Short-grass and Mixed-grass Ecosystems in the Southern Plains, U.S.A.: Conceptual Ecosystem Models

Prepared by Daniel Tinker and Ann Hild
Departments of Botany and Renewable Resources
University of Wyoming
Laramie, Wyoming

for

The Great Plains Cooperative Ecosystem Studies Unit
And the National Park Service and
Southern Plains Inventory and Monitoring Program

September, 2005

OVERVIEW OF MODEL DEVELOPMENT AND MODEL TYPES

The National Park Service (NPS) Inventory and Monitoring (I & M) program plans to initiate long-term monitoring of natural resources within its parks. In the Southern Plains Network (SOPN), mixed- and short-grass prairies are the dominant ecosystem. However, due to the relatively small size of Southern Plains parks, many of the prairies within the parks are isolated fragments and no longer function as did historical grasslands. Land management within and outside the parks can have a major impact on the ecological processes and functions on these prairie fragments. Understanding how these prairie systems have functioned historically, as well as how they currently function, is critical for identification of ecological indicators, or ecological vital signs, that represent the condition of a variety of natural resources. Conceptual models that describe the structure and function of these prairie fragments will aid land managers in the identification and selection of appropriate vital signs for long-term monitoring.

Various forms of conceptual models, including Jenny-Chapin, conceptual diagrams, State-Transition models, and Driver-Stressor schematic models were developed for SOPN, and are described separately in the following sections. We first provide some general background information for short-grass and mixed-grass prairie communities.

Introduction to Grassland Communities

Grasslands were historically the largest vegetation type in North America, covering more than 300 million ha (Küchler 1964), yet still occupy over 125 million ha in the United States (U.S. Forest Service 1980). However, due to widespread changes in land use and conversion to agricultural lands, short-grass and mixed-grass prairie grasslands are currently some of the most endangered ecosystems in North America (Rickletts et al. 1999). Short-grass prairies are dominated by two species of grass, blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*), but other species such as needle and thread grass (*Stipa comata*), prairie june grass (*Koeleria macrantha*), and sand dropseed (*Sporobolus cryptandus*) are also important components. These ecosystems are found primarily east of the Rocky Mountains, from Nebraska and Wyoming southward through the High Plains (Sims and Risser 2000). Mixed-grass prairies, which extend from south-central Canadian provinces to central Texas, are more floristically rich, and are characterized by vegetation intermediate to tallgrass and short-grass prairies. Dominant species vary across a latitudinal gradient, and include species of *Elymus*, *Pseudoroegneria*, *Bouteloua*, along with various species of sedges (*Carex* sp.) (Barbour et al. 1987).

CONCEPTUAL MODEL DEVELOPMENT AND DESCRIPTIONS

General Ecosystem Model – Jenny-Chapin Model

Jenny (1941) developed a simple model containing five state variables, including global climate, topography, parent material, potential biota, and time that control the formation of soils, as well as control many ecosystem processes. Chapin et al. (1996) expanded the state variable approach to include four interactive controls (regional climate, disturbance regime, soil processes, and functional groups) that not only help to control ecosystem structure and function, but also respond to ecosystem characteristics. We have modified each of these models slightly to better represent the state variables and interactive controls of the grassland systems in the Southern Plains, resulting in a general grassland model that describes at a very basic level the important feedbacks and drivers of grassland ecosystems (Figure 1). While time, as included in Jenny's original model for explaining soil formation, is certainly important in grassland ecosystems, we have substituted Land Use Legacies as a much more direct and potentially important constraint on grasslands of the Southern Plains. Land use legacies pertain to the past history of the land, (grazing, fire, agriculture) which can dramatically affect future grassland conditions.

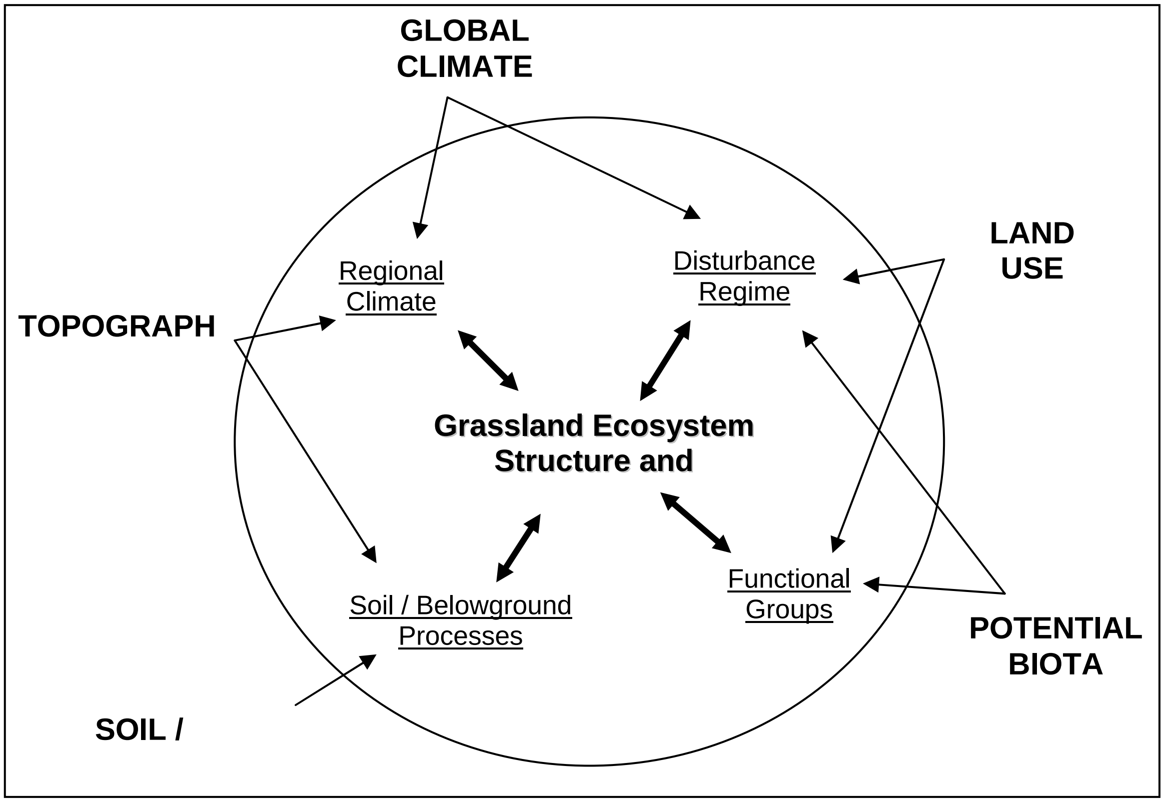

Figure 1. Generalized Jenny-Chapin Grassland Ecosystem Model

Short-grass and Mixed-grass Prairie Pictorial Model Overview

The various environmental variables, along with critical ecosystem drivers, stressors, and responses are depicted here in a non-hierarchical, general grassland pictorial model, included as Figure 2. This pictorial drawing also depicts many of the important interactions among various biotic and abiotic components of grassland ecosystems, and suggests ways that management and/or human activities may affect these interactions and outcomes.

