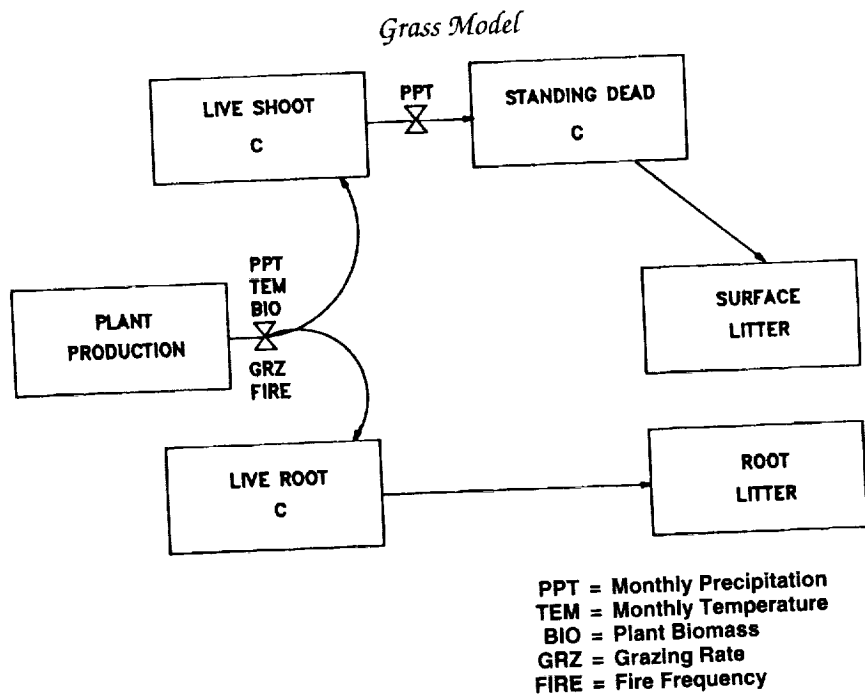


Figure 2. Plant production submodel flow diagram for grassland systems.

fine branches, large wood, and coarse roots. Wood decomposition is simulated in the forest model for three dead wood boxes (large wood, fine branches, and coarse roots). A detailed description of Century is presented in two papers (Parton et al., 1987, 1988) and in a user's manual for the PC version.

During the last few years, a number of simple ecosystem models have been developed that are amenable to regional studies over a long time period. Linkages (Pastor and Post, 1986) is a forest growth model that has been used extensively to simulate growth of different forest species and feedbacks between litter quality and plant growth. A comparison of the two models shows that soil texture, plant nitrogen and lignin contents, and climatic factors are the major controls over nutrient cycling in both models. A major difference is that Linkages uses a litter cohort approach, where the decomposition of each year's litter cohort is represented separately, while in Century new litter is aggregated into either the metabolic or the structural litter component (see Figure 3). Another major difference is that Linkages has one SOM pool while Century has three pools. We (J. Pastor and W. Parton) plan on making a formal comparison between Linkages and Century and anticipate that the utilization of the litter cohort approach will be more important for forest systems since litter quality (i.e., lignin and nitrogen content) is much more variable for forest species and litter types (e.g., large wood, fine wood, fine roots, and leaves) than for those observed in grassland ecosystems.

The model structure used in Century is similar to that used in some new simple ecosystem models such as the Vegie model (Aber et al., 1991) and the General Ecosystem Model (GEM) (Rastetter et al., in press). There are a substantial number of similarities between the Century, Vegie, and GEM models; however, decomposition of plant residue and plant production are calculated using different approaches. The importance of model differences is not clear, and we plan on making a formal comparison of these models.

Model Simplification and Parameter Determination

Century was developed by using a simple representation of biological processes to represent the dynamics of plant-soil systems. Two major model simplification processes were used: the hierarchical approach and the conceptual procedure.

Hierarchical Model Simplification Approach

The hierarchical approach is based on ideas presented by Kittel and Coughenour (1988) and Allen and Starr (1982). This approach takes advantage of high-resolution models with fine time and space

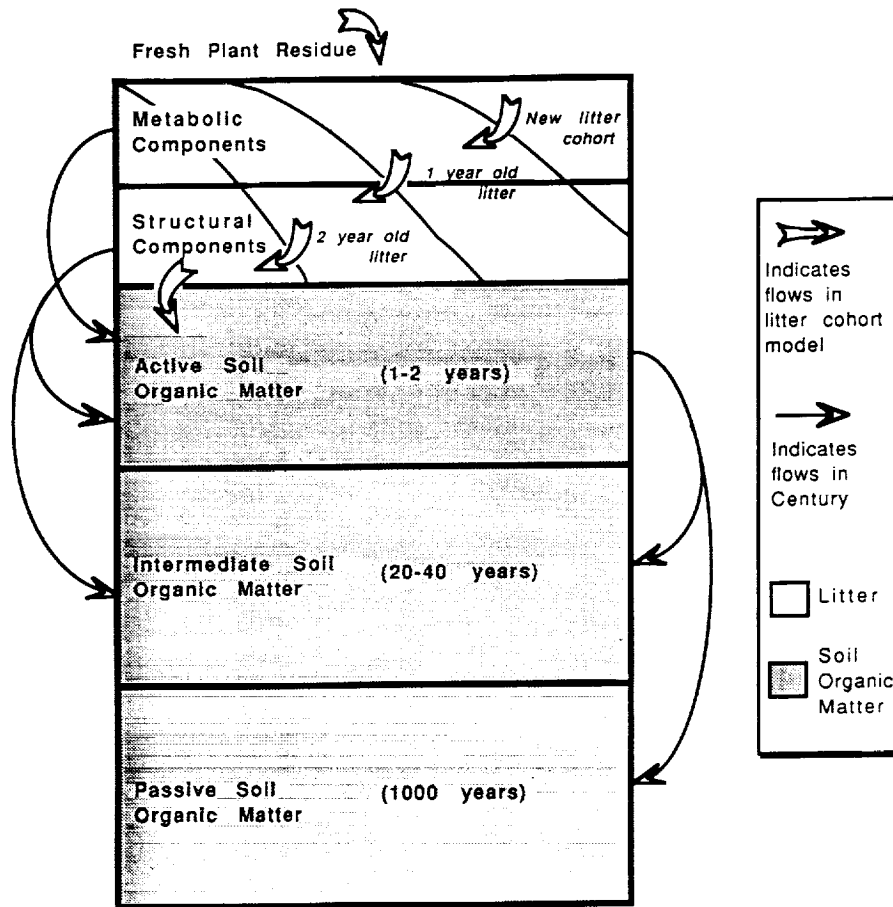


Figure 3. Comparison of Century model structure with cohort models (from Schimel et al., 1991).

scales to develop simplified relationships for coarser-scaled models. Model output from a fine-scaled model is transformed into an equation that is appropriate for a coarse model.

