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Modeling vegetation structure–ecosystem process interactions across sites and ecosystems

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ABSTRACT

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We describe an approach to investigating and understanding the interactions between vegetation structure and ecosystem processes that uses simulation models as a framework for comparison and synthesis across ecosystems arrayed along environmental gradients. The models are individual-based vegetation simulators and compartment models of nutrient cycling and soil water relations. Applications focus on interactions and feedbacks between vegetation structure (species composition, size structure) and ecosystem processes (water balance, nutrient cycling), and how these relationships vary across environmental gradients. Preliminary results indicate that life-history traits of plants have a profound influence on system-level behaviors, and that differences between grasslands and forests can be attributed largely to contrasting traits of grasses and trees. Experiments with linked vegetation–ecosystem process models diverge from simulations with either model run independently, suggesting the importance of feedbacks between details of vegetation pattern and ecosystem processes. The development of a fully coupled vegetation–ecosystem process model that is sufficiently general to simulate systems dominated by multiple lifeforms presents several conceptual, logistical, and scaling challenges, but also provides for new opportunities in ecosystem theory.

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INTRODUCTION

The relationship between pattern and process is a classic ecological theme (Lindeman, 1942; Watt, 1947; Whittaker and Levin, 1977). Bormann and Likens (1979) and others recently have pointed out the effects of changes in vegetation structure on processes such as productivity and nutrient cycling. Many ecologists recognize that pattern and process are mutually causal; changing ecosystem structure can feed back to alter rates of processes which, in turn, can cause additional changes in structure. Pastor and Post (1986) used a simulation model of forest nutrient cycling to illustrate feedbacks between nitrogen (N) dynamics in the soil, N content of litter, and N requirements of tree species. They found self-amplifying species compositional patterns that, depending on initial conditions, diverged with respect to the pathway of forest development.

The factors governing vegetation structure and ecosystem processes vary considerably within and among ecosystem types or biomes. In mesic forests, the availability of light is a frequent constraint on vegetation structure. As a forest environment tends from mesic to xeric or nutrient-poor, the effective constraint shifts from above- to belowground (Webb et al., 1978; Tilman, 1988; Smith and Huston, 1989). Under still drier conditions, the forest changes to grassland in which the principal constraint is belowground, suggesting patterns in the influence of environmental constraints in structuring ecosystems across broad environmental gradients.

Ecosystem types can be arrayed along environmental gradients (Holdridge, 1967; Whittaker, 1975) to investigate systematically trends in structure or function. For example, temperate forest and grassland can be represented as domains in an environmental space defined by mean annual temperature and precipitation (Fig. 1). Two fundamental issues regarding ecosystem behaviors along such gradients are: (1) changes *within* a particular environmental domain or biome are associated with changes in species composition, plant density or cover, and rates of processes; (2) changes *between* domains involve changes in the dominant lifeform with attendant potential feedbacks on ecosystem processes.

The objective of this paper is to describe an approach to investigating some of the relationships between vegetation structure and ecosystem processes using simulation models and environmental gradients represented by a collection of sites within the Long-Term Ecological Research (LTER) program in the United States (Fig. 2, Table 1). The sites include three grasslands, three forests, and two sites that we consider transitional. The models are individual-based vegetation simulators (Shugart, 1984; Huston et al., 1988) and compartment models of ecosystem processes (Parton, 1978; Parton et al., 1987).

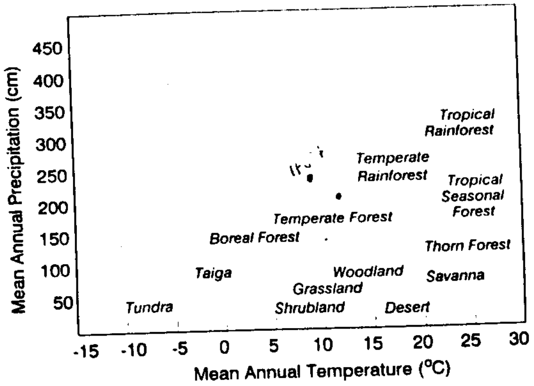


Fig. 1. Distribution of ecosystem types as domains in an environmental space defined by mean annual temperature and precipitation (redrawn from Whittaker, 1975).

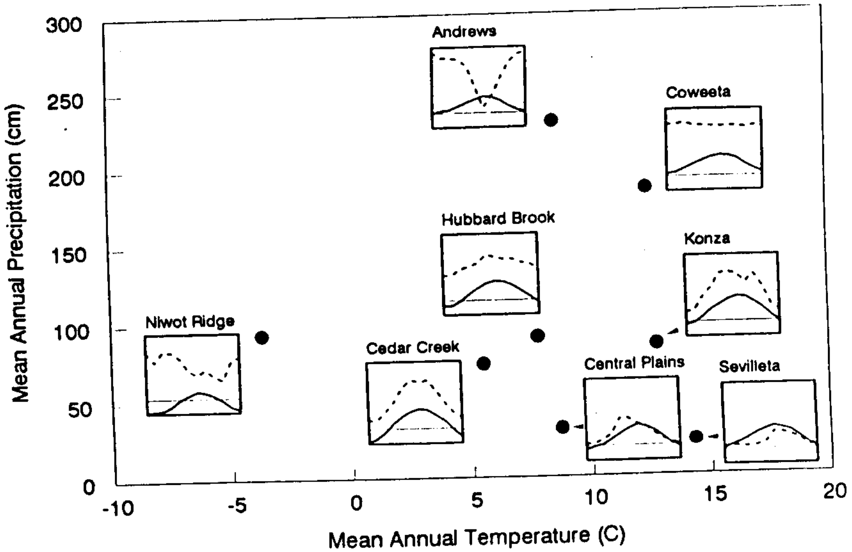


Fig. 2. Climatic distribution of LTER sites involved in cross-site comparisons. Insets are Walter diagrams (Walter, 1973), depicting monthly temperature (solid line) and precipitation (dashed line) on a scale such that 10°C = 2 cm precipitation; moisture deficits occur when the temperature line exceeds the precipitation line.

CONCEPTUAL APPROACH

Despite rapidly accumulating evidence of its importance, it is difficult, and in some cases impossible, to investigate empirically the feedback between pattern and process. The approach we are taking to the exploration of the link between vegetation pattern and ecosystem process across environmental gradients is the development, testing and application of ecosystem models representing an explicit set of assumptions concerning vegetation and soil processes. Our approach is underlain by a few general hypotheses, which reflect the current state of ecosystems theory and recent empirical studies. The hypotheses contrast woody and herbaceous lifeforms with respect to the role of above- (light) and belowground (water, nutrients) constraints, and system response to disturbances.

Patterns of constraint

Water availability. Walter (1971) described grasses and woody plants in savanna as "antagonistic plant types" differing in their root systems and water economy. Walter's ideas stimulated a substantial amount of interest in the analysis of relationships between grasses and woody plants as functional types (Walker et al., 1981; Eagleson, 1982, 1986; Walker and Noy-Meir, 1982; McMurtrie and Wolf, 1983; Knoop and Walker, 1985). Our working hypotheses embody these ideas as follows:

(1) Grasses, because of their adventitious root systems, will have most of their roots in the upper soil layer, and will thus be limited in their ability to exploit deep soil resources. They will, because of their dense fibrous roots, be very effective at exploiting resources in the upper soil layers (approx. 2–60 cm).

(2) Succulents have the capability to store water in modified stems, and therefore can exist on water resources with brief residence times in the soil. Our observations and those of others (Weaver, 1920) suggest that the roots of succulents are limited to the upper soil layers (5–20 cm).

