Articles

Using Mechanistic Models to Scale Ecological Processes across Space and Time

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Human activities affect the natural environment at local to global scales. To understand these effects, knowledge derived from short-term studies on small plots needs to be projected to much broader spatial and temporal scales. One way to project short-term, plot-scale knowledge to broader scales is to embed that knowledge in a mechanistic model of the ecosystem. The National Science Foundation's Long Term Ecological Research (LTER) Network makes two vital contributions to this type of modeling effort: (1) a commitment to multidisciplinary research at individual sites, which results in a broad range of mutually consistent data, and (2) long-term data sets essential for estimating rate constants for slow ecosystem processes that dominate long-term ecosystem dynamics. In this article, we present four examples of how a mechanistic approach to modeling ecological processes can be used to make projections to broader scales. The models are all applied to sites in the LTER Network.

Keywords: scaling, ecosystem models, long-term ecological research, spatial projection, mechanistic models

Human activities now alter the natural environment at a global scale. The understanding of ecological processes affected by, and interacting with, these global alterations is generally derived from short-term studies of less than a few years made on small plots of less than 10,000 square meters (m^2) at a few intensively studied sites (e.g., the International Biosphere Program [IBP] sites; Blair 1977). Therefore, to fully assess the implications of human activities on the globe, this short-term, plot-derived understanding must be projected to much broader spatial and temporal scales.

There are two general approaches to projecting to broader scales. The first is an empirical approach based on correlative relationships between the ecological processes of interest and some physical property of the environment that is more readily measured at broader scales (e.g., productivity estimated from satellite images). This empirical approach is the subject of the accompanying article by Kratz and colleagues (2003). The second approach is a mechanistic approach in which the interactions and mutual constraints among ecological processes are simulated with a mathematical model, which is then used to predict broader-scale properties of ecosystems, landscapes, regions, and the globe.

Although this mechanistic approach has significant development and implementation costs, it also has several advantages. One advantage is that it can make use of the vast store of knowledge on fine-scale biological, geological, and chemical processes that underlie ecosystem function. However, this fine-scale knowledge needs to be appropriately scaled. Scaling involves a change in the spatial and temporal resolution of a model to be consistent with the data available to drive it. For example, Farquhar and von Caemmerer (1982) developed a well-corroborated model of the responses of photosynthesis to changes in carbon dioxide (CO_2), temperature, and light, but this model is only applicable to individual leaves on a minute-to-minute time scale. It would have to be scaled before it could be used with daily weather records and whole-canopy characteristics to predict daily whole-canopy productivity. This scaling might also incorporate new processes that act at the broader scale (e.g., light extinction through the canopy). Alternatively, the model might be projected up to the canopy scale. Projection involves repeated application of a model across space or time without changing its scale. For ex-

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Articles

ample, the Farquhar–von Caemmerer model might be applied with minute-by-minute weather data to every leaf in the canopy to predict productivity throughout the canopy for the entire day. Prediction of broader-scale ecological characteristics often involves a combination of scaling and projection.

Another advantage of a mechanistic approach is that changes in ecosystem properties in response to changes in the environment are incorporated in the underlying model. These changes in ecosystem properties can impede an empirical approach because there are limits to how far the correlative relationship underlying the approach can be extrapolated. For example, a relationship between satellite imagery and productivity might change under different moisture or soil fertility conditions. A mechanistic approach would predict how that relationship might change. The ability to predict changes in ecosystem properties is particularly important for projections into the future when the data needed to make an empirical projection do not yet exist (e.g., satellite imagery to estimate productivity for the year 2100).

A major problem with mechanistic scaling is that the coarse-scale predictions of the model can be difficult to test. Indeed, the motivation for the scaling or projection may be a lack of data at the coarser scale. This lack of data is particularly problematic if the scaling is intended to make long-term projections into the future. Such projections will likely involve very slowly responding components of the ecosystem (e.g., soil organic matter). Thus, data likely to be available to parameterize the model might not be sufficient to constrain the representation of these slowly responding components.

The National Science Foundation (NSF) Long Term Ecological Research (LTER) Network makes two vital contributions to a mechanistic scaling effort. First, the long-term commitment to individual sites attracts researchers from many disciplines to work on the same ecosystem, resulting in a broad range of mutually consistent data from a single site. These data would otherwise have to be inferred from several sites with different characteristics and under different conditions. Second, the LTER program provides the long-term data sets essential for estimating rate constants for the slow ecosystem processes that are likely to dominate the long-term responses of ecosystems to global change. Below we present four examples of mechanistic scaling using models derived from work at various LTER sites.

