CENTRAL PLAINS EXPERIMENTAL RANGE
LONG TERM ECOLOGICAL RESEARCH

SITE REVIEW
JUNE 1989

The Central Plains Experimental Range
Long Term Ecological Research Project

Our approach to the LTER program has explicitly considered system behavior across a range of spatial and temporal scales. Our work has spanned spatial scales from individual plants to the central grassland region of the United States (Figure 1), focusing on annual to century level implications. In our approach to LTER we assumed that an important criterion for judging the significance of our LTER-funded work at the Central Plains Experimental Range would be our ability to generalize results beyond the boundaries of the site. Because we are interested in spatial and temporal scales that exceed the boundaries of a single site, we have emphasized observations and experiments with a spatially explicit dimension, as well as technologies to deal with the analysis and extrapolation of spatial information. These technologies include simulation modeling and geographic information systems.

Overview of Activities and Accomplishments

Core Topics

1. Pattern and control of primary production.

Our approach to this topic has emphasized the full range of spatial scales from individual plants to the central grassland region. We have been most concerned about controls on production at the various scales. We have benefitted substantially from historical and collaborative research on this topic.

Data from the US IBP program for the late 1960's and early 1970's provided background for estimates of both above- and belowground net primary production. The USDA has estimated aboveground forage production at a number of locations on the site for most of the years since 1939 which provides us with a long term database. Beyond the boundaries of the CPER, we have obtained a Soil Conservation Service database of soils and forage production for approximately 9000 sites throughout the central grassland region.

Our current data collection activities include:

> 1. Estimating net aboveground production at several locations at the CPER which differ in soil texture. Additionally, at one of these locations, estimates have been made for three landscape positions.

> 2. Estimating belowground production using a harvest technique and a ^{14}C dilution technique.
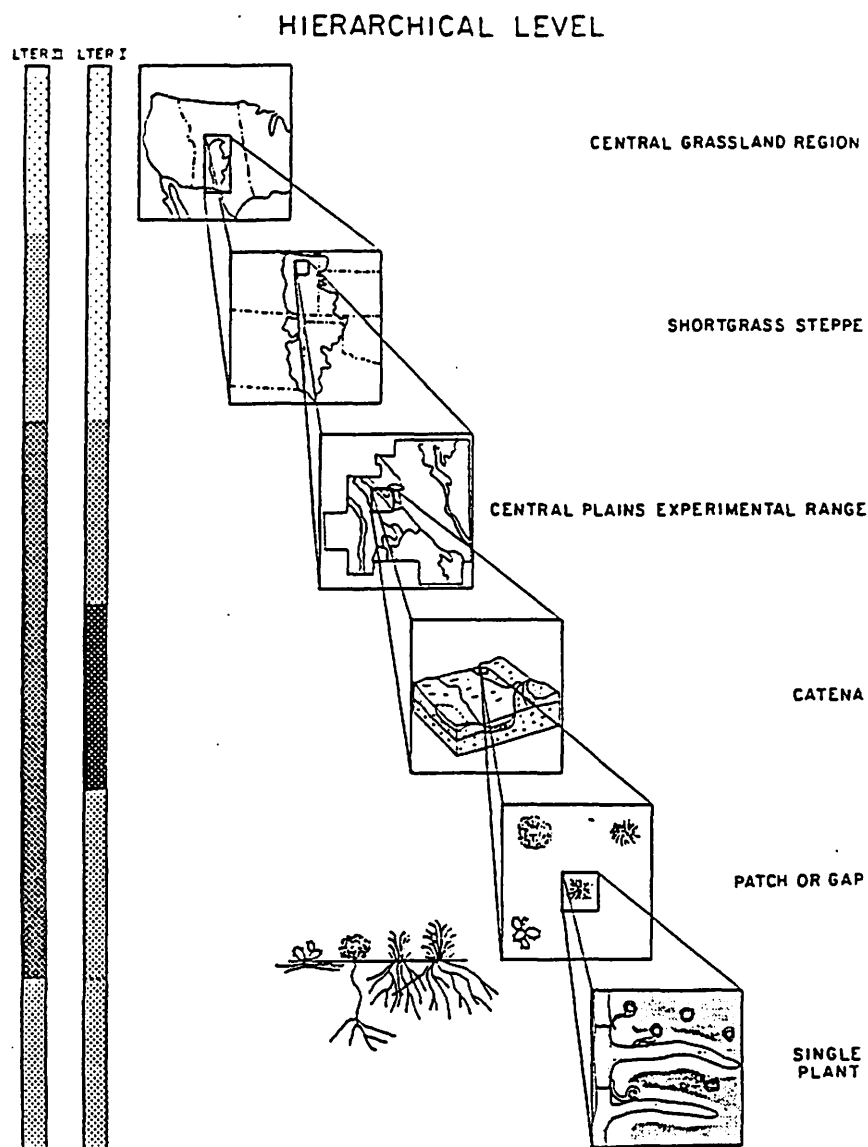
Fig. I. Nested hierarchy of spatial pattern. (1) Central Grassland Region: 1.8×10^6 km^2 of grassland and cropland derived from grassland in the Great Plains and Central Lowlands physiographic provinces of the United States. (2) The Shortgrass Steppe: 2.8×10^5 km^2 of grassland and cropland derived from grassland in the west central section of the Great Plains physiographic province. (3) The Central Plains Experimental Range: 70 km^2 of grassland in the northern portion of the Shortgrass Steppe. The CPER is composed of several physiographic units. (4) Catena: Physiographic units are made up of catenas with sites which range between 0.5 to 1 km^2. Different positions (summit, backslope, toeslope) along catenas are associated with the same soil and vegetation characteristics. (5) Patch or gap: Bare soil patches of approximately 0.1 m^2 are intermingled with patches of grass, shrub, herb, or succulents. (6) Single plant: Single plants are associated with microorganisms in the rhizosphere and non-rhizosphere environment. The shading of the vertical bars indicate how research effort was allocated over spatial scale during LTER I and our proposal for allocating effort during LTER II.

Recent Products

Michunas, D.G., W.K. Lauenroth, J.S. Singh, C.V. Cole, and H.W. Hunt. 1985. Root turnover and production by ^{14}C dilution: implications of carbon partitioning in plants. Plant Soil 88:353-365.