(3) Forbs consist almost entirely of annual and perennial cryptophytes and hemicryptophytes. They grow rapidly under conditions of high resource availability. Their root systems overlap with grasses and woody plants, but they are poor competitors for resources, and so are abundant only when resources are available in excess of the amounts that can be used by grasses and woody plants.

(4) Woody plants, because of their characteristic rooting behavior (less dense, not fibrous, but with a strong taproot), will be inefficient at exploiting resources in upper soil layers but capable of exploiting resources stored deep in the soil. Shrubs differ from trees in degree, with trees potentially having deeper roots. Conifers, in general, are more tolerant of drought and use water more efficiently than deciduous trees. Drought tolerance reflects water storage in the stems of gymnosperms, and the needle-leaf habit confers greater water use efficiency via lower conductance (Waring and Schlesinger, 1985).

TABLE 1

The eight Long-Term Ecological Research sites to be used in the analysis of the interactions between vegetation structure and ecosystem processes

Central Plains Experimental Range (CPER) in northeastern Colorado (40°49′N 107°47′W) is a shortgrass-dominated site.

Niwot Ridge/Green Lakes Valley site (CULTER) in the Rocky Mountains of northcentral Colorado (40°N 105°W) is an alpine tundra site located at 3500 to 4000 m elevation.

Konza Prairie Natural Research Area (Konza) in eastern Kansas (39°6′N 96°36′W) is a tallgrass prairie site.

Sevilleta research site (Sevilleta) in central New Mexico (34°13′ to 34°25′N 106°30′ to 107°05′W) is a transition site. The vegetation may be dominated by short-, mid- or tallgrasses, shrubs or small trees.

Cedar Creek Natural History Area, on the sand plains of Minnesota (45°24′N 93°12′W, 175–288 m), encompasses a mix of prairie, oak savanna and deciduous hardwood forest.

H.J. Andrews Experimental Forest in western Oregon (44°14′N 122°11′W; elevation range 425–1620 m) represents Pacific northwestern conifer forest.

Coweeta Hydrological Laboratory in western North Carolina (35°N 83°30′W; 679–1592 m) supports deciduous forests ranging from Appalachian cove hardwoods at low elevations to northern hardwoods at higher elevations.

Hubbard Brook Experimental Forest in New Hampshire (43°56′N 71°45′W; 229–1015 m) represents northern hardwood forest with a transition to spruce-fir at high elevations.

Temperature. We distinguish two effects of temperature, one direct and the second indirect:

(1) Temperature has a direct effect on plant growth and decomposition processes which is reflected in specific temperature–growth response functions as mediated by ecophysiological mechanisms (i.e., the Q_{10}s of photosynthesis versus respiration; Landsberg, 1986; Reynolds et al., 1986; Sprugel, 1989);

(2) Temperature has an indirect influence on vegetation and ecosystem processes via its effect on potential evapotranspiration (PET) and soil water availability.

This influence on PET dictates that the seasonal distribution of precipitation relative to temperatures will have an important effect on soil water availability. In particular, Neilson et al. (1989) suggested that the overlap between growing-season evaporative demand and precipitation largely determines water availability; they argue that late-winter or early-spring precipitation is critical in providing the deep soil water essential to woody plants. The climatic regimes at the collaborating LTER sites vary considerably in terms of the amount and seasonality of precipitation relative to temperature (Fig. 2), which should have profound influences on vegetation and soil processes (Walter, 1973; Neilson et al., 1989; Stephenson, 1990).

Nutrient use. Feedbacks between plants and their environment via nutrient cycling are effected by two links:

(1) Plants modify nutrient cycling rates and availability as a result of species-specific differences in litter quantity and quality (lignin content, C:N ratio).

(2) Changes in nutrient availability can alter plant species composition and stature as a result of species- and size-specific demand for limiting nutrients.

These two ideas are fundamental to most nutrient-cycling studies, with differences mostly a matter of degree or resolution (Aber and Melillo, 1982; Pastor and Post, 1986, 1988; Parton et al., 1988; Rastetter et al., 1991). Evidence in support of the former hypothesis is available from experiments at the Cedar Creek LTER site (Tilman, 1988; Wedin and Tilman, 1990) and forest studies (Pastor and Post, 1986). Empirical evidence to quantify species-specific responses is not available for all species, and so we will make explicit assumptions. One suggestion supported by experimental evidence (Mitchell and Chandler, 1939; Pastor and Post, 1986; Ojima et al., 1988; Wedin and Tilman, unpublished data) is:

> Early seral species do better under conditions of high N availability, compared to late-seral species of the same lifeform.

This would be the case if above- versus belowground allocation strategies differed for early versus late seral species, a reasonable hypothesis (Tilman, 1988; Smith and Huston, 1989) but one that requires further testing. Finally, we make a simple assumption about nutrient demands for a given plant:

> A plant's requirements for nutrients can be estimated according to the nutrient concentration in new tissues, and so are proportional to fresh biomass increments during growth.

Available light. At a coarse level of resolution the role of available light in controlling ecosystems is straightforward:

> A plant affects its light environment via the amount and distribution of its leaf area; these effects vary among lifeforms. In the extreme, light is nonlimiting to semiarid grasslands, but can represent a boundary condition to moist, fertile forests. In intermediate cases, light plays an intermediate role in controlling ecosystems.

We also assume that once a forest is established on a site, the trees characterize the ecosystem in terms of system structure and function; herbaceous species can be ignored with little loss of information. We will, however, attend the role of competition among lifeforms in the early stages of tree establishment (Burton and Urban, 1989).

This collection of working hypotheses is being implemented as simulation models at a spectrum of LTER sites. This parallel effort for very different ecosystems requires special considerations about the general ecosystem model, and demands sites with well established research programs and empirical bases for estimating model parameters and testing results.

SIMULATION MODELS

Modeling is playing an increasing role in the development of ecological theory at several scales, from understanding carbon fixation (Farquhar and Sharkey, 1982; Farquhar and von Caemmerer, 1982) and plant water balance (Cowan, 1982, 1986); to scaling of physiological processes to whole-plant responses (Reynolds et al., 1986); to exploring how ecosystem processes of carbon and nitrogen cycling operate at regional to global scales (Emanuel et al., 1985; Burke et al., 1991). Modeling is especially important in exploring phenomena at spatial and temporal scales for which extensive direct observation and experimentation are prohibitive, if not impossible. Recent examples include the role of spatial and temporal variation in competition on ecosystem functioning (Sharpe et al., 1985, 1986; Wu et al., 1985; Walker and Sharpe, 1989), extrapolation of the processes of carbon fixation and water balance to the landscape scale to enable linking ecosystem models with remotely sensed data (Running and Coughlan, 1988), and exploring the implications of the evolution of plant adaptations to varying environmental conditions on current patterns of ecosystem structure across environmental gradients (Tilman, 1988).

Our objectives require a model of the interactions between vegetation structure and ecosystem processes which satisfies the following criteria:

(1) Estimating parameters must be possible from data generally available at LTER sites representing a variety of ecosystems, and the model must provide predictions that can be tested against data on ecosystem structure or process rates.

(2) The model must be sufficiently general to accommodate ecosystems dominated by different lifeforms (e.g., grasses, trees) and constrained by different environmental factors (water, light, nitrogen, temperature).

This is necessary to conduct within- and between-biome comparisons under the same framework and set of assumptions.

(3) The implementation of this model must be sufficiently robust and general so that it can span the parametric domains of two adjacent biomes by incorporating the relevant mechanisms and constraints of both biomes.

Criteria 2 and 3 represent a new challenge in ecosystem research. The conventional approach has been to focus narrowly on systems at scales and parametric domains that can be simply and unambiguously defined, which has resulted in site-specific models that cannot be extended easily to different sites or other systems.

