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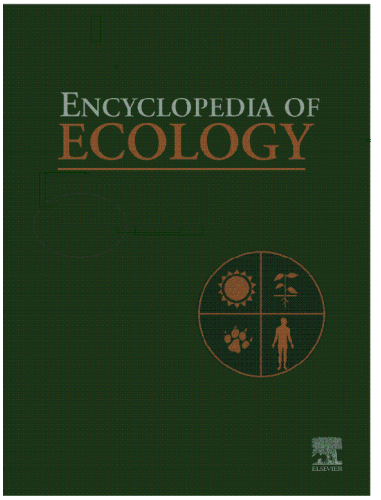


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T Wiegand, K Wiegand, and S Pütz. Grassland Models. In Sven Erik Jørgensen and Brian D. Fath (Editor-in-Chief), Ecological Models. Vol. [3] of Encyclopedia of Ecology, 5 vols. pp. [1754-1765] Oxford: Elsevier.

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some general conclusions that are in full agreement with everyday observations and general systems knowledge:

- Generalists have a better survival chance than others if moved to an environment of greater variety.
- Cautious types have a better survival chance than others if moved to a less reliable environment.
- Training in more unreliable and/or more diverse environments increases satisfaction of the security and/or freedom of action orientors at the cost of the effectiveness orientor.
- Training in an uncertain environment teaches caution and improves fitness in a different environment.
- Learning caution (better satisfaction of the security orientor) takes time and decreases effectiveness, but increases overall fitness.
- Investment in learning (exergy cost of learning in the animat) pays off in better fitness; the learning investment is (usually) much smaller than the pay-off gain.

Animat individuals not only develop behavior that can be interpreted as intelligent, they also develop a complex goal function (balanced attention to basic orientors), or value orientation. Serious attention to basic values (basic orientors: existence, effectiveness, freedom, security, adaptability, coexistence) is therefore an objective requirement emerging in, and characterizing self-organizing systems. These basic values are not subjective human inventions; they are objective consequences of the process of self-organization in response to normal environmental properties.

*See also*: Ecological Network Analysis, Ascendency; Ecological Network Analysis, Environ Analysis; Emergy and Network Analysis; Exergy; Fundamental Laws in Ecology; Structural Dynamic Models.

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# Grassland Models

**T Wiegand**, UFZ Helmholtz Centre for Environmental Research, Leipzig, Germany

**K Wiegand**, University of Jena, Jena, Germany

**S Pütz**, UFZ Helmholtz Centre for Environmental Research, Leipzig, Germany

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## Introduction

### Grasslands

A large proportion of the surface of the Earth is covered with grasslands (**Figures 1** and **2**), which are ecosystems where the vegetation component is herbaceous in character, with grasses being predominant. Grasslands can be divided into tropical grasslands that occur in the same regions as savannas (see Savanna), that is, grasslands with scattered individual trees, and temperate grasslands. The major manifestations of temperate grasslands are, for example, the veldts of South Africa, the puszta of

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**Figure 1** Examples of grasslands in South Africa (top) and Argentina (bottom). (Top) Experimental plots of a *Themeda triandra* – *Cymbopogon plurinodis* grassland located at Bloemfontein, South Africa (28°50′ S; 26°15′ E, altitude 1350 m). The left photo shows a nondegraded state dominated by the perennial bunchgrass *T. triandra* and the right photo shows a degraded plot dominated by the stoloniferous perennial *Tragus koelerioides* and the short-lived perennial bunchgrass *Aristida congesta*. (Bottom) View of a grass steppe dominated by *Festuca pallescens* ('coiron blanco') that characterize the sub-Andean district of the Patagonian Phytogeographic Province located in a narrow north–south strip between 71° W and 71° 30′ W. (Top) Thorsten Wiegand. (Bottom) Nestor Fernandez.

Hungary, the pampas of Argentina and Uruguay, the steppes of the former Soviet Union, and the plains and prairies of central North America. Grasslands are important ecosystems because they are frequently used for livestock grazing, they provide important ecosystem services, and may serve as carbon sinks.

Very roughly, grasslands can be classified as natural grasslands where grassland without trees constitutes the vegetation climax, seminatural grasslands which are mostly natural grasslands but modified by low intensity (grazing) management, and man-made grasslands which are either intensively managed natural grasslands that have been substantially altered or secondary grasslands, for example, created by the removal of natural forests for livestock production. The latter is common in temperate, Mediterranean, and tropical regions. In natural grasslands