Liang, Y.M, D.L. Hazlett, and W.K. Lauenroth. 1989. Biomass dynamics and water use efficiencies of five plant communities in the shortgrass steppe. Oecologia (Berl.) (in press).

Our current and recent synthesis activities include:

1. Analysis of controls on aboveground primary production for the central grassland region of the United States using the database compiled by the Soil Conservation Service.

2. Comparisons of spatial patterns of aboveground primary production for the Central Plains Experimental Range and the entire Shortgrass Steppe region. The long-term USDA database will be used for the Central Plains Experimental Range and the Soil Conservation Service database for the Shortgrass Steppe.

3. Analysis of the relationship between precipitation and net aboveground production at individual sites. The long-term USDA database will be used along with a database from Manyberries, Alberta provided by Argiculture Canada.

Recent Products

Sala, O.E., W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1988. Primary production of the central grassland region of the United States. Ecology 69:40-45.

2. <u>Spatial and temporal distribution of populations selected to represent trophic structure.</u>

The trophic structure of shortgrass ecosystems is dominated aboveground by grasses, cattle, and macroarthropods such as grasshoppers and belowground by grasses, nematodes, fungi, bacteria, and protozoans. The asymmetry in the complexity of the trophic structure between the above- and belowground portions is typical of semiarid regions with greater complexity belowground. Our approach has been to focus on grasses above- and belowground and consumers aboveground. Because of historical research during and following the IBP program, the CPER has a substantial database of population level-work.

The physiognomic as well as the trophic structure of shortgrass steppe ecosystems is dominated by <u>Bouteloua gracilis</u>. Much of our population work has focused on recruitment and mortality of

<u>Bouteloua</u> <u>gracilis</u> and the consequences for other plant populations. Our consumer work has included grasshoppers and birds; the USDA is responsible for the work with cattle.

Our current data collection activities include:

1. Monitoring population dynamics of grasshoppers at several locations on the Central Plains Experimental Range.

2. Analysis of population processes in <u>Bouteloua</u> <u>gracilis</u>. Our focus is on reproduction and mortality. This work is closely related to the small scale disturbance work under core topic 5.

Recent Products

Capinera, J. L. and D. C. Thompson. 1987. Dynamics and structure of grasshopper assemblages in shortgrass prairie. Can. Ent. 119(6):567-575.

Shaw, R. B., C. M. Bern and G. L. Winkler. 1987. Sex ratios of <u>Buchloe</u> <u>dactyloides</u> (Nutt.) Engelm. along catenas in the shortgrass steppe. Bot.Gaz. 148:85-89.

Thompson, D. C. 1987. Sampling rangeland grasshoppers. pp 219-233 IN J. L. Capinera (ed). Integrated pest management on rangeland: a shortgrass prairie perspective. Westview Press, Boulder, CO.

Our current and recent synthesis activities include:

1. Analysis of factors causing mortality in <u>Bouteloua</u> <u>gracilis</u> as a function of landscape position and grazing management. This work used data collected at the Central Plains Experimental Range and a spatially explicit simulation model.

2. Analysis of the return time for climatic and soil water requirements for the germination and establishment of <u>Bouteloua</u> <u>gracilis</u> at the Central Plains Experimental Range. This is a simulation analysis using a soil water model, a stochastic weather generator based upon 30 years of data at the Central Plains Experimental Range. The model will be parameterized and run for the range of different soils at the Central Plains Experimental Range.

3. Analysis and comparison of responses of shortgrass plant communities to grazing with other grassland communities worldwide. This work was largely theoretical relying on data from a variety of grasslands for examples.

4. Theoretical analysis of foraging strategies of large generalist herbivores.

5. Synthesis of grazing studies in grasslands worldwide. This work is in progress and utilizes published results from grazing studies as well as a ranking of the evolutionary histories of the study areas by a group of experts.

Recent Products

Coffin, D.P. and W.K. Lauenroth. 1988. The effects of disturbance size and frequency on a shortgrass plant community. Ecology 69:1609-1617.

Milchunas, D.G., O.E. Sala and W.K. Lauenroth. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. American Naturalist 132:87-106.

Senft, R.L., M.B. Coughenour, D.W. Bailey, L.R. Rittenhouse, O.E. Sala, and D.M. Swift. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37:789-799.

3. <u>Pattern and control of organic matter accumulation in surface layers and sediments;</u> and

4. <u>Pattern of inorganic inputs and movements of nutrients through soils, groundwater, and surface waters.</u>

In semiarid regions, the inputs and movements of nutrients are so closely tied to the inputs and fate of soil organic matter that they are best dealt with together. Our work on these topics has spanned spatial scales from single patches to the central grassland region. We have benefitted substantially from both historical and collaborative research on this topic.

Soil organic matter (SOM) has been the key focus of this work and our interests span the patch to central grassland region scales. At the patch, landscape, and site level we have concerned ourselves with processes controlling the formation and losses of SOM. These include interactions with mineral nutrient availability. Because of the large time scales associated with the formation and turnover of SOM, we have also investigated relationships among geologic, geomorphologic, and pedologic processes.

At the scales of the shortgrass steppe and central grassland region we have been mostly concerned with geographic patterns and soil and climatic correlates of SOM. Much of this work has utilized region-wide databases and simulation modeling.

Our current data collection activities include:

1. Sampling of soils along a 8-km transect on the Central Plains Experimental Range to estimate the range of

variability in soil properties as well as relationships with landscape position.

2. Monitoring of the movement of eolian material using equipment and techniques developed by the Agricultural Research Service. The equipment is located in conjunction with a study to measure downslope movement of material by water.

3. Landscape-scale ^{15}N experiment to investigate interactions among grazing, landscape position, soil organic carbon, and nitrogen.

Recent Products

Schimel, D., M.A. Stillwell, and R.G. Woodmansee. 1985. Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. Ecology 66:276-282.

Yonker, C. M., D. S. Schimel, E. Paroussis and R. D. Heil. 1988. Patterns of organic carbon accumulation in a semiarid shortgrass steppe, Colorado. Soil Sci. Soc. Amer. J. 52:478-483.

Our current and recent synthesis activities include:

1. Analysis of controls on soil organic matter in central grassland region of the United States. This work relies on a Soil Conservation Service database.

2. Production of a surface geology map for the Central Plains Experimental Range including interpretation based upon regional geologic histories.