The hierarchical approach was used to derive the equation for the effect of monthly precipitation on the decomposition rate. A daily decomposition model and daily soil water and temperature models (Parton, 1978, 1984) were used to simulate daily decomposition rates for a 40-year time series using observed weather data to drive the models. These simulated daily decomposition rates were then aggregated on a monthly basis and used to develop a simplified equation for the effect of monthly precipitation on decomposition. A nonlinear least squares data-fitting procedure (Powell, 1965) was used to estimate the coefficients in the equation (Figure 4). This relationship is being refined in a new version of Century to include the effect of soil

texture on modifying the relationship shown in Figure 4. This hierarchical approach provides a methodology to determine the effect of precipitation on decomposition for a time step (monthly) that was not easily derived from existing decomposition data.

Conceptual Model Simplification Procedure

A conceptual procedure was used to develop the overall structure of Century (Figure 1). This process incorporates the essential concepts of more detailed nutrient cycling models that are needed to simulate the dynamics of the soil system for a monthly time step. Simplification of the model structure is based on extensive experience from field and laboratory studies in establishing these concepts and provides the basis to extend the concepts over longer time domains (decades to centuries) and over greater and more diverse geographic regions.

The structure of Century represents a simplification of concepts found in the process-oriented nutrient cycling models developed by

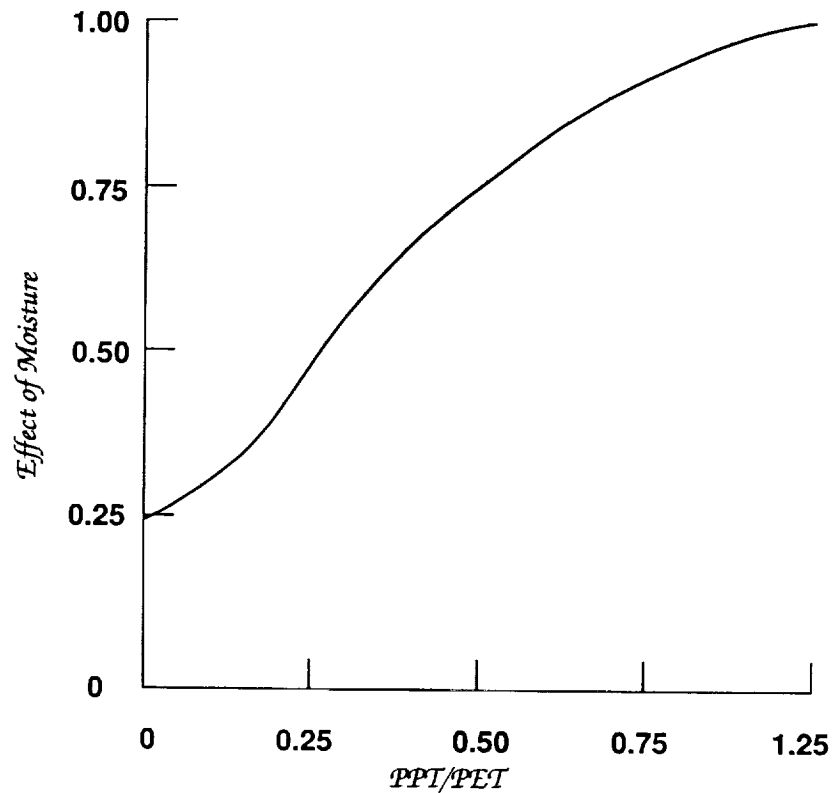


Figure 4. The effect of the ratio of precipitation (ppt) to potential evaporation (pet) on monthly decomposition rates (from Parton et al., 1987).

Hunt (1977) and McGill et al. (1981). McGill et al.'s model (Phoenix) is a detailed process-oriented nitrogen cycling and soil organic matter model (Figure 5) with a 0.2-day time step. The major structural simplification of the Phoenix model was accomplished by combining bacteria, fungi, and microbial products into a single state variable (active SOM). The specific effects of bacteria and fungi on the system were incorporated by using different microbial growth efficiencies for plant material decomposed at the soil surface and that decomposed in the soil. Surface litter is primarily decomposed by fungi, while soil litter is primarily decomposed by bacteria. This allowed us to simplify the model and still include the major role of bacteria and fungi. The conceptual simplification and aggregation of state variables in Century have resulted in the ability to test the potential role of microbial populations on SOM decomposition. In this case, the