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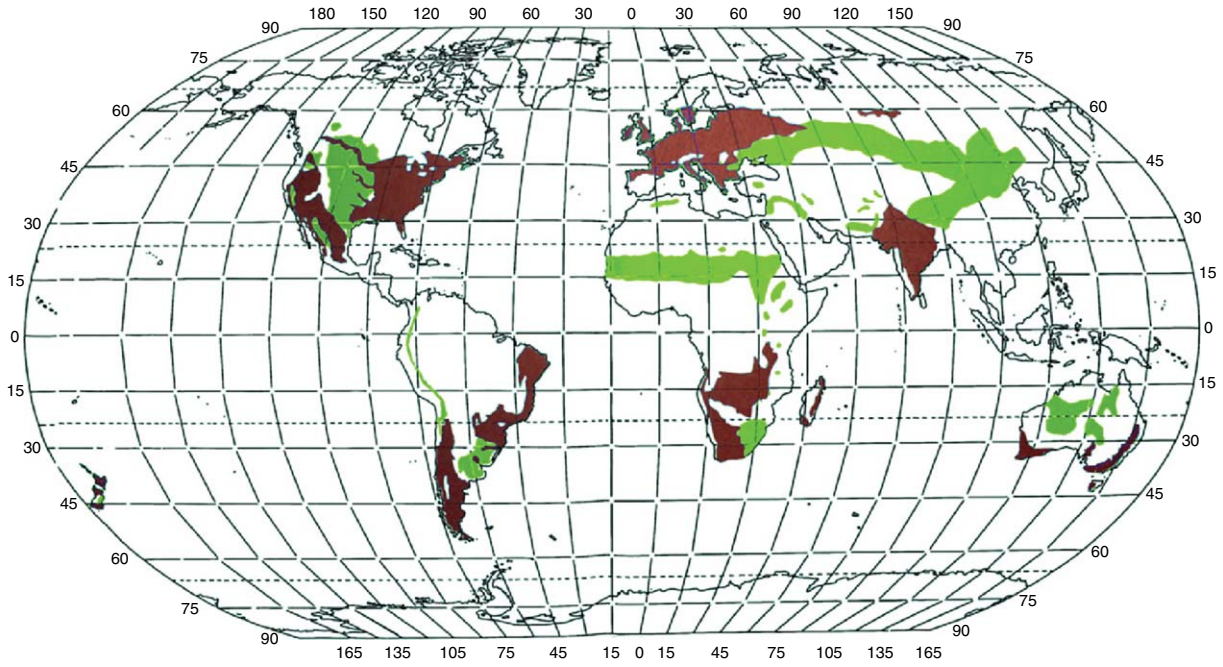


**Figure 2** Grassland vegetation map of the world. Green: regions in which grassland without trees is the vegetation climax over most of the area, and brown: man-made grasslands. Adapted from Snaydon RW (1987) Managed Grasslands. *Ecosystems of the World*, vol. 17B. Amsterdam: Elsevier, and Coupland RT (ed.) (1992) Natural Grasslands. *Ecosystems of the World*, vol. 8A. Amsterdam: Elsevier.

of pristine climax condition, perennial grasses and sedges are dominant and annual grasses are often restricted to locations where perennial plant cover has been disturbed. On the other hand, in seminatural grasslands, grazing often reduces the palatable perennials which are replaced by unpalatable and/or annual grasses.

As one of the world's major ecosystems, grasslands have been an important subject of basic and applied ecological research attempting to understand the ecological processes and factors occurring in grasslands and their effects on grassland dynamics, productivity, and diversity. Grasslands are model ecosystems for basic ecological research to investigate the effects of processes such as competition, seed dispersal, and reproductive strategies on coexistence and diversity. They are of interest in rangeland science where ecological understanding is needed to derive optimal grazing management strategies that maximize fodder or animal production and minimize the risk of degradation. More recently, grassland ecosystems gained interest in climate change ecology because of their importance as carbon sinks.

## Overview Over Models of Grasslands

Grasslands are complex ecosystems, and understanding the ecological processes and factors determining its dynamics, productivity, and biodiversity requires use of combined approaches of field measurements, experimentation, data analysis, and modeling. Thus, ecological models are important tools for ecologists working in grasslands. However, the term 'model' has been used in such a variety of contexts that it has become almost meaningless, unless used with some qualifications. In the present context, models may be regarded as a simplified and formalized representation of ecological processes, either using mathematical or computer simulation techniques, which produce, based on a set of assumptions, a quantitative output. Grassland models are as varied as the purposes for which they have been constructed, and cover various spatial and temporal scales and various degrees of detail. Our focus lies on ecological models which are concerned with grassland population and community dynamics with less attention to grassland models of matter and energy flows or biophysical processes. In this article, most grassland models are conceptual, empirical, analytical, or simulation models.

## Modeling Questions and Models

In the following, we present an overview over the most important grassland models, structured by their scientific questions rather than by model type. A summary of these models is given in **Table 1**. The major variables and properties of ecological grassland models are temporal and spatial grassland dynamics and diversity, grassland

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**Table 1** Overview of different exemplary modeling studies in grasslands