Synergy between modeling and long-term data sets: The Harvard Forest and Hubbard Brook LTER sites

We illustrate synergy between modeling and long-term data sets with an example from the Harvard Forest and Hubbard Brook LTER sites. The establishment of the LTER Network was predicated on the value of long-term data. The LTER sites serve both as hosts for the kinds of experiments that must continue beyond the usual 2- to 3-year funding cycle and as places to continually take the pulse of native ecosystems. There is a third and perhaps equally important role for the accumulating long-term data sets flowing from the LTER sites: They provide essential data for testing the validity of the ecosystem

models used to predict ecosystem characteristics across space and time.

The development of the PnET (photosynthesis and evapotranspiration) models (Aber et al. 1995, 1996, 1997, Aber and Driscoll 1997) is a case in point. Conceived as part of an integrated approach to regional-scale research, and first presented at the initial LTER All Scientists Meeting (Aber et al. 1993), the PnET models were designed expressly for use in conjunction with spatial data sets and for the prediction of ecosystem processes at the regional scale. As such, they are lumped-parameter models (Federer and Lash 1978) in which every effort has been made to capture the important dynamics of forest ecosystems with the fewest input parameter requirements.

At the heart of lumped-parameter models is an emphasis on simple, elegant formulations of whole-ecosystem processes. Thus, the PnET models employ neither the correlative equations of a purely empirical approach nor the complex theoretical or physiologically explicit formulations depicting very fine-scale interactions within the ecosystem. Instead, they employ some widely tested phenomenological functions that have a strong basis in fundamental plot-scale physiology. For example, photosynthesis is not coded from the Farquhar–von Caemmerer equations discussed in the introduction, but rather as a function of foliar nitrogen (N) concentration, which establishes maximum photosynthetic rates (Reich et al. 1995), and of well-established relationships with vapor-pressure deficit (VPD), light, and temperature (Aber et al. 1995). Rather than using the theoretically correct, but difficult to parameterize, Penman-Monteith equation to estimate transpiration, the PnET models use a simpler reasoning developed by Sinclair and colleagues (1984) that expresses water use efficiency as a function of VPD. By combining these two approaches, which are strongly rooted in data, researchers can estimate photosynthetic capacity, water use efficiency, and transpiration with just a few equations. Only foliar N content, daily maximum and minimum temperature (T_{max} and T_{min}), and photosynthetically active radiation (PAR) are required as inputs. (VPD is estimated from T_{max} and T_{min}.)

The PnET models are structured as a nested set of three models. The PnET-Day model (Aber et al. 1996) is a daily time-step canopy photosynthesis model that estimates gross and net carbon (C) gain only. This is nested within the PnET-II model (Aber et al. 1995), which adds allocation, respiration, and water balance algorithms to predict net C and water fluxes at variable time steps. This in turn is nested within the PnET-CN model (Aber et al. 1997, Aber and Driscoll 1997), which adds biomass pools, litter fall, decomposition, and N cycling, including deposition inputs and leaching losses. This nested structure allows independent testing of the individual model components.

The PnET models predict the integrated function of ecosystems. There are very few direct measurements of whole-ecosystem function, and even fewer that provide continuous whole-ecosystem data over several years. Thus, it can be difficult to find independent whole-ecosystem data to both pa-

rameterize and test the models. However, the PnET models are applied without calibration. That is, parameters used in the model have a physiological meaning and are estimated from data in the literature, leaving the existing whole-system data for independent testing. Thus, when the model is run, the input parameters are not optimized to improve the fit between model predictions and measured data. Because the model is not optimized, it is possible to learn from the discrepancies between prediction and measurement; that is, the model can be used to direct research. The analysis of the discrepancies illustrates yet another interaction of the models with the LTER data.

Work with the PnET models has been carried out as part of the Harvard Forest and Hubbard Brook LTER programs. Central data sets at these sites include the long-term, high-resolution gross and net C balance measured at the Harvard Forest by eddy covariance (Goulden et al. 1996) and the long-term water and nutrient-balance data sets at Hubbard Brook (Likens and Bormann 1995). These data sets have been used to challenge the PnET models. The PnET models do well predicting water and nutrient balances at Hubbard Brook, wood production at both Harvard Forest and Hubbard Brook, and net ecosystem C flux at Harvard Forest when data on several environmental stresses and land use are accurately specified (Aber et al. 1995, 1997, Ollinger et al. 2002).

Models reveal more when they fail than when they succeed in matching measured values. The PnET models fail to capture accurately the effects of water stress on gross C exchange (Aber et al. 1995). They also fail spectacularly in estimating N retention in the chronic N-amendment experiment at the Harvard Forest; the models predict rapid increases in nitrate loss when none occurred for 8 years (Aber et al. 1997). These failures guide research. What processes in the hydrologic and N cycles are either structured incorrectly or parameterized improperly in the model? Where are the gaps in knowledge about how these ecosystems work?

