

Handbook of Ecological Models Used in Ecosystem and Environmental Management

Edited by
Sven Erik Jørgensen



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Grassland Simulation Models: A Synthesis of Current Models and Future Challenges

Debra P. C. Peters

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7.1 Introduction

Grasslands occur on all continents, except Antarctica, in areas that are transitional between deserts that are drier and forests that are wetter. Historically, grasslands comprised almost 42% of the world's plant cover (Anderson 2006). However, many perennial grasslands have converted to other system states (degraded shrublands or shrub steppes, savannas, woodlands, cultivated fields) or have been susceptible to invasion by nonnative species over the past several centuries. For example, North American grasslands are now listed as critically endangered with declines in spatial extent as high as 98% in some locations (Noss et al. 1995). Consequences of these vegetation conversions are consistent across grasslands globally: local ecosystem properties are modified, including primary production, biodiversity, and rates and patterns of nutrient cycling (Schlesinger et al. 1990; Ricketts et al. 1999; Huenneke et al. 2002; Briggs et al. 2005; Knapp et al. 2008). Regional to global processes are altered, including transport of dust to the atmosphere, redistribution of

water to the oceans and groundwater reserves, and feedbacks to weather (Jaffe et al. 2003; McKergow et al. 2005; Pielke et al. 2007).

Aside from conversion to cultivation, historic shifts in grass species composition and dominance are related to changes in environmental drivers, in particular climate (i.e., periodic drought), fire, and grazing animals (Oesterheld et al. 1999); the relative importance of these drivers to ecosystem dynamics varies by grassland type (Pieper 2005). Dry grasslands change to more desertlike systems as xerophytic shrubs increase in density and cover with livestock overgrazing in times of drought (Schlesinger et al. 1990; Archer 1994). Mesic grasslands shift to more forest-like systems as trees increase in density and cover with a reduction in grazing and fire frequency, particularly in extended wet periods (Briggs et al. 2005). Shifts in species composition can occur in grasslands containing mixtures of C₃ and C₄ species when temperature and water availability are modified to favor one physiology over another (Steuter 1987; Paruelo and Lauenroth 1996). Shifts in dominance between species that are grazing- or fire-adapted occur with changes in grazing management or fire frequency (Knapp et al. 1998). Invasion by non-native species depends on the availability of their propagules in the presence of disturbance under appropriate environmental conditions that favor their recruitment and expansion (Sheley and Petroff 1999).

Although many studies have been conducted in grasslands, it is often difficult experimentally to quantify and distinguish the role of each driver to grassland dynamics, and the consequences of changing species composition and dominance to other ecosystem processes (Peters et al. 2006). In addition, the environmental drivers continue to change, thus making predictions about future states increasingly difficult (Smith et al. 2009). Simulation models provide a powerful approach to improving our understanding of historic dynamics, and to synthesizing the importance of changing drivers to future dynamics.

7.2 Overview of Available Models

Five major classes of simulation models are commonly used to study grasslands (Tables 7.1 to 7.5). Each class is discussed below in terms of its drivers and key response variables relative to the types of questions typically addressed by that class of model. Specific models are described for each class that differ in the drivers (climate, grazing, fire), input parameters, unit of response, processes simulated, and response or output variables that determine the questions that can be addressed. An exhaustive description of all possible grassland models is not intended, but rather specific models are given as examples. In addition, a representation of each model is given rather than all possible applications that may, in some cases, include different plot

sizes, functional types, input parameters, and response variables. The discussion is limited to simulation models such that theoretical and mathematical models are not discussed here (e.g., Rietkerk et al. 1997; HilleRisLambers et al. 2001).

7.2.1 Demographic Models

Demographic models include both individual-based models (IBMs), models that simulate an aggregate of individuals, and cellular automata (CA) models (Table 7.1). IBMs simulate the recruitment, growth, and mortality of individual plants, and how these demographic processes are affected by competition for resources with neighboring plants. The models are often deterministic in competition for resources that affect growth, and have stochastic elements for recruitment and mortality. IBMs have a long history of use in forests where individual trees compete primarily for light, although more recent applications include simple submodels of water and nitrogen (Botkin et al. 1972; Shugart 1984; Smith and Urban 1988; Pacala et al. 1996; Moorcroft et al. 2001). The forest modeling paradigm was adapted to grasslands where plants compete for belowground resources (water, nitrogen) (Coffin and Lauenroth 1990; Peters 2002).

IBMs are often gap models where individual plants are simulated on a plot scaled to the resource space associated with a full-size plant of the dominant species. Forest models use light gaps associated with the canopy of a full-size dominant tree (Shugart 1984), whereas grassland models define a gap as the belowground resource space (i.e., active rooting volume) associated with a full-size grass of the dominant species (Coffin and Lauenroth 1990). Because grass plants are small, the plot size of grassland models is much smaller (0.1 to 1 m²) compared with forest gap models (>100 m²). Time step is typically annual for incrementing plant growth, although other dynamics, such as soil water, may be simulated at a finer resolution (daily, weekly, monthly), and this information is aggregated to obtain an annual amount of water available for growth by each plant. Grids of plots are used to simulate landscapes, either with or without spatial processes such as seed dispersal, that connect plots (Coffin and Lauenroth 1989; Rastetter et al. 2003).