| *Authors* | *Type of model* | *Description* | *Area* |
|---|---|---|---|
| *Rangeland models* | | | |
| Westoby *et al.* (1989) | Conceptual | Alternative stable states with discontinuous and irreversible transitions, nonequilibrium dynamics | Arid and semiarid rangelands |
| Noy-Meir (1975) | Nonspatial differential equation | Applies classical predator–prey models to plant–herbivore systems, detects dual stability | |
| Fernandez-Gimenez and Allen-Diaz (1999) | Conceptual | Assesses the extent to which the current nonequilibrium models of rangeland vegetation dynamics apply | Mongolian rangeland ecosystems |
| Bosch and Gauch (1991) | Statistical | Description of degradation gradient method for range condition assessment | Grasslands of South Africa |
| Phelps and Bosch (2002) | Statistical | Degradation gradient method in conjunction with state-and-transition models of rangeland dynamics and condition | Mitchell grasslands, central western Queensland, Australia |
| *Spatially explicit models on succession and disturbance in grasslands* | | | |
| Coffin and Lauenroth (1989, 1990) | Gap model, simulations | Introduction to STEPPE model, evaluates the effects of disturbances at the scale of a landscape for a semiarid grassland | Semiarid grassland in north-central Colorado, USA |
| Coffin and Urban (1993) | Gap models, simulations | Compares the STEPPE model to a structurally similar gap model for forest dynamics (ZELIG) | |
| Lauenroth *et al.* (1993) | STEPPE, CENTURY, simulations | Couples two models to study interactions between vegetation structure and ecosystem processes | Semiarid grassland in north-central Colorado, USA |
| Peters (2002) | Gap model, similar to STEPPE, simulations | Studies effects of climatic fluctuations and disturbance on regional patterns of vegetation dynamics at an arid–semiarid grassland ecotone | Chihuahuan desert, central New Mexico, USA |
| Moloney and Levin (1996) | Spatially explicit, grid-based, simulations | Varies components of disturbance architecture systematically to determine their impact on population dynamics at the scale of the landscape | Jasper Ridge serpentine grassland, USA |
| Wu and Levin (1994) | Spatially explicit patch-based model | Studies landscape pattern and process dynamics | Jasper Ridge serpentine grassland, USA |
| Tan and Smeins (1996) | Statistical model, neural networks | Predicts grassland community changes with an artificial neural network model | Grassland communities near Hays, Kansas, USA |
| O'Connor (1993) | Size–structured matrix models | Investigates how population growth rate depends on factors such as rainfall or grazing | Perennial grasses of two African savannas |
| *Optimal life-history strategies, competition, coexistence, and biodiversity* | | | |
| Lavorel *et al.* (1994) | Spatially explicit, two-species, simulation | Spatiotemporal dispersal strategies and annual plant species coexistence in a structured landscape | Species-rich Mediterranean old-fields |
| Matsinos and Troumbis (2002) | Cellular automaton model | Models competition, dispersal and effects of disturbance in the dynamics of a grassland community | Grasslands in Lesbos, Greece |
| Schwinning and Parsons (1996) | Spatially explicit cellular automaton model | Extends a pasture model by Thornley *et al.* in 1995 to study coexistence mechanisms for grasses and legumes including selective grazing and spatial considerations | Perennial rye-grass and white clover communities |
| Thornley *et al.* (1995) | Physiological models | Studies complex dynamics in a carbon–nitrogen model of a grass–legume pasture | |
| Winkler and Fischer (2002) | Grid-based model | Investigates the role of vegetative and seed dispersal within habitats for optimal life histories of clonal plants | |
| Bolker and Pacala (1999) | Analytical model, moment equations | Aims to understand at a general level how plants coexist in communities | |
| *Spatial structures in arid and semiarid grasslands* | | | |
| Dunkerley (1997) | Cellular automaton model | Investigates the development of banded vegetation communities in grass- and shrublands | Western NSW grass- and shrublands, Australia |

(*Continued*)

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**Table 1** (Continued)

| *Authors* | *Type of model* | *Description* | *Area* |
|---|---|---|---|
| Rietkerk *et al.* (2004) | Partial differential equations, numerical simulations | Investigates vegetation pattern formation in arid ecosystems and hypothesizes that they may be the result of spatial self-organization, caused by net displacement of surface water to vegetated patches | |
| *Modeling primary production in grasslands* | | | |
| Le Houèrou *et al.* (1988) | Regression models | Relationship between the variability of primary production and the variability of annual precipitation in world arid lands | Arid lands of the world |
| Paruelo *et al.* (1999) | Regression models and NDVI | Studies how grassland precipitation-use efficiency varies across a resource gradient. Uses 11 temperate grassland sites worldwide, and 19 grassland sites across the central grassland region of North America | Grassland sites worldwide |
| Paruelo *et al.* (1997, 2000) | Regression models, NDVI | Estimates ANPP for the central grassland region of the US and subhumid pampa rangelands in Argentina | Central grassland (USA), subhumid pampa (Argentina) |
| Prince (1991) | Satellite remote sensing | Determines primary production for Sahelian grasslands, 1981–88 | Sahelian grasslands |
| *Ecosystem modeling and flows of energy and matter in grasslands* | | | |
| Nouvellon *et al.* (2001) | Remote sensing, ecosystem model | Couples a grassland ecosystem model for semiarid perennial grasslands with Landsat imagery to calibrate parameters of ecosystem model | Grasslands in southeastern Arizona (USA) |
| Van Dyne (1972) | | Describes organization and management of an IBP 'big biology' program. | |
| Coughenour and Chen (1997) | Linked ecosystem model | Assessment of grassland ecosystem responses to atmospheric change using linked plant-soil process models | Grasslands of Colorado and Kansas (USA) and Kenya |
| Parton *et al.* (1993) | CENTURY | Parametrizes CENTURY for the world's major grassland types to model biomass and soil organic-matter dynamics in grasslands | Grassland biome worldwide |
| Gilmanov *et al.* (1997) | CENTURY | Uses long-term data from several sites to assess the performance of CENTURY | |
| Hibbard *et al.* (2003) | CENTURY and matrix transition model | Linked CENTURY to a transition matrix model to simulate the displacement of grassland communities under heavy livestock grazing and climate events | Grassland and thorn woodland in southern Texas (USA) |
| Paruelo and Sala (1995) | Water balance model | Calculates the amount of water evaporated from the soil and transpirated by the canopy to estimate water losses in a Patagonian steppe | Shrub–grass steppe in Patagonia (Argentina) |

productivity, water dynamics, and flow of other matter and nutrients. Grazing is a predominant theme in grassland models. It has been discussed in Grazing Models.

## Grassland Dynamics and Processes of Coexistence

An important topic in grassland research, both from theoretical and applied point of view, is the temporal and spatial dynamics of species abundance and composition. In applied rangeland science, the dominant question is how to manage grasslands for maximal long-term domestic livestock production without degrading the grassland to an extent that would make it unsuitable for further grazing. In applied conservation ecology, the main question is how to promote survival of small and fragmented remnants of natural grasslands. A specific conservation problem in central Europe is that an increasing intensification of agriculture leads at the same time to abandonment of former secondary grasslands maintained by grazing. From a more theoretical perspective, grassland ecologists are interested in the processes and factors that determine the dynamics of grasslands and maintain their biodiversity. Grasslands are good systems to study questions of coexistence and biodiversity in sessile organisms (e.g., vascular plants), because they are relatively easy to monitor, and are less complex than tropical forests or coral reefs but still species rich enough for studying questions of coexistence. Another theoretical question in biogeography is why and under which climatic and environmental conditions grasslands can exist.