The PnET models have been used to make regional-scale predictions of changes in net primary production, net ecosystem production, water yield, and nitrate leaching into the future under a number of different scenarios including changes in climate, N deposition, tropospheric ozone, and CO_2 concentration, all for different land-use histories (see earlier references). These regional-scale simulations provide valuable insights into the future of the environment that would have been unavailable without the continuous high-quality measurements of critical indicators of ecosystem function provided by the two LTER sites.

Long-term carbon budget for arctic tundra: The Arctic LTER site

The Arctic LTER site on the North Slope of Alaska has maintained a series of long-term experiments designed to assess responses of tussock tundra to changes in climate (Chapin et al. 1995, Shaver and Chapin 1995). These long-term data, along with earlier data from the same site on ecosystem responses

to elevated CO_2 (Grulke et al.1990) and established physiological and biogeochemical knowledge, have been synthesized in a series of three models to assess responses of arctic tundra to changes in CO_2 concentration and climate. These models depict processes at different scales, and the finer-scale models are used to derive the next coarser-scaled model. The models were used in concert to scale information, derived from a few decades of work on small experimental plots, to assess changes in the C budget of the 9000-square-kilometer (km^2) Kuparuk River watershed over the next century.

The first of these models is the soil–plant–atmosphere (SPA) model of canopy photosynthesis (Williams et al. 1996), which was derived using eddy covariance data from the Harvard Forest LTER (Goulden et al. 1996) and has been successfully applied to other eddy covariance data, including data from arctic tundra (Williams et al. 2000). It incorporates several well-established physiological and biophysical relationships like the Farquhar–von Caemmerer photosynthesis, the Penman-Monteith transpiration, and the Jones soil-to-leaf hydraulic models (Williams et al. 1996). It requires fine-scale data on canopy leaf and N distribution as well as half-hourly data on temperature, light, soil moisture, and CO_2. The SPA model was applied to data from the footprint of 14 eddy covariance towers distributed in the Kuparuk River watershed, which includes the Arctic LTER site (Williams et al. 2000). These towers were placed in the four major types of tundra on the North Slope of Alaska: heath, shrub, moist tussock, and wet sedge tundra. The model was successful at simulating CO_2 exchanges for all four tundra types *(r^2 = 0.2 to 0.8; Williams et al. 2000).

To apply the SPA model to the whole Kuparuk River watershed would require not only data on canopy leaf area and N distribution over the entire watershed but also all the climatic data over the watershed for every half hour of the simulation. These data are difficult to obtain over such a large area at such a high frequency. In addition, because the model includes so much detail, running it for enough sites to represent the spatial pattern of photosynthesis over the region would be computationally prohibitive. Williams and colleagues (1997) took an alternate approach; they scaled the SPA model to develop an aggregated canopy model (ACM) that requires only daily climate data and is structurally far simpler than the SPA model, so is far less computationally demanding (about 1000 times faster).

To develop the ACM empirically would require a large set of daily photosynthesis data for a broad range of climatic conditions and vegetation properties. Such data sets are not available. Williams and colleagues (1997) therefore generated several thousand artificial days of data for a wide range of daily patterns in temperature and light. These were combined randomly with a wide range of possible soil moisture conditions, CO_2 concentrations, leaf areas, and leaf N concentrations. The SPA model was used to simulate photosynthesis for each of these artificial days and environmental conditions. This rich set of artificial data was then used to develop a set of simple equations relating daily total photosynthesis to soil mois-

Articles

ture, CO_2 concentration, total canopy leaf area, total canopy N, maximum and minimum daily temperature, and daily total incident radiation (analogous to PnET-Day). The development of these simple equations used a nonlinear regression approach, with the form of the equations guided by knowledge of the underlying processes. The resulting equations capture about 96% of the day-to-day pattern in photosynthesis predicted by the SPA model and are consistent with daily estimates of photosynthesis from the eddy covariance towers $(r^2 = 0.96)$. The ACM was used to project estimates of daily photosynthesis over the Kuparuk River watershed using interpolated climate variables, a satellite-based estimate of leaf area, and a linear relationship between leaf area and canopy N derived from a survey of vegetation within the watershed (figure 1; Williams et al. 2001).

To project the ACM estimates of photosynthesis into the future requires both a predicted time series of climate change and a prediction of how leaf area and canopy N change in response to changing climate. These changes in vegetation properties might be generated with an independent ecosystem model. However, such an approach would not allow feedback between the ACM and the ecosystem model, and the predicted changes in leaf area and N therefore might not be consistent with the ACM predictions of photosynthesis. To incorporate this feedback, Le Dizes and colleagues (2003) incorporated the ACM into the general ecosystem model (GEM). The GEM has been used in the past to analyze interactions between the C and N cycles in experimental plots of tussock tundra at the Arctic LTER site (McKane et al. 1997) and to project responses of tussock tundra to changes in climate over the next century (Clein et al. 2000).