The climate found in short-grass and mixed-grass ecosystems is quite variable across central North America. Notably, in the majority of these systems, approximately two-thirds of the annual rainfall in central grasslands occurs during the growing season. The usual rainfall deficiency that occurs late in the growing seasons provides conditions more favorable for the maintenance of grasslands than to deciduous forests (Sims and Risser 2000). In particular, grasslands of the Great Plains are strongly influenced by north-south and east-west climatic patterns, with precipitation decreasing from east to west, and air temperature increasing from north to south (Singh et al. 1983). Precipitation also acts as a strong driver of grassland ecosystem processes, and the relationship between rainfall and productivity is generally linear (Lauenroth 1979). The distribution of grasslands within the central U.S., as well as their vegetative composition, is further related to the interactions of a variety of other environmental and edaphic factors, including physiographic and topographic conditions, elevation, and herbivory (McNaughton et al. 1982). With respect to bedrock geology and soils, Mollisols are typically associated with cool, wet grasslands of the central plains, while more arid sites are most often characterized by Aridisols (Sims and Risser 2000). In the southern plains, soil texture varies from fine sandy soils to clay soils. There is a swath of relatively fertile Alfisols that stretches from southeastern Kansas into central Texas, following the general distribution of the cross timbers vegetation, as mapped by Küchler (1984), while Mollisols are most abundant throughout the rest of the southern plains (Sims and Risser 2000). Finally, land use change, primarily brought about by human uses and

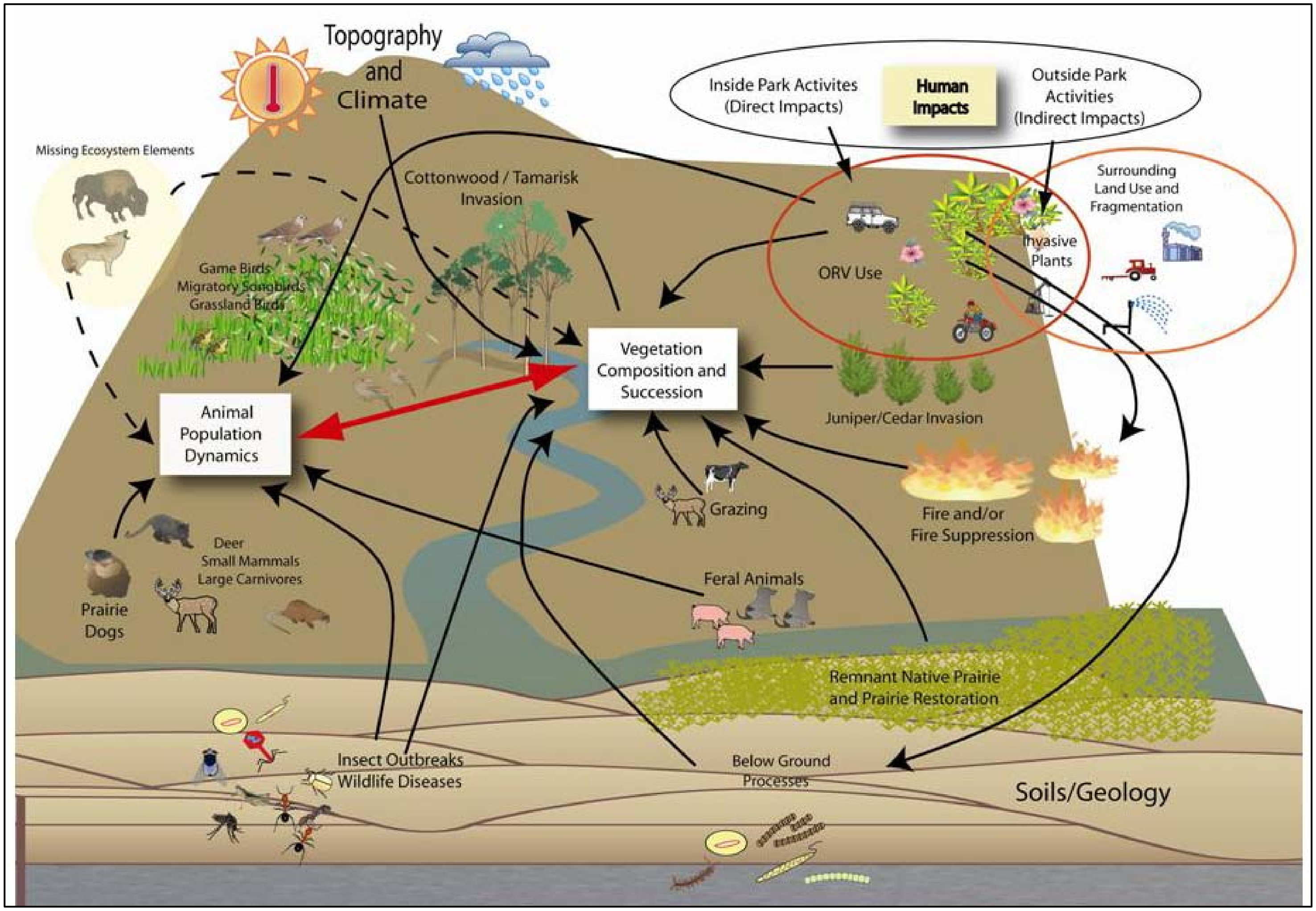

Figure 2. Grassland pictorial model.

impacts such as agriculture and urban development, may cause dramatic impacts on grassland ecosystems, including the loss of soil fertility and biological diversity, as well as hydrologic changes and increases in soil erosion (Paruelo et al. 2001).

Wet and dry cycles, along with periodic drought in short-grass systems, may be both harmful and beneficial, depending on the timing and intensity of the cycles. Dickinson and Dodd (1976) found that increases in water may affect the phenology of some grass species, e.g., blue grama, and flowering may occur earlier than in drier periods. Soil water, along with nitrogen, is thought to be the most important resources for determining community structure and plant growth in semiarid grasslands (Sala et al. 1992; Lauenroth et al. 1978). Notably, some grassland systems have developed adaptations to aridity, which may manifest themselves as morphological changes such as small stature and basal meristems (Coughenour 1985). These adaptations may also be advantageous for recovery from herbivore grazing. In general, grassland ecosystem responses to herbivory and defoliation are quite variable, and many systems have evolved grazing resistance to herbivory (e.g., Milchunas and Lauenroth 1993). However, grazing may be detrimental to many short-grass and mixed-grass ecosystems, depending on the intensity and duration of the grazing activity. Grazing impacts also vary along gradients of interaction with fire, and these interactions are more fully discussed later in the Grazing-Fire Submodel section of this narrative (Figure 3).

Erosion of surficial soils may occur as a result of intense, episodic rainfall events, or from road building, agricultural activities, and other human land uses. Stream bank erosion may also occur from land use practices such as grazing. For example, excessive grazing, which can cause increases in bare ground, may be positively correlated with increases in runoff following precipitation events (Hart et al. 1988; Hart and Frasier 2003). Similarly, flooding of rivers and streams can occur in arid areas where human activities have rerouted water courses and where soil texture prevents rapid infiltration.

Fire may also be a stressor, although most grassland systems have evolved with relatively frequent recurring fires (Sauer 1950; Curtis 1962; Axelrod 1985). Consequently, the suppression and removal of fire as an ecological process could actually act as a more direct stressor than fire itself, although fire may be detrimental in some short-grass prairie ecosystems (Wright and Bailey 1980). The impacts of fire on grassland systems and of the absence of fire, along with its interaction with grazing practices are more fully discussed in the Grazing-Fire Submodel section (Figure 3).