Because of the challenges and uncertainties in explicitly simulating belowground resources and rooting distributions at the temporal and spatial resolution required for individual grasses, IBMs have not been used as extensively in grasslands compared to the number and variety of forest models (Bugmann 2001; Perry and Enright 2006). One approach to simulating competition for water is to link an IBM to a multilayer soil water model that simulates water dynamics (i.e., interception, evaporation, transpiration, infiltration, and deep drainage) at a fine-scale resolution in time (daily) and space (single plot with detailed soil layers). The approach is to compare the distribution of simulated soil water content with the distribution of active root biomass for each individual relative to total root biomass on the plot to determine the amount

TABLE 7.1

Demographic Models: Examples of Specific Models and Their Key Characteristics

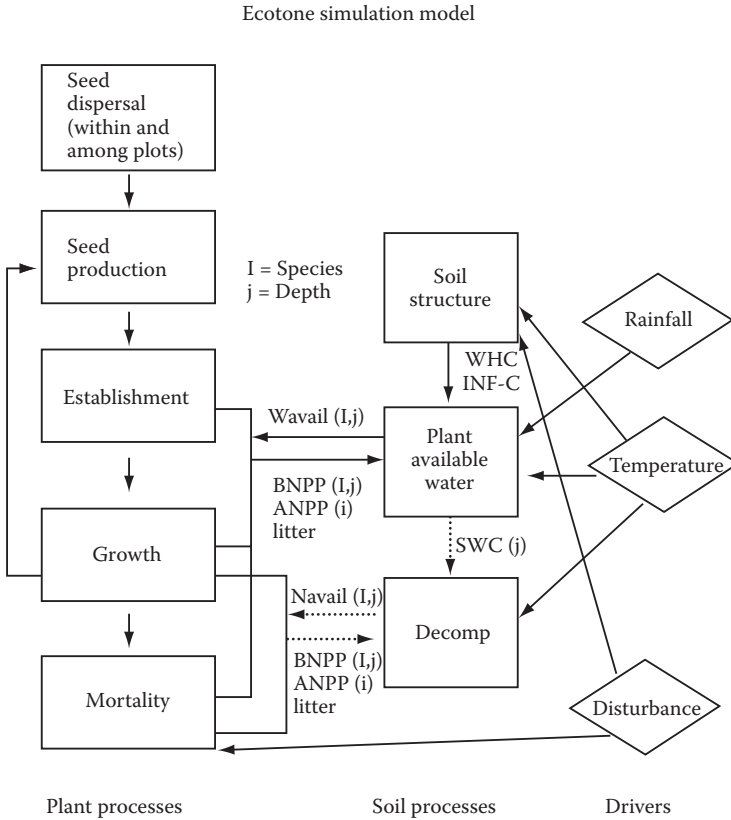
Model Type	Model Name	Ecosystem Type	Unit of Response	Plot Size	Time Step	Drivers	Plot-Scale Processes	Spatially Explicit Processes	Response Variables	References
IBM	STEPPE + SOILWAT	Semi-arid grasslands	Individual	0.12 m ²	Annual Annual, daily	PPT, temp. disturbance	Competition for water – rule based – dynamic	Dispersal Dispersal	Production biomass for herbaceous plants individuals, populations, communities	Coffin and Lauenroth (1989, 1990) Coffin et al. (1993)
IBM	Ecotone	Arid to semi-arid grasslands	Individual	0.1 to 1 m ²	Annual	PPT, temp. disturbance	Competition for water (dynamic)	Dispersal	Grass–shrub state changes individuals, populations, communities	Peters (2002) Peters and Herrick (2002) Rastetter et al. (2003)
IBM	COIRON	Grass steppes of Patagonia (<i>Festuca paltescens</i>)	Individual	0.09 m ²	Annual	PPT grazing (intensity, seasonality)	Competition for water (rule-based)	Lateral water movement grazing	Density of individuals Species ANPP	Paruelo et al. (2008)
PFT	FATE LAMOS	Semi-arid grasslands (Sweden)	Groups of individuals of four life stages	20 × 20 m	Annual	Grazing, fragmentation	Competition for light	Grazing frequency, intensity; seed dispersal	Biomass by group	Moore and Noble (1990) Cousins et al. (2003)
Cellular automata		Artificial landscapes	Populations	100s of meters	Annual	Weather, fragmentation	Competition (rule-based)	Seed dispersal	Population size, turnover rate, portion of occupied habitats	Körner and Jeltsch (2007)

Note: ANPP, aboveground net primary production; Pops, populations; PPT, precipitation.

of water allocated to a plant (Coffin et al. 1993; Peters 2002). Soil water content per layer is simulated daily by a soil water model using information on daily precipitation and temperature and soil properties. Active root biomass simulated by the vegetation model is determined for each plant based on the temperature of that day relative to optimum temperature for growth. Water is allocated proportionally to each plant daily based on its proportion of the total active root biomass in that layer. Total amount of water available to each plant in each year (cm water/year) is found by summing across layers and days. Water-use efficiency values (g production/cm water) are then used to convert water (cm) to plant production (grams) per year. Root to shoot ratios are used to allocate total production to above- and belowground. Root production by layer is distributed based on the proportion of water available to a plant in each layer relative to the total water in the profile. This approach to competition for soil water has been used successfully to link the SOILWAT model (Parton 1978) to two grassland models (STEPPE, Coffin et al. 1993; Ecotone, Peters 2002).

Grassland IBMs have been used to examine the role of different drivers and key processes on species dominance and composition, primarily in arid and semiarid grasslands where competition for light can be ignored (Table 7.1). STEPPE was developed to examine the importance of local (competition for water) and spatial (seed dispersal) processes to successional dynamics of semiarid grasslands (Coffin and Lauenroth 1989, 1990). Although the model successfully represented successional patterns for a range of disturbance sizes (Coffin and Lauenroth 1989, 1994), the rate of recovery was too slow as disturbance size increased to include abandoned agricultural fields (Coffin et al. 1993). The model assumes that recovery is dependent solely on wind dispersal of seeds from the undisturbed edge of a field. Results suggest that additional processes besides wind are operating to disperse seeds over long distances to result in faster recovery times than simulated (Coffin et al. 1993).