In addition to the ACM photosynthesis module, the GEM includes equations to allocate C and N among plant tissues, to decompose organic matter in the soil, to cycle N between soil and vegetation, and to simulate the responses of all these processes to changes in temperature and moisture. The interactions among these processes impose constraints on leaf area and leaf N and therefore on the photosynthetic rate predicted by the ACM. The GEM was calibrated to be simultaneously consistent with the 3-year and 10-year results from an experiment at the Arctic LTER site in which plots were subjected to warming, fertilization, shading, and elevated CO_2 concentration (McKane et al. 1997). Although these experiments cannot mimic future changes in CO_2 and climate directly, they do elicit process-level responses likely to be important in the ecosystem response to future changes in the environment. Calibration of the GEM to the experimental plots provides a means to make the model consistent with these process-level responses. Le Dizes and colleagues (2003) used the calibrated GEM to predict changes in photosynthesis and C storage across the Kuparuk River watershed between 1920 and 2100 (figure 1). The estimated spatial pattern of production using the GEM correlates well with satellite-based production estimates for years between 1992 and 1998 $(r^2 = 0.88$ to 0.94). The results of this spatial–temporal projection have been compared to results from the

terrestrial ecosystem model (Clein et al. 2000) to help understand changes in ecosystem C budgets throughout the Arctic.

Spatial interactions among species: The Shortgrass Steppe, Sevilleta, and Jornada Basin LTER sites

The final step in the previous examples was a plot-by-plot projection to a regional scale, which ignored any spatial interactions among the plots. However, broad-scale spatial interactions can be important in the response of landscapes to changes in climate or land use. Fire and seed dispersal are the most common spatially explicit processes used in models to examine these types of interaction (e.g., Miller and Urban 1999, Peters and Herrick 2001). At the Shortgrass Steppe, Sevilleta, and Jornada LTER sites, a landscape-level seed dispersal algorithm has been coupled with individual-based models to simulate species invasions, geographic shifts in species ranges, and local species dynamics as climate or disturbance regime changes.

These individual-based models use plant life-history traits to simulate recruitment, growth, and mortality of individual plants on small plots. These models have been used in several capacities that build on the long-term data sets available at three LTER sites in Colorado and New Mexico. In particular, they have been used (a) to synthesize and integrate existing knowledge to improve understanding of vegetation recovery following disturbance, (b) to identify key processes limiting that recovery, and (c) to predict long-term recovery dynamics for different climate and disturbance regimes. In these analyses, an iterative procedure is employed in which data from short- and long-term experiments are used to parameterize and test the models. Model results lead to new insights that are used to generate hypotheses about key processes; these hypotheses are then tested with new experiments. The LTER sites are critical to this process, both in providing the broad suite of plant, soil, and climate data needed for model parameterization and testing and in providing the continuity needed to conduct long-term, interrelated experiments.