Invasive exotic plant species may colonize disturbed areas in and around NPS lands, and can be transported into parks via humans, vehicles, or other biotic vectors. These plants may outcompete some native vegetation, may persist for decades, and may even exert greater effects on community composition than other factors such as water availability (Clarke et al. 2005). Exotic animal species and feral domestic species can also compete with native species for limited resources. Along with invasive species, insect outbreaks and both natural and exotic wildlife diseases may infest native populations of plants and animals. While they may not be exotic, black-tailed prairie dogs (*Cynomys ludovicianus*) and their colonies play a significant role as a stressor in avian community structure and composition in some areas of short-grass plains (Smith and Lomolino 2004); however, their presence may be either beneficial or detrimental to other fauna and flora. This important dynamic is considered more fully later in this report in a prairie dog gradient model (Figure 5).

An interrelated set of critical factors in grassland systems of the Southern Plains are human impacts, along with adjacent land use and land use change. The many different ways that humans use the land is an important contributor to landscape pattern and process (Turner et al. 2001). For example, residential, commercial, and industrial development on adjacent lands are the direct result of human use (Meyer 1995), and may create hard boundaries around parks that can interrupt natural flows and fluxes of ecosystem processes and services, including recycling of nutrients and maintenance of clean air and water – this may be particularly problematic for some of the smaller parks in the Southern Plains Network. Many of the historically intact landscapes are rapidly becoming fragmented, largely through human land uses (Harris 1984). Unfortunately, these human “footprints” on the landscape are usually one-directional and are long-lasting legacies on the landscape (Turner et al. 1988). Species-area relationships are important for identifying biodiversity hotspots (Myers et al. 2000), and for helping predict reductions in populations or species in areas subjected to habitat fragmentation (Pimm and Askins 1995). This increases the difficulty in managing small areas, as are common for some parks within SOPN. Closely related to human land uses is the issue of non-park source pollution, which may include a variety of unwanted materials such as fertilizers and airborne pollutants.

Based on the ecosystem components and relationships identified and described in this pictorial model, as well as specific concerns of many of the SOPN parks, we developed three additional submodels that were deemed critical for understanding ecosystem function within SOPN grasslands. The following submodels focus on three key areas of grassland structure and function: fire and grazing; soil carbon and nutrients; and prairie dogs.

SUBMODEL DESCRIPTIONS

State-and-Transition Submodels

In contrast to basic succession-retrogression models for grasslands and rangelands, resource managers recognize that most semiarid grasslands may be transformed into shrub- or tree-dominated woodlands that may not return to typical grassland communities using grazing management techniques (Laycock 1991). Rather, multi-equilibrial states may exist in space and time, driven by a variety of mechanisms that cause often rapid and unanticipated shifts among the various states (Westoby et al. 1989). Conceptual models that use the state-and-transition approach to non-equilibrium conditions in grassland ecosystems provide more desirable means by which to anticipate such changes and, through monitoring and assessment, mitigate or restore grassland community structure and function (Allen-Diaz and Bartolome 1998; Rodriguez et al. 1997). We have included three such models, or variations thereof, in this report and they are described below and in Figures 3-5.

Fire and Grazing State-Transition Submodel

This submodel (Figure 3) describes the various grassland community types that may occur, along with the mechanisms that cause transitioning, such as the presence or absence of fire and grazing. In addition, the direct conversion of native grassland to agricultural lands such as croplands or hayfields, and the potential for restoration of the grassland community to a condition approaching that of the native composition is also considered. Grassland prairie communities in the central and western US have evolved over millennia with both fire and grazing (Collins 1992; Stebbins 1981). Both of these processes directly and strongly influence community composition, and much of the research on these two important variables has focused on the main effects of each independently. Yet, the interaction of fire and grazing may be more important in determining grassland community composition and condition than the sum of the individual processes. Indeed, fires often concentrate grazing in recently burned areas, where forage quality and quantity is higher (Fuhlendorf and Engle 2004).

The Fire-Grazing submodel (Figure 3) depicts three potential pathways for community composition changes that result from interactions of fire and grazing, as well as a fourth pathway that results in the conversion of any grassland community to agricultural lands.

The first pathway emphasizes intensive, heavy grazing regimes, along with the absence of fire, either through fire suppression, or the inability of managers to apply prescribed fire. These transitions will likely result in a reduction in native plant species, an increase in annuals and other invasives such as prickly pear cactus (*Opuntia sp.*), and a higher abundance of bare soil (e.g., Sims and Risser 2000; Belsky 1992; Albertson 1937). Intermediate vegetative states may be

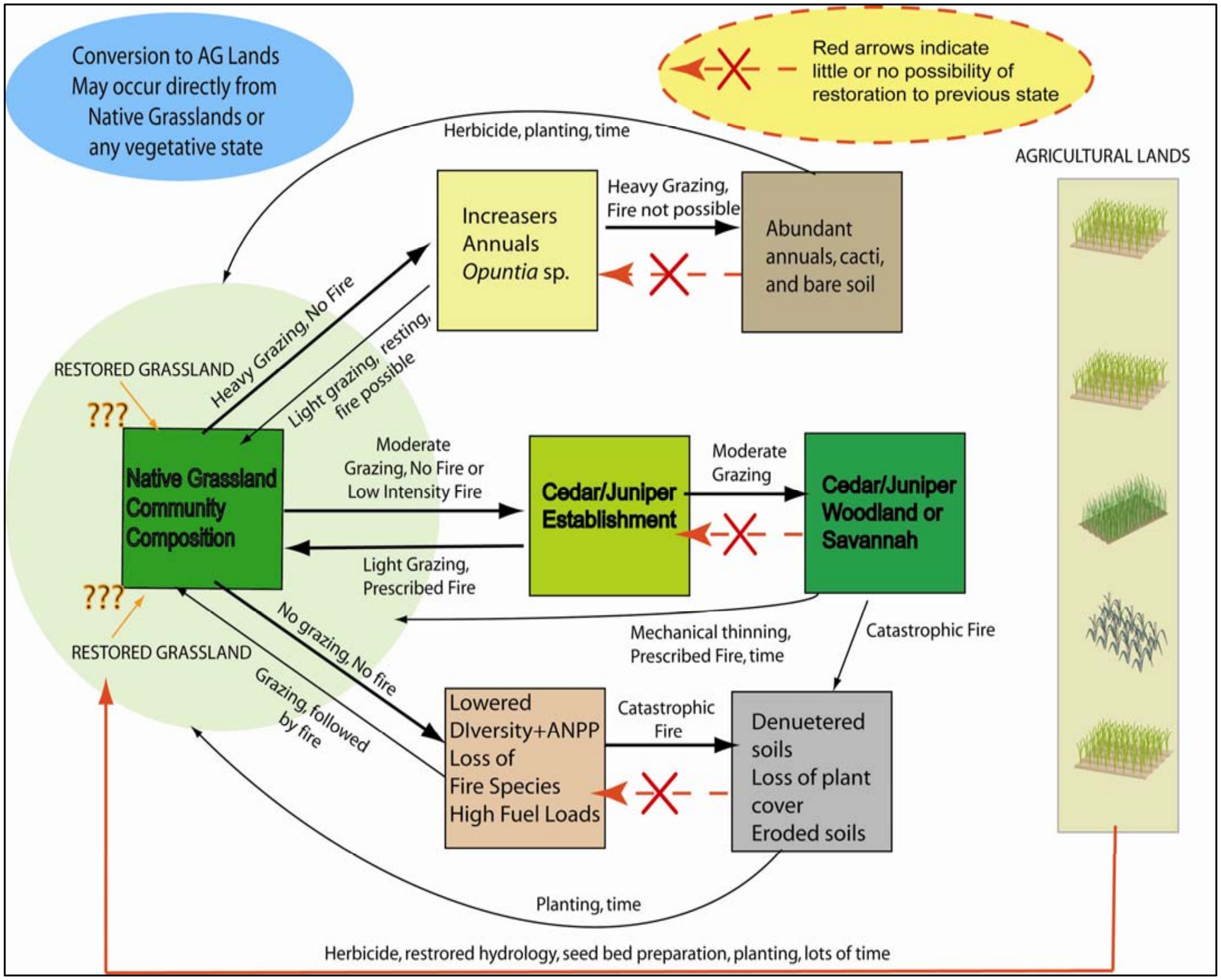

Figure 3. Fire-grazing state and transition model.

restored to native communities through a reduction in grazing and occasional fire use; however, highly degraded sites may require much more intensive restoration efforts, including herbicide application, reseeding, and considerable time.