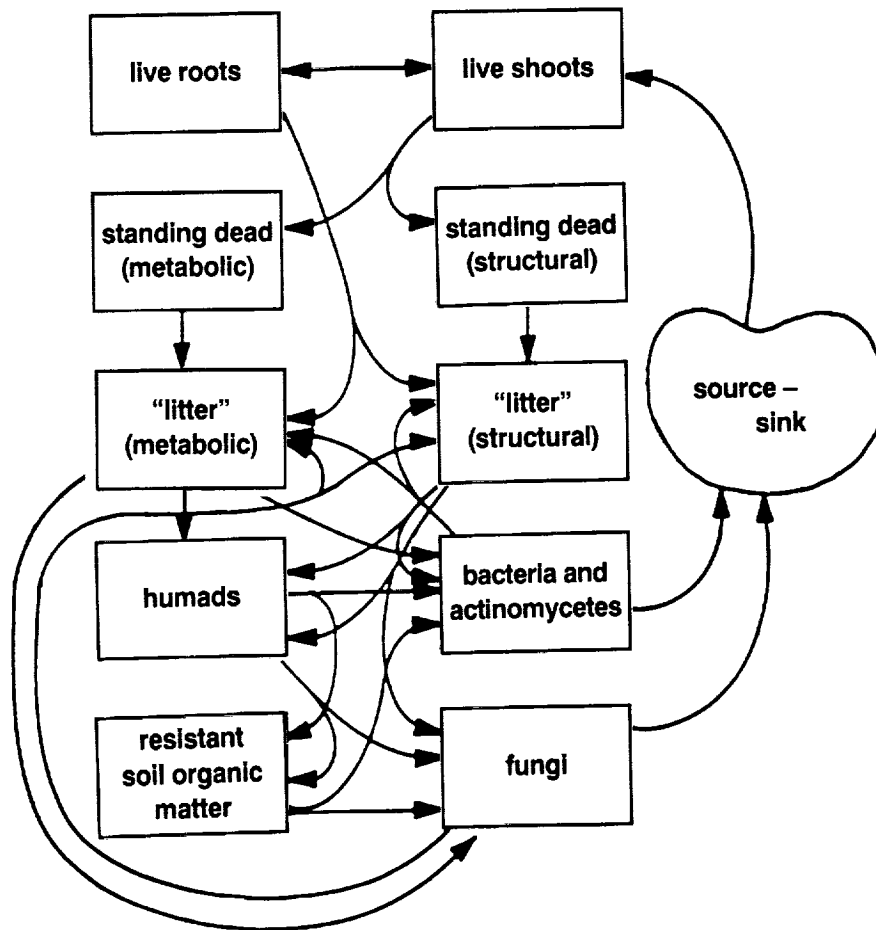


Figure 5. Carbon flow diagram for Phoenix soil organic matter model (from McGill et al., 1981).

model is testing a hypothesis that is based on literature data that is not definitive, and it could potentially be used to formulate a new hypothesis about the role of fungi and bacteria during decomposition. The Century model is also now being used to test the potential impact of earthworms on SOM dynamics. Some of the model parameters that are being modified include the decay rate for slow SOM and microbial growth efficiency for slow SOM.

Parameters Used

Most of the parameters in Century were determined by fitting the model to 15 long-term soil incubations where different types of plant material were added to the soil. A nonlinear data-fitting procedure (Powell, 1965) was used to determine the specific coefficients used in the model. A major contribution of the Century model was to include the effect of the soil texture on the stabilization of SOM. A comparison of the observed (Sorenson, 1981) and simulated effect of soil texture on soil C stabilization is shown in Figure 6. It is important to note that model coefficients determined during the original model fitting procedure have not been changed.

Model Testing and Development

The initial version of Century (Parton et al., 1987) was tested by comparing simulated long-term average plant production and steady state soil C and N levels with observed data from the U.S. Great Plains. The observed vs. simulated comparisons for soil C (Figure 7a) and plant production (Figure 7b) show that the model did an

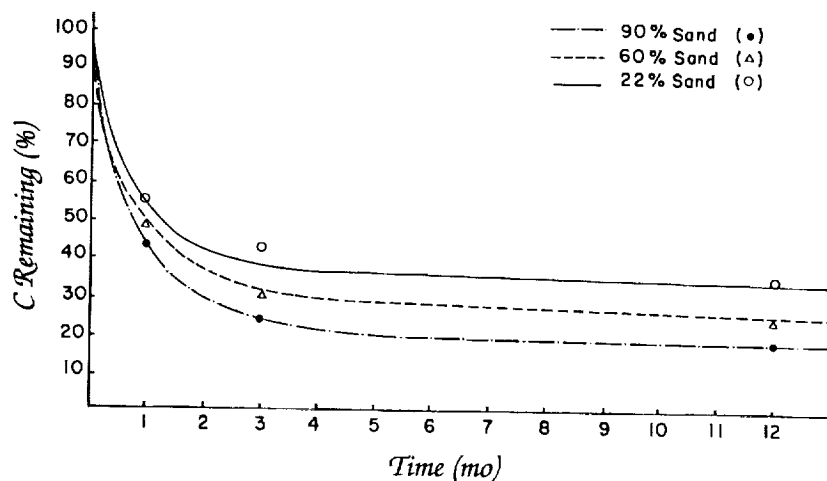


Figure 6. A comparison of observed and simulated effect of soil texture on soil C stabilization (from Parton et al., 1987).

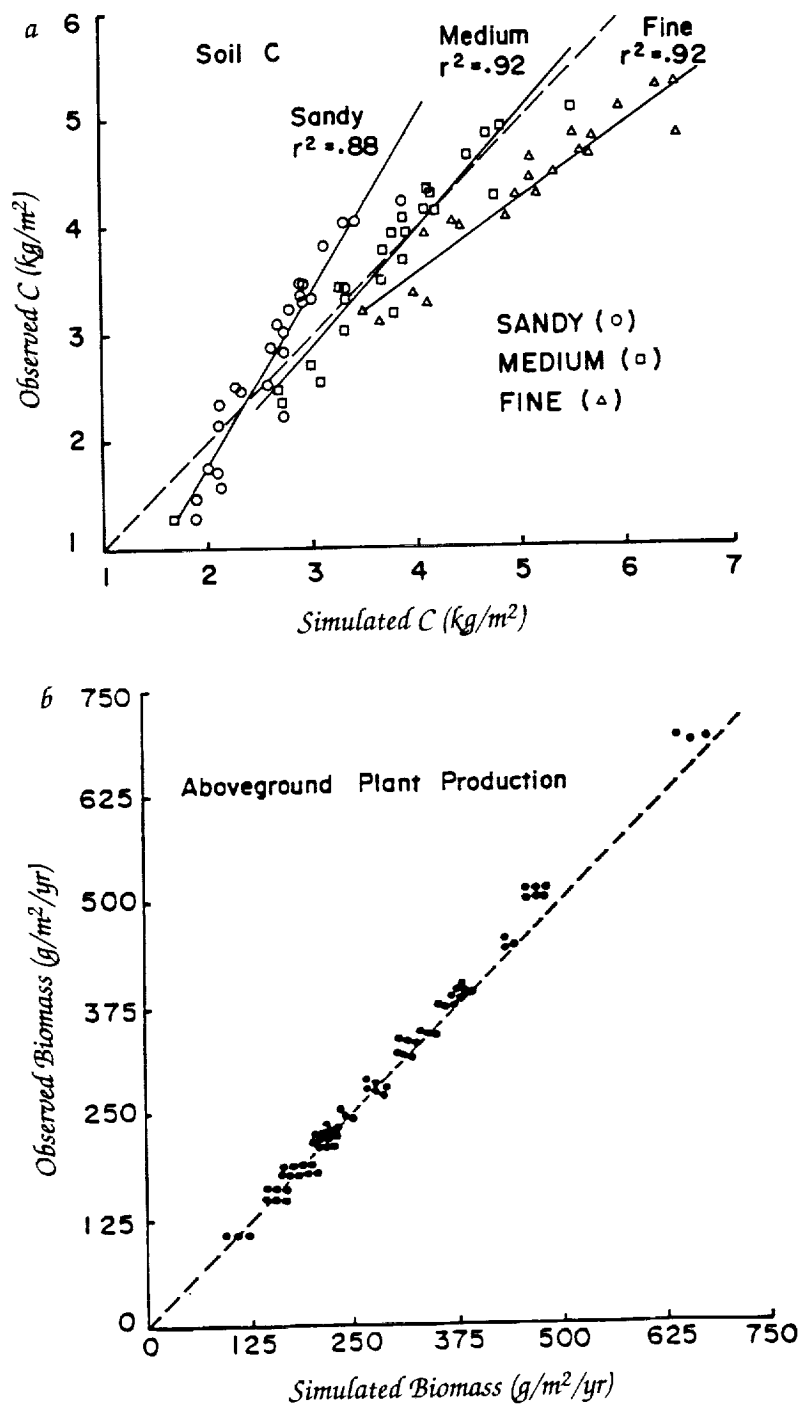


Figure 7. Comparison of observed and simulated (a) soil C levels and (b) plant production for different sites in the Great Plains (from Parton et al., 1987).