At the Shortgrass Steppe LTER site in northern Colorado, an individual-based gap dynamics model (STEPPE) was developed to simulate the response of semiarid grasslands to disturbances of different sizes. STEPPE was the first attempt to apply an individual-based gap dynamics approach to grasslands; most individual-based models have been applied to forests (reviewed in Urban and Shugart 1992). The model was used in combination with a series of experiments conducted at the LTER site to examine the role of different recruitment processes on the recovery of species from disturbances of various sizes. Like gap dynamics models of forests, STEPPE simulates vegetation dynamics on small plots at an annual time step. Plot size (0.12 m^2) is smaller than in forest models, and is based on the belowground resource space occupied by a full-size individual of the dominant grass, *Bouteloua gracilis* (blue grama). Competition is determined by the overlap in the distribution of roots for each species and the distribution of available soil water, which is controlled in part by soil texture.
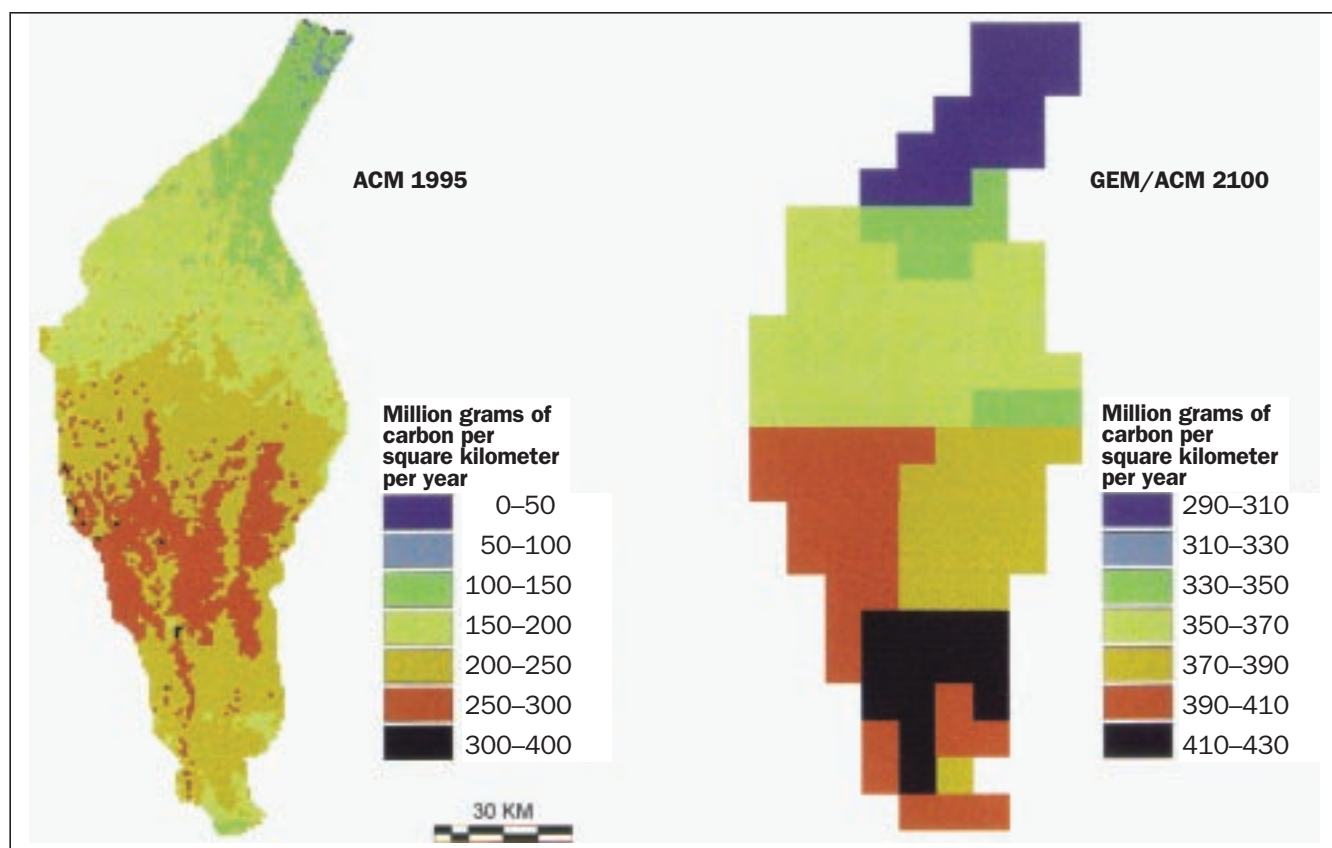
Figure 1. Gross primary production (GPP) for the Kuparuk River basin on the North Slope of Alaska for the years 1995 and 2100. Through a formal aggregation procedure described in the text, the soil–plant–atmosphere model was used to derive an aggregated canopy model (ACM), which is less computationally demanding and has more modest data requirements. On the left is the prediction of GPP produced by the ACM for 1995 using interpolated climate data, satellite imagery to estimate leaf area, and an empirical relationship between leaf area and foliar nitrogen (redrawn from Williams et al. 2001). On the right is the prediction of GPP by the ACM for 2100 using a projected climate. Because no satellite data are available to run ACM for the year 2100, it was embedded into the general ecosystem model (GEM), which predicts both leaf area and foliar N (derived from data in Le Dizes et al. 2003).

The model simulates responses to disturbance and to changes in annual precipitation and temperature.

Initial simulations using STEPPE examined vegetation dynamics following disturbances similar in size to individual plots, either with or without seed production constraints (Coffin and Lauenroth 1990). The model was successful in simulating dynamics on these small plots. However, on disturbances larger than a single plot, the recovery times of the dominant species were too fast compared with field observations, suggesting that other processes are important as disturbance size increases. To simulate intermediate and large disturbed areas (2 m^2 to 1 km^2), an interactive grid of plots was used to allow seed dispersal by wind to operate in the model. Results indicated longer recovery times for the dominant species as disturbance size increased; these results were modified by soil texture that influenced seedling establishment of the dominant grasses (Coffin and Lauenroth 1994, Coffin et al. 1996). The recovery time in the spatially explicit model is similar to field results from intermediate disturbance size (less than 16 m^2; Coffin and Lauenroth 1989), but is still too fast for large disturbances such as abandoned agricultural fields (Coffin et al. 1996). These results led to new studies showing that the redistribution of seeds by cattle is another process that may influence patterns in recovery on large areas (Fraleigh 1999). Thus, experimentation combined with simulation model development and analysis significantly improved the understanding of the response of shortgrass steppe to disturbances of different sizes. Scaling model results beyond single plots using a grid of interactive plots was important in capturing vegetation dynamics of the landscape.