A second transitional pathway that includes more moderate levels of grazing, with fire being absent or very infrequent and low intensity, will likely allow for the establishment of cedar or juniper (*Juniperus spp.*) shrubs and trees, with this establishment resulting in the conversion of grasslands to cedar/juniper woodland or savannahs, given sufficient time (Bragg and Hulbert 1976; Briggs et al. 2002; Hoch et al. 2002). As described above, restoration to an approximation of native grassland community would again require intensive management actions such as mechanical thinning, prescribed fire, and long time periods.

However, a third pathway exists that can result from the complete absence of both fire and grazing. Such a trajectory could initially lead to lower plant species diversity, including fire-adapted species, and would likely increase fine fuel loadings considerably (Belsky 1992; Collins 1987). Such conditions could result in higher frequency of catastrophic fire (e.g., Stinson and Wright 1969), which leads to short-term decreases in plant cover and concomitant increases in runoff and erosion (Hart et al. 1988).

Finally, as mentioned previously, conversion of grassland ecosystems, regardless of condition, to agricultural land is always possible, resulting in the immediate conversion of vegetative composition. It is believed that it would be extremely difficult to restore such land to native grassland, or perhaps even to an approximation of native grassland, and only then if intensive restoration efforts that include herbicide, reseeding, restoration of hydrology, and long periods of time are implemented.

Soil Carbon and Nutrient Submodel

This submodel (Figure 4) is a bit different from more traditional state-and-transition models in that, in addition to suggesting possible pathways for vegetative change, it also represents, in a very simplified manner, basic pools and processes associated with carbon and nutrients in a grassland ecosystem.

Soil carbon and nutrient dynamics for grasslands and other ecosystem types have been thoroughly described in literally hundreds of books and scientific journals (sensu Aber and Melillo 2001). Aboveground net primary productivity (ANPP) by grassland plants contributes to the processes of litterfall, decomposition, and mineralization, which, in turn, provide the release of nutrients for uptake by the microbial and plant communities. Because fire, grazing, and human land use most directly impact ANPP in grassland ecosystems, it is these transitions and resulting conditions that are discussed in this submodel. Indeed, the transitional pathways described here are quite similar to those discussed in the Fire-Grazing submodel, and focus on fire, grazing, their interactions, and the conversion of grassland to agricultural lands.

When fire is present, along with moderate grazing, accumulated fuels and litter are combusted and many important nutrients are released. Although some of these nutrients are lost during volatization, those that remain are often in forms more available to plants, which may result in higher ANPP (Aber and Melillo 2001). Some of the microbial community may be lost, especially in the upper organic layers of the soil, but soil heating in mineral soil, which could further reduce the abundance of microbes, is rare (Whelan 1995).

When both fire and grazing are removed from these systems, the effect is less dramatic than when both are present. For example, without periodic releases of available nutrients as provided by fires, ANPP may actually decrease slightly in the long-term, which also somewhat reduces inputs to litter and fine fuels. Consequently, there is minimal short- or long-term effect on the belowground community structure.

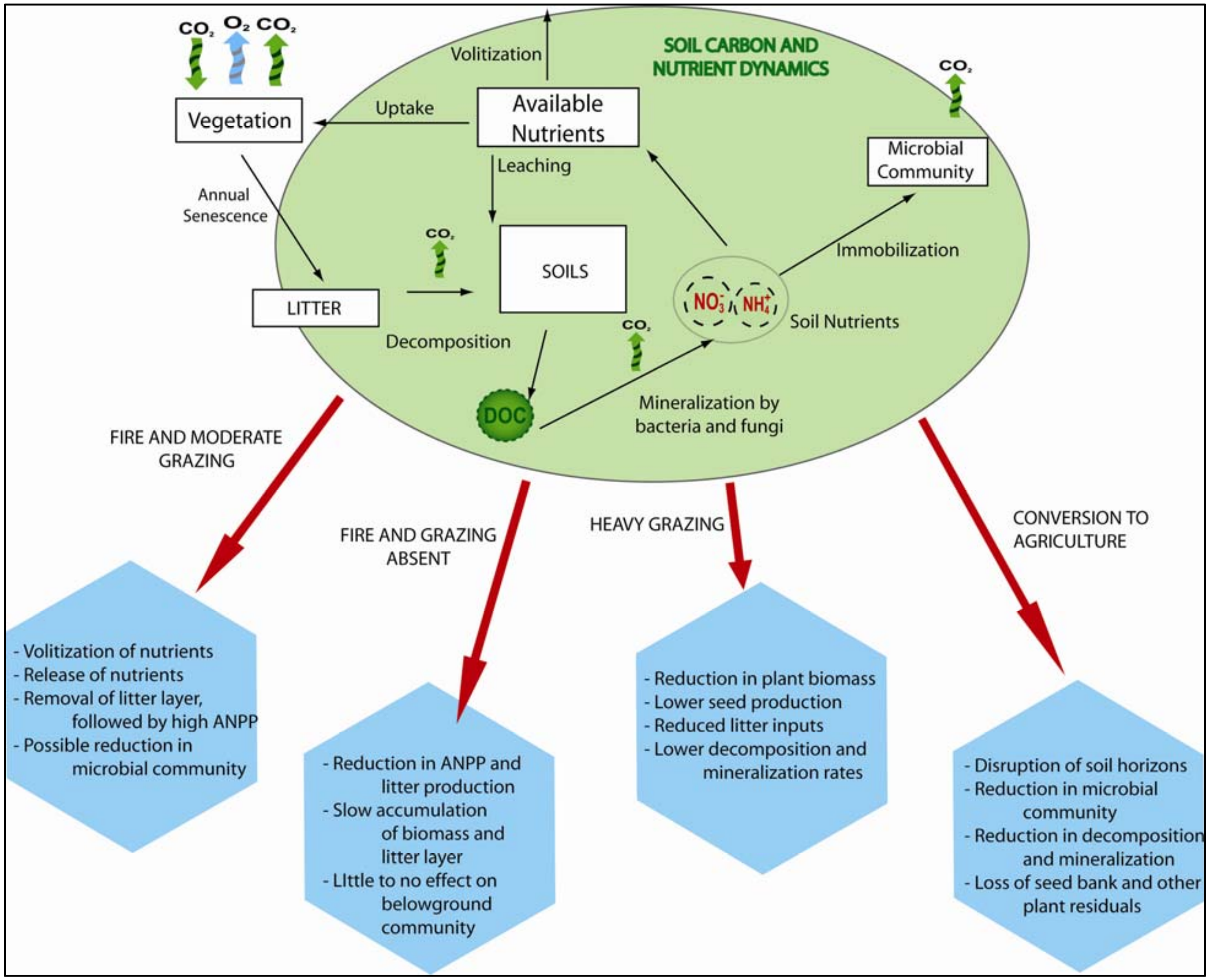

Figure 4. Soil carbon and nutrient dynamic submodel.