The Ecotone IBM (Figure 7.1) was developed to examine shifts in species dominance between grasses and shrubs in arid and semiarid grasslands, either with (Rastetter et al. 2003) or without seed dispersal (Peters 2002). This model explicitly includes competitive interactions among grasses and shrubs, and the drivers that promote shrub expansion or grass dominance. Results showed that soil properties can overwhelm climatic conditions that favor shrub expansion to allow grass persistence (Peters 2002), and that seed dispersal can limit the suitable microsites for grass dominance in a shrub-dominated landscape (Rastetter et al. 2003). Ecotone has also been used to simulate conditions that limit or promote the spread of herbaceous invasive species (Goslee et al. 2001, 2006), and to identify thresholds in disturbance frequency where dominance shifts from perennial grasses to shrubs (Peters and Herrick 2002). The COIRON model was developed to examine effects of precipitation and livestock grazing on density of perennial grasses in South America (Paruelo et al. 2008). Interannual variability in precipitation

**FIGURE 7.1**

The Ecotone IBM for grasslands simulates plant (recruitment, competition, mortality), water, and soil processes within a plot as well as seed dispersal among plots. (From Peters, D.P.C., *Ecological Modelling* 152, 5–32, 2002. With permission.) Competition for soil water is determined using water availability and rooting distribution by depth for each plant relative to all plants on a plot. Time scales vary from days to years depending on the process simulated. Spatial scales range from individual plants to groups of plants (patches), landscape units, and geomorphic units. Environmental drivers include climate (precipitation, temperature) and disturbances, such as human and animal activities, that kill plants and modify soil structure.

was found to be more important than grazing regime in explaining plant density.

Two models similar to IBMs deserve mention here. First, the FATE model simulates groups of individuals in similar life stages rather than simulating individual plants (Moore and Noble 1990). Linking the model to LAMOS allowed simulation of the effects of grazing frequency and intensity on plant species persistence at the landscape scale, and the relative effects of grassland size and pattern (Cousins et al. 2003). Results showed that continuous, low intensity grazing is more favorable to grasslands than discontinuous,

high intensity grazing. Second, cellular automata (CA) models have been used to simulate plant populations across landscapes using rules for population dynamics in each cell. In CA models, each particular cell is affected by its neighbors in a simple, rule-based manner. A CA model for grasslands showed that plant functional groups selected to represent populations with different traits have different vulnerabilities to fragmentation (Körner and Jeltsch 2007).

Advantages. Demographic models, and in particular, IBMs, are relevant to many key questions in grasslands that deal with invasion by woody plants or herbaceous, nonnative species. A focus on individual plant dynamics, including recruitment and dispersal, allows the simulation of invasion and recovery dynamics by populations and species. In addition, IBMs allow an examination of how system properties emerge from the behavior of individuals, and how system dynamics affect individuals. Variation among individuals, local interactions such as competition for limiting resources, complete life cycles, and individual responses to changing environmental conditions can all be studied within the context of multiple levels of organization (populations, communities, ecosystems) (Grimm et al. 2006). IBMs are intuitively appealing because of the use of individuals as the fundamental unit, and of life cycle stages with stochastic elements (recruitment, mortality) that can often be parameterized based on natural history information for each species.

Limitations. IBMs can be difficult to parameterize for grasslands given that competition among individuals is simulated, and little is known about how plants compete for belowground resources. IBMs are computationally intensive as spatial extent increases because many small plots with many individuals on each plot need to be simulated. Thus, simulations can become prohibitive for large landscapes and regions. IBMs require many data for calibration and validation, although simple functional relationships are often possible for some parameters, in particular those related to recruitment and mortality when they are assumed to be stochastic processes. The models can not simulate conservation of mass and energy, and can become complex if many processes are included. Developing IBMs for mesic grasslands where both above- and belowground competition need to be explicitly simulated is a challenge for the future.

Approaches to address limitations. Approaches have been developed to address some of these limitations in forest models; these approaches are also expected to be applicable to grassland models. For example, the HYBRID model replaces species-specific functions with physiological and biogeochemical relationships similar to ecosystem models (e.g., Century described below). This approach reduces the number of parameters required, yet maintains mechanistic relationships. To scale up, each 1° Global Climate Model (GCM) grid cell is assumed to be homogeneous, and is simulated using the ensemble average of 10 tree-size plots (Friend et al. 1997). Hundreds or thousands of tree-size plots would be required to account for within GCM

grid cell heterogeneity. More recent approaches have focused on developing equations that govern the ensemble average of an IBM directly from fine-scale processes without simulating each plant (Moorcroft et al. 2001). More tractable macroscopic equations have been developed to predict mean densities and size structures for each species using only individual-level parameter values and functional forms in an IBM (Strigul et al. 2008). These equations can be solved analytically to significantly reduce computational time for large spatial extents.

Meta-modeling is a different approach where many simulations of an IBM are used to develop relationships between state variables and drivers or to create transition probabilities from one state to another (Urban 2005). These relationships or transition probabilities can then be used to simulate large spatial extents, by using a CA model, a semi-Markov model, or a stage-based transition model, depending on the level of detail included in the processes in the original IBM (Urban et al. 1999).