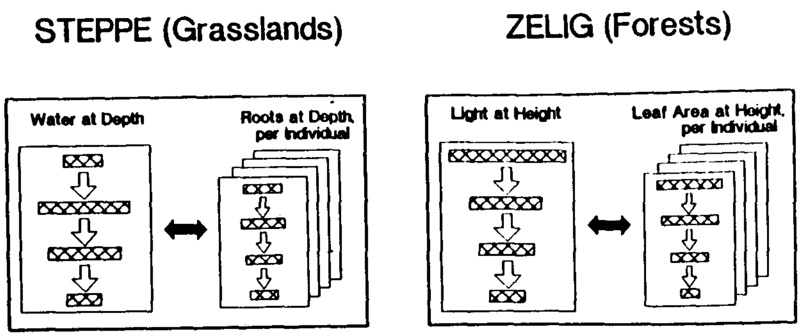
We are using a set of coupled and interactive simulation models as components of a unifying conceptual model of ecosystem structure and function. These models represent vegetation dynamics and the ecosystem processes of nutrient cycling and soil water balance. The vegetation models are individual-based gap models (Shugart and West, 1980; Shugart, 1984), which incorporate a rich array of life history mechanisms to simulate mixed-species, mixed-age communities. The ecosystem process models are compartment models, which emphasize transfer rates among compartments such as soil organic matter and aboveground biomass. The models have a long history of development, application, and testing, and have been developed to the point where it is reasonable to synthesize a general model.

Vegetation models

The three vegetation models are individual-based gap models (Shugart and West, 1980; Shugart, 1984). The models simulate the establishment, growth, and mortality of individual plants at an annual timestep on a plot of defined size. The general approach has been widely applied in forests and the same structure was used as the basis of STEPPE, a model of semiarid grasslands (Coffin and Lauenroth, 1990). All individual-based gap models share a common set of characteristics and demographic processes.

The various versions of the models differ in their attention to details judged important at a particular site. Unfortunately, the differences among local models tend to confound efforts to conduct controlled cross-site comparisons. As a first step toward synthesis, we are encoding a single generic forest model and likewise, a single grassland model. These two common models will serve as benchmarks for the more complicated, fully coupled ecosystem model we plan to develop.

There are important differences between the forest and the grassland models. The forest model emphasizes light competition and simplifies belowground interactions, while the grassland model emphasizes competition for soil water and assumes no competition for light (Fig. 3). Because gap models are explicitly scaled by the size of a dominant individual, there are large differences in plot size for forest (roughly 0.1 ha) versus grassland (0.1 m^2). This presents a problem in simulating conditions under which different lifeforms coexist. We are reconciling this problem with a third vegetation model (VEGOMAT), using a framework for linking gap models operating at different spatial scales in a manner analogous to nested-quadrat sampling schemes (see below).



Plot Size:	0.1 m^2	500 m^2
Constraints:		
Water:	Individual–level	Species–level
Light:	not included	Individual–level
Nutrients:	not included	Species–level
Temperature:	Species–level	Species–level

Fig. 3. Schematic representation of the individual-based grassland model (STEPPE) and the forest model (ZELIG), emphasizing their parallel structure. Both models aggregate plot-level competitive environments (root depth distribution, leaf area profile) from individuals and model resource capture in terms of the overlap between capturing organs (roots, leaves) and the vertical distribution of available resources (water, light). The models differ in scale (plot size) and the level of detail with which environmental constraints are simulated.

Ecosystem process models

The CENTURY model simulates soil organic matter dynamics and plant production (Parton et al., 1987). The dynamics of C, N, P, and S in the soil–plant system are tracked, on a monthly timestep, in compartments defined by process rates. Soil organic matter is divided into: (1) an active soil fraction consisting of live microbes and microbial products with a 1- to 2-year turnover time; (2) a protected fraction resistant to decomposition with a 20- to 40-year turnover time; and (3) a fraction that is physically or chemically isolated with a 800- to 1200-year turnover time. Plant residue is divided into structural (2–5-year turnover time) and metabolic (0.1 - 1-year turnover time) pools as a function of the lignin to nitrogen ratio. Decomposition is calculated by multiplying the decay rate for each state variable by the combined effect of soil moisture and soil temperature on decomposition. The decay rate of the structural material is also a function of its lignin content. The active soil organic matter decay rate changes as a function of the soil silt and clay content. Submodels for N and P parallel the carbon structure with the appropriate modifications.

The plant production submodel simulates the monthly dynamics of C, N, P, and S in the live and dead above- and belowground plant material. Maximum potential plant growth is estimated as a function of annual precipitation and is reduced if sufficient N, P or S is not available.

The CENTURY model has been run for a large number of grassland sites, and has predicted patterns of plant productivity, soil organic C, N, and P in the central grassland region of the USA. These patterns have been validated using extensive regional databases (Parton et al., 1987, 1990).

The SOILWAT model simulates the flow of water through a plant canopy and soil layers. Rainfall interception, infiltration of water into soil, rapid and slow soil water drainage, and evaporation of water from the plant canopy and the soil layers are simulated on a daily timestep. The model can treat an arbitrary number of soil layers in each of which depth and soil type are specified. A detailed description is provided in Parton (1978).

MODEL DEVELOPMENT

Evaluating relationships between vegetation structure and ecosystem processes over a range of environmental conditions represented by the LTER sites has required modifications of the existing models as well as development of a new model and development of a new method for simultaneously running vegetation and ecosystem process models. This entails two levels of activity. The first is a set of generalized component models (the benchmark versions of STEPPE, ZELIG, VEGOMAT, CENTURY and SOILWAT).

Extensions to the vegetation models

As the second phase of this modeling task, we are extending the vegetation models to be fully coupled and integrative with the water and nutrient models. Plant response to environmental constraints is computed on a supply/demand basis. The models estimate the amount of a given resource a plant needs to achieve optimal growth (its demand), then compute the amount of the resource available to that plant (its supply). Actual growth is less than optimal if demand is not met. Demand computations vary with the resource considered. Demand for nitrogen or other mineral nutrients is based on the absolute amount implied by net biomass increment under optimal growth, corrected for nutrient concentrations in plant tissues. Water demand can be estimated for small plants by measuring whole-plant water-use efficiency (mm water/g plant production) using watering trials. For large plants (trees) we are exploring several complementary estimates of water demand, including estimates based on heat loading and pipe model theory (Shinozaki et al., 1964; Makela, 1986; Leemans and Prentice, 1987), relative transpiration demand that partitions total plot-level evapotranspiration by the proportion of total stand leaf area accounted for by each tree, and indirect (stand-level) estimates of water-use efficiency used by other models (Running and Coughlan, 1988). In the case of light, a first approximation of demand can be estimated from basic growth analyses (e.g., Larcher, 1980, see also Leemans and Prentice, 1987).

Resource supply is a function of the amount of the resource and its spatial and temporal distribution. The supply of a resource to a plant is computed by the overlap in the distribution of a resource and the distribution of capturing organs (leaves or roots). For light, the vertical distribution of leaf area for each plant is estimated using allometric functions; the aggregation of these for all plants on the plot provides a leaf-area profile for the plot, and the relative light level at each height interval is estimated by attenuating incident light through the profile (Botkin et al., 1972a,b, as modified by Leemans and Prentice, 1987). Similarly, the depth-distribution of roots per plant and total roots per soil layer is simulated, and the depth distribution of soil water and nitrogen from the soil process models is determined. In both the above- and belowground case, the density of organs of a plant at each height or depth relative to the stand total will determine that plant's share of the available resource. These amounts summed for all heights or depths is the supply of the resource for the plant.