In contrast, under intensive grazing practices, the chronic reduction in plant biomass may result in dramatic decreases in plant litter inputs. This, in turn, will cause a reduction in decomposition and mineralization rates and, potential reductions in available nutrients. Notably, heavy grazing will also result in lower seed production and, therefore, lower dispersal and recruitment of new individual plants.

Conversion of grassland sod-forming plants to agriculture will disrupt belowground structure and function dramatically compared to the other three pathways described above. The disruption of surficial soil horizons increases evaporation and water loss, which can reduce decomposition and mineralization of soil organic matter. Perhaps most importantly, the loss of plant residuals and other forms of the seed bank may preclude restoration to native grassland community composition without very intensive and extended reclamation treatments.

Prairie Dog Submodel

The black-tailed prairie dog is usually considered to be a keystone species in grassland and prairie ecosystems (Kotilar et al. 1999). The influences and roles of prairie dogs in short-grass and mixed-grass systems will be examined in the following submodel (Figure 5) in the context of a gradient of prairie dog abundance, from absent to high, and under various stressors that may affect prairie dog populations, regardless of density.

Over the past century, prairie dogs have been subjected to widespread eradication efforts, yet still persist, albeit in much reduced numbers when compared to historical population densities (Clark 1989). In addition, other stressors to population numbers include the destruction of habitat, mostly through land use change, extended drought, epidemics of Sylvatic plague, and, indirectly, the removal of wolves (*Canis lupus*) from most grassland and prairie ecosystems, which results in an increase of a primary prairie dog predator, the coyote (Miller et al. 1994; Cully 1993). This increase in coyote abundance may negate any increases in swift fox and ferret abundance, as described below (Laliberte and Ripple 2004).

In the absence of prairie dogs and their burrows from grassland and prairie ecosystems, structural changes to the landscape occur, including a shift to a more static landscape pattern (Kotilar et al. 1999). Additionally, the vertical structure of vegetation is higher, resulting in an increase of fine fuels. This increase may eventually lead to a higher frequency of intense fires (Whelan 1995), which may create large patches of bare ground and increase the likelihood of exotic plant invasion. Many of these consequences are important management considerations in many, if not most, of the parks in the SOPN.

At high population densities, many benefits of prairie dogs and their burrows have been documented. One of the many roles they serve is that of prey for a variety of predators, including swift fox (*Vulpes velox*), coyote (*Canis latrans*), and black-footed ferrets (*Mustella nigripes*). Their presence also creates a decrease in vertical structure of vegetation. While perhaps not intuitive, this reduction in vertical structure may have important implications for many other species. For example, visibility for swift foxes is increased (Agnew et al. 1986), mountain plovers (*Charadrius montanus*) are more likely to nest in such landscapes (Knowles et al. 1982), and there is a greater likelihood that ferruginous hawks (*Buteo regalis*) and burrowing owls (*Athene cunicularia*) will occupy these lands (Cook et al. 2003; Desmond et al. 1995). Notably, the decrease in vertical structure may also increase habitat for relatively rare species such as the lesser prairie chicken (*Tympanuchus pallidicnctus*) (Barko et al. 1999).

Finally, at lower densities, populations may become isolated, resulting in genetic isolation, reduced gene flow, and reduced genetic diversity, all critical factors in maintenance of persistent and adaptable populations of organisms (Dobzhansky 1970).

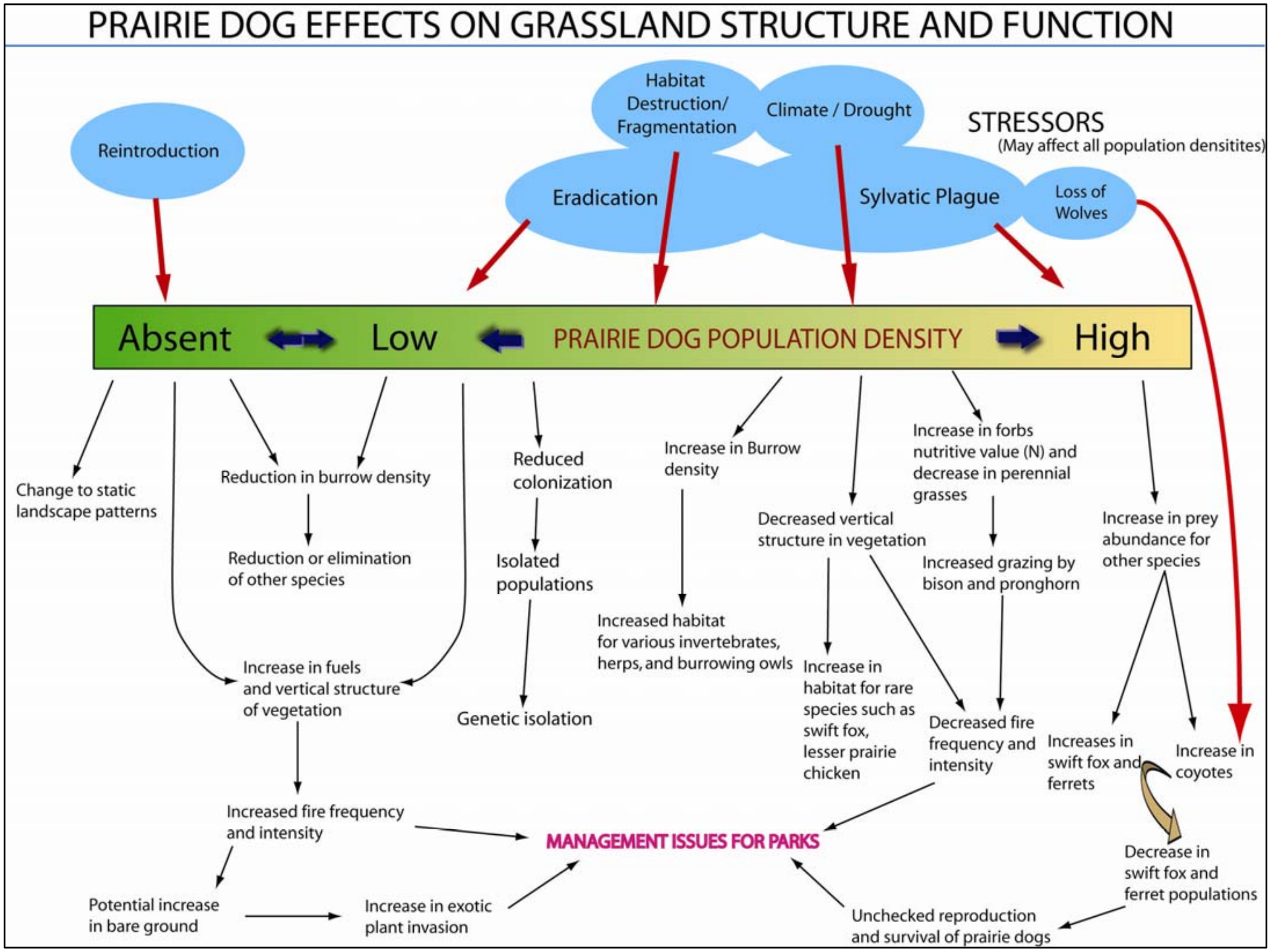

Figure 5. Prairie dog effects submodel.