More recently, a similar modeling exercise was used to examine the importance of plant processes, at multiple spatial scales, interacting with soil texture and climate to affect perennial grass and shrub response to climate change. For this question, another individual-based gap dynamics model (ECOTONE) was developed that simulates arid and semiarid grasslands and shrublands as well as ecotones between vegetation types. ECOTONE contains more sophisticated recruitment and competition routines than STEPPE, and can

Articles ●━━━━━━━━━━━━━━━━━━━━━━━━━━━━━

handle multiple dominant life forms (Peters 2002, Peters and Herrick 2001). Soil water is simulated daily and feedbacks between vegetation and soil properties occur monthly or annually.

ECOTONE was used to examine the importance of spatial processes to perennial grass recovery following shrub invasion on sites with different soils and with or without a directional change in climate. The Jornada LTER site was used to parameterize and test the model because of its long history of research (1912 to the present). This history includes a period of extensive shrub invasion into perennial grasslands. Predictions about perennial grass dominance and recovery were made for the Sevilleta LTER site, located approximately 250 km to the north of the Jornada site, with similar soils and precipitation but cooler temperatures. Landscapes at the Sevilleta site are a mosaic of perennial grasslands and shrublands; thus, the importance of seed dispersal to recovery for sites on different soils could be evaluated. A 20,000-hectare (ha) area of the McKenzie Flats was gridded into a series of 1 ha macroplots. Each macroplot was simulated by extrapolating results from the average of 25 ECOTONE plots, each 1 m^2, with the same soil texture and climatic conditions. Seed availability of the dominant grass, *Bouteloua eriopoda* (black grama), to a plot was determined both by seeds produced within that plot and by seeds dispersed from neighboring plots. The probability of seed dispersal was a function of distance between macroplots and biomass of grasses on a plot.

Under current climatic conditions, ECOTONE successfully simulated the dominance of *B. eriopoda* on soils with high water availability (loamy sand and sandy loam; figure 2). *Larrea tridentata* (creosote bush) dominated gravelly loam soils with low available water. Loam soils with intermediate water availability contained both species. Under a climate change scenario with an increase in summer precipitation and year-round increase in temperature, *B. eriopoda* increased in biomass on all soils when seeds were always available. On soils with low available water, shrubs maintained dominance through time. If seeds were limited by dispersal, then biomass of *B. eriopoda* decreased in the transition zone where both species coexisted. Thus, multiple plant processes interacting with soil texture and climate affected perennial grass response to climate change. Large-scale shifts in dominance between life-forms are often predicted by continental scale models based on competition. The results from the ECOTONE model illustrate that seed dispersal and seedling establishment are also important constraints on the response by perennial grasses to climate change, particularly at the landscape scale.

Predicting regional land–atmospheric exchanges: The Shortgrass Steppe LTER site

In the earlier examples, the ecosystem models responded to changes in climate, but there was no ecosystem feedback to the atmosphere. On long time scales and regional or global spatial scales, these feedbacks can be very important. For example, "In studies of...climate change, terrestrial ecosystem dy-

namics are as important as changes in atmospheric dynamics and composition, ocean circulation, ice sheet extent, and [Earth] orbit perturbations" (Pielke et al. 1998, p. 461), and inclusion of ecosystem characteristics can markedly improve regional atmospheric modeling (Pielke et al. 1997). However, the very different space and time scales used to study ecosystems as opposed to atmospheric processes have hampered a complete understanding of the coupling between the two. For example, ecosystem models are generally applied to plots less than 100 m across, at monthly or yearly time steps, while atmospheric models are generally applied to cells thousands of kilometers across, at subdaily time steps. Before two-way communication can be set up between these two types of models, this difference in scale has to be reconciled.

The long-term commitment provided by the LTER program has made it possible to address some of these differences in scale between ecosystem and atmospheric perspectives. Researchers at the Shortgrass Steppe LTER site have been able to test various hypotheses related to changes in land use and land cover on regional atmospheric dynamics (Eastman et al. 1998, Lu et al. 2001). Development of this regional land–atmosphere perspective started from plot-level studies of water vapor exchange, greenhouse gas fluxes, and land-use effects on these exchanges (Parton et al. 1998). The CENTURY ecosystem model was applied to these data using a monthly time step (Parton et al. 1987, 1996). This model has been well tested with site-level studies to evaluate the system response to changes across gradients of soil texture, moisture, temperature, and land use at the Center Plains Experimental Range on the Shortgrass Steppe LTER site (Schimel et al. 1990, Burke et al. 1991, Schimel et al. 1994, Lapitan and Parton 1996, Mosier et al. 1996, 1997). The monthly time step in the CENTURY model provided the appropriate temporal resolution to represent the feedback between vegetation and soil-microbial processes, but not the feedback between ecosystems and the atmosphere.