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### Succession in grasslands

Understanding succession (see Succession), that is, the change in vegetation of an area over time, is fundamental for the theoretical understanding of grasslands as well for an understanding of the reactions of grasslands to management. Models of grassland succession, especially applied models, are mostly based on the Clementsian theory of ecological succession. Models which explicitly deal with spatial structures are more influenced by the work of A. S. Watt in the 1940s, who proposed that plant communities are composed of a mosaic of patches in different states of a natural cycle of disturbance and regeneration.

### Rangeland models

*The range succession model.* The range succession model based on the Clementsian theory of ecological succession formed the conceptual framework for most grazing management up to the 1980s. It is supposed that, in the absence of grazing, a rangeland has a single persistent state (the climax), whereas grazing causes continuous and reversible transitions of the grassland state along a single, monotonic gradient between an undisturbed climax and an overgrazed subclimax vegetation state. Therefore, the grazing pressure can be made equal and opposite to the successional tendency, producing an equilibrium in the vegetation at a set stocking rate (**Figure 3a**). A sustainable yield of livestock products can be harvested from such an equilibrium. The model recognizes that vegetation is affected when rainfall varies from year to year and supposes that grazing and interannual variation in rainfall cause equivalent changes in the vegetation. Therefore, management should respond to drought by reducing grazing.

*State-and-transition models.* Over the years, however, substantial empirical evidence accumulated of cases where the assumptions of the range succession model were not met, especially in arid and semiarid environments. To deal with the complex dynamics of semiarid and arid ecosystems, scientists such as M. Westoby, B. Walker, and I. Noy-Meir suggested (by the end of the 1980s) that these ecosystems could be described in terms of discrete states and inter-state transitions (**Figure 3c**). Transitions could be triggered by natural events (e.g., rainfall, drought, and fire) or by management actions (e.g., removal of herbivores, altered intensity or timing of herbivory, and burning). Changes in range condition are not unidirectional, but multiple pathways of system transitions to alternative states may exist, depending on the particular sequence of driving events (**Figure 3c**).

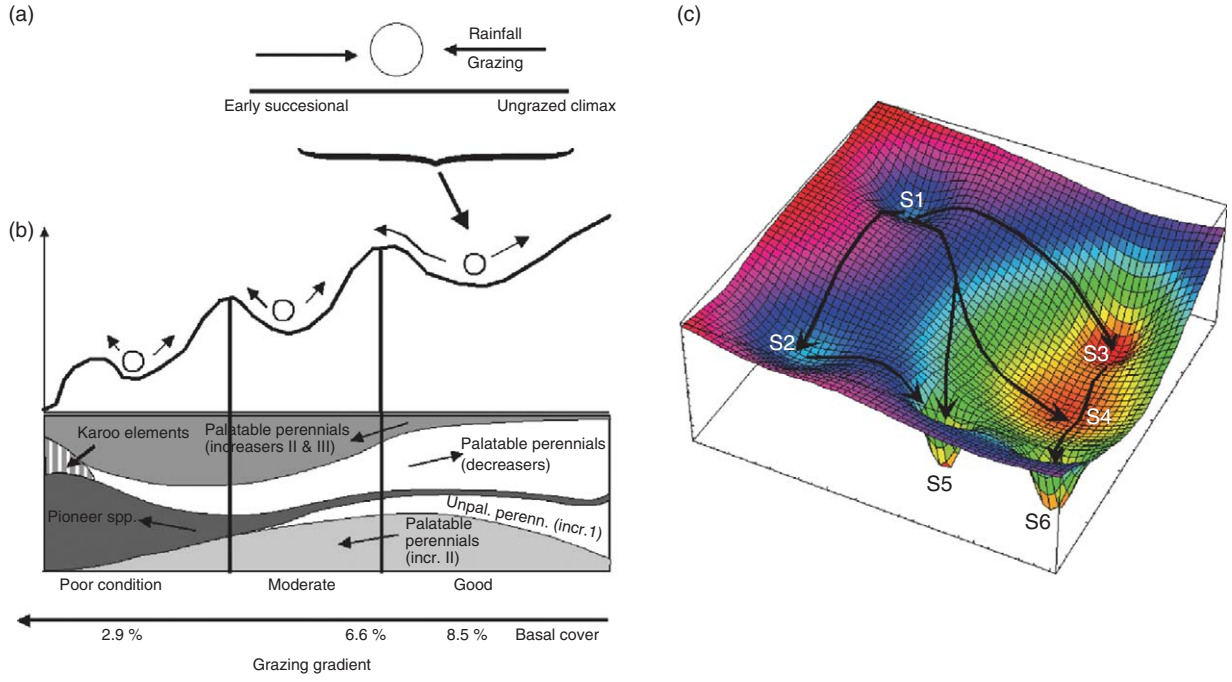


**Figure 3** Illustration of different conceptual rangeland models. (a) Range succession model. Vegetation changes are reversible and unidirectional in response to grazing and rainfall. (b) Degradation gradient model for South African grasslands. The system responds to smaller perturbations (grazing and rainfall) unidirectionally and reversibly as predicted by the range succession. Larger perturbations (drought, overgrazing) may cause the system to cross an irreversible threshold where changes in soil conditions (related to reduced basal cover) and species composition may hinder the system to return. The pathway of degradation is unidirectional. (c) State and transition model. Multiple equilibria and multidirectional pathways of degradation in response to different driving events. S1, S2: good condition domains; S3, S4: moderate condition domains; and S5, S6: poor condition domain.