Driver-Stressor Schematic Models for Short-grass and Mixed-grass Prairie

Driver-stressor models are often useful for identifying linkages among various state variables and ecosystem properties and responses (e.g., Gentile et al. 2001), but are also useful for identifying important ecosystem indicators, or “vital signs” along with appropriate means of measurement of the indicators. Most of the forcing factors depicted in the following two schematic models have been discussed above in the section describing the grassland pictorial model, but the following figures may serve as summaries of the various components and linkages, as well as serve to identify critical ecological indicators. Although separate models were developed for short-grass and mixed-grass prairie, differences between the two systems and, therefore, between the two models are minimal. For Figures 6 and 7, the hierarchy of organization for the models includes: drivers (boxes), which are major external factors or forcings that have large-scale influences; stressors (ovals) that represent physical, chemical, or biological agents that cause significant changes in ecological components, patterns, or relationships in natural systems; ecological outcomes or processes (diamonds), defined as physical, chemical, or biological responses to drivers or stressors, and which may be either positive or negative (these processes are more fully described in the submodels section); indicators (hexagons) that represent living or nonliving, information-rich features of an ecosystem that can be measured or estimated, and that are somehow indicative of the quality or integrity of the larger ecological system; and measurements (parallelograms) of the above described indicators.

INDICATORS

The following section will focus only on the Indicators depicted in the schematic models. Suggested measurements for each indicator are included in Figures 6 and 7, but are not specifically discussed in this report.

Bird and other wildlife populations are directly and indirectly affected by many of the stressors contained in the pictorial submodel (Figure 2), including direct and indirect human impacts such as land use change, and the invasion of exotic and feral species. Inventories of big game, ungulates and other small mammals may serve as important indicators of ecosystem function. The interactions of temperature, precipitation, and soil type, along with annual and decadal wet and dry cycles can determine the structure and activity of **wetland areas and upland springs**.

Regeneration of **Cottonwood (*Populus deltoides*) riparian woods** relies heavily on episodic flooding events. Regulation of water flows, through impoundments and irrigation, may reduce the likelihood of such events and, consequently inhibit natural regeneration of new individuals along these important corridors. Tamarisk (*Tamarix spp.*) and other non-native plants may encroach on cottonwood habitat in the absence of cottonwood regeneration, altering the community composition in such areas. In mixed-grass ecosystems in particular, small patches of **deciduous hardwood forests** are quite sensitive to many stressors such as human impacts, grazing, fire, and invasive plant species.

Grassland community composition is perhaps the best indicator of the condition of these ecosystems. Changes in the natural fire regimes, along with varying intensities of domestic livestock grazing, can shift community composition to a range of conditions that may or may not resemble native grasslands (Figure 3). Also, dramatic alterations in community structure and composition, such as those that occur with the conversion of native grasslands to agricultural areas, require substantial restoration efforts to recreate grassland communities that even remotely resemble original, native ecosystems. Such restoration is rarely, if ever successful in completely restoring converted agricultural land to native grassland communities. Resource islands in these temperate grasslands, which develop from spatially heterogeneous plant cover, can be areas of accumulated soil materials. These islands may take decades to create, but can disappear within three years of the death of an individual plant, and may be good indicators of ecosystem condition (Burke et al. 1998). Further, the **habitat quality** of the grassland ecosystems responds to a variety of drivers and stressors, most notably human impacts, grazing,

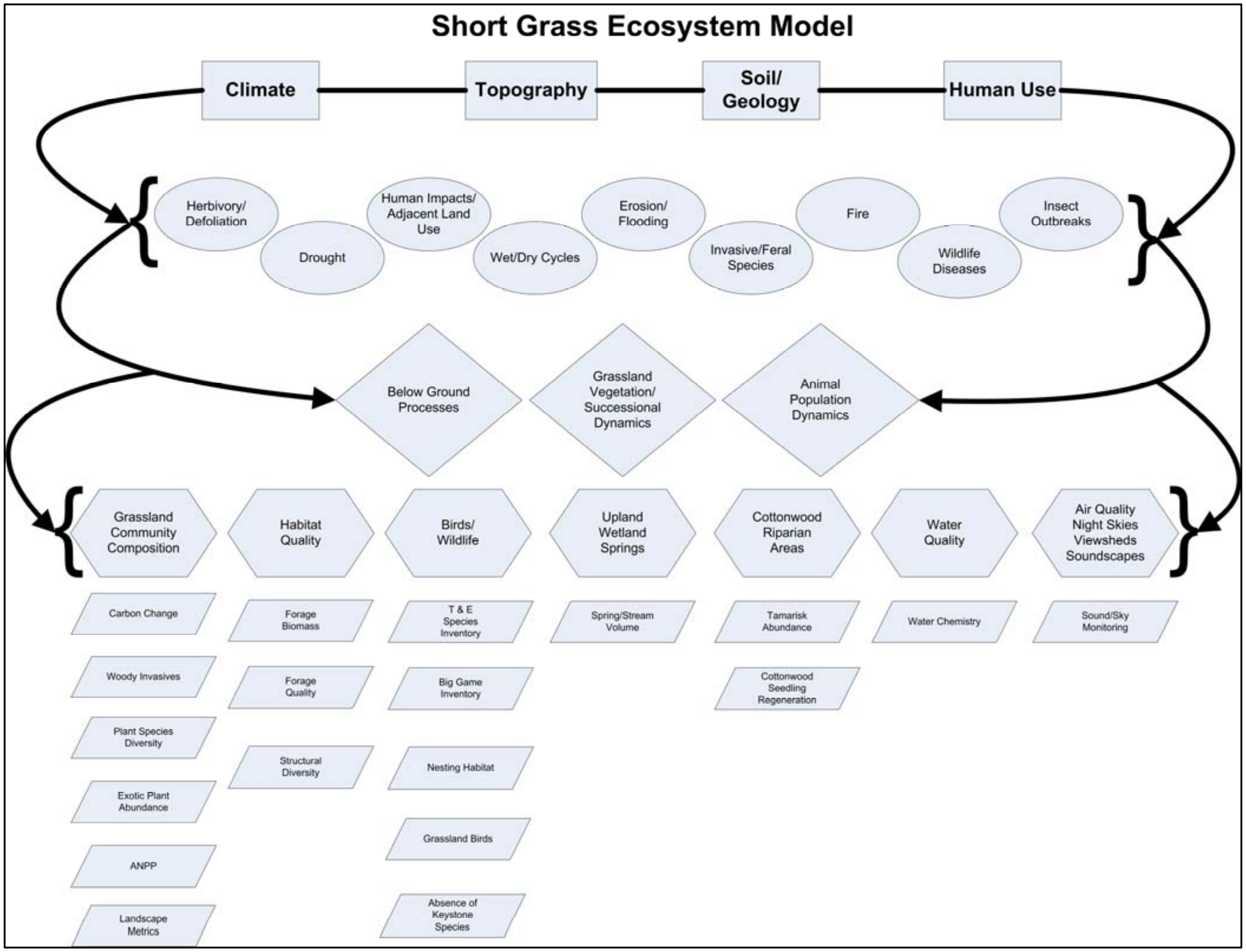

Figure 6. Short-grass ecosystem driver-stressor schematic model.