The demand and supply of resources vary temporally. Soil processes are modeled at a daily (for water) or monthly (for mineral nutrients) time step. Vegetation structure is simulated on an annual time step. To exchange information between the models, aggregation techniques are used to translate fine-scale information to the coarse scale, and seasonal distributions are used for the inverse coarse- to fine-scale translation. Resource levels, especially belowground, vary in response to seasonality of precipitation and temperature, and resource capture per plant varies in time as a result of the relative activity of plants on the plot. Activity is determined from a phenological response function defined for each plant species or functional type.

Extensions to the ecosystem process models

A forest version of CENTURY has recently been developed and includes three woody compartments (fine branches, large wood, and coarse roots) as well as fine root and leaf compartments. This new model is currently being tested and coupled to the ZELIG model, which will be used to provide estimates of plant residues to CENTURY.

Four different FORET-style vegetation models already exist which simulate nutrient cycling (Aber and Melillo, 1982; Weinstein et al., 1982; Pastor and Post, 1986, 1988; Bonan, 1990). These models, while not sufficiently general for our purposes, provide estimates of allometries to predict leaf, branch, bole, and root biomass from stem diameter, as well as the C:N ratio and lignin content of these tissues. Our major task is to incorporate these relationships into the ZELIG model to allow direct coupling to the CENTURY model.

We intend to generalize SOILWAT, which was originally developed as part of the ELM grassland model during the International Biosphere Programme (Parton, 1978). The model simulates a multilayer soil, allows us to explore the implications of various rooting depths of different species or lifeforms. To maintain the geographic generality required by our overall goals, hydraulic properties of soils will be inferred from soil texture data (Clapp and Hornberger, 1978; Cosby et al., 1984). The model uses daily time steps, and output is aggregated for exchange with the vegetation and nutrient-cycling modules.

A major modification for SOILWAT is to include relationships specific to forests. These include a means of estimating interception losses from the canopy (Running and Coughlan, 1988), and distributing evapotranspirational demand on the canopy to appropriate rooting depths (which we base on explicit assumptions about above : belowground symmetry).

Scaling issues: modeling mixed lifeforms

VEGOMAT (Smith et al., 1989) is a framework for linking individual-based gap models which can operate simultaneously at number of spatial scales. The prototype version operates at three spatial scales corresponding to plot sizes for simulating the dynamics of herbs, shrubs and trees. Each spatial scale operates as a separate submodel; these interface via plant influence on environmental conditions and the process of recruitment. The largest spatial scale corresponds to a gap-model plot for trees, with pro-

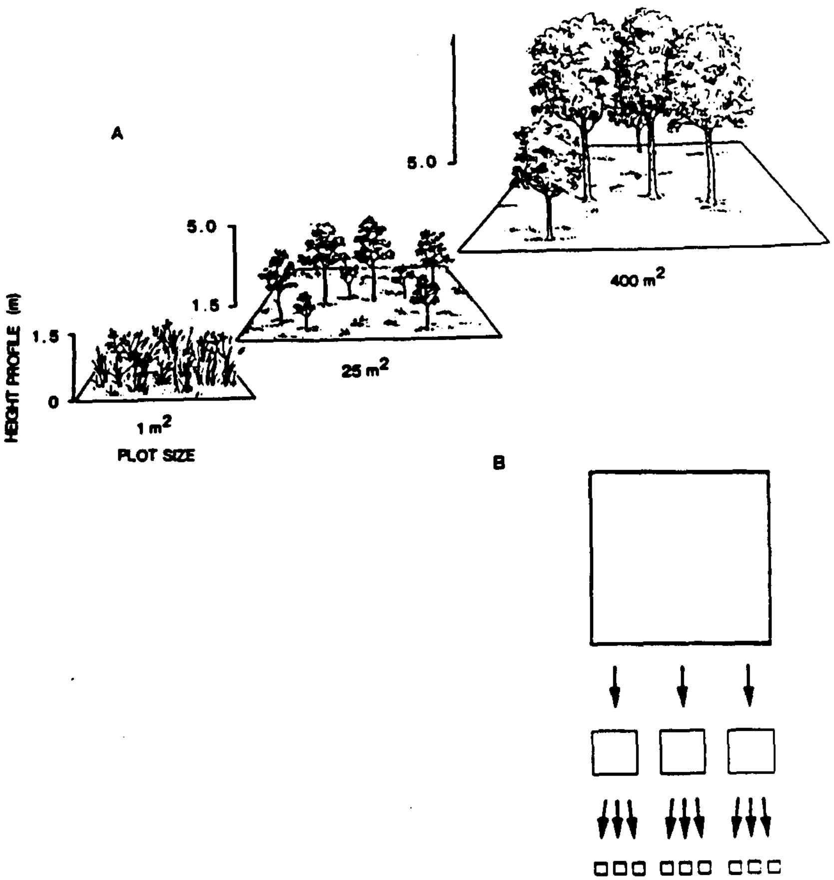


Fig. 4. Schematic of a mixed-lifeform, multi-scaled vegetation model (VEGOMAT). (A) Nested submodels are defined by height classes, at spatial scales corresponding to herbs and woody seedlings, shrubs and saplings and trees. (B) Subplots are nested spatially, with multiple herb/seedling plots per shrub/sapling plot and multiple shrub/sapling plots per tree plot.

gressively smaller plots for shrubs and grasses. The plots are nested in that each of the smaller plots is a sub-plot of the plot at the next larger scale, thus maintaining the spatial context of nestedness: the shrub plots can be viewed as samples within the larger tree plot, and similarly the grass plots as samples within the shrub plots (Fig. 4).

The vertical profile is continuous, with a defined minimum and maximum height for each spatial scale (submodel). Each scale operates as a conventional gap model; however, as individuals grow they can pass from one scale to the next larger as they increase in height. This process of recruitment from one scale (i.e., submodel) to the next is carried out as a probabilistic process based on sample statistics for replicate plots at the next lower level. In turn, the large plots act as a constraint on the small scales by modifying the environmental conditions of plots within them. For example, the available light at the top of the vertical profile for a shrub plot is defined by the leaf area of the larger tree plot to which it belongs. Thus, the framework is one of the large plots acting as a context for the small, and the small plots providing a statistical distribution of recruitment to the large.

This structure is ideal for examining vegetation dynamics across environmental gradients (either spatial or temporal) where the dominant lifeform changes. Under xeric conditions, or on mesic sites following disturbance, the model structure is one of independent replicate plots at the smallest scale, and is roughly equivalent to the STEPPE model. Under wetter site conditions or as succession proceeds on mesic sites, woody plants become established and grow. As these individuals increase to a size corresponding to the next largest scale the structure of the model becomes one of a sample of intermediate scaled plots and a series of smaller scale plots nested within. This continues until trees dominate, with the shrub and herbaceous/woody seedling plots representing subsamples of the large forest plot. For closed-canopy forests, VEGOMAT should approximate ZELIG; for dry grasslands it should approximate STEPPE. Thus, this single modeling framework can simulate a range of conditions from grassland to forest using the same model paradigm, and bridges STEPPE and ZELIG.

Linking models: concurrent processing

To assemble a general ecosystem model, we plan to link the component models that are appropriate to a particular application. Each combination would include the soil water model, CENTURY, and one vegetation model (STEPPE, ZELIG, or VEGOMAT, for grasslands, forests, and transitional cases, respectively) (Fig. 5).

The traditional technique to combine two or more models into a single simulation tool is to merge the computer code. This often requires extensive modifications to the programs to resolve symbolic and input/output conflicts, plus differences in design factors such as time steps; this often takes considerable effort and collaboration by the modelers.

An alternative technique, which can be implemented in many computer networking environments, allows two or more models to be executed concurrently. Concurrent processing under the UNIX operating system is handled by interprocess communication. Models may be executed on different computers, or on a single multitasking computer. Information exchange between the models and synchronization of the models is handled using network functions. A separate, master control program is used to synchronize execution and to transfer data between models.