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Such state-and-transition models are valuable tools for describing the structure of the ecosystem to identify irreversible transitions and alternate stable states; however, they provide little information applicable to forecasting and prediction. Additional models are needed to quantify the temporal scales of the transitions, to identify rare events that drive semiarid and arid ecosystems, and to improve the user's understanding of ecosystem dynamics over a long temporal scale.

*Degradation gradient models.* The degradation gradient model combines in some sense the concepts of Clementsian succession and state-and-transition models (**Figure 3b**). It is based on the idea that vegetation compositional changes along a grazing gradient are indicative for the ecological condition. This statistical method was developed in the 1990s by O. J. H. Bosch and H. G. Gauch for the semiarid South African grasslands. Key element of the approach is a classification of the species according to their response to grazing as increaser and decreaser species (**Figure 3b**). This classification is derived by means of multivariate statistics. Species composition data are collected from grasslands in various stages of degradation. Based on a series of statistical analyses of these data, the degradation gradient is constructed. The model recognizes that irreversible transitions may exist which are caused by soil loss or major changes in floristic composition. This method is used for range assessment where species composition data of a sample is compared to the gradient.

### *Spatially explicit models on succession and disturbance in grasslands*

Disturbance can play a major role in structuring grasslands by producing a spatiotemporal mosaic of patches by locally resetting the successional clock after a disturbance. The spatiotemporal distribution of species within the resulting mosaic depends upon an interaction between species' life-history traits and the spatial and temporal structure of the ecological processes controlling species' distributions. The availability of powerful computers and the advent of spatially explicit simulation models revitalized the conceptual work done by Watts in the 1940s and allowed to elucidate process from patterns. In this line, several spatially explicit plant dynamics models investigate questions related to succession and disturbance.

*The Steppe model.* D. B. Coffin and W. Lauenroth developed at the end of the 1980s a spatially explicit gap dynamics simulation model (STEPPE) to evaluate the effects of disturbances at the scale of a landscape for a semiarid grassland in north-central Colorado, USA. The approach goes back to spatially implicit gap models of forest succession (see Forest Models). These models simulate succession in a gap left after the death of a large tree. Succession dynamics are then estimated by the average behavior of 50–100 plots of the size of a single large tree. The exact location of each individual is not used to compute competition in these models. However, gap models can be made spatially explicit by linking several individual plots together.

The STEPPE model is a gap model and simulates the establishment, growth, and death of individual grass plants on a small plot (0.12 $m^2$) through time at an annual time step. Landscapes were simulated either as a collection of independent plots or as a collection of interacting plots. In the 1990s, extending their first approach, W. Lauenroth and colleagues coupled compartment models of nutrient cycling and soil water–plant relation with the STEPPE model. The aim was to understand the interactions between vegetation structure and ecosystem processes across ecosystems. However, the approach of coupling several models was quickly abandoned, probably because of problems with increased model complexity.

A gap model similar to STEPPE was developed at the beginning of the 2000s by D. B. Peters (formerly Coffin). This individual-based, gap dynamics model (ECOTONE) was used to predict the effects of climatic fluctuations on regional patterns of vegetation dynamics, and the effects of disturbance on vegetation dynamics at an arid–semiarid ecotone between shortgrass steppe grassland and a Chihuahuan desert community in central New Mexico, USA.

*The Jasper model.* K. A. Moloney and S. A. Levin developed in the 1990s a spatially explicit simulation model of a serpentine grassland, focusing primarily on the role of disturbance. The model is hierarchical in design and population dynamics were modeled as occurring within local sites, which were then arranged to form a landscape and interact primarily through seed dispersal. Several components of the disturbance architecture were varied systematically among model runs to determine their impact on population dynamics at the scale of the landscape. Results suggested that predicting the impact of disturbance on ecological communities will require an explicit understanding of at least some aspects of the spatial and temporal architecture of the disturbance regime.

*Neural networks.* Where long-term site data on species composition and environmental factors are available, an approach using artificial neural networks may be feasible to predict grassland succession. The method takes advantage of the ability of neural networks to learn, recognize, and generalize from patterns contained in the ecological data. In the 1990s, S. S. Tan applied this approach to a 30-year data set on vegetation changes and climatic factors in grassland communities in Kansas (USA). Their model predicted future community composition using input data on present conditions that have not been used to develop the model. The model performs well for 1–4 year predictions and performance significantly deteriorated from the

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fifth year on. One disadvantage of the neural networks is that it is purely descriptive and gives little insight into underlying causes and mechanisms of grassland succession. On the other hand, if predictions are required for highly complex systems as they occur in natural rangeland communities, they are an appropriate technique for qualitative analysis and statistical forecasting.

*Matrix models*. Matrix models of succession are mathematically and conceptually the most straightforward among the succession models. Matrix models are constructed by determining the probability that the vegetation on a local plot will transform to some other vegetation state after a given time interval. To construct the model, the vegetation must be classified into identifiable states. The model consists of a vector representing the state variables of the system and a matrix containing the (usually) constant probabilities of possible state transitions. A question of interest is how a population growth rate depends on factors such as rainfall or grazing. Matrix models provide the means for calculating population growth rates, thereby allowing for an assessment of the influence of different population processes such as seed production and growth and mortality. For example, T. G. O'Connor used in the 1990s stage-structured matrix models to assess the influence of rainfall and grazing on the demography of some African savanna grasses. Results showed that the population growth rates of most species were positively correlated, indicating that an extrinsic force, presumably rainfall, had the greatest effect on population growth.