3. Construction of a hierarchical spatial database of grasslands and agroecosystems for a box-transect that encompasses all of Colorado east of the Rockies, all of Kansas, and the southern half of Nebraska. The initial objective for the database is analysis of carbon and nitrogen dynamics and their responses to a variety of land-use and management scenarios using a simulation model (CENTURY). The long-term objective is to evaluate global change scenarios. Data types to be included in the database include: climate, soils, land-use, rangeland and cropland production, output from general circulation models, and TM and AVHRR imagery. ARC/INFO software will be used to manage and manipulate the data.

Recent Products

Burke, I.C, D.S. Schimel, C.M. Yonker, W.J. Parton, L.A. Joyce, and W.K. Lauenroth. 1989. Regional modeling of grassland biogeochemistry using GIS. Landscape Ecology 2:(in press).

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. J. 51:1173-1179.

5. <u>Patterns and frequency of disturbance to the research site.</u>

   Most of our disturbance work to date has focused on the range of spatial scales from individual plants to the research site. We plan to deal with larger scale land-use and vegetation type scales in the next two years.

   The disturbance work falls into two categories. A relatively large-scale category deals with the recovery of hectare size areas from a variety of disturbances ranging from long-term (50 years) heavy grazing to several years of application of water and mineral nitrogen fertilizer. The second category is small-scale disturbances dealing with areas of 0.1 to several square meters. This work has utilized gap-phase dynamics concepts to explain the response of shortgrass plant communities to disturbances. This work is closely related to the recruitment and mortality work with <u>Bouteloua gracilis</u>.

   Our current data collection activities include:

   1. Annual or biannual sampling of density and basal cover of plants on plots subjected to 50 years of heavy grazing, 50 years of protection from large herbivore grazing, and recovery from several years of application of mineral, nitrogen, and/or water.

   2. Annual or biannual sampling of density and basal cover on small (0.5-2m^2) artificially produced disturbances, and disturbances produced by western harvester ants, small mammals, and cattle fecal pats.

Recent Products

Coffin, D.P. and W.K. Lauenroth. 1989. Spatial and temporal variation in the seed bank of a semiarid grassland. Amer. J. Bot. 76:53-58.

Milchunas. D.G., W.K. Lauenroth, P.L. Chapman, and M.K. Kazempour. 1989. Plant communities in relation to grazing, topography, and precipitation in a semiarid grassland. Vegetatio (in press)

Milchunas, D.G. and W.K. Lauenroth. 1989. Three-dimensional distribution of plant biomass in relation to grazing and topography in the shortgrass steppe. Oikos 55:(in press)

Our current and recent synthesis activities include:

1. Construction and testing of an individual-based gap dynamics model (STEPPE) for shortgrass ecosystems. The objective for the model was to test current concepts of recovery following disturbances.

2. Analysis of alternate concepts of landscape interactions in recovery processes following disturbance in shortgrass ecosystems. Phase 1 of this is complete and reported in a paper in Landscape Ecology. Phase 2 will focus on verifying interactions between and among cells in the landscape.

3. Evaluation of nutrient cycling processes and their role in recovery following disturbances in shortgrass ecosystems. This work will be a simulation analysis utilizing an individual-based gap dynamics model of plant recovery (STEPPE) and a soil process model (CENTURY).

Recent Products

Coffin, D.P. and W.K. Lauenroth. 1989. Disturbances and gap dynamics in a semiarid grassland: A landscape level approach. Landscape Ecology 2:(in press).

Coffin, D.P. and W.K. Lauenroth. 1989. A gap dynamics simulation model of succession in a semiarid grassland. Ecological Modelling (in press)

Soil Water Dynamics

Inputs, storage, and losses of water from soils at the Central Plains Experimental Range and in semiarid regions in general, is of such importance that we chose to make this a separate topic in organizing and reporting our LTER work. We are dealing with the dynamics of water at the individual plant, patch, and catena spatial scales.

At the individual plant scale we are just beginning to collect data on the effects of a single individual of _Bouteloua gracilis_ on the availability of water to other plants. We have relatively long term (10-15 years) data at the patch scale and 3-5 years of data at the catena scale.

A new experiment, by USDA cooperators, was initiated in conjunction with our LTER project to provide information about run-off and run-on of water along catena segments of varying

length. This work is just beginning to provide new information.

Our current data collection activities include:

1. Regular monitoring of soil water at several depths on three catenas and within three exclosures. Each of the catenas has approximately 8 sample points beginning at a ridgetop and ending in a swale. The exclosures have 1 to several sample points. Two of the exclosures have been monitored since 1970. Sampling is approximately biweekly during the growing season and monthly for the remainder of the year.

2. Monitoring of a 3-m diameter lysimeter for soil water content and water loss. The lysimeter was constructed in 1970. Monitoring was discontinuous during the 1970's because of the state of recorder technology. Monitoring has been almost continuous during the 1980's.

Recent Products

Hazlett, D.L., Y.M. Liang, and W.K. Lauenroth. Effects of soil texture and vegetation on the dynamics of soil water in five steppe communities. Amer. Midl. Nat. (in review)

Our current and recent synthesis activities include:

1. Simulation of soil water dynamics using the past 30 years of weather data from the Central Plains Experimental Range. This work is now in the writing stage. All of the simulations and data analyses are complete.

2. Analysis of the spatial pattern and temporal frequency of soil water conditions appropriate for the germination and establishment of <u>Bouteloua gracilis</u> in the shortgrass steppe. This will utilize a simulation model and a spatial database of soils and climatic conditions for the shortgrass steppe region.

Intersite (LTER) Syntheses

Many of our LTER activities have ignored the boundaries of the Central Plains Experimental Range. Much of this work gains its significance from applications to areas larger than our specific LTER site. In addition to this work which is a logical extension of our site specific research, project personnel have been involved in a number of efforts with the specific objective of comparative analysis of one or more LTER sites. Some of these efforts have been supported by the LTER grant, some by the Coordinating Committee grant, and others by separate grants from NSF and other agencies. These activities include:

1. Box-transect database which includes both the Central Plains Experimental Range and the Konza sites. This is also discussed under core topics 3 and 4. Support is from supplements to the Central Plains LTER grant.