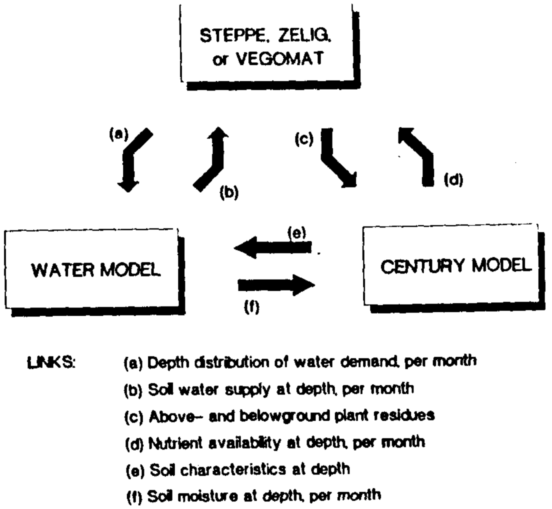


Fig. 5. Transfer of information among component models of the fully coupled ecosystem model, which consists of a vegetation model, the soil water model and the CENTURY nutrient-cycling model. A master program controls the interactions among the separate models.

PRELIMINARY RESULTS

Vegetation-nutrient cycling relationships

STEPPE–CENTURY coupling. Our initial attempt at concurrent processing involved linking the STEPPE grassland model with the CENTURY soil process model. The linkage of the models provided CENTURY with information about above- and belowground plant biomass production from a more detailed model of plant dynamics (STEPPE) and provided STEPPE with more detailed information about soil water and information about nitrogen availability for plant growth. Both models required modification to accommodate the information exchange. STEPPE required that information about the effect of nitrogen availability on the growth of individual plants be added to the code. This was accomplished using the approach outlined above using the concept of a maximum nitrogen-use efficiency at the species level. STEPPE was also modified to use soil water information from CENTURY instead of its internal functions. CENTURY was modified to accept above- and belowground biomass information from STEPPE rather than use its internal functions.

CENTURY and STEPPE were run under UNIX and linked using stream sockets. Within each model, data to be sent or received are associated with variables within common blocks. FORTRAN-callable C routines were used to establish the sockets and to read and write all data. A control program was used to synchronize the execution of the two models, to transfer data from the common blocks of the sender to that of the receiver, and to act as a filter for the data. The filtering functions

included conversion of units (cm to mm of precipitation) and the disaggregation of annual estimates of production and standing biomass from STEPPE into monthly quantities for CENTURY.

Each model was started and given time to perform any initialization required for the simulation. Each model called a routine which created a socket for data transfer and waited for a message from the control program indicating that it could proceed. After the control program was started, it found the sockets created by the models and sent them initial data plus the message to proceed. Each model then simulated 1 year and wrote its data to the socket. The control program received the data, made appropriate conversions and transfers, and signaled the models to simulate another year. This was continued until the end of the simulation.

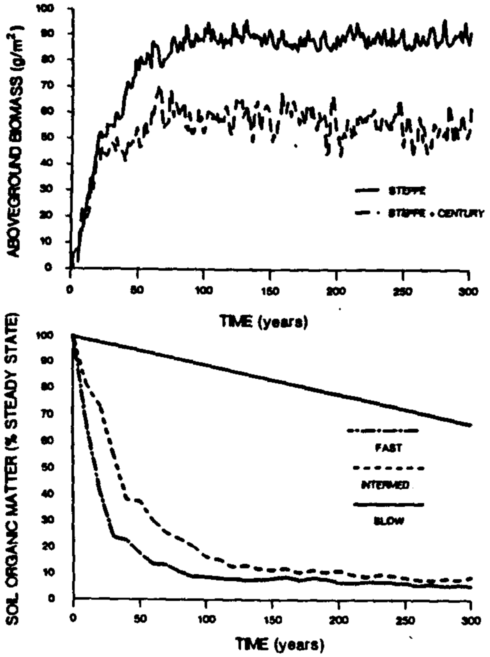


Fig. 6. Comparison of model behavior of STEPPE independently and STEPPE-CENTURY models linked under concurrent processing. Top: above-ground biomass for STEPPE as caompared to the linked models; N-limitation via CENTURY reduced productivity in STEPPE. Bottom: soil organic matter (SOM) pools simulated by CENTURY, with plant biomass produced by STEPPE.

The results for the linked models showed substantial effects compared to results for each model running separately (Fig. 6), underscoring the importance of the link between vegetation and ecosystem processes. STEPPE running alone assumes that nitrogen is never limiting, or alternatively, that accounting for the effects of water also accounts for the effects of nitrogen. Providing STEPPE with a nitrogen constraint and information about nitrogen availability suggested that nitrogen may be a frequently limiting resource (Fig. 6).

A portion of the apparent effect of nitrogen on steady-state aboveground biomass is the result of a mismatch in the spatial scales that the two models represent. STEPPE has an explicit spatial scale of 0.12 m^2. The spatial scale of CENTURY is not explicit and most likely represents an average over several m^2. This results in STEPPE being provided with an average nitrogen availability that may be a substantial underestimate of what may happen at a spatial scale of the area influenced by an individual plant.

The effect of the mismatch in spatial scales is even more apparent in the CENTURY results than it was for STEPPE. By coupling CENTURY to an individual plant model that represents a scale at which equilibrium plant biomass is never achieved (Shugart, 1984), the steady-state condition of each of the soil organic matter pools is drastically altered. The simulation was initialized at steady-state values of soil organic matter (Fig. 6). After 100 years of running with STEPPE the fast and intermediate pools reached new steady-state conditions that were approximately 10 and 20% of initial values respectively. The slow pool declined continuously and after 300 years was 65% of the initial value. We are working on resolution of the problems associated with coupling the models and these initial results are useful in helping us focus our efforts.

Extensions. The results concerning the importance of N to vegetation dynamics, as illustrated with the STEPPE–CENTURY coupling, are consistent with results from forest gap models which include N effects explicitly (e.g. Pastor and Post, 1986) as compared to those gap models which do not simulate N (e.g. Shugart and West, 1977). Pastor and Post (1986) found N to be limiting in many cases, especially in early succession; their model produces lower annual productivity and slower tree growth rates compared to the baseline ZELIG model, which does not simulate N explicitly. To pursue the importance of forest-N feedbacks more fully we will require the version of CENTURY which incorporates woody tissues explicitly.

Vegetation–soil water relations

SOILWAT. We subjected the soil water model to an initial qualitative test by running it for a loamy sand soil texture at three of the LTER grassland sites: Jornada, a desert grassland; CPER, a shortgrass steppe; and Konza, a tallgrass prairie. Our objective was to verify that the model would produce different depth-distributions of available soil water for the three sites. The output variable evaluated was the annual average number of days at each depth when soil water potential was greater than −1.5 MPa. These data were then summarized as the relative frequency of water available by depth for each site.

There is a clear trend in the depth of available soil water across the three sites (Fig. 7). Jornada, the driest site, has the shallowest depth distribution of water with approximately 70% of the available water occurring in the top 15 cm of the soil. By contrast, the Konza site had less than 25% of the average annual amount of available water in the top 15 cm. The CPER was intermediate but much more similar to the Jornada site than to the Konza. Both the CPER and Jornada sites had essentially all of their available water in the top 80 cm, whereas the Konza site had water available down to 135 cm. These results suggest a much greater potential to support deep rooted plants on loamy sand soils at the Konza site than either the CPER or the Jornada sites.