excellent job of simulating long-term grassland plant production for the Great Plains and did an adequate job of simulating soil C levels for different soil textures and abiotic environments in the region. One of the major parts of the model testing procedure was an analysis of observed regional plant production data (Sala et al., 1988) and soil C and N data (Burke et al., 1989) to develop a validation data set, since an adequate regional data set was not otherwise available for testing the model.

This regional soil data base for the Great Plains (Burke et al., 1989) was used to test and validate the ability of Century to simulate regional patterns of soil C and N for grassland soils (Parton et al., 1987). This data base is now being used to test new concepts about the formation of passive soil C (old soil C) and to test the ability of Century to simulate C and N losses due to cultivation. Recent data indicate that the slow SOM pool is not the primary source of passive soil C (the assumption made during the initial model development) and that the amount of passive soil C is higher for clay soils. The inability of Century to predict SOM dynamics for forest soils and to predict observed differences in C-to-N ratios of SOM for different soil textures (i.e., 13 to 14 for silty soils and 10 to 11 for clayey soils) has also helped to formulate these concepts. In the recent formulation, most of the passive soil C is derived from the turnover of active SOM, and passive SOM increases with clay content. By incorporating these concepts, the model correctly predicts observed differences in soil C-to-N ratios and predicts that the fraction of soil C in the passive pool will range from 30% for silty soils to 50% for clay soils. The regional soil data base is being used to test how well the model simulates soil textural differences in C-to-N ratios and steady state soil C and N levels. This demonstrates the importance of using regional data bases to test model performance and to help reformulate the model. Testing of general ecosystem models with a large number of sites is an essential part of the model development and testing procedure.

The original version of the model was tested by comparing simulated plant production and soil C and N levels with extensive data on plant production and soil organic matter (C and N) from the U.S. Great Plains (Parton et al., 1987). We are presently testing the model by using grassland plant production and soil organic matter data from 15 sites around the world. The testing of the model using data from many different grassland ecosystems has been an important part of the model development process and has suggested model changes which were necessary to formulate a truly general grassland ecosystem model.

During the last two years we have developed a more mechanistic version of the grassland plant production submodel with the objec-

tive of being able to simulate year-to-year variations in annual plant production and to simulate the seasonal dynamics of live plant biomass. The new model calculates maximum monthly plant production as a function of soil temperature, monthly precipitation, and the ratio of live shoots to dead shoots. The model also includes the effects of grazing and fire on plant root-to-shoot ratio and N content of the plant material (Holland et al., in press; Ojima et al., 1990). This new model was developed using long-term (1928–89) plant production data from a tallgrass prairie in eastern Kansas (Towne and Owensby, 1984; Owensby, unpublished data) and a seven-year time series of plant production data from a shortgrass prairie site in Colorado (Dodd and Lauenroth, 1978). Researchers measured plant production from 1970 to 1976 for control, irrigated (only), fertilized (only), and irrigated plus fertilized sites. Simulated annual plant production for the different treatments in the shortgrass prairie (Figure 8a) and a comparison of observed and simulated production (Figure 8b) show that the model reasonably simulates plant production for the different treatments ($r^2 = 0.85$). A comparison of observed and simulated annual aboveground plant production data from 1930 to 1968 for the tallgrass prairie site (Figure 9a) shows that the model has an observed and simulated r^2 of 0.60. Note that the observed plant production for these years is underestimated since the biomass measurements were made by clipping the biomass at a height of 5 cm, thereby omitting a portion of the grass biomass. Figure 9b shows the comparison of observed and simulated biomass data from 1970 to 1989 for the late-spring-burned and unburned sites. The model correctly estimated plant production for the very dry years (1981 and 1989) and correctly predicted the mean difference between the burned and unburned sites. Year-to-year variability was not as well predicted by the model; however, it is important to note that the standard deviation associated with the production estimates ranges from 100 to 200 g/m²/yr and makes it difficult to assess the significance of differences between modeled and observed data. In summary, Century reasonably simulated the impacts of fertilization, irrigation, and burning on plant production over an extended period of time, but further refinements may be needed to simulate smaller year-to-year variations in production.

The ability of the model to simulate seasonal biomass dynamics for live and standing dead biomass is now being tested by comparing the model results to monthly plant biomass data from four tropical grassland sites (Mexico, Kenya, Ivory Coast, and Thailand) and temperate grassland sites in the former USSR and Ireland. The results for the tropical sites are very promising and show that the model can correctly simulate the seasonal dynamics of live and dead