2. Regional ecological response to climatic variability. The objective of this work is to evaluate the effect of continental and global-scale climatic variability on interseasonal and interannual ecological variability across North America. Regions containing LTER sites are emphasized in the analyses. This work is supported by the Coordinating Committee and the Central Plains LTER grant.

3. Comparison of eolian processes in deserts and semiarid regions. This is a comparison of processes at the Jornada site with the Central Plains Experimental Range. This work is being supported by the LTER grants at each site.

4. Exotic plants at LTER sites. This work entails a comparison of the exotic components of the flora at each of the LTER sites. The objective is detection of differences in invasiveness of a variety of ecosystem types. This work is being supported by the Central Plains LTER grant.

5. Modeling plant community structure across gradients. This is a cooperative project with H.H. Shugart at the University of Virginia. The objectives are: (1) to evaluate the controls on the dynamics of vegetation structure in the transition zone between forests and grasslands in North America and (2) to compare the responses of vegetation to climatic change at LTER sites. This research is being supported by a NSF grant as well as by the Central Plains LTER grant.

6. Surface biophysical properties and trace gas exchange in tallgrass prairie. This work builds on NSF-funded research at the Konza site, and uses a simulation model built with that funding. The current objectives are to develop a spatial simulation model of surface biophysical processes, generate dynamic maps, and compare them to GOES and AVHRR satellite data. This research is funded by NASA.

Root turnover and production by ^{14}C dilution: implications of carbon partitioning in plants

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Summary   Estimates of belowground net primary production (BNP) obtained by using traditional soil core harvest data are subject to a variety of potentially serious errors. In a controlled growth chamber experiment, we examined the aboveground-belowground, labile to structural tissue, and plant to soil dynamics of carbon to formulate a ^{14}C dilution technique for potential successful application in the field and to quantify sources of error in production estimates.

Despite the fact that the majority of net ^{14}C movement between above- and belowground plant parts occurred between the initial labeling and day 5, significant quantities of ^{14}C were incorporated into cell-wall tissue throughout the growing period. The rate of this increase at late sampling dates was greater for roots than for shoots. Total loss of assimilated ^{14}C was 47% in wheat and 28% in blue grama. Exudation and sloughing in wheat and blue grama, respectively, was 15 and 6% of total uptake and 22 and 8% of total plant production.

When root production estimates by ^{14}C dilution were corrected for the quantities of labile ^{14}C incorporated into structural carbon between two sampling dates, good agreement with actual production was found. The error associated with these estimates was ± 2% compared with a range of −119 to −57% for the uncorrected estimates. Our results suggest that this technique has potential field application if sampling is performed the year after labelling.

Sources of errors in harvest versus ^{14}C dilution estimates of BNP are discussed.

Introduction

Belowground net primary production (BNP) is the major source of organic matter input for a wide variety of biome types[3]. This is especially apparent in semiarid grasslands of the Great Plains of North America. The contribution of BNP to net primary production (NPP) has been estimated to be 80% in the northern mixed-grass prairie[14] and 85% in the shortgrass steppe[9]. Despite the importance of BNP to energy flow and nutrient cycling in ecological systems, current methods of estimating BNP from harvest data are subject to several serious errors[10].

Two types of errors are inherent in all estimates of BNP by the harvest technique. The first concerns maxima and minima in root biomass. Missing the true max-min values tends to underestimate

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BNP. Increasing sampling frequency in an attempt to better define maxima and minima may result in an overestimation of BNP because of the artificial maxima and minima that can be generated by random-sampling with variance[10]. Furthermore, different computational schemes yield different estimates of BNP from the same set of data[9,10]. The second type of error concerns unaccounted for losses as a result of root exudation, sloughing, and belowground grazing.

A technique that measures root turnover and production based on the dilution of $^{14}C:^{12}C$ ratios in the structural carbon of root systems after pulse labeling has been purported to avoid many of the problems associated with traditional methods of measuring BNP[2]. The technique is based on the reduction of the ratio of $^{14}C:^{12}C$ in the structural carbon of the root system of pulse-labeled plants, as the plants grow and assimilate only ^{12}C. The turnover coefficient is expressed as

$$TC = (R_1C_1/R_2C_2) - 1,$$

where R_1 and R_2 are the ratios of $^{14}C:^{12}C$ in structural tissue at times 1 and 2, and C_1 and C_2 are the percent structural tissue at times 1 and 2. The turnover coefficient is based on structural tissue only, thereby eliminating complications posed by fluxes of labile material between shoots and roots. BNP is determined by multiplying TC by the total biomass (structural plus labile) at time 1.

Our initial attempt to use this technique in the field resulted in negative turnover coefficients. That the technique did not work, although it appeared conceptually promising, prompted us to examine an assumption associated with this technique. Caldwell and Camp[2] stated that the turnover coefficient would be underestimated if new ^{14}C were incorporated into cell wall materials of the root system between the time of the first and end-of-season samplings. They referred to a related study and data from a pot experiment to conclude that the underestimation would be small if sampling occurred 5 days after labeling.

Our objectives were to (1) test Caldwell and Camp's[2] assumption by examining labile to structural tissue, above- to belowground dynamics of ^{14}C in pulse-labeled plants and compare estimates of root production obtained by ^{14}C dilution with those obtained by complete harvest of potted plants; (2) assess exudation losses; and (3) compare sources of error in harvest versus ^{14}C dilution methods of estimating BNP.

Methods

Blue grama [*Bouteloua gracilis* (H.B.K.) Lag.] and spring wheat (*Triticum aestivum* L.) were grown in a growth chamber from seed in sifted, thoroughly mixed, native Ascalon soil.

The ascalon series are fine-loamy, mixed, mesic aridic argiustolls. The growth chamber was maintained at 30°C day and 15°C night temperatures with a 14-hour photoperiod. Wheat plants were 45 days old, and blue grama plants were 95 days old when they were exposed to $^{14}CO_2$. The wheat plants senesced 62 days after exposure.

Ten blue grama plants were composited for each of three replicates for each of the sample dates 0, 5, 8, and 11 days after labeling; and nine plants were composited for each replicate for each of days 25 and 40. Each of the three wheat replicates for each of days 0, 5, 8, and 11 was a composite of eight plants and for days 25, 40 and 62 was a composite of five plants. Values were equalized to the number of composites on day 0. Three pots of bare soil were removed on each harvest date and used to correct for the influence of atmospheric input of ^{14}C to soil.