STEPPE–SOILWAT coupling. We have made sufficient progress linking STEPPE and SOILWAT so that we no longer use the original soil water functions in STEPPE. All soil water information for recruitment, growth, and mortality is supplied by SOILWAT via network functions. SOILWAT has a spatial resolution that can easily accommodate the plot size of STEPPE. SOILWAT is run for a year (daily time step) and information about conditions for establishment of *Bouteloua gracilis* and the availability of soil water are summarized and passed to STEPPE, which uses it to update the size and age of each individual on the plot. STEPPE then provides SOILWAT with information about aboveground and belowground biomass and litter for the next year. This information exchange continues on an annual basis for the length of the simulation.

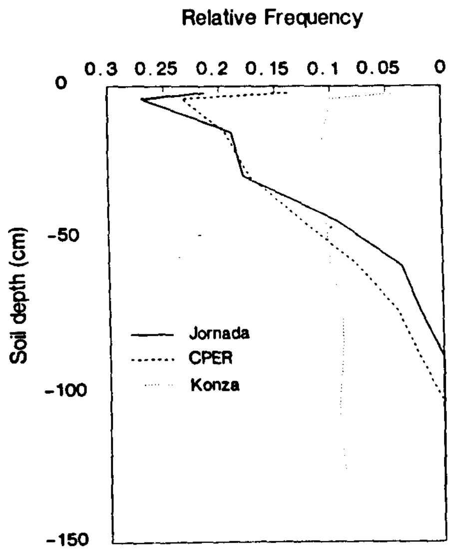


Fig. 7. Depth distribution of available soil water at three LTER sites with contrasting climatic conditions (see Fig. 2 for climatic conditions). Values are relative frequency of days for which soil water was greater than −1.5 MPa, based on 20-year simulations.

The results presented here are for a transect 12 m long and 2 m wide (216 plots, all of which were initialized with zero plant biomass). The results represent the average of 25 Monte Carlo simulations. One edge of the transect was adjacent to undisturbed vegetation but the remaining edges were adjacent to bare ground. This is the situation encountered at the edge of an abandoned agricultural field. Average annual precipitation over the 100-year simulation was 330 mm with a standard deviation of 90 mm.

The output that is different from previous versions has to do with the interactions between root distributions and soil water extraction. Over the 100-year simulation, average distributions of root biomass for each depth were biased toward the upper layers, which is a reflection of the distribution of soil water (Fig. 8). Approximately 50% of the roots were in the upper 30 cm of the soil which contained approximately 90% of the available water. The variability in root biomass in the upper 30 cm of the soil is in response to the temporal variability in available soil water. The variability in the lower layers of the soil is in response to variability in lifeform composition.

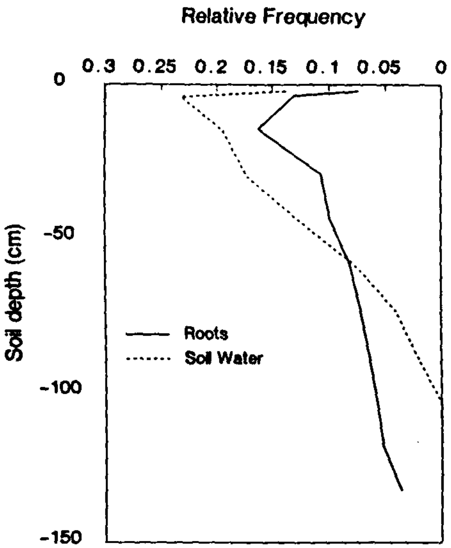


Fig. 8. Depth distribution of available soil water and root biomass at the CPER site. Results are for a 100-year simulation of STEPPE and SOILWAT running concurrently.

Extensions. Results thus far indicate the SOILWAT model is capable of simulating soil water relationships and vegetation-water feedbacks via root distributions for a range of grassland conditions. We are currently extending this model to forest conditions, by incorporating interception losses to the canopy (Running and Coughlan, 1988). With the appropriate modifications to ZELIG (tree root distributions and monthly tree phenology) we will be able to couple SOILWAT and ZELIG as well.

Cross-site comparisons

Alpine tundra grasslands. A version of STEPPE has been created for the Niwot Ridge LTER site (Humphries et al., 1990). The current model simulates the responses of alpine plants over a snow deposition and soil water gradient from a ridge to a swale. One of the most extensive community types is the dry meadow dominated by *Kobresia myosuroides. Kobresia* is a perennial caespitose sedge with a very long lifespan and infrequent reproduction. The most important modifications required to adapt the model to the alpine were to estimate parameters for alpine species and incorporate the effects of snow on soil water and the length of the growing season.

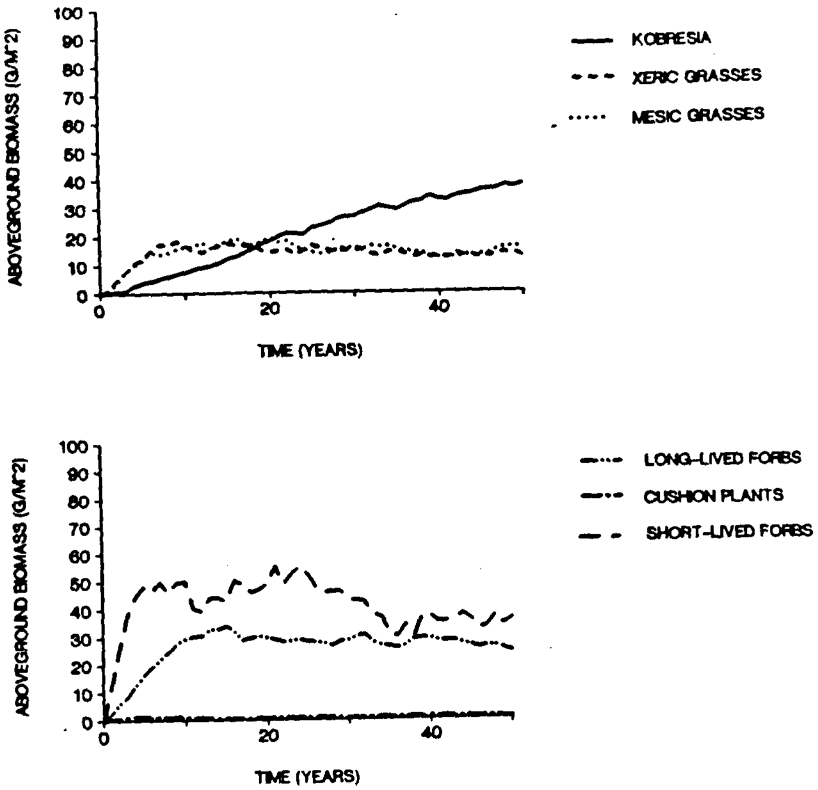


Fig. 9. Simulation results for a dry meadow plant community at Niwot Ridge. The simulation was begun following a disturbance that killed all of the plants.

Simulations of dry meadows at Niwot Ridge produced distributions of biomass among species that agree quite well with observations (Fig. 9). Plant biomass was zero at time zero and colonization was allowed to proceed over a 50-year period. For the first 20 years the plant community was dominated by grasses and forbs. *Kobresia* became established 2 or 3 years after the simulation began and slowly increased in biomass over the 50 years. Long-term simulations indicate that *Kobresia* may take up to 250 years to reach a steady-state biomass. The major increase is in the first 50 years but a slow increase continues over the next 200 years.

Relative to the semiarid grasslands of the Central Plains, the alpine communities at Niwot Ridge are governed more by cold temperatures and snow distribution than by low water availability. The dominant species

(*Bouteloua* vs *Kobresia*) are both long-lived perennials, yet the successional dynamics at the sites vary: *Bouteloua* assumes immediate dominance during succession whereas *Kobresia* becomes dominant only after an initial phase characterized by grasses and forbs. A more detailed comparison of the two systems is in preparation (Humphries et al., 1990).