Ecosystem–atmosphere feedbacks operate on a wide range of time scales. For example, weather is strongly influenced by the fast coupling of water and energy exchange between ecosystems and the atmosphere (Schimel et al. 1990, Walko et al. 2000). The fluxes of trace gases such as nitrous oxide (N_2O), nitric oxide (NO), and methane (CH_4) to the atmosphere respond to daily changes in temperature and soil water content (Mosier et al. 1996). The exchange of CO_2 between ecosystems and the atmosphere, and the net sequestration of atmospheric C in ecosystems, is constrained by seasonal and longer-term climate restrictions (Parton et al. 1987). All these temporal scales need to be represented in an ecosystem model to adequately accommodate ecosystem–atmosphere feedbacks. This range in temporal scale creates some important challenges for representing complex process interactions in ecosystem models (Rastetter et al. 1992). The work at the Shortgrass Steppe LTER site has made it possible to address some of these challenges.

One project that required the reconciliation of ecosystem and atmospheric time scales was the derivation of the
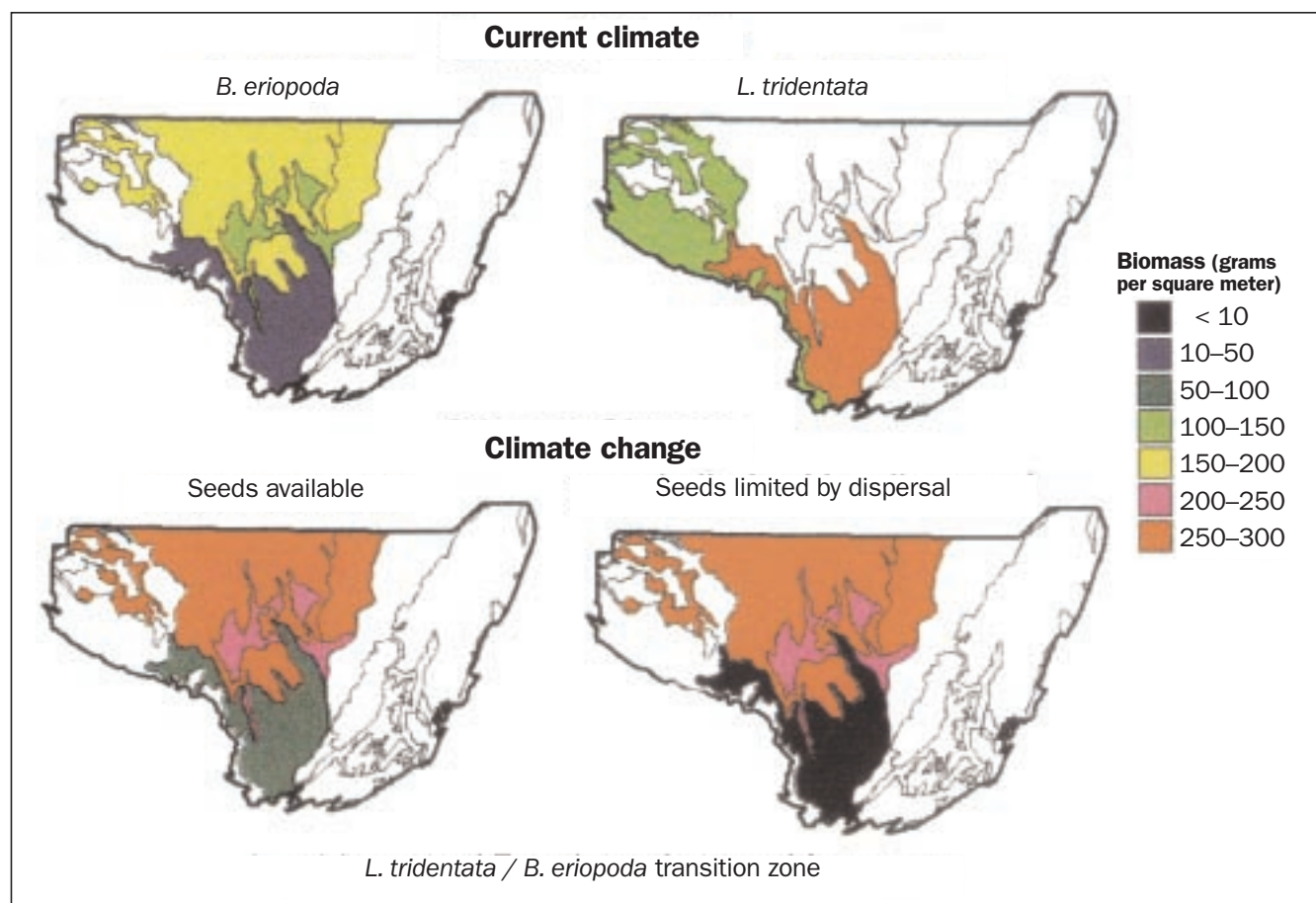
Figure 2. Simulation results from ECOTONE for vegetation dynamics at the Sevilleta LTER. Top panel: biomass of **Bouteloua eriopoda** *(black grama) and* **Larrea tridentata** *(creosote bush) under current climatic conditions on four soils differing in plant-available water. Bottom panel: biomass of* **B. eriopoda** *under a GFDL (Geophysical Fluid Dynamics Laboratory) climatic-change scenario. Lower left panel: seeds always available. Lower right panel: seeds limited by dispersal from neighboring plots with* **B. eriopoda** *present.*