Wheat plants were placed inside a 0.6 m³ clear-plastic tent equipped with a fan to circulate air. The CO_2 level inside the tent was allowed to decline from 700 ppm to 150 ppm (1 hour), at which time 9.2×10^6 Bq (249 μCi) of $^{14}CO_2$ was released. The objective was to supply approximately 14.8×10^4 Bq.g^{-1} (4 μCi.g^{-1}) aboveground plant tissue. After the CO_2 level again declined to 150 ppm, the plants were flushed with $^{12}CO_2$ and the drawdown repeated. The plants were removed and time 0 plants randomly selected for harvest. Total time of labeling was 2.5 hours, and harvesting required another 1 hour. Labeling of blue grama plants was similar except that more $^{14}CO_2$ was released.

Harvested plants were separated into above- and belowground portions and dried at 55°C. The soil was dried and sifted through 2, 1.1, and 0.02 mm sieves and refrigerated. The fine roots and other organic matter were removed from the soil in each sieve by vacuuming with a fine-mesh cloth over the nozzle. Roots were then separated from other organic matter. Plant samples were ground for chemical analysis.

Cell wall constituents (CWC) of roots and shoots were isolated by the neutral-detergent fiber (NDF) procedure[12,13]. Whole-plant and cell-wall fractions were combusted in a Packard Model 306 tri-carb sample oxidizer, using Carbosorb as a trap and a Permaflour cocktail. ^{14}C activity was determined by liquid scintillation counting. The ash content of root cell walls was determined by the ash content of whole roots times a coefficient of ash solubility in the NDF procedure because of difficulties in obtaining a homogeneous, small subsample from the NDF residue (i.e., fluffy cell wall and coarse ash residue). Correcting for ash content in this manner reduced the variability of the CWC data. The activitites of the inorganic and organic fractions of the soil carbon pool were assayed using the wet oxidation procedure of Snyder and Trofymow[11] with carbon traps modified (phenethylamine rather than NaOH) for compatibility with a scintillation cocktail containing 630 ml toluene, 370 ml methanol, 5 g PPO, and 0.1 g POPOP.

The data were subjected to analysis of variance. Significant differences ($P < 0.05$) between means were determined by Tukey's HSD procedure[15].

Results

The blue grama and wheat plants were grown from seed under optimal conditions in a growth chamber. Phenology and growth, therefore, may be different from what would occur in the field. The wheat plants developed from seedlings to senescent plants with fully developed inflorescences in 107 days. Labeling (day 0) occurred at what may be considered 40% into the growing season; heading occurred between the day 40 and day 62 sample dates. The perennial blue grama grows indeterminately under optimal conditions and develops inflorescences but does not senesce. In terms of growth characteristics, the aboveground portion of blue grama plants was greater than that
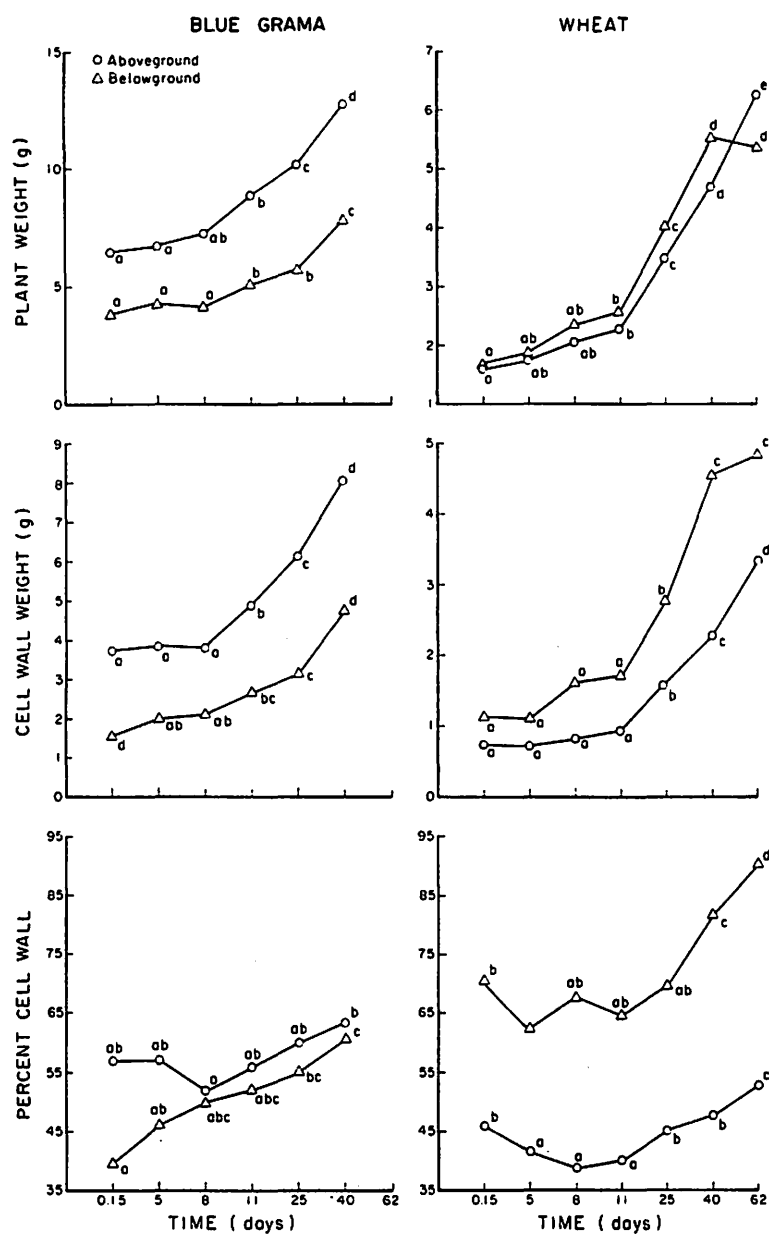
Fig. 1. Growth characteristics of above- and belowground components of blue grama and wheat plants from 3.5 hours after start of labeling with $^{14}CO_2$ to the time of fully developed inflorescence. Points in time not sharing *a common letter* are significantly different ($P \leq 0.05$). Values represent standing live and dead plus shed parts. *N.B. Scale x-axis not proportional.*

of the belowground portion (Fig. 1). In the field, 85% of the biomass occurs belowground[9].