7.2.2 Physiological Models

Physiological models simulate carbon assimilation, allocation, and growth by plant functional types (PFTs) or species (Table 7.2). Models typically include additional processes, such as local water and nitrogen dynamics, and spatial processes associated with water redistribution and seed dispersal. The time step is daily to weekly, and key response variables are biomass and production by PFTs or key species. Plot size is sufficiently large to assume homogeneity within a patch (tens to hundreds of meters). PALS is an example of these models that have been used to explore effects of rainfall variability on primary production and plant–soil water dynamics (Reynolds et al. 2000), and decomposition and nutrient cycling (Kemp et al. 2003). MALS is a spatially explicit version of PALS that includes water redistribution and seed dispersal among plots (Gao and Reynolds 2003). Results generally support the hypothesis that wetter winters and drier summers decrease grasses and increase shrubs, but the model was unable to reproduce major shifts in state from grasslands to shrublands.

The SAVANNA model is included here, although this model also includes simple demographic processes of plants as well as detailed livestock grazing processes at local, landscape, and regional scales (Coughenour 1993). In this model, flows of biomass, nitrogen, and organisms are simulated weekly, and vegetation and ungulate production are related to climate, soils, and topography. SAVANNA was originally developed for studies of African pastoralism, and has been applied to western U.S. and Canadian national parks, and to savannas in Australia as an ecosystem management tool (Ludwig et al. 2001; Weisberg and Coughenour 2003). SAVANNA has also been used to examine the effects of climate change (precipitation, temperature, CO₂) on grazing system sustainability in steppe grasslands of Inner Mongolia (Christensen et al. 2004). Large increases in precipitation, temperature, and CO₂ left the

TABLE 7.2
Physiological Models: Examples of Specific Models and Their Key Characteristics

Model Type	Model Name	Ecosystem Type	Unit of Response	Plot Size	Time Step	Drivers	Plot-Scale Processes	Spatially Explicit Processes	Response Variables	Citations
PFT	PALS	Chihuahuan Desert	PFT	10 × 30 m	Day	Weather	Carbon assimilation allocation growth	None	Biomass, ANPP, nutrient cycling by PFT	Reynolds et al. (2000) Kemp et al. (2003)
PFT	MALS	Chihuahuan Desert	PFT	10 × 30 m	Day	Weather	Carbon assimilation allocation growth	Water run-off runoff Seed dispersal	Biomass by PFT	Gao and Reynolds (2003)
PFT	SAVANNA	Arid and semiarid grasslands	PFT (trees, shrubs, grasses) Animal FT	Scaled to landsc	Week	Weather, soil properties, elevation, aspect plus CO ₂	Carbon assimilation allocation growth Competition for water, N, light, demog	Seed dispersal	Plant biomass, production by PFT number of animals	Coughenour (1993) Boone et al. (2004) Christensen et al. (2004)
PFT	STEP STEP-RT	Annuals in Sahel	PFT (C ₃ /C ₄ ; proportion of dicots/grasses)	Day	Day	Weather (rainfall daily, temp., PET, radiation decade), soil depth, texture Radiative transfer functions	Carbon assimilation allocation growth	None	Biomass, LAI Canopy height, fraction green vegetation All above plus land surface reflectance	Mougin et al. (1995) Tracol et al. (2006) Jarlan et al. (2008)

Note: Animal FT, animal functional type; ANPP, aboveground net primary production; demog, demography; landsc, landscape; N, nitrogen; PET, potential evapotranspiration; PFT, plant functional type; PPT, precipitation.

simulated system vulnerable to shrub invasion when grazed. SAVANNA has also been used to guide management decisions in Africa where simulated production was improved if livestock stocking was reduced before a forecasted drought (Boone et al. 2004).

A set of physiologically based models have been developed for use with remotely sensed images. The STEP model simulates daily water fluxes, photosynthesis, respiration, growth, and senescence driven by weather and global radiation (Mougin et al. 1995). STEP was coupled with radiative transfer models in the optical (Lo Seen et al. 1995) and active/passive microwave domains (Frison et al. 1998) to interpret temporal variations of satellite observations over the Sahel. Normalized Difference Vegetation Index (NDVI) values were also assimilated into STEP to estimate grassland production in Mali (Jarlan et al. 2008). Values simulated by a canopy process model were also used in canopy radiative transfer equations to determine effects of vegetation change on energy balance with feedbacks to the atmosphere (Cayrol et al. 2000).

Advantages. Physiological models account for fine-scale temporal resolution in carbon, nitrogen, and water dynamics (daily), and are used for questions related to controls on carbon assimilation and allocation as related to photosynthesis. The focus is on biomass and production of PFTs or key species, thus the spatial resolution assumes homogeneity within plots sufficiently large to support multiple PFTs (e.g., SAVANNA: trees, shrubs, grasses) or to reduce heterogeneous responses (PALS). Detailed vegetation–herbivore interactions can be simulated at fine temporal scales needed to understand the effects of livestock grazing on grassland production.

Limitations. Because demographic processes are not included, physiological models are limited in their ability to simulate shifts in species dominance or state changes from grasslands to woody plant dominance. The short time steps (daily, weekly) require intensive parameterization of plant physiological processes.