DAYCENT model from the CENTURY model (Parton et al. 1998). The DAYCENT model was designed to predict fluxes of the greenhouse gases N_2O, NO_x (other nitrogen oxides), and CH_4 to the atmosphere. These fluxes are sensitive to daily changes in soil moisture and temperature, and could therefore not be reliably predicted with the monthly time step in the CENTURY model. In the DAYCENT model, above- and belowground biomasses were updated weekly, but water and nutrient flux rates were calculated daily. In addition, to adequately simulate the distribution and movement of soil water, the model was modified to accommodate finer depth resolution in the soil (layers 1 to 15 cm thick) and a 2-hour time step to simulate water redistribution among soil layers. These changes improved the simulated linkage between ecosystems and atmosphere in terms of both the trace gas fluxes and the water and energy balance (Parton et al. 1998).

The rescaling of the monthly time-step CENTURY model to the daily time-step DAYCENT model enabled a direct two-way linkage between the DAYCENT model and an atmospheric model (ClimRAMS [climate version of the Re-

gional Atmospheric Modeling System]; Lu et al. 2001). This linkage allows feedbacks associated with changes in transpiring leaf area, soil moisture dynamics, and related changes in land surface to influence atmospheric dynamics (Lu et al. 2001). Inclusion of these feedbacks is essential for predicting regional weather patterns (Pielke et al. 1997).

An understanding of the processes mediating this ecosystem–atmosphere coupling was derived largely from the extensive field observations over the course of a decade at the Shortgrass Steppe LTER site (Lapitan and Parton 1996, Mosier et al. 1996, 1997). The models developed as part of the Shortgrass Steppe LTER program represent a synthesis of many years of research by many researchers with a broad range of expertise. Without the long-term commitment to ongoing research at a single site provided by the LTER program, this degree of understanding and synthesis would be more difficult to acquire.

Conclusion

We have presented four examples of how data derived from six LTER sites have been used to project estimates of ecosys-

tem properties across space and time based on a mechanistic understanding of the underlying ecosystem processes. This mechanistic understanding serves as the basis for models that are then used with spatial and time-series data to project to broad regions and into the future. The PnET models in the first example are based on a plot-scale understanding of ecosystem processes that are constrained by the physiology of photosynthesis and the cycling of nutrients and water. In the second example, the mechanistic understanding is progressively scaled from tissue physiology to the ecosystem level through a series of three models (SPA, ACM, and GEM); the finer-scale models are used to derive or serve as parts of the coarser-scale models, and the ecosystem-scale model imposes nutrient cycling constraints on the finer-scale parts. The two models (STEPPE and ECOTONE) in the third example are based on the plot-scale competitive interactions among individual plants and incorporate spatial interactions among plots through the dispersal of seeds. Spatial interactions are extended to even broader scales in the third example, in which the CENTURY model was rescaled to allow two-way interactions between ecosystems and the overlying atmosphere. This two-way interaction allows changes in ecosystem characteristics to affect simulated patterns in regional weather and therefore allows changes in ecosystems on one part of the landscape to affect the simulation of ecosystems elsewhere on the landscape. These spatial interactions among plots or across regions can have important local effects on ecosystem function, but are as yet poorly represented in ecosystem models, particularly biogeochemical models (e.g., hillslope interactions mediated by the movement of water and nutrients). The continuing commitment provided by the LTER program makes possible the long-term experiments necessary to understand these interactions.

The mechanistic understanding of ecosystem processes that underlies the models presented here has been derived from many studies from several related disciplines over many years, but the contribution of research at the LTER sites is of particular importance. The LTER program has allowed the commitment of resources to long-term monitoring and experimentation. Because of this long-term perspective, an understanding of slow-responding ecosystem components and feedbacks is emerging. This depth of knowledge is vital for scaling ecological processes across space and time. The LTER program has also made it possible for work in many disciplines to be conducted on the same ecosystem. The modeling-based scaling efforts described here are greatly enhanced by the resulting broad range of mutually consistent data.

Acknowledgments

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