Wheat grew at a faster rate and had higher belowground-to-above-ground ratios than blue grama (Fig. 1). Cell wall constituents (CWC) of blue grama shoots were greater than that of wheat shoots, whereas wheat roots had a higher CWC than blue grama roots. Very little information concerning the cell wall content of roots is available in the literature. Dormaar et al.[4] reported seasonal values for root structural tissue (lignin + pentosans + hexosans) of blue grama ranging from 60% in the spring to 68% in the fall. This is comparable to the 61% CWC of blue grama roots at the end of this experiment. In contrast, wheat roots were 82% CWC.

The majority of net ^{14}C movement between above- and belowground plant parts occurred between the initial labeling and day 5 (Fig. 2). Differences in the quantity of ^{14}C in aboveground to belowground plant parts were observed, however, after day 5; and this was significant in blue grama. Carbon-14 appeared to move from above- to below-ground organs in blue grama and from below- to above-ground organs in wheat at the end of the experiment. This probably represents translocation to perennial belowground organs in blue grama and development of the inflorescence in wheat.

Contrary to aboveground-belowground fluxes, significant quantities of ^{14}C were incorporated into cell-wall tissue throughout the growth period (Fig. 2). The rate of this increase at late sampling dates was greater for roots than for shoots. The ^{14}C in cell-wall tissue as a percentage of the above- or belowground total increased as a function of the incorporation of ^{14}C into cell walls and the fluxes of labile ^{14}C between roots and shoots.

The largest losses of ^{14}C from the plants occurred within 5 days of labeling (Fig. 2). Only small losses were measured through the remainder of the growth period. Aboveground dead tissue was harvseted as it senesced; therefore, losses represent exudation, sloughing, and respiration.

The ^{14}C balance of the plant-soil system and the plant (Fig. 3) were calculated according to the following equations. Each quantity is represented with a subscript that indicates the time in days of the measurement.

$$\text{Total loss}_{62} = \text{total uptake}_{0.15} - \text{plant activity}_{62}$$
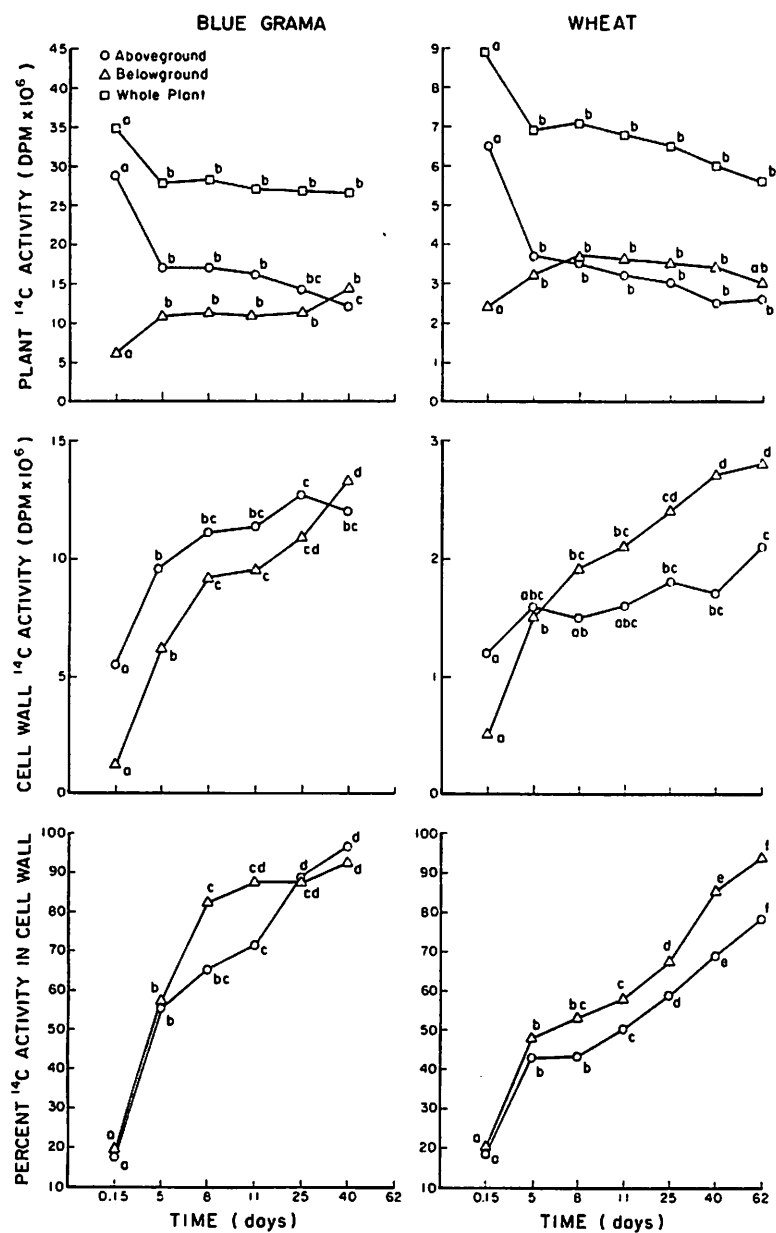$$- \sum_{t=0.15}^{62} (\text{leaf death}_t),$$

where

Fig. 2. Distribution of ^{14}C through time in the aboveground, belowground, and cell-wall components of pulse-labeled blue grama and wheat plants. Points in time not sharing *a common letter* are significantly different ($P \leqq 0.05$). Values represent standing live and dead plus shed parts. *N.B. Scale x-axis not proportional.*

$$\text{Total uptake}_{0.15} = \text{plant activity}_{0.15} + \text{soil activity}_{0.15}$$
$$- \text{soil blank}_{0.15}$$

Total losses were partitioned into exudation plus sloughing and respiration:

$$\text{Exudation} + \text{sloughing} = \max_{t=0.15}^{62} (\text{soil activity}_t - \text{soil blank}_t)$$

$$\text{Respiration} = \text{total loss} - (\text{exudation} + \text{sloughing})$$

Exudation plus sloughing is discussed as a percent of (1) total uptake, (2) total plant production – *i.e.*, total uptake-respiration, and (3) final plant activity – *i.e.*, total uptake–(exudation + respiration).