7.2.3 Physical Models

Physical models simulate physical processes, typically soil water dynamics and other environmental variables, then rules or functional relationships are used to calculate vegetation responses (Table 7.3). One model, the SOILWAT model of soil water dynamics, has been used extensively to calculate the probability of germination and establishment for perennial grasses in North America. SOILWAT is a daily time step, multilayer soil water dynamics model of interception, evaporation, transpiration, infiltration, and deep storage (percolation) (Parton 1978). Combining this model of soil water dynamics with detailed growth chamber studies of the sequence of microenvironmental conditions required for germination and establishment has allowed recruitment probabilities to be calculated for a dominant perennial grass in the shortgrass steppe for different soil properties (Lauenroth

TABLE 7.3
Physical Models: Examples of Specific Models and Their Key Characteristics

Model Type	Model Name	Ecosystem Type	Unit of Response	Plot Size	Time Step	Drivers	Plot-Scale Processes	Spatially Explicit Processes	Response Variables	References
Tippling bucket	SOILWAT	Shortgrass steppe SGS-CD CD	Plot	1 × 1 m	Day	Biomass, weather, soil properties	Soil water dynamics	None	Soil water content Estab. from rules	Lauenroth et al. (1994) Minnick and Coffin (1999) Peters (2000) Peters et al. (2010)
Membership functions		Mediterranean: semiarid	Plot	25 × 25 m	Day	Weather, topography, soil hydraulic properties, rock cover, radiation flux	Soil water dynamics	Runoff	Germination and production calculated from rules	Svoray et al. (2008)
Niche-based	Biomod	Mostly forests	Species	0.5° grid	Month	Temp. PPT PET	Statistical relationships	Migration rates	Species presence/absence	Thuiller (2003) Morin and Thueller (2009)

Note: CD, Chihuahuan Desert; estab, establishment; PET, potential evapotranspiration; PPT, precipitation; SGS, shortgrass steppe; Temp, air temperature.

et al. 1994). Results showed that infrequent recruitment (1/10 to >1/100 years) can explain, at least in part, the inability of this species to recover following disturbance. The model was also extended to a dominant species in the Chihuahuan Desert grasslands, and was used to explore the importance of recruitment to the geographic distributions of dominant grass in the short-grass steppe and Chihuahuan Desert grasslands (Minnick and Coffin 1999). Effects of seasonality and decadal patterns in rainfall on establishment of grasses were examined at an ecotonal site between the two grassland types (Peters 2000), and more recently to examine effects of soil properties, climate, and historical shifts from grass to shrub dominance on grass establishment in the Chihuahuan Desert (Peters et al. 2010).

A similar approach was used for germination and production of annuals in Israel (Svoray et al. 2008). TOPMODEL was used to simulate soil moisture dynamics within and among topographic units, and relationships for other environmental variables were used in a fuzzy logic (rule based) approach to determine combined effects on germination and production of annuals in the Negev. Results showed that water redistribution and climate are of similar importance in explaining variation in ANPP (Svoray et al. 2008). Another type of physical model is a niche-based model where the establishment of statistical or theoretical relationships between environmental drivers and observed species distributions are used to predict future distributions as the drivers change. Niche-based models have been used to predict effects of climate and land use change on species distributions globally, including grasslands (e.g., Thomas et al. 2004; Thuiller 2003).

Advantages. Physical models are relatively easy to parameterize depending on the complexity of the underlying physical processes and the relationships with biotic responses. Niche-based models are relatively simple, yet can project modeled niches of many species given distribution data.

Limitations. No biology is explicitly included, thus many assumptions are needed for these models to work well. These models do not include biotic interactions, mortality, or growth, and rely on observed patterns based on historical drivers that may change nonlinearly in the future (Hampe 2004).

7.2.4 Biogeochemical Models

Biogeochemical models simulate changes in the cycling of carbon, water, and nutrients with fixed vegetation types (Table 7.4). Consequences of changes in vegetation type can be examined by imposing a change in vegetation or management regime. Although similar drivers (climate, soils) are used, the specific models within this class of models use very different approaches that can generate different results at the grid scale for the same input parameters, yet all models examined in one analysis converged on continental scale total values for NPP and total carbon storage (Schimel et al. 1997). In many cases, the models have been used for both global simulations as well as local, site-

TABLE 7.4
Biogeochemical Models: Examples of Specific Models and Their Key Characteristics

Model Type	Model Name	Ecosystem Type	Unit of Response	Plot Size	Time Step	Drivers	Plot-Scale Processes	Spatially Explicit Processes	Response Variables	Citations
Nutrient cycling	CENTURY	C ₃ -C ₄ Grasslands globally (also forests, shrublands)	Ecosystem	Plot to 0.5° grid	Month	Maximum, minimum ATEMP PPT Soil texture/Depth CO ₂	Soil carbon pools/fluxes Nitrogen, phosphorus, Sulfur Same as above	None	ANPP, SOC, net N min, E-T	Parton et al. (1987, 1993)
	DAYCENT	C ₃ -C ₄ grasslands	Ecosystem	Plot to 0.5° grid	Day	Same as above and manage. type, timing	Same as above	None	ANPP, SOC, trace gas flux	Parton et al. (1998)
Nutrient cycling	TEM	Grasslands globally (also forests, shrublands, tundra)	Ecosystem	Plot to 0.5° grid	Month	Maximum, minimum Temp PPT Soil texture/ Depth CO ₂	E-T photosyn. decomp. Soil N turnover	None	ANPP, SOC net N min, E-T	McGuire et al. (1993) Clein et al. (2000)
Nutrient cycling	BIOME-BGC	C ₃ -C ₄ Grasslands globally (also forests, shrublands)	Ecosystem	Plot to 0.5° grid	Day/ annual	Maximum, minimum Temp PPT Soil texture/ Depth CO ₂ N dep	E-T photosyn decomp. Soil N	None	ANPP, SOC net N min, E-T, LAI	Running and Hunt (1993) White et al. (2000) Thornton and Rosenbloom (2005)

Note: ANPP, aboveground net primary production; decomp, decomposition; E-T, evapotranspiration; LAI, leaf area index; N, nitrogen; net N min, net nitrogen mineralization; photosyn, photosynthesis; PPT, precipitation; SOC, soil organic carbon.

specific conditions. A large number of these models have been developed that allow model comparisons (e.g., Cramer et al. 1999); only a few are shown in Table 7.4 that include grasslands as part of one of many vegetation types simulated globally. One model was developed specifically for grasslands (CENTURY) that is described in more detail here.