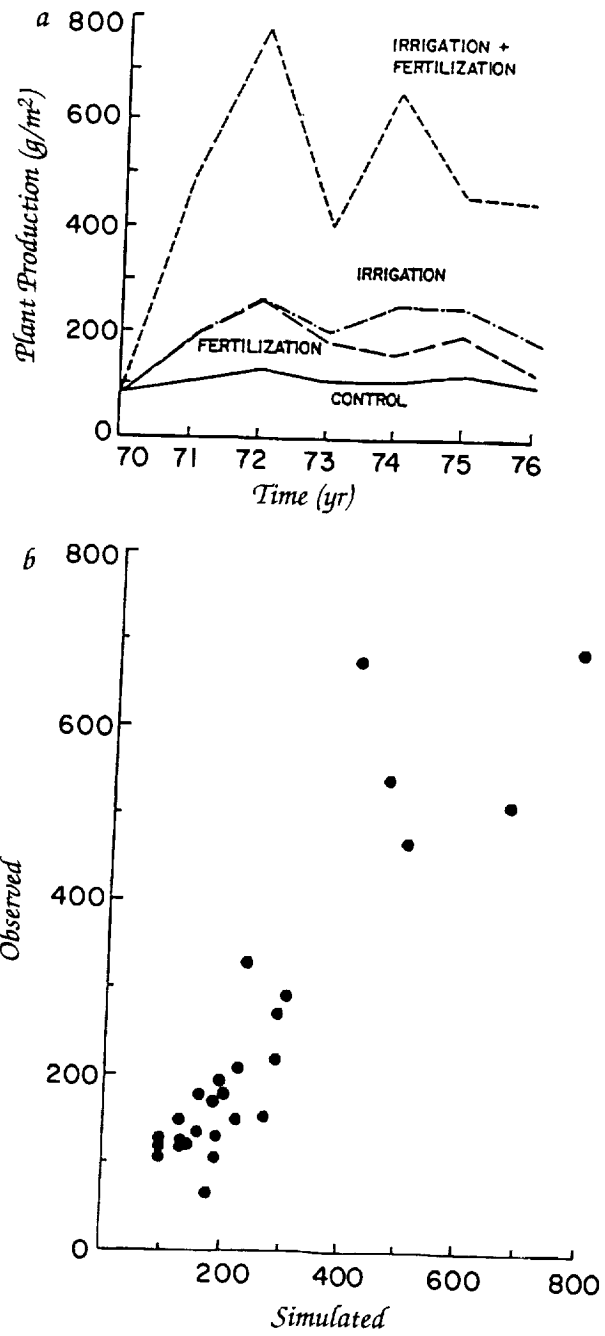


Figure 8. (a) Simulated patterns of plant production for control, fertilizer, irrigation, and irrigation plus fertilization treatments at a shortgrass prairie site and (b) comparison of observed and simulated plant production (g/m²) for these treatments.

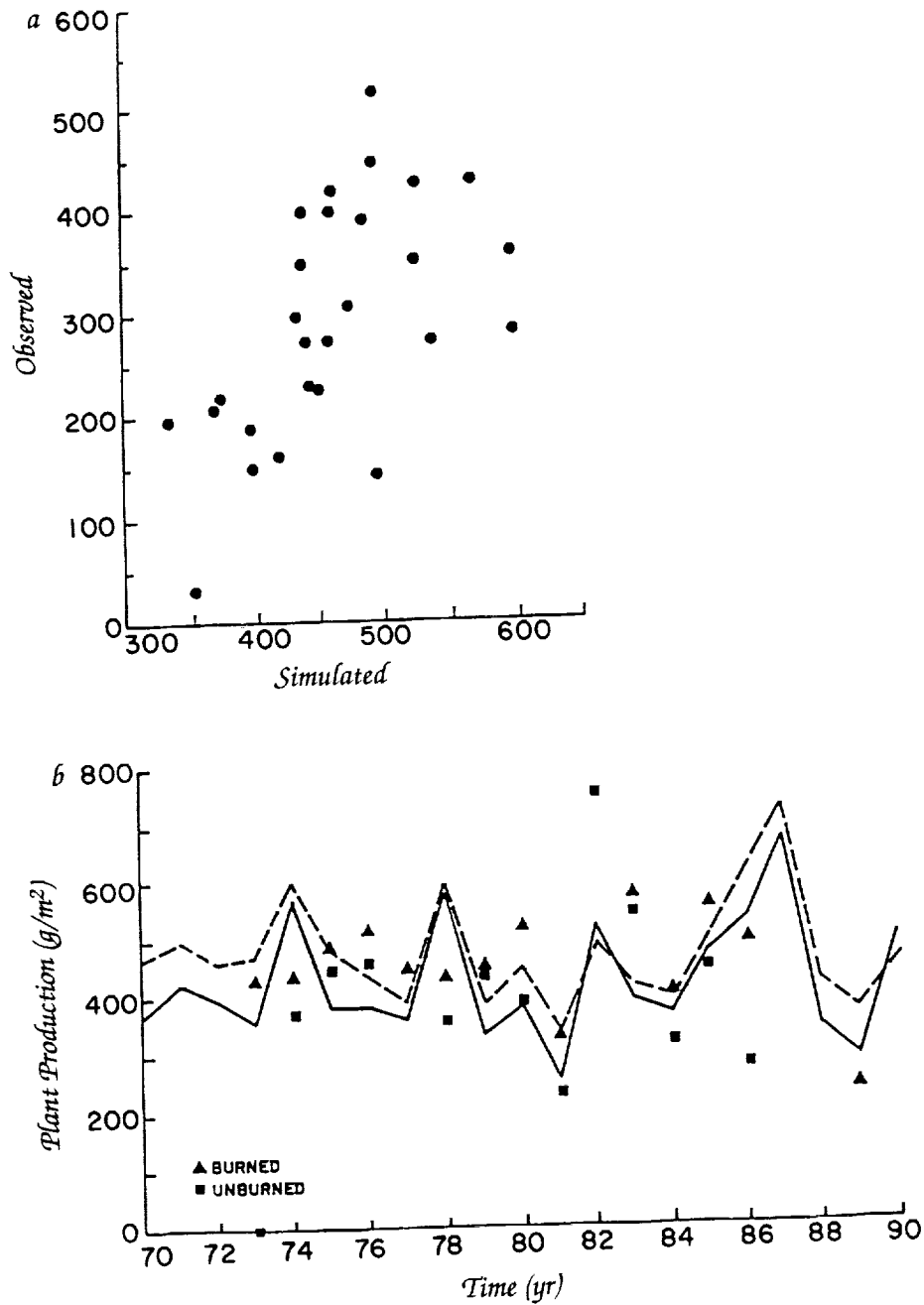


Figure 9. (a) Comparison of observed and simulated plant production (g/m²) for a tallgrass site from 1930 to 1968. (b) Comparison of observed and simulated plant production from 1972 to 1989 for an unburned (squares = observed, solid line = simulated) site and a late-spring-burned (triangles = observed, dashed line = simulated) site.

biomass and respond appropriately to fire events. The turnover rate of live roots, the rate of transfer from standing dead biomass to litter, and the root-to-shoot ratio are parameters that vary considerably among the sites. These differences are caused by plant-specific differences and abiotic factors such as snow. The observed and simulated live biomass for the Lamto site in Ivory Coast agree reasonably well (Figure 10). The results for the Russian grassland sites indicate that the model underestimated plant production and soil N inputs to these systems and suggest that the equations for the effect of rainfall on plant production and soil N inputs need modification. Such testing of the model at sites with diverse climatic conditions is an important part of model testing and validation and has led to the development of a more accurate and general grassland model.