For wheat, peak soil activity was observed at the first sampling, only 3.5 hours after the start of labeling (Table 1). The activity of the wheat soil declined 55% between the initial sampling and day 5 and declined very slowly thereafter. A peak in soil activity for blue grama was less clear. No distinct relationship was apparent between root labile ^{14}C and the activity of the soil (Table 1). The labile ^{14}C content of roots is a function of fluxes of soluble ^{14}C between roots and shoots and the incorporation of ^{14}C into structural tissue, as well as losses by exudation. For both wheat and blue grama approximately 90% of the total soil activity was associated with the rhizosphere. Inorganic ^{14}C in the soil was always less than 1% of the total. Dry deposition and/or fixation of ^{14}C to soil blanks ranged from 14 to 16% of the activity of the soil with plants.

Total loss of ^{14}C from the plants was 47% in wheat and 28% in blue grama and total loss as a percent of plant production was 68% in wheat and 36% in blue grama. Possible explanations for the large difference between the species are that blue grama may conserve photoassimilate more than wheat; and age differences can have a large influence on respiration/assimilation values[8].

Exudation and sloughing in wheat and blue grama, respectively, accounted for 15 and 6% of total uptake, 22 and 8% of total plant production, and 29 and 9% of the final plant activity. Exudation and sloughing was 33 and 22% of the total losses, and respiration was 31 and 22% of total uptake, in wheat and blue grama, respectively.

The time scale of ^{14}C partitioning in both wheat and blue grama influenced estimates of BNP by ^{14}C dilution. The incorporation of labile ^{14}C into root structural carbon during latter periods of growth had large negative effects on estimates of BNP by ^{14}C dilution compared with complete harvest (Table 2). Errors associated with the ^{14}C

Table 1. Time course of soil organic ^{14}C and root labile ^{14}C in pulse-labeled wheat and blue grama. Soil values were corrected for deposition of ^{14}C to bare soil. Values not sharing a common superscript within a row are significantly different ($P \le 0.05$)

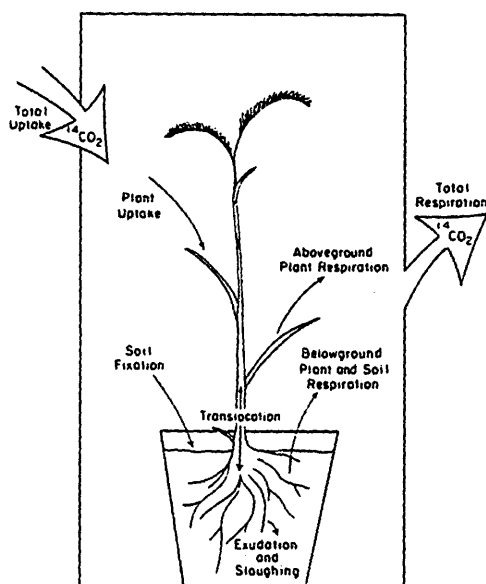| Compartment	Time (days)						
	0.15	5	8	11	25	40	62
Wheat							
Soil organic ^{14}C (DPM × 10^6)	1.6^a	0.7^b	0.7^b	0.6^b	0.7^b	0.6^b	0.4^b
Root labile ^{14}C (DPM × 10^6)	1.9^a	1.7^{ab}	1.7^{ab}	1.5^b	1.1^c	0.7^d	0.2^d
Blue grama							
Soil organic ^{14}C (DPM × 10^6)	2.2^a	2.3^a	1.6^b	1.9^{ab}	1.7^b	1.7^b	
Root labile ^{14}C (DPM × 10^6)	4.9^a	4.6^{ab}	2.0^c	1.4^c	1.6^c	1.1^c	

Fig. 3. The ^{14}C balance of the plant-soil system.

dilution method, when positive increments in biomass were observed, ranged from -119 to -64% for blue grama and from -70 to -57% for wheat. The errors increased as the time period between R_1 and R_2 increased.

When root production estimates by ^{14}C dilution were corrected for the quantities of labile ^{14}C incorporated into structural carbon between R_1 and R_2, good agreement with actual production was found (Table 2). The errors associated with these estimates ranged from -2 to 1% for blue grama and $\pm$ 2% for wheat during periods of positive

Table 2. Comparison of increments in the belowground biomass of blue grama and wheat as determined by complete harvest and $^{14}C/^{12}C$ diution techniques. Values are expressed on an ash-free dry-weight basis

Cell-wall carbon					Belowground production*				
Time	^{12}C (g)	^{14}C (g × 10^{-4})†	R (× 10^{-4})§	R$_C$ (× 10^{-4})¶	Harvest	$(R_1C_1/R_2C_2-1)B_1$ ψ	Error (%)δ	$(R_1C_1/R_CC_2-1)B_1$ ψ	Error (%)δ
Blue grama									
0.15	0.70	4.37	6.23						
5	0.90	22.56	25.07	10.58	3.52	-0.65	-118	3.48	-1
8	0.95	33.48	35.26	15.70	3.64	1.22	-66	3.56	-2
11	1.19	34.57	28.99	16.21	2.70	0.53	-80	2.73	1
25	1.40	39.67	28.25	18.60	2.15	0.78	-64	2.14	0
40	2.13	48.04	22.52						
Wheat									
0.15	0.53	1.82	3.46						
5	0.52	5.46	10.46	2.52	3.45	1.02	-70	3.53	2
8	0.72	6.91	9.60	3.19	2.96	1.25	-58	2.97	0
11	0.77	7.64	9.99	3.52	2.73	1.35	-50	2.68	-2
25	1.26	8.73	6.95	4.02	1.31	0.51	-56	1.33	2
40	2.02	9.83	4.87	4.53	-0.20	-0.35	75	-0.15	-25
62	2.17	10.19	4.70						

* Increment is grams of total root (structural plus labile) between that sampling time and the last sampling time.

† ^{14}C = (DPM sample) (60 s/min) [Ci/(3.7 × 10^{10} DPS)] (0.22442 g/Ci).

§ R = $^{14}C/^{12}C$; R$_1$ = $^{14}C/^{12}C$ for that sampling time; and R$_2$ = $^{14}C/^{12}C$ for the last sampling time.

¶ R$_C$ = R$_2$ corrected for the amount of ^{14}C incorporated into structural material between that sampling time and the last sampling time.

ψ C = % cell wall at time 1 or 2; B$_1$ = biomass (structural plus labile) at time 1.