The CENTURY model was originally developed to simulate Great Plains grasslands of North America (Parton et al. 1987). This model simulates carbon, nitrogen, and phosphorus cycling as well as plant production at a monthly time step. Multiple plant, litter, and carbon pools are simulated. Soil respiration is computed from decomposition of litter, and SOM is regulated by soil temperature and moisture. Runoff from a plot is calculated from ecosystem water balance. CENTURY has been used extensively to simulate grasslands both in the United States (Burke et al. 1991; Schimel et al. 2000) and globally (Parton et al. 1993; Cramer et al. 1999). DAYCENT is a more recent formulation that uses a daily time step, and more detailed submodels for simulating soil moisture, temperature, and nitrogen, trace gas flux, and soil organic matter (Parton et al. 1998; Gerten et al. 2008).

Advantages. Biogeochemical models are based on conservation principles. These models are easy to parameterize, apply to new systems, and use for predictions. Models have been developed for individual sites and ecosystem types as well as applied globally.

Limitations. These models cannot represent population or spatial variability, or dynamic state changes (grasses to shrubs). Although multiple PFTs can be simulated, species composition cannot be simulated. Proportional biomass by C_3 and C_4 functional groups has been used to represent total biomass and production.

7.2.5 Dynamic Global Vegetation Models

Dynamic global vegetation models (DGVMs) were designed to simulate vegetation functional and structural dynamics at the global scale, thus they are not specific to grassland dynamics. However, grasslands are one of several PFTs simulated globally, and some models have been used at the landscape scale to simulate grassland–forest ecotones. Thus, this class of models is briefly described here with particular reference to the models relevant to grasslands (Table 7.5).

DGVMs simulate vegetation dynamics within a coarse resolution grid cell (typically $0.5^\circ \times 0.5^\circ$, $1^\circ \times 1^\circ$) as a fractional coverage of populations of different PFTs. The general structure of DGVMs is similar, although the level of detail varies among models (Cramer et al. 2001). Fast processes (e.g., energy and gas exchange at the canopy–atmosphere interface, photosynthesis, plant–soil water exchange) are simulated hourly or daily, seasonal dynamics (e.g., plant phenology, growth and soil organic matter dynamics) are simulated monthly, and vegetation dynamics are simulated annually (Prentice et al.

TABLE 7.5
Dynamic Global Vegetation Models: Examples of Specific Models and Their Key Characteristics

Model Type	Model Name	Ecosystem Type	Unit of Response	Plot Size	Time Step	Drivers	Plot-Scale Processes	Spatially Explicit Processes	Response Variables	Citations
Biogeography- biogeo- chemistry	LPJ	Global	PFT Average individual	0.5° grid	Day Month Annual	PFT Temp CO ₂ Soil properties	Establishment Growth Mortality Above, belowground carbon, water	None	ANPP, carbon, water fluxes	Sitch et al. (2003) Gerten et al. (2004)
+ Land surface model	LPJ + LSM	Global	PFT Average individual	3° grid	20 min Day Month Annual	Same as above	Above plus energy, moisture, momentum fluxes between land and atmosphere, hydrologic cycle, soil temperature	None	ANPP, cover, biomass, respiration, net ecosystem production	Bonan et al. (2003)
Biogeography + biogeo- chemistry	MAPSS	Grasslands	PFT	200 m 10 km 0.5° grid	Month	PFT Temp. Soils	Plant production Water, energy	Fire	Production Biomass LAI	Neilson (1995)
	MC1 (MAPSS + CENTURY + fire)	C ₃ , C ₄ grasslands	PFT	50 m 0.5° grid	Month Annual	PFT Temp. soils	Above plus Soil organic matter decomp. nutrient cycling grazing		Production Biomass LAI	Bachelet et al. (2000) Daly et al. (2000)

Note: ANPP, aboveground net primary production; decomp, decomposition; LAI, leaf area index; PFT, plant functional type; PPT, precipitation; Temp, air temperature.

2007). Some models provide more detail to plant physiological processes (e.g., HYBRID; Friend et al. 1997). Other models simulate energy and water fluxes needed by atmospheric circulation models (e.g., IBIS; Foley et al. 1996) or were designed as vegetation dynamics models and include scaling of individual-level processes to the grid cell (e.g., LPJ; Sitch et al. 2003). DGVMs have also been coupled interactively with climate models to allow vegetation feedbacks to climate (e.g., Foley et al. 1998; Bonan et al. 2003). A number of studies have compared DGVMs and have shown uncertainties in the way ecosystem responses to climate are simulated, in particular for water-limited systems (Cramer et al. 2001; Bachelet et al. 2003). These uncertainties led to models where biogeochemistry and water dynamics are explicitly simulated using ecosystem models such as Century (Daly et al. 2000).

The use of DGVMs in grasslands has been primarily to include grassland types as one or more PFTs in global simulations. Grasslands have been distinguished either based on physiology and photosynthetic pathway (C_3 and C_4 ; Bonan et al. 2003), vegetation structure (tall and short grasses; Hickler et al. 2006) or drought and fire tolerance (Hély et al. 2006). More detailed representations of water fluxes in the soil profile and wildfire effects are likely needed in global models to accurately distinguish grassland types (Hickler et al. 2006). In some cases, DGVMs have been used at the landscape scale to simulate effects of fire, grazing, and climate on grassland–forest ecotones (Bachelet et al. 2000; Daly et al. 2000). Woody encroachment was enhanced by grazing and limited by frequent fires, similar to observed patterns in the field (Bachelet et al. 2000). A warmer and slightly wetter future simulated climate increased the extent of grasslands, and reduced the spatial distributions of forests and savannas (Daly et al. 2000). In addition, model results were sensitive to rooting distributions suggesting that large-scale models will require more detailed accurate belowground representations before shifts in life form can be accurately simulated.