### Optimal life-history strategies, competition, coexistence, and biodiversity

A considerable number of models on grassland dynamics and processes are motivated from general theory in ecology and are often put into a spatially explicit context. These models, developing since the mid-1990s, are concerned with tradeoffs in optimal reproduction strategies, and investigate how optimal strategies depend on disturbance and other spatially explicit factors such as a patchy habitat. One early example of this approach is a spatially explicit, two-species simulation model by S. Lavorel to examine the interaction between dispersal, dormancy, and small-scale disturbances on coexistence of two annual plant species in landscapes with varying degree of patchiness. Coexistence patterns depended on the degree of suitability and the patchiness of the landscape, mostly in relation to the interactions between landscape structure and mean dispersal distance.

A model of grassland community dynamics developed in the 2000s by Y. G. Matsinos and A. Y Troumbis aimed to quantify the role of competition and dispersal under disturbance, and investigated the resilience of the communities with respect to gap-creating disturbances that were imposed at different spatial extent. Model results showed that plants with longer seed dispersal distances may have a competitive advantage in their colonization success as compared to the better competitors, especially in the cases of a disturbance-mediated creation of gaps in the landscape. An increase of the species number led to more stable end communities and a higher vegetation cover in the landscape.

A series of papers by S. Schwinning and A. J. Parsons investigated, in the 1990s, coexistence mechanisms for grasses and legumes in grazing systems. This is an important question since legumes fix nitrogen which in turn is beneficial for grasses.

Other questions investigated with spatially explicit models attempt to gain an understanding of clonal growth and ramification of grass tillers in grasslands. For example, E. Winkler and colleagues developed a series of grid-based models of grassland communities to investigate long-term control of species abundances and reproduction strategies in patchy landscapes undergoing disturbances. One example is a study with M. Fischer investigating tradeoffs between sexual and vegetative reproduction of clonal plants. Depending on spatial habitat structure and disturbances, different reproduction strategies lead to different long-term fitness. The model simulated plant population dynamics on a two-dimensional cellular grid consisting of $70 \times 70$ square cells. In an extension of this approach, J. Stöcklin and E. Winkler used a spatially explicit, individual-based metapopulation model of *Hieracium pilosella* to examine the consequences of tradeoffs between vegetative and sexual reproduction and between short and far-distance dispersal of seeds. They found that in a spatially heterogeneous landscape, sexual seed production in a clonal plant is advantageous even at the expense of local vegetative growth.

While most of the questions from this section were analyzed by means of grid-based models, advances in analytical modeling made by B. M. Bolker, S. W. Pacala, and others at the end of the 1990s suggested that spatial interactions may be approximated by means of moment equations that describe changes in the mean densities and spatial patterns (covariances) of competing species. The formalism of moment equations is borrowed from physics where it was used to describe phase transitions and is an elegant way to approximate simple spatial dynamics by tracking the dynamics of the first moments (mean densities) and second moments (variances and covariances or spatial covariances) of the spatial distributions of populations. For example, to understand at a general level how plants coexist in communities, Bolker and Pacala studied three different strategies to compete for resources in a spatially variable environment: colonizing new areas, exploiting resources in those areas quickly before other plants arrive, or tolerating competition once other plants arrive. However when adding more realism the moment equations become quickly lengthy, simulations are often required to find an appropriate moment closure.

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### *Spatial structures in arid and semiarid grasslands*

In mesic regions, patchy spatial vegetation patterns arise through the interplay of succession and disturbances. In the past, this has been shown in many studies of patch dynamics for mesic forests and grasslands, for example, summarized in the classic book by S. T. A. Pickett and P. S. White. However, patchy structures are also frequently observed in water-limited arid and semiarid ecosystems, where distinct banded and spotted vegetation patterns are often found. There are numerous hypotheses on the origin of the distinctive patterning. For example, banded vegetation may be a remnant of more complete vegetation cover diminished by climatic deterioration or by grazing disturbance. Other hypotheses assume these patterns to be natural with downslope water re-allocation from bare areas to vegetated bands as a key-process or are based solely on the intrinsic dynamics of the vegetation without slope-induced anisotropy.

A number of cellular simulation models were developed to investigate the robustness and origin of such patterns. For example, end of the 1990s, D. L. Dunkerley modeled banded vegetation communities in western New South Wales Australian grassland and shrublands to test the hypothesis that water partitioning in spatially unstructured plant communities may lead to the development of banding. The model shows that without any climatic change or external disturbance, strongly developed banding can emerge from an initially random distribution of plants.

Other models used differential equations to search for possible unifying mechanisms to explain these spatial patterns. One hypothesis is that spatial patterns establish themselves through a Turing-like spatial instability depending only on a tradeoff between facilitative and competitive interactions among plants. This hypothesis goes back to the 1950s where A. M. Turing described morphogenesis in chemical systems. These models produce patterns superficially similar to banded and spotted vegetation, which then is taken as evidence for the validity of the underlying hypothesis. However, reproduction of a pattern is not proof that the modeled processes represent the natural processes. Since these top-down models are usually not explicitly related to specific spatial and temporal scales, they are difficult to test and their ecological content remains unclear.