Regional Modeling

The Century model has been used to simulate regional patterns of grassland biogeochemistry (Burke et al., 1990; Parton et al., 1989). A hierarchical approach is used to simulate the regional ecosystem dynamics (Figure 11). Century is a patch model which represents plant production as an aggregate variable from a mixture of plant species. The external driving variables for the model are soil texture and monthly climatic data. In scaling up from patch to toposequence in a landscape or to a physiographic unit, the diversity of soil types tends to increase. In making a regional simulation with Century, soil variability is accounted for by identifying key soil types

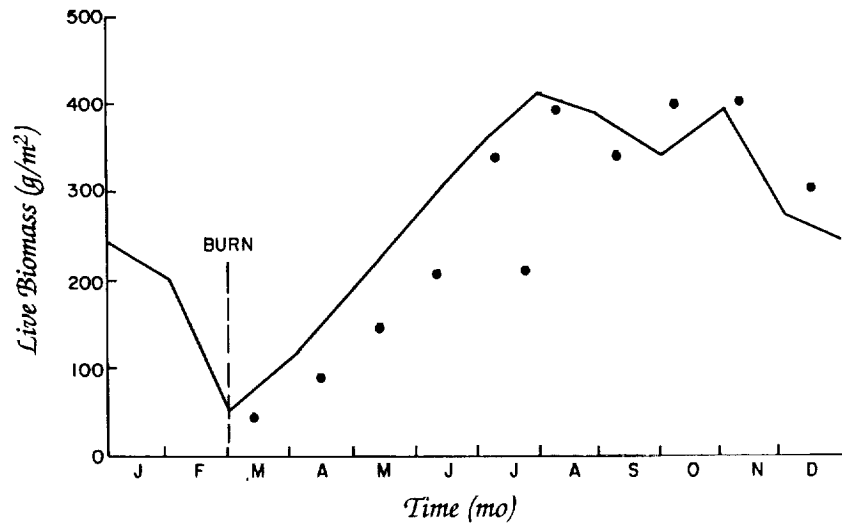


Figure 10. Comparison of observed and simulated live biomass for a burned grassland site in West Africa.

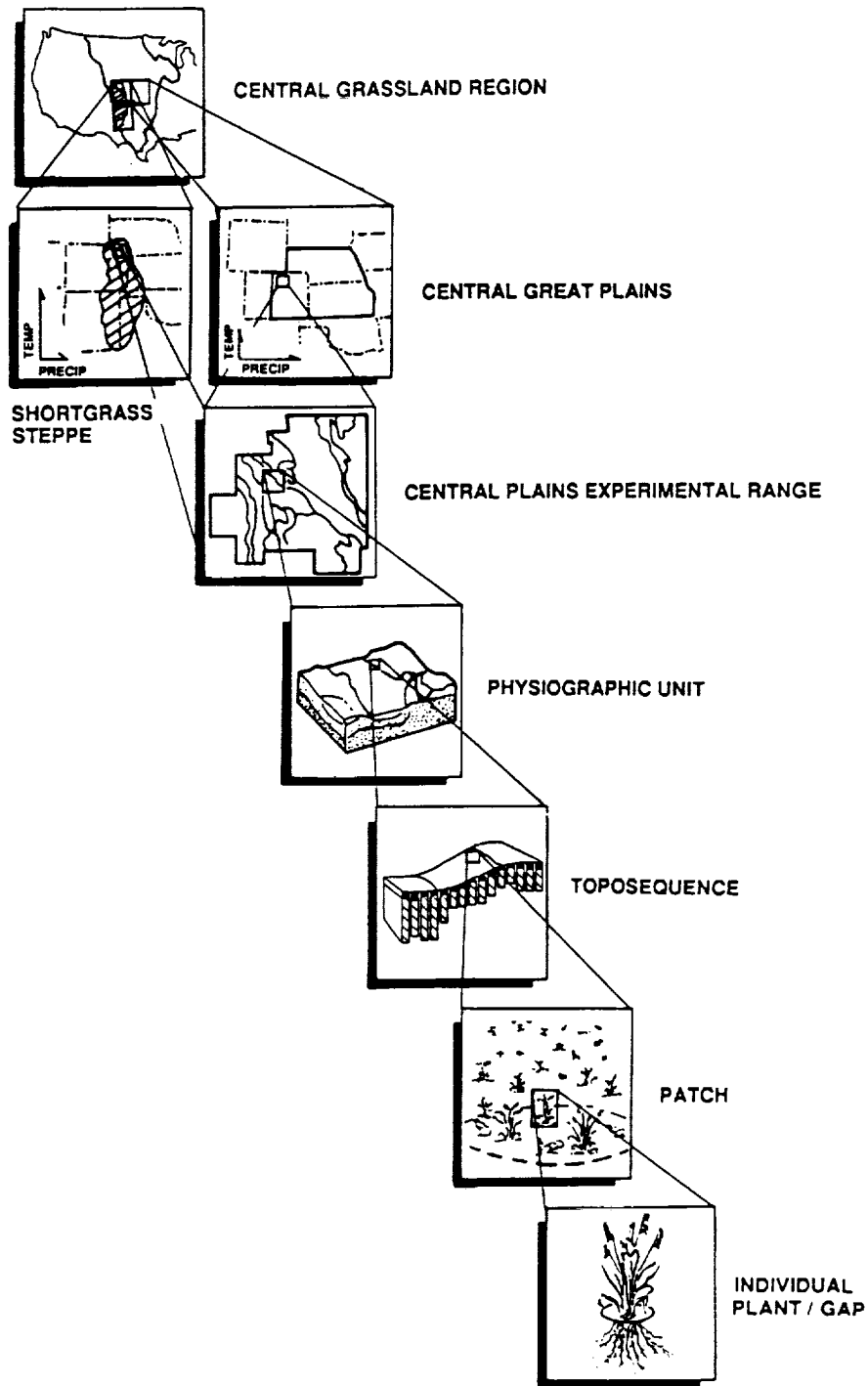


Figure 11. Hierarchical levels used in the regional modelling activity (from Kittel and Coughenour, 1988).

and parameterizing Century for each individual type. The results can then be aggregated as an areal average weighted mean. In addition, the range in climatic factors increases with the size of a region.

Overlaying regional soil variability on climatic variability within a region defines unique sets of driving variables for Century. This is facilitated by a geographic information system (GIS) that contains information on the spatial patterns of soil texture and monthly climatic data. A regional grassland simulation for northeastern Colorado (Burke et al., 1990) required 160 model runs to represent the unique combinations of soil texture and climate.