Advantages. Broad spatial extents, from landscapes to the globe, can be simulated for different PFTs, including grassland types. Effects of drivers on dynamics of groups of species can be simulated for large areas. Landscapes and regions can be simulated at finer resolution of PFTs for a greater range of drivers, including fire spread. Broad-scale changes in carbon and nitrogen pools and cycling as a result of interactions between the terrestrial biome and the atmosphere can be simulated as well as patterns in potential natural vegetation.

Limitations. DGVMs assume PFTs migrate rapidly and remain in equilibrium with the climate. At the global scale, the models do not include dispersal, disturbance, or human activities, although there are exceptions at the continental (Lenihan et al. 2008) and landscape scales that include these processes, either within or among grid cells (e.g., Bachelet et al. 2000). Range distribution shifts and extinction for particular species cannot be simulated without detailed knowledge of potential migration rates (Midgley et al. 2007). Detailed parameters for many processes are needed at multiple

temporal scales. There is no variation within PFT responses, for example, species-specific variability in growth responses, age, and phenological patterns are not accounted for. These models also do not currently include human activities such as logging, habitat fragmentation, and introduction of invasive species.

7.3 Recommendations on Model Selection

In general, the unit of response is an important determinant of the question that can be addressed by each class of model, and can be used with the needed response variables to guide model class selection. Because demographic models simulate individual plants or populations, they can be used to address controls on shifts in species composition and invasive species dynamics as well as state changes between grasses and woody plants. Size and age class distributions of individuals as well as population density can be output from these models. Because many questions related to future grassland dynamics require an understanding of shifts in dominance, more detail is provided below on demographic models. Physiological models simulate carbon assimilation, allocation, and growth differences among PFTs in response to drivers, and are restricted to dynamics of broad categories of plants (grasses, woody plants) rather than individual plants or populations. Physical models simulate physical properties of a system, such as soil water dynamics, and then use rules to generate biological responses; the resolution of the rules determines the details of the response. Biogeochemical models simulate carbon, water, and nitrogen cycling to generate plant production and soil organic carbon as response variables. DGVMs are described in terms of their ability to simulate grasslands within a broader context of multiple ecosystem types across regions, continents, and the globe.

The selection of a particular model within each class often depends on the way processes are represented relative to the specific question or system being simulated. Model comparisons have been used very effectively to highlight variability in responses driven by different processes included in each model (Cramer et al. 2001; Gerten et al. 2008). These comparisons involve the use of the same input parameters and generation of the same output responses; thus the differences in response depend on which processes are included, assumptions about these processes and their relationships with the drivers, and how the processes are represented (Schimel et al. 1997; Cramer et al. 1999). Similar responses across multiple models can be used to generate testable hypotheses about key processes (Luo et al. 2008), and to provide greater certainty on modeled estimates, such as the annual carbon sink or species range shifts (Schimel et al. 2000; Morin and Thuiller 2009).

7.4 Future Challenges in Grassland Modeling

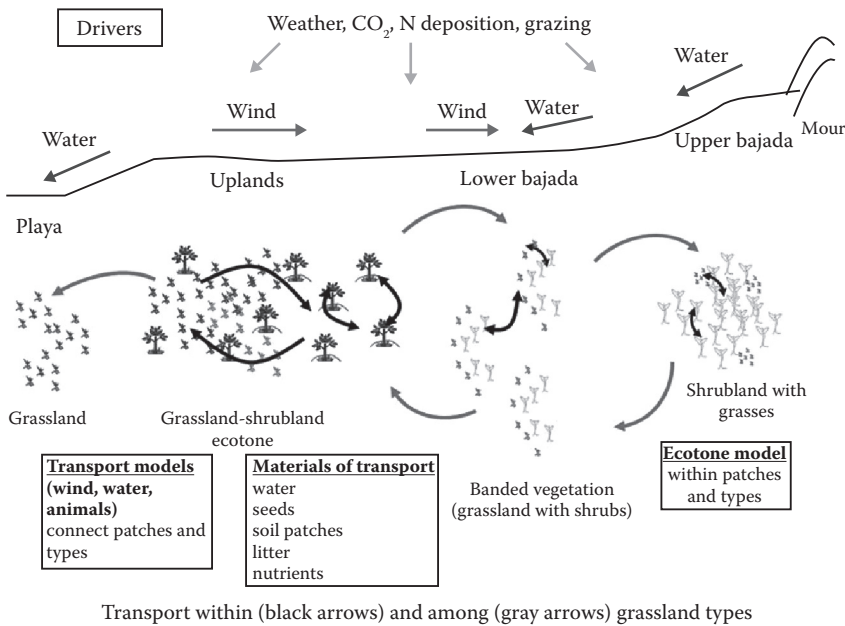
Many of the future science questions to be addressed in perennial grasslands globally will revolve around the conditions that shift these grasslands to alternative states, dominated by woody plants, by nonnative herbaceous species, or by novel assemblages of species, and the consequences of these state changes to ecosystem services, including biodiversity and primary production, rates of nutrient cycling and carbon storage, and air and water quality and quantity. In many cases, these state changes are “ecological surprises” in that they are observed and confirmed after they occur. These surprises result from an inability to understand the full suite of mechanisms and interactions occurring across spatial and temporal scales that act to drive and maintain these shifts (Peters et al. 2004). In addition, there is increasing interest in identifying the weather–vegetation–soil conditions that may allow a reversal of these states back to perennial grasslands under global changes in drivers (e.g., Holmgren and Scheffer 2001; Allington and Valone 2010).