Pacific northwestern vs. eastern deciduous forests. The original version of ZELIG (Smith and Urban, 1988) was developed for eastern deciduous forests. A new version of ZELIG has been created that can simulate Pacific Northwestern (PNW) coniferous forests as well as eastern deciduous forests. This approach is in contrast to previous implementations of gap models at various sites, which have thus far resulted in site-specific versions which are not directly comparable (e.g., Botkin et al., 1972a,b, Weinstein et al., 1982, and Dale and Hemstrom, 1984, for forests at or near Hubbard Brook, Coweeta and Andrews, respectively).

PNW forests are characterized by species that differ considerably in terms of life-history traits, relative to eastern deciduous species (Waring and Franklin, 1979). For example, *Pseudotsuga menziesii*, a PNW dominant, may live more than twice as long as the longest-lived eastern species, yet is considered a successional species in PNW forests. Similarly, PNW trees may achieve diameters on the order of 2–3 m and heights of 100 m; no eastern trees achieve this stature.

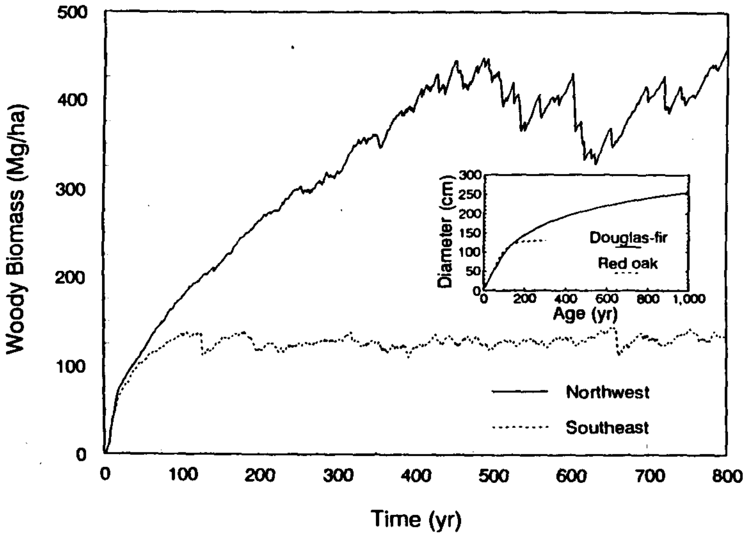


Fig. 10. Comparison of forest biomass dynamics as simulated for Pacific Northwestern conifers and Appalachian hardwoods. Inset: the dominant species in the northwest, Douglas-fir (*Pseudotsuga menziesii*), lives longer and achieves larger size than the eastern oaks (*Quercus rubra*), illustrating the influence of species life-history traits on system-level dynamics.

Simulations with ZELIG suggest that these life-history attributes have a profound effect on forest productivity and steady-state standing biomass (Fig. 10). A detailed comparison of eastern and northwestern forests is in preparation (Urban et al., in prep).

Grassland–forest comparisons. We have used the baseline STEPPE and ZELIG models as a framework to assess the implications of grass and tree life-history traits in determining system-level behaviors of grasslands and forests (Coffin and Urban, 1993). Plant stature determines the inherent spatial grain in grasslands and forests, but the models showed that plant growth habit influenced system response to spatial and temporal variability. Clonal grasses were able to adjust their size by adding or losing tillers, to track variability in environmental patchiness (as plot size, Fig. 11) as well as temporal variability (as periodic variation in soil moisture, Fig. 12). Trees, in contrast, had a much narrower response to patchiness because of their incremental growth and a minimum necessary plot size for adequate growth (Fig. 11). Incremental, deterministic growth by trees also imparts a natural frequency to gap dynamics corresponding to the lifespan of trees (Fig. 12).

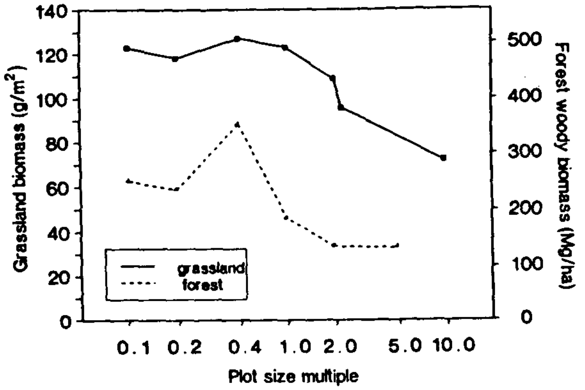


Fig. 11. Response of STEPPE and ZELIG to variation in model plot size, as mean biomass for 50 plots averaged over 100 years. Plot sizes are multiples of baseline size defined by maximum size of a dominant individual. The peak in forest biomass corresponds to canopy size of a large tree; in the grassland, the dominant bunchgrass grows clonally to adjust itself to a wider range of plot sizes, hence does not show as pronounced a peak.

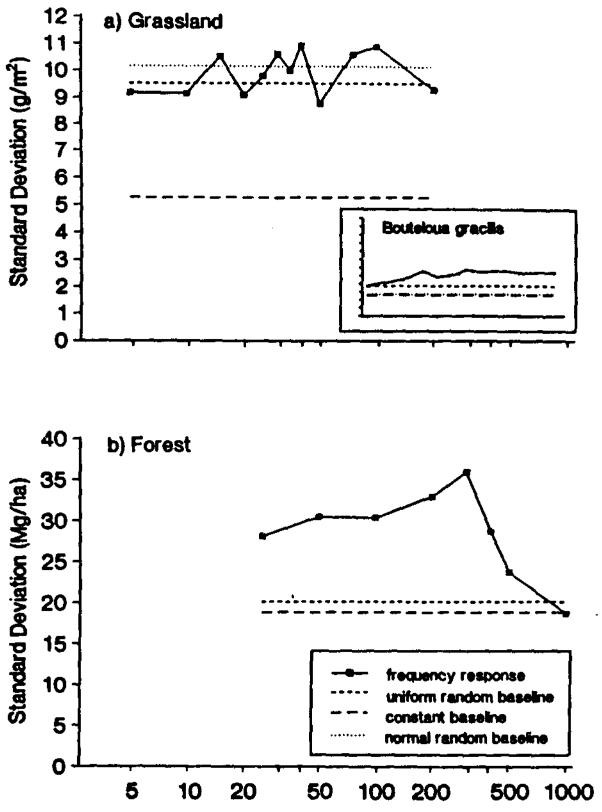


Fig. 12. Response of (a) STEPPE and (b) ZELIG to periodic variation in soil moisture, as standard deviation in biomass for 50 plots over 100 years. Amplitude of drivers were +/− 1 standard deviation of long-term records from each site. The grassland responds to a number of frequencies because its several lifeforms have varying natural frequencies (longevities, timing of reproduction). Note that response of dominant *Bouteloua gracilis* (inset) differs from the mixed-species stand. The forest responds strongly to a single frequency, amplifying variation at a timescale that corresponds to the lifespan of trees.

The mode of competition also varies in grasslands vs. forests, reflecting the importance of water vs. light as an important constraint on the systems. Competition for water is symmetric in STEPPE, in that each plant has access to soil water in direct proportion to its relative root biomass (a plant with 10% of the roots gets 10% of the water). In forest gap models, competition for light is asymmetric in that a tall tree has full access to available light while short trees have access only to light that is not absorbed by tall trees. This difference in the two models had important consequences at the system level: a forest exhibits a characteristic "thinning curve" whereas a grassland does not (Fig. 13). The mode of competition also has a direct effect on plant size distribution; in STEPPE most of the individuals of the dominant species were nearly full-size and other individuals were of all sizes; in ZELIG tree sizes assumed a "reverse J" distribution and most of the individuals were very small (see also Huston et al., 1988).