Across larger areas, dominant plant species changes may result in modifications to certain key ecosystem characteristics, such as the root-to-shoot ratio and plant lignin and nutrient content. For the Great Plains region we have developed equations which predict how the root-to-shoot ratio and plant lignin and nutrient contents change as a function of the annual precipitation. These equations work because plant communities change as a function of annual precipitation.

Simulated annual patterns for aboveground production, soil organic C, net N mineralization, and N gas flux (N_2O , NO_x , and NH_3) in northeastern Colorado (Figure 12) show that soil organic C is primarily controlled by soil texture, while regional patterns of the other variables correspond to annual precipitation (Burke et al., 1990). The effect of spatial resolution of input data indicates that regional estimates of the average plant production and N gas flux are relatively insensitive to changes in spatial resolution of inputs from 2.5 to 4000 km². In contrast, average soil C levels are substantially underestimated (14%) when the spatial resolution of inputs is decreased from 1500 to 4000 km². These results suggest that aggregation errors are noticeable for soil C levels when the spatial grid is coarse because of the nonlinear impact of soil texture on soil C levels.

Regional patterns for grassland ecosystem properties have been simulated for the North American Central Grasslands (Parton et al., 1989; Schimel et al., in press) based on regional variation in climate. While results are limited by the lack of detailed soil and land use data, the regional pattern of net primary production compares well with that of the annual integral of satellite-based vegetation index data (Schimel et al., 1991). At present, development of a regional GIS data base that includes climatic, land use, and soil data for the North American Central Grasslands is ongoing, and the data base will be used to more accurately simulate patterns of soil C and plant production.

Sensitivity of ecosystem processes and of fluxes of C and N to changes in climate and atmospheric CO₂ level has been evaluated

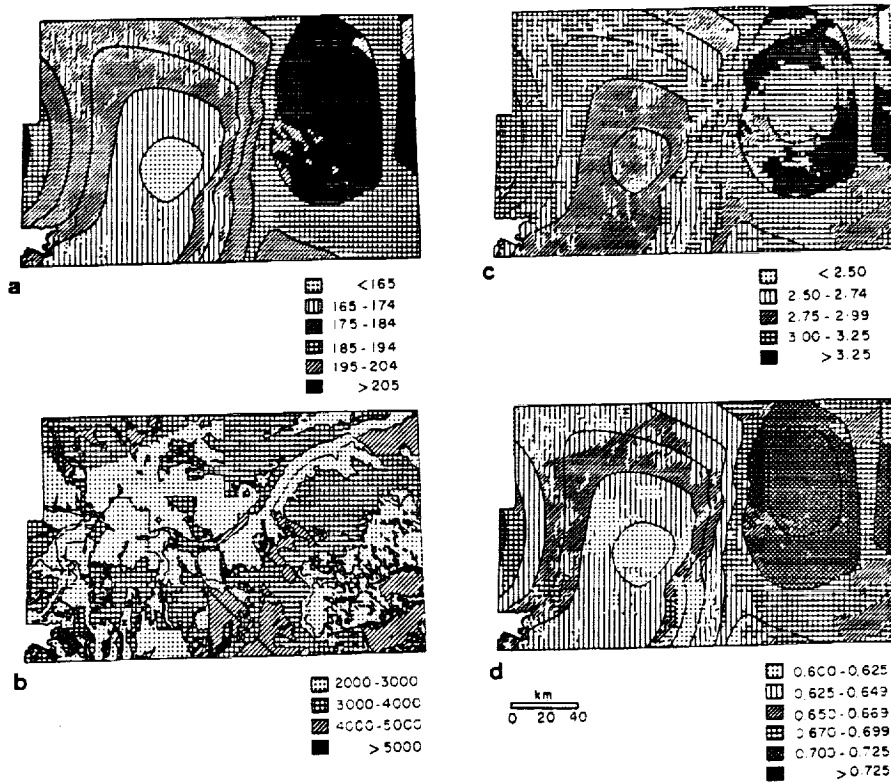


Figure 12. Simulated output from the Century ecosystem model for (a) net primary production in $g\ C/m^2/yr$, (b) soil organic carbon in $g\ C/m^2$ to 20 cm depth, (c) net annual N mineralization in $g\ N/m^2/yr$ to 20 cm depth, and (d) net annual N gas flux in northeastern Colorado in $g\ N/m^2/yr$. Lines overlaid represent annual precipitation contours (a, c, d) and soil texture classes (b) (from Burke et al., 1990).

for Century. Results from simulating the effects of a GCM CO_2 -doubling climate scenario (Hansen et al., 1988) suggest that plant production will generally increase in the northern portion of the North American Central Grasslands and decrease in the southern portion, largely in response to precipitation (Schimel et al., 1990; Kittel et al., in preparation). In addition, throughout the region there will be a net release of C from the soil and an increase in fluxes of nitrogenous gases (N_2 , N_2O , and NH_3).

Conclusions

There has been substantial progress in the development of simplified ecosystem models which have the potential to be incorporated into earth system models and to address regional issues regarding changes in land use or climatic conditions. An essential part of the

development of these models is detailed comparison of models with data from a large number of sites having different climate and soil characteristics. These comparisons are critical for testing this class of models and have greatly enhanced our understanding of the complex interactions, leading to substantial improvements in their structure. These models are capable of simulating the impact of climatic change on different ecosystems and can provide insight to potential changes in carbon (e.g., CO₂) and nutrient (e.g., N₂O) fluxes from ecosystems that, as radiatively active gases, play a role in global climate. A significant problem with including simple ecosystem models in earth system models is that the spatial scale of the atmospheric GCM models is still too coarse to incorporate the spatial heterogeneity in surface climate and land surface properties (e.g., topography) needed to represent natural ecosystems. This is illustrated by the fact that the southern part of the Great Plains, which includes short-grass, mid-grass, and tallgrass prairie ecosystems; montane systems; and agroecosystems that range from wheat-fallow to continuous corn systems, is covered by a single grid with 7.8° latitude × 10° longitude in the GCM at the Goddard Institute for Space Studies. Even with a very fine GCM grid network, it is anticipated that a need to consider subgrid diversity in agricultural land use and natural ecosystems must be explicitly addressed. This level of resolution will be necessary to represent the potential interactions between the atmosphere and the biosphere (Pielke and Avissar, in press; Avissar and Pielke, 1989; Avissar and Verstraete, 1990).