## Models on the Impact of Grazing on Grasslands

The impact of grazing on the dynamics and productivity of grasslands has been an important subject of basic and applied ecological research. Theoretical and applied questions are intimately linked since developing sustainable grazing management requires an understanding on the dynamics of the grazing system. Early models on grazing systems were based on the Clementsian theory of ecological succession, and since the 1970s biomass–herbivore grazing systems were modeled in analog to predator–prey models developed one decade earlier. Since the 1980s, however, the equilibrium concept was increasingly challenged, and in the late 1980s nonequilibrium concepts and models emerged which stipulated environmental variation (due to rainfall variability) and spatial heterogeneity. Numerous grazing models have modified the early predator–prey differential equation models, and spatially explicit and rule-based simulation models are increasingly used to analyze specific grazing systems. For a detailed treatment of grazing models, see Grazing Models.

## Modeling Primary Production in Grasslands

Regional and global patterns in aboveground net primary production (ANPP) and their determinants have long interested ecologists. Understanding ANPP patterns and controls through time is particularly important in grasslands where grazing is the most important economic activity. Coping with temporal changes in the availability of forage is a prerequisite for the efficient and sustainable use of natural vegetation. More recently, interest in ANPP has intensified as projected global changes in climate, nitrogen deposition, and land use threaten to alter ecosystem carbon and energy flow. Data on primary production are also important to calibrate, parametrize, and evaluate terrestrial biosphere models and for modeling the global carbon cycle.

### *Regression models*

Early approaches to assess primary production in grasslands, such as the work by H. N. Le Houérou in the 1980s, used empirical models which correlated primary productivity with mean annual precipitation or evapotranspiration. In general, the relationships of production with environmental variables were derived from long-term averages for many sites distributed across environmental gradients (spatial models). ANPP increases linearly along spatial precipitation gradients within the range of 200–1300 mm $yr^{-1}$ in North American, South American, and African grasslands.

However, much less is known about the controls of the temporal, inter-annual variation of productivity at a given site (temporal models). Temporal models relating time series of ANPP and annual precipitation for single sites have shown lower slopes (= water use efficiency) and regression coefficients than the spatial models. Additionally, memory and carryover effects, for example, due to storage of carbohydrates in the root system and structural inertia, might play an important role in the functioning of semiarid grasslands. Memory and carryover effects buffer fluctuations in production if wet, productive years alternate with dry, less productive years and amplify fluctuations if wet or dry sequences of several years take place. Identifying and quantifying such memory and carryover effects is an important

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challenge for global models which mostly use simple linear relationships with precipitation.

### Use of remote sensing data

Biomass harvesting is the most common way to estimate ANPP in grasslands, but because of the large effort and the detailed spatial scale, harvesting methods are rather limited in their spatial and temporal extent. Remote-sensing techniques are a fast and nondestructive method for estimating ANPP at a regional scale over longer time periods. NDVI is the most commonly used radiometric index for estimating ANPP in grasslands and the annual summed NDVI can be used as a surrogate for annual ANPP because, in ecosystems dominated by grasses or deciduous life forms, the absorbed photosynthetically active radiation of plant canopies (APAR) and net primary production are directly related. Biomass estimates for grassland using NDVI have been performed, for example, by the group of J. M. Paruelo in the late 1990s and 2000s for the Central Grassland Region of the United States, and for subhumid pampa rangelands and the Patagonia steppes in Argentina. S. D. Prince determined in the early 1990s primary production for Sahelian grasslands.

Additionally, NDVI data allow determination of other important ecosystem characteristics such as the degree of seasonality, and the start and the end of the growing season. Relating NDVI characteristics over regional gradients with climatic and other environmental variables allow for inference on the controls of primary production and ecosystem functioning. Remote-sensing data may also be used to calibrate ecosystem models, for example, by minimizing the difference between the measured and the simulated NDVI. The utility of this approach was demonstrated by a study of Y. S. Nouvellon in the 2000s who coupled a grassland ecosystem model for semiarid perennial grasslands in southeastern Arizona (USA) with Landsat imagery for a 10-year simulation of carbon and water budgets.

## Ecosystem Modeling and Flows of Energy and Matter in Grasslands

Although the first interest in ecosystem modeling peaked in the 1970s with the International Biological Program (IBP), it is now having a rebirth with the recent interest in predicting ecosystem effects of global change. In the 1960s and 1970s 'big biology' projects were initiated by G. M. Van Dyne to study ecosystems including grasslands. One of the main problems of this big biology project was the attempt to model everything without a clear and focused research question. At the end, the resulting models were nearly as complex as nature itself and they could not be properly analyzed and thus understood. The objective of the IBP grassland simulation model was to simulate biomass dynamics in a variety of grassland types and the response of the system to irrigation, fertilization, and cattle grazing. The model comprises several submodels, that is, abiotic, producers, mammals, grasshoppers, decomposers, nitrogen, and phosphorus. Some of the submodels originally designed to be incorporated into the ELM model never reached this objective but developed a life of their own.

### Plant growth and production

A number of models, reviewed in detail by J. D. Hanson and colleagues in the mid-1980s, simulated/predicted plant growth and production of grassland ecosystems. For example, the AFRICA model included processes like shoot growth, tillering, root growth, photosynthesis, and nitrogen uptake for single plants. The aim of AFRICA was to model primary production of perennial graminoids and it unites physiological processes and morphometric traits. In a study in the late 1990s, M. B. Coughenour and D.- X. Chen linked models of photosynthesis, plant growth, and biophysical processes with models that simulate water, nutrient, and carbon flows through plant–soil ecosystems. The linked ecosystem model was applied to examine ecosystem-level responses to $CO_2$, temperature, precipitation, and global-warming scenarios in grasslands of Colorado and Kansas (USA) and Kenya. Using similar ecosystem model approaches, several models have been developed for semiarid perennial grasslands that allow multiyear simulations of plant growth patterns by accounting for carbohydrate storage in root systems and further translocation to aboveground regrowth.