New modeling approaches will be needed to improve understanding of these mechanisms in order to detect, predict or promote state changes, in particular those that impact the delivery of goods and services to human populations (Peters et al. 2009). Modeling approaches will be needed that enhance our understanding of cross-scale interactions and elucidate the role of these interactions in determining ecosystem thresholds (the level or magnitude of an ecosystem process that results in a sudden or rapid change in ecosystem state). Critical thresholds are often crossed during or following a state change such that a return to the original state is difficult or seemingly impossible (Bestelmeyer 2006). Thresholds can occur either in the environmental driver, the rate of a process, or a state variable. Thresholds indicate that a change in a dominant process has occurred and that distinct exogenous drivers or endogenous positive feedbacks are governing rates of change (Peters et al. 2004). Feedbacks tend to maintain a state, and it is often the change in these feedbacks and the resultant alteration in pattern–process relationships that differentiate a regime shift from a reversible ecosystem change that is not maintained through time (Carpenter 2003). For example, shifts from grasslands to woodlands can be maintained for hundreds of years by positive feedbacks between woody plants and soil properties. In some cases, state changes are driven by processes at one spatial or temporal scale interacting with processes at another scale (Carpenter and Turner 2000; Peters et al. 2007).

Modeling approaches that explicitly account for thresholds and cross-scale interactions are expected to improve our understanding of the mechanisms driving state changes in grasslands, and to allow more informed predictions of impending changes (Bestelmeyer et al. 2006). Most studies of cross-scale interactions have documented changing patterns in vegetation through time and across space, and then assumed changing patterns resulted from changing ecological processes (Peters et al. 2004). However, an approach that

combines pattern analyses with experimental manipulation of processes and simulation modeling of rates of ecosystem change under different drivers is needed to tease apart the role of role of drivers and processes in determining patterns at different scales (Peters et al. 2009).

In order to address these science questions, thresholds, feedbacks, and cross-scale interactions will need to be included in models that simulate shifts from grasslands to dominance by other species or assemblages. In some cases, this can be accomplished by linking models of different types



Transport within (black arrows) and among (gray arrows) grassland types

FIGURE 7.2

The ENSEMBLE model for grasslands is being developed to link existing models of vegetation, water, and soil processes at the scale of individual plants (Ecotone) with transport models of wind, water, and animals. Transfer of materials is simulated both within (black arrows) and among spatial units (gray arrows) across a range of scales to represent different grassland types that typically occur along an elevation gradient in the Basin and Range Province of North America. A stylized landscape for the Jornada Basin USDA-LTER site in the northern Chihuahuan Desert is shown as an example. The relative importance of each driver (weather, CO₂, nitrogen deposition, grazing, wind, and water) varies along this gradient as a result of interactions among patterns in atmospheric circulation, elevation, soils, vegetation cover, composition, and spatial distribution of vegetated and bare soil gaps. (From Peters et al., in Miao et al., eds., *Real World Ecology: Large-Scale and Long-Term Case Studies and Methods*, Springer, New York, 2009. With permission.) These interactions across scales can generate nonlinear responses and threshold dynamics in the conversion of grasslands to other states (from Peters et al., *Proceedings of the National Academy Sciences* 101: 15130–15135, 2004; with permission), and are hypothesized to be important to grass recovery. Both native woody plants and nonnative herbaceous plants can be simulated as invasive species that shift dominance to alternative states of the system with consequences for species composition and cycling of carbon, water, and nutrients.

identified in Tables 7.1–7.5, and by adding processes and functional relationships to account for nonlinear dynamics and interactions. At a minimum, models will need to maintain species parameters and within-plot responses to drivers, and include biogeochemical processes that feedback to the vegetation. For example, IBMs have been linked with nutrient cycling models or incorporated nutrient cycling routines from these models to simulate landscapes (e.g., Ecotone with SOILWAT and Century routines) (Figure 7.1) or regions (MAPSS + Century, Bachelet et al. 2000; Daly et al. 2000). Linking vegetation dynamics models with landscape-scale physical models (e.g., SWEMO of wind erosion–deposition, Okin 2008) or mesoscale climate models (e.g., RAMS, Beltrán-Przekurat et al. 2008) will allow more realistic simulations of additional processes known to be important to grassland–shrubland dynamics. More detailed soil development routines will be needed with wind and water movement of materials as soil is added or removed. Using IBMs in these linked models will require a reduction in complexity through statistical or numerical approaches to maintain detailed species information on many small plots, yet simulate large spatial extents (described in Section 7.2.1).

Under conditions where spatial processes are important to connect spatial units, transport of materials will also need to be simulated. Seed dispersal, spread of fire, and water runoff are the most commonly simulated spatial processes (e.g., MALS, Gao and Reynolds 2003; SAVANNA, Coughenour 1993). However, natural landscapes may include multiple drivers occurring across a range of spatial and temporal scales that act to transport materials both within and among spatial units corresponding to different assemblages of grasslands and shrublands (Figure 7.2). Simulating realistic landscapes will require more complicated approaches that include multiple spatial and temporal scales as well as vegetation–soil feedbacks. Scaling this landscape-scale approach to broader spatial extents, such as continents containing connected ecosystem types, is possible with a robust conceptual framework (Peters et al. 2008).

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