References

- Aber, J.D., J.M. Melillo, K.J. Nadelhoffer, J. Pastor, and R.D. Boone. 1991. Factors controlling nitrogen cycling and nitrogen saturation in northern temperate forest ecosystems. *Ecological Applications* 1, 303–315.
- Allen, T.F.H., and T.B. Starr. 1982. *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago, Illinois.
- Avissar, R., and R.A. Pielke. 1989. A parameterization of heterogeneous land surfaces for atmospheric numerical models and its impact on regional meteorology. *Monthly Weather Review* 117, 2113–2136.
- Avissar, R., and M.M. Verstraete. 1990. The representation of continental surface processes in atmospheric models. *Reviews of Geophysics* 28(1), 35–52.
- Burke, I.C., C.M. Yonker, W.J. Parton, C.V. Cole, K. Flach, and D.S. Schimel. 1989. Texture, climate, and cultivation effects on soil organic matter context in U.S. grassland soils. *Soil Science Society of America Journal* 53(3), 800–805.

- Burke, I.C., D.S. Schimel, C.M. Yonker, W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1990. Regional modeling of grassland biogeochemistry using GIS. *Landscape Ecology* 4, 45-54.
- Cole, C.V., D.S. Ojima, W.J. Parton, J.W.B. Stewart, and D.S. Schimel. 1989. Modeling land use effect on soil organic matter dynamics in the central grassland region of the U.S. In *Ecology of Arable Land: Perspectives and Challenges* (M. Clarholm and L. Bergstrom, eds.), Kluwer Academic Publishers, Dordrecht, The Netherlands, 89-99.
- Dodd, J.D., and W.K. Lauenroth. 1978. Analyses of the response of a grassland ecosystem to stress. In *Perspectives in Grassland Ecology* (N. R. French, ed.), Springer-Verlag, New York, 43-58.
- Hansen, J., I. Fung, A. Lacis, D. Rind, G. Russel, S. Lebedeff, R. Ruedy, and P. Stone. 1988. Global climate changes as forecast by the GISS 3-D model. *Journal of Geophysical Research* 93, 9341-9364.
- Holland, E.A., W.J. Parton, J.K. Detling, and D.L. Coppock. Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient. *American Naturalist*, in press.
- Hunt, H.W. 1977. A simulation model for decomposition in grasslands. *Ecology* 58, 469-484.
- Kittel, T.G.F., and M.B. Coughenour. 1988. Prediction of regional and local ecological change from global climate model results: A hierarchical modeling approach. In *Monitoring Climate for the Effects of Increasing Greenhouse Gas Concentrations* (R.A. Pielke and T.G.F. Kittel, eds.), Cooperative Institute for Research in the Atmosphere Workshop, Colorado State University, Fort Collins, 173-193.
- Kittel, T.G.F., D.S. Schimel, and W.J. Parton. Sensitivity of the North American Central Grassland ecosystems to climate change (in preparation).
- McGill, W.B., H.W. Hunt, R.G. Woodmansee, and J.O. Reuss. 1981. Dynamics of carbon and nitrogen in grassland soils. In *Terrestrial Nitrogen Cycles: Processes, Ecosystem Strategies and Management Impacts* (F.E. Clark and T. Rosswall, eds.), Ecological Bulletin, Stockholm, Sweden.
- Ojima, D.S., W.J. Parton, D.S. Schimel, and C.E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. In *Fire in North American Prairies* (S.L. Collins and L. Wallace, eds.), University of Oklahoma Press, Norman, Oklahoma.
- Parton, W.J. 1978. Abiotic section of ELM. In *Grassland Simulation Model* (G.S. Innis, ed.), Springer-Verlag, New York, 31-53.
- Parton, W.J. 1984. Predicting soil temperature in a shortgrass steppe. *Soil Science* 138, 93-101.

- Parton, W.J., J. Persson, and D.W. Anderson. 1983. Simulation of soil organic matter changes in Swedish soils. In *Analysis of Ecological Systems: State-of-the-Art in Ecological Systems* (W.K. Lauenroth, G.V. Skogerboe, and M. Flug, eds.), Elsevier, New York, 511-516.
- Parton, W.J., D.S. Schimel, C.V. Cole, and D. Ojima. 1987. Analysis of factors controlling soil organic levels of grasslands in the Great Plains. *Soil Science Society of America Journal* 51, 1173-1179.
- Parton, W.J., J.W.B. Stewart, and C.V. Cole. 1988. Dynamics of C, N, P, and S in grassland soils: A model. *Biogeochemistry* 5, 109-131.
- Parton, W.J., C.V. Cole, J.W.B. Stewart, D.S. Ojima, and D.S. Schimel. 1989. Simulating regional patterns of soil C, N, and P dynamics in the U.S. central grassland region. In *Ecology of Arable Land: Perspectives and Challenges* (M. Clarholm and L. Bergstrom, eds.), Kluwer Academic Publishers, Dordrecht, The Netherlands, 99-108.
- Pastor, J., and W.M. Post. 1986. Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. *Biogeochemistry* 2, 3-27.
- Pielke, R.A., and R. Avissar. Influence of landscape structure on local and regional climate. *Landscape Ecology*, in press.
- Powell, M.J.D. 1965. A method for minimizing a sum of squares of nonlinear function without calculating derivatives. *Computer Journal* 7, 303-307.
- Rastetter, E.B., M.G. Ryan, G.R. Shaver, J.M. Melillo, K.J. Nadelhoffer, J.E. Hobbie, and J.D. Aber. A general biogeochemical model describing the responses of the C and N cycles in terrestrial ecosystems to changes in CO₂, climate and N deposition. *Tree Physiology*, in press.
- Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the Central Grassland Region of the United States. *Ecology* 69(1), 40-45.
- Sanford, R.L., W.J. Parton, D.S. Ojima, and D.J. Lodge. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: Results of simulation modeling. *Biotropica* 23(4), 364-373.
- Schimel, D.S., T.G.F. Kittel, and W.J. Parton. 1991. Terrestrial biogeochemical cycles: Global interactions with the atmosphere and hydrology. *Tellus* 43(AB), 188-203.
- Schimel, D.S., W.J. Parton, T.G.F. Kittel, D.S. Ojima, and C.V. Cole. Regional simulation of grassland biogeochemistry. *Climatic Change*, in press.

Sorensen, L.H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biology and Biochemistry* 13, 313-321.

Towne, G., and C. Owensby. 1984. Long-term effects of annual burning at different dates in ungrazed Kansas tallgrass prairie. *Journal of Range Management* 37, 392-397.