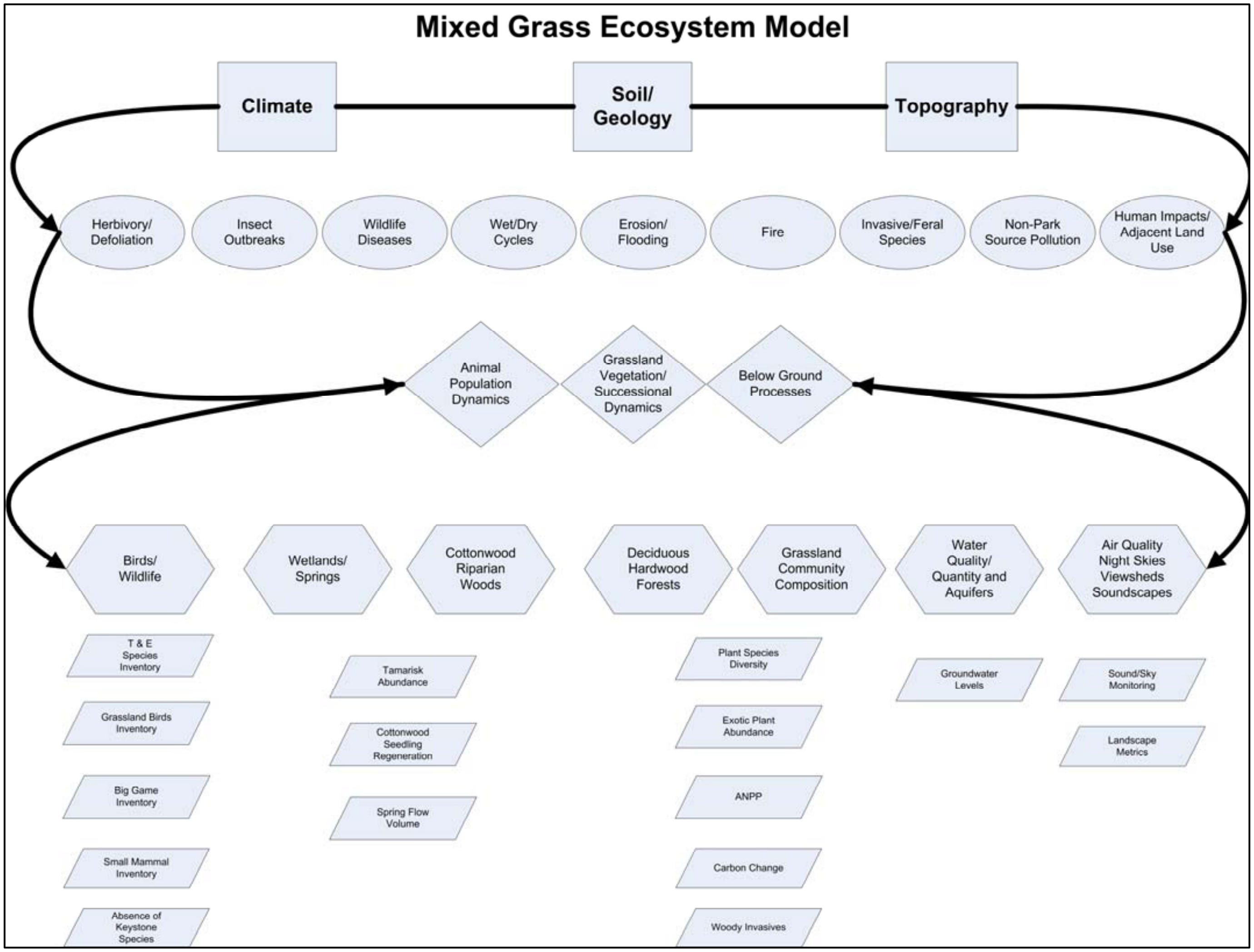

Figure 7. Mixed-grass ecosystem driver-stressor schematic model.

and periodic drought. Also, fire, or the absence of fire, can either adversely affect or benefit habitat conditions for many ungulates, small mammals, and birds (Figures 2 and 3). As discussed in an earlier section of this report (See Prairie Dog Submodel; Figure 5), prairie dogs exert a disproportionate influence on habitat quality and quantity for a variety of organisms, including burrowing owls, swift fox, and lesser prairie chicken. Further, changes in land use and, therefore, community composition, can alter many soil processes such as decomposition and mineralization, which may result in reduced productivity and lower habitat quality for herbivores and obligate carnivores.

Water quality and quantity respond to a myriad of drivers and stressors. **Water quantity** is directly affected by annual precipitation and periodic drought, along with water allocation by human uses. **Water quality** may be impacted by specific non-park source pollution, and also by non-point source pollution such as atmospheric deposition. More detail on aquatic systems is included in a separate report prepared elsewhere for the SOPN grasslands. **Night skies and soundscapes**, arguably some of the most desired resources in national parks and recreation areas, are primarily affected by human impacts and adjacent land uses, including construction of roads and buildings. Other impacts to soundscapes can include fire suppression efforts and direct impacts of intense fires, such as smoke and haze. However, night skies may also be impacted by other natural causes such as dust, which may be caused by extended periods of drought.

REFERENCES

Aber, J.D., and J.M. Melillo. 2001. Terrestrial Ecosystems. Harcourt Academic Press. San Diego, CA. Second Edition.

Agnew, W. D., W. Ursek, and R. M. Hansen. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. J. Range Management 39:135-139.

Albertson, F.W. 1937. Ecology of mixed prairie in west central Kansas. Ecological Monographs 7: 481-547.

Allen-Diaz, B., and J.W. Bartolome. 1998. Sagebrush-grass vegetation dynamics: comparing classical and state-transition models. Ecological Applications 8: 795-804.

Axelrod, D.I. 1985. Rise of the grassland biome, central North America. Bio. Rev. 51: 163-201.

Barbour, M.G., J.H. Burk, and W.D. Pitts. 1987. Terrestrial Plant Ecology. Second Edition. Benjamin/Cummings Publishing, Menlo Park, CA.

Barko, V.A., J.H. Shaw, and D.M Leslie, Jr. 1999. Birds associated with black-tailed prairie dog colonies in southern shortgrass prairie. Southwest Naturalist 44: 484-489.

Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. J. Vegetation Science 3: 187-200.

Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Management 29: 19-24.

Briggs, J.M., A.K. Knapp, and B.L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a 15 year study of fire and fire-grazing interactions. Am. Midland Naturalist 147: 287-294.

Burke, I.C., W.K. Lauenroth, M.A. Vinton, P.B. Hook, R.H. Kelly, H.E. Epstein, M.R. Aguiar, M.D. Robles, M.O. Aguilera, K.L. Murphy, and R.A. Gill. 1998. Plant-soil interactions in temperate grasslands. Biogeochemistry 42: 121-143.

Chapin, F.S., III, M.S. Torn, and M. Tateno. 1996. Principles of ecosystem sustainability. American Midland Naturalist. 148: 1016-1037.

Clark, T.W. 1989. Conservation biology of the black-footed ferret. Wildlife Preservation Trust International, Special Scientific Report No. 3.