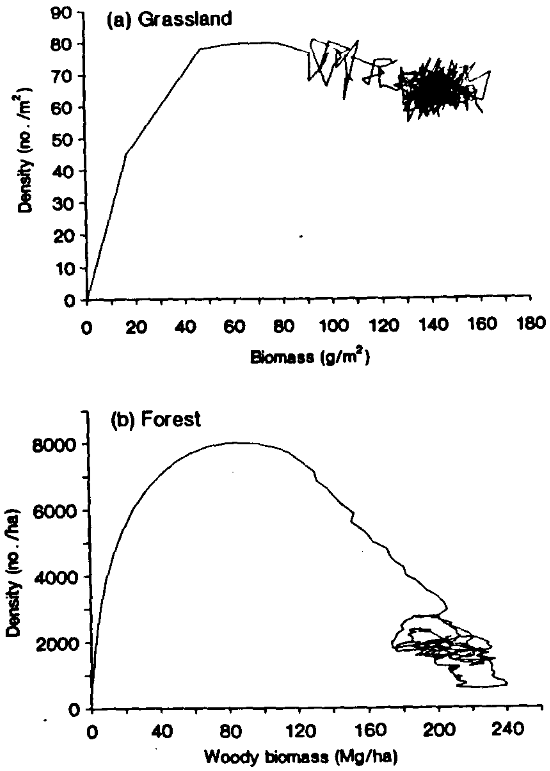


Fig. 13. Dynamics of stand density versus biomass for a grassland (from STEPPE) as compared to a forest (from ZELIG). Competition for water is symmetric in STEPPE, while light competition is asymmetric in ZELIG, which results in qualitatively different thinning curves and stand dynamics.

Thus, life-history traits of grasses and trees had important implications to system-level behavior of both grassland and forest vegetation. We anticipate that life-history traits of various plant lifeforms will have important feedbacks to ecosystem processes of nutrient cycling and water relations.

PROSPECTUS

Preliminary results underscore the importance of interactions and feedbacks between vegetation pattern and ecosystem processes. Thus far, our focus has been on ecosystem behaviors for natural conditions under ambient environmental regimes. Yet the development of a robust, general model of ecosystem dynamics has important implications for exploring system response to disturbances and under the specter of global environmental change.

The role of disturbance

Temporal patterns in disturbances can have profound effects on ecosystem structure and processes, in some cases overriding the effects of environmental constraints. For vegetation structure, the interactions between disturbance characteristics, such as size and frequency, and plant life-history traits are important (Denslow, 1980; Sousa, 1984), while for system processes the characteristics of the disturbance determine whether the effects will be quantitative or qualitative (Odum, 1969; Vitousek and Reiners, 1975; Bormann and Likens, 1979; Vitousek et al., 1989). Disturbance frequency may coincide with natural frequencies of plant growth (i.e., phenology, time to first reproduction, longevity) to amplify environmental patterns (Neilson, 1986). Thus, there may be an interaction between abiotic constraints and biotic natural-history phenomena which results in system-specific spatial and dynamical patterns (Allen and Wyleto, 1983; O'Neill et al., 1986; Urban et al., 1987; Shugart and Urban, 1989).

Interactions between disturbance characteristics, life history traits, and ecosystem processes are important in determining the balance of dominance among species, particularly among lifeforms at transition zones. Where climatic conditions are suitable to support mixed lifeforms, disturbance rate had important effects on the dominant lifeform because lifeforms differ in their natural frequencies (i.e., time to first reproduction, lifespan). High disturbance rates should select for fast-growing plants that reproduce early and are short-lived (Grime, 1974, 1977); the successful lifeforms will be those that can mature in the interval between disturbances. In addition, the pulses of nutrient availability that occur after disturbances will select for plants with rapid growth rates that can respond to the nutrient pulses (Mooney and Dunn, 1970; Orians and Solbrig, 1977).

At low disturbance rates, lifeforms with slow growth rates, which reproduce late in life and are long-lived should dominate (Tilman, 1988). In general, these lifeforms should be taller and should allocate a higher proportion of biomass to supportive structures and less to leaves than lifeforms that dominate under high disturbance rates (Tilman, 1988). The low relative growth rates of these plants confers tolerance to low annual resource availability. Therefore, these lifeforms will have a competitive advantage through time, as compared to lifeforms with fast growth rates that require high resource levels. The several LTER sites vary considerably with respect to regional disturbance regimes. The grassland sites are grazed to varying extent, and Konza in particular is heavily influenced by its fire regime. Western conifer forests have also developed under a history of fire, while mesic eastern forests are less prone to fires but experience other disturbances such as hurricanes and severe storms. Inasmuch as species response to disturbance will vary according to life-history traits and the nature of the disturbance, we expect system response to disturbances to vary considerably across sites. In particular, we anticipate that fire will play an important role in determining the prairie-forest transition (Anderson, 1982).

Environmental change

One of the most significant problems confronting ecologists in the next several decades is global climate change. Our work on modeling vegetation structure and ecosystem processes across LTER sites will put us in a good position to make predictions about the potential effects of climate change. Our approach will rely on a "space-for-time" substitution. In this, we presume that a model that is sufficiently general to simulate vegetation pattern and ecosystem process across a wide spectrum of environments, will also be useful in predicting system response to a temporally changing environment. To be sure, there are other aspects of environmental change that render space-for-time substitution inadequate. For example, the transient response of a forest to a rapidly changing climate depends strongly on stand age and composition (Urban et al., 1989); belowground conditions are similarly important (Perry et al., 1990). The potential for life-history traits to key system-level feedbacks that may lead to self-amplifying behavior (Shugart et al., 1981; Pastor and Post, 1986; Shugart and Urban, 1989) suggests that hysteretic behavior might develop under a changing environmental regime. Thus, a model that explicitly incorporates the details of vegetation (multiple lifeforms, species composition, age structure) as well as belowground processes (nutrient pools and decomposition processes, water relations) will be a valuable tool for assessing climate-change implications for a variety of ecosystems.

CONCLUSIONS

The final, fully coupled ecosystem model (Fig. 5) will offer three novel capabilities compared to previous efforts. First, the vegetation models can provide realistically scheduled inputs of organic material to the nutrient cycling model, with these inputs determined by demographic mechanisms rather than modeled as continuous transfer rates. These inputs will make it possible for the nutrient model to handle organic material from various species differently. Second, the linked models can account for system-level feedbacks and synergisms between plant structure, composition, and demography and the processes of nutrient cycling and water use. Finally, the models can be used to explore the temporal and spatial variability inherent in these processes at small spatial scales (i.e., the scale of vegetation dynamics). This last capability is in contrast to most previous ecosystem modeling studies, which typically invoke the assumptions of spatial homogeneity and near-equilibrium conditions implicit in compartment models encoded as differential equations.

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Statistical modelling of regional GIS data: an overview

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ABSTRACT

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Rapid advances in computing technology have facilitated the storage and manipulation of large sets of data in Geographic Information Systems. These data present new opportunities for modelling spatial distribution and change to distribution at a regional scale. The models used should take account of the special nature of GIS data, particularly the differing resolution associated with different variables. Likewise, inferences, either concerning model selection or model predictions, should be made with reference to the sampling units on which the estimates are based. Computer-intensive statistical methods, especially the bootstrap, are suitable for studying the variability of predictions. Presentation of results in map form should be accompanied by estimates of error.

1. INTRODUCTION

One of the major driving forces of scientific development in the last ten years has been the rapid development of computers and associated software. This development manifests itself to the user firstly by the ability to handle large sets of data, with rapid access and condensed storage using databasing techniques, secondly by the immense processing power of the most modern machines, which enables users to manipulate the data stores, and thirdly by the facility to display results of calculations using sophisticated graphical technology. It is the simultaneous advances on these three fronts which have made geographic information systems (GIS) powerful

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