### Biochemistry models

Other models analyzed the soil organic matter dynamics in response to changes in management and climate. These models described the flow of energy and matter (Conceptual Diagrams and Flow Diagrams) in form of balance equations. Following the approach of H. T. Odum, the focus of these models was not on biotic interactions between species but rather on the flows of energy and nutrients, treating plants basically as composers and decomposers.

The most prominent model of this type is the 'CENTURY model' (**Figure 4**) developed by W. J. Parton in the 1980s. CENTURY is a model of terrestrial biochemistry of grasslands based on the relationships between climate, human management (fire, grazing), soil properties, plant productivity, and decomposition. Studies performed with this model include efforts to link models describing plant and soil responses to the large-scale modeling of global change effects. The model is intended as a generic model whose basic balances of the different flows in grasslands can be calibrated to specific systems. In the 1990s, Parton and colleagues parametrized CENTURY for the world's major grassland types to predict the biomass and soil organic matter dynamics of the grassland biome worldwide.

In the late 1990s, the performance of CENTURY was assessed by T. G. Gilmanov and colleagues using long-term

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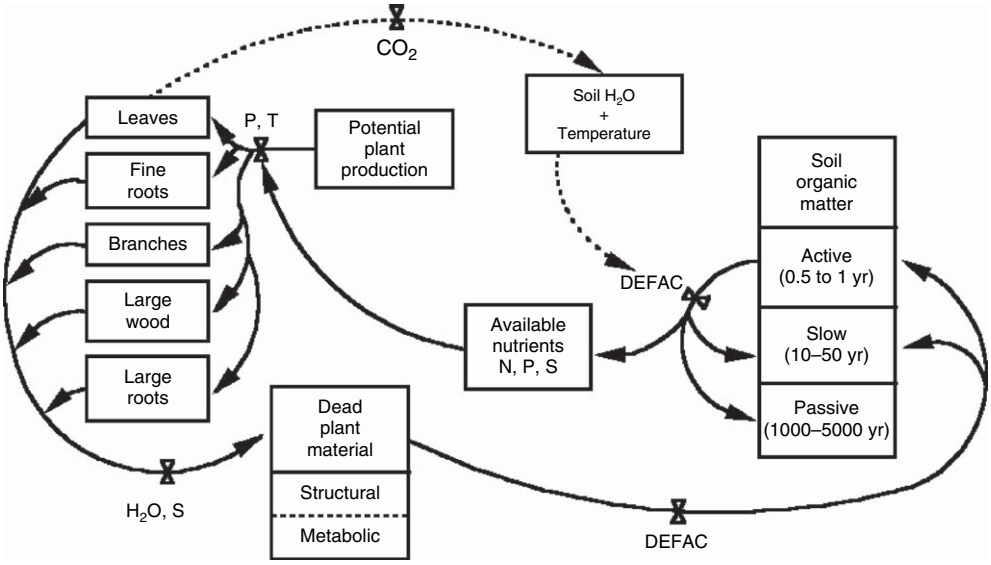


**Figure 4** Flowchart of the CENTURY model. Supplement to Metherell *et al*. 1993. Century Manual. CENTURY Soil organic matter model environment. Technical documentation. Agroecosystem version 4.0. Great Plains System Research Unit Technical Report No.4. USDA-ARS, Fort Collins, Colorado, USA. Freely available at http://www.nrel.colostate.edu/projects/century/Century_Slides.ppt

data collected under IBP and at research stations within the former USSR. They found that CENTURY reproduced the seasonal, mid-term, and, in some cases, long-term dynamics in aboveground biomass in a wide range of grassland ecosystems. Model discrepancies were attributed to changes in species composition and short-term responses to intermittent rainfall that are missed by the monthly timestep of the model. In another application, K. A. Hibbard and colleagues assessed in the 2000s the magnitude of changes in plant and soil carbon and nitrogen pools in a subtropical landscape undergoing succession from grassland to thorn woodland in southern Texas (USA). They linked CENTURY to a transition matrix model and parametrized grass and tree production submodels of CENTURY with field data. The Markov transition matrix model simulated the displacement of grassland communities under land-use practices (heavy livestock grazing, no fire) and climate events.

### *Water-balance models*

Other models, such as a model of water balance developed by J. M. Paruelo in the 1990s, calculate the amount of water evaporated from the soil and transpirated by the canopy. Typical questions asked with such models are: What are, on a long-term basis, the magnitude of evaporation, transpiration, and deep percolation in a water-limited steppe? How will elevated $CO_2$ change the fluxes of soil water to the atmosphere and ground water?

*See also*: Forest Models; Grazing Models; Savanna; Steppes and Prairies.

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**Grasslands** *See* Steppes and Prairies

# Grazing

**A J Underwood**, University of Sydney, NSW, Australia

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Grazing in Terrestrial Environments: Why Is the World Green?
The Paradox of the Plankton
Modeling Grazing Processes
Grazing and Indirect Interactions among Species
Switching and Facilitation by Grazers: Mechanisms Sustaining Biodiversity
Defenses against Herbivores
Grazing Promoting the Growth of Plants: Examples of Gardening
Grazers and Indirect Effects
Further Reading

## Grazing in Terrestrial Environments: Why Is the World Green?

Because grazing is so commonly considered to be a widespread and important process, it has been debated how it comes about that the majority of terrestrial habitats remain dominated by plants. Why have the grazers not removed most of the biomass and cover of their food?

Under most natural conditions, the plants are limited in production by availability of light, which has seasonal patterns in temperate regions and extreme limitation for long periods of the year near the poles. In addition to