Clarke, P.J., P.K. Latz, and D.E. Albrecht. 2005. Long-term changes in semi-arid vegetation: invasion of an exotic perennial grass has larger effects than rainfall variability. J. Vegetation Science 16: 237-248.

Collins, S.L. 1992. Fire frequency and community heterogeneity in tallgrass prairie: a field experiment. Ecology 73: 2001-2006.

Collins, S.L. 1987. Interactions of disturbances in tallgrass prairie: a field experiment. Ecology 68: 1243-1250.

Cook, R. R., J. E. Cartron, and P. J. Plocheta, Jr. 2003. The importance of prairie dogs to nesting ferruginous hawks in grassland ecosystems. Wildlife Society Bulletin 31:1073-1082.

Coughenour, M.B. 1985. Graminoid responses to grazing by large herbivores: adaptations, exaptations and interacting processes. Annals of the Missouri Botanical Garden 72: 852-863.

Cully, J.F. 1993. Plague, prairie dogs and black-footed ferrets. Pages 38-48 in J.L. Oldemeyer, D.E. Biggins, B.J. Miller, and R. Crete, eds.: Management of prairie dog complexes for the reintroduction of the black-footed ferret. Biological report 13. US Department of the Interior, US Fish and Wildlife Service.

Curtis, J.T. 1962. the modification of mid-latitude grasslands and forests by man, pp. 721-736 in W.L. Thomas, Jr., ed., Man's role in changing the face of the earth. University of Chicago Press, Chicago.

Desmond, M. J., J. A. Savidge, and T. F. Seibert. 1995. Spatial patterns of burrowing owl (*Speotyto cunicularia*) nests within black-tailed prairie dog (*Cynomys ludovicianus*) towns. Can. J. of Zoology 73:1375-1379.

Dickinson, C.E., and J.L. Dodd. 1976. Phenological pattern in the shortgrass prairie. American Midland Naturalist 96: 367-378.

Dobzhansky, T. 1970. Genetics of the evolutionary process. Columbia University Press. New York, NY.

Fuhlendorf, S.D., and D.M. Engle. 2004. Application of the fire-grazing interaction to restore a shirting mosaic on tallgrass prairie. Journal of Applied Ecology 41: 604-614.

Gentile, J.H., M.A. Harwell, W. Cropper, Jr., C.C. Harwell, D. DeAngelis, S. Davis, J.C. Ogden, and D. Lirman. 2001. Ecological conceptual models: a framework and case study on ecosystem management for South Florida sustainability. The Science of the Total Environment 274: 231-253.

Harris, L.D. 1984. The Fragmented Forest. University of Chicago Press, Chicago, Illinois, USA.

Hart, R.H., M.J. Samuel, P.S. Tewst, and M.A. Smith. 1988. Cattle, vegetation and economic responses to grazing systems and grazing pressure. J. Range Management 41: 282-286.

Hart, R.H., and G.W. Frasier. 2003. Bare ground and litter as estimators of runoff on short- and mixed-grass prairie. Arid Land Research and Management. 17: 485-490.

Hoch, J.A., J.M. Briggs, and L.C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. Ecosystems 5: 578-586.

Jenny, H. 1941. Factors of soil formation. McGraw-Hill. New York.

Knowles, C.J., C.J. Stoner, and S.P. Gieb. 1982. Selective use of black-tailed prairie dog towns by Mountain Plovers. Condor 84:71-74.

Kotilar, N.B., B.W. Baker, A.D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24: 177-192.

Küchler, A.W. 1964. Potential natural vegetation of the conterminous United States. American Geographical Society special publication 36, New York.

Laliberte, A. S., and W. J. Ripple. 2004. Range contractions of North American carnivores and ungulates. BioScience 54(2): 123-138.

Lauenroth, W.K. 1979. Grassland primary production: North American grasslands in perspective, pp. 3-24 in N.R. French, ed., Perspectives in grassland ecology. Springer-Verlag, New York.

Lauenroth, W.K., J.L. Dodd, and P.L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. Oecologia 36: 211-222.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. J. Range Management 44: 427-733.

McNaughton, S.J., M.B. Coughenhour, and L.L. Wallace. 1982. Interactive processes in grassland ecosystems, pp. 167-193 n J.R. Estes, R.J. Tyrl, and J.N. Brunken (eds.), Grasses and grasslands, systematics and ecology. University of Oklahoma Press, Norman, OK.

Meyer, W.B. 1995. Past and present land use and land cover in the USA. Consequences, Spring 1995: 25-33.

Milchunas, D.G., and W.K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecological Monographs 63: 327-366.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology 8: 677-681.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Paruelo, J.M., I.C. Burke, and W.K. Lauenroth. 2001. Land-use impact on ecosystem functioning in eastern Colorado, USA. Global Change Biology 7: 631-639.

Pimm, S.L., and R.A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. Proceedings of the National Academy of Sciences (USA) 92: 9343-9347.

Rickletts, T.H., E. Dinerstein, D.M. Olsen, C.J. Loucks, W. Eichbaum, D. DellaSala, K. Kavanagh, P. Hedao, P.T. Hurley, K.M. Carney, R. Abel, and S. Waiters. 1999. Terrestrial ecoregions of North America. Island Press, Washington, D.C.

Rodriguez Iglesias, R.M., and M.M. Kothman. 1997. Structure and causes of vegetation change in state and transition model applications. J. Range Management 50: 399-408.

Sala, O.E., W.K. Lauenroth, and W.J. Parton. 1992. Long-term soil water dynamics in the shortgrass steppe. Ecology 73: 1175-1181.

Sauer, C.O. 1950. Grassland, climax, fire, and man. J. Range Mgt. 3: 16-22.

Sims, P.L., and P.G. Risser. 2000. Grasslands. *In*: Barbour, M.G., and W.D. Billings, eds., North American Terrestrial Vegetation, Second Edition. Cambridge University Press, New York, pp. 323-356.

Singh, J.S., W.K. Lauenroth, R.K. Heitschmidt, and J.L. Dodd. 1983. Structural and functional attributes of the vegetation of the mixed prairie of North America. Bot. Rev. 489: 117-149.

Smith, G.A., and M.V. Lomolino. 2004. Black-tailed prairie dogs and the structure of avian communities on the shortgrass plains. Oecologia 138: 592-602.

Stebbins, G.L. 1981. Coevolution of grasses and large herbivores. Annals of the Missouri Botanical Garden 68: 75-86.

Stinson, K.J. and H.A. Wright. 1969. Temperature and headfires in the southern mixed prairie of Texas. J. Rangeland Management 22: 169-174.

Turner, M.G., S.R. Carpenter, E.J. Gustafson, R.J. Naiman, and S.M. Pearson. 1988. Land use. *In*: M.J. Mac, P.A. Opler, P. Doran, and C. Haecker, eds. Status and Trends of Our Nation's biological Resources, volume 1, pp. 37-61. National Biological Service, Washington, DC, USA.

Turner, M.G., R.H. Gardner, and R.V. O'Neill. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer-Verlag, New York.

U.S. Forest Service. 1980. An assessment of the forest and range land situation in the United States. USDA publication FS-345. Forest Service, Washington, D.C.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. J. Range Management 42: 266-274.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press. Cambridge, UK.

Wright, H.A., and A.W. Bailey. 1980. Fire ecology and prescribed burning in the Great Plains – a research review. USDA Forest Service general technical report INT-77. Intermountain Forest and Range Experiment Station, Ogden, Utah.