δ (Dilution − harvest)/harvest × 100.

increments in actual biomass. There was no relationship between the errors and the length of time between R_1 and R_2.

Discussion

Caldwell and Camp[2] assumed that the error to BNP estimates resulting from incorporation of labile ^{14}C into structural carbon during the growing season would be small. Our results indicate that this assumption did not hold for wheat or blue grama and resulted in large errors in the estimate of BNP. Caldwell and Camp[2] also reported that the proportions of total ^{14}C in roots to total ^{14}C in shoots were similar throughout the growing season. Our results did not support that finding. The ratios for the last two sample dates were 0.9 and 1.2 for blue grama and 1.4 and 1.1 for wheat. Our results indicate that estimates of BNP based on total ^{14}C will be biased by fluxes of ^{14}C between shoots and roots, as well as by seasonal differences in the amount of labile ^{12}C in roots.

Identification of these errors led to a refinement of the technique that appears to have promise for field estimates of BNP. Once the errors associated with the incorporation of ^{14}C in structural root carbon during the growing season were corrected, the estimates of BNP were very good (Table 2). This suggests that the technique may be used successfully if labelling occurred early in one growing season and R_1C_1 and R_2C_2 calculations were made from samples obtained at the beginning and end of the following growing season. Although there will be a period of two growing seasons between the initial labeling and the final sampling, errors should result only from the decomposition of roots in the period between R_1 and R_2. The error will be negative if $R_t:R_d < 1$, positive if $R_t:R_d > 1$, and there will be no effect of decomposition on the estimate of BNP if $R_t:R_d = 1$ (where R_t is $^{14}C:^{12}C$ during the R_1 to R_2 period and R_d is decomposition of $^{14}C:^{12}C$ during the same period). Similar arguments can be used to explain the effect of losses due to herbivory. In contrast, the effect of losses due to decomposition or herbivory on estimates of BNP by harvest methods will always be negative and will be equal to the amount of decomposition or herbivory that occurred in the period between the maximum and minimum of biomass. Growth after the maximum and differences in species maxima will both cause an underestimation of BNP by harvest methods, whereas neither will affect the estimate by ^{14}C dilution.

Large underestimations of BNP due to exudation and sloughing were observed for both blue grama and wheat, and there were large differences between species. Our estimates of exudation and sloughing

Table 3. Summary of errors affecting the harvest and the ^{14}C dilution techniques of estimating BNP

Error factor	Technique			
	Harvest, peak-trough		[14]C dilution	
	Amount*	Direction	Amount*	Direction
Missing time peaks-troughs	All	Negative	None	—
Inflated peaks-troughs due to variance[†]	All	Positive	None	—
Individual species peaks	All	Negative	None	—
Growth after peak	All	Negative	None	—
Exudation, sloughing	All	Negative	Partial[§]	Negative[§]
Decomposition	All	Negative	All to none[¶]	Positive, negative, or none[¶]
Herbivory	All	Negative	All to none[¶]	Positive, negative, or none[¶]
Presence of annuals	None	—	Partial[ψ]	Positive

* The proportion of the amount of the error incorporated in the estimate of BNP.

[†] See Singh et al.[10]

[§] Partial and negative due to microbial respiration losses and exudation after the peak in soil ^{14}C but may overestimate the contribution of exudation and sloughing because of possible contamination of soil samples with root hairs. See text.

[¶] See text.

[ψ] Dependent on decomposition rate of previous year's labeled roots of annual plants, all of which are dead and decomposing the following year. See text.

were influenced by three factors. First, the peak in exudation may have occurred between the start of labeling and the first sampling at 3.5 hours. Minchin and McNaughton[7] observed peaks in the activity of wheat root bathing solutions approximately 80 minutes after labeling, whereas McDougall[6] observed a 2-hour interval between exposure of wheat and activity in the apices of roots. Microbial respiration of labeled exudates during the initial 3.5 hours of our experiment, as well as exudation occurred after the initial peak in soil activity, were not accounted for. Second, exudation may have been overestimated by root hairs in the soil samples. This would not, however, affect estimates of BNP corrected by this estimate of exudation. Third, ^{14}C in the soil and microbes that were firmly attached to roots would have been partitioned to root activity. While this would affect values of the partioning of carbon, it would not affect estimates of BNP that were corrected for exudation. Our estimates of a 15% loss due to exudation (as a percent of total uptake) in wheat compares with reported values for wheat of 14–25%[5] and 12–18%[1], suggesting that microbial respiratory losses of ^{14}C from the soil during the short interval between the 3.5-hour harvest and the peak in exudation were not large.

A summary of errors affecting both the harvest and the ^{14}C dilution technique is presented in Table 3. Seven of eight error factors affect estimates of BNP by the harvest method. All of the error for each of the factors is incorporated into estimates of BNP by the harvest method, and all except one tend to result in an underestimation. In contrast, only four of the error factors affect estimates of BNP by ^{14}C dilution and the amount and the direction of the error varies. Limitations to the use of the ^{14}C dilution technique may occur in plant communities with a large composition of annuals, and in forests where an unmanageably large amount of ^{14}C may be necessary to adequately label roots.

The partioning of carbon by plants reported herein is based on a single time of labeling. Labeling at different phenological stages may have resulted in different patterns of carbon partitioning. Although our results suggest that the ^{14}C dilution technique has promise for field estimates of BNP, the technique has not been tested in the field. The error associated with differential decomposition of roots with ^{14}C versus roots with only ^{12}C is of primary concern. We are currently in the process of evaluating the technique in the field.

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Biomass dynamics and water use efficiencies of five plant communities in the shortgrass steppe

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Summary. Standing crop biomass and water-use efficiency were estimated for five plant communities of the Central Plains Experimental Range in north central Colorado. Aboveground biomass by functional groups, surface litter amounts, and standing dead biomass were compared, as were vertical and size-class distributions of belowground biomass. Greater production and water-use efficiency values were found: (1) at coarse-textured sites, indicating the importance of the inverse texture effect, and (2) wherever site characteristics favored the establishment of life-forms other than grasses, e.g., succulents and shrubs. Seasonal aboveground biomass and water-use efficiencies for the grass component were similar among sites, even though the mixes of C_3 and C_4 grass species were different. Similar grass biomass values in very different communities suggested that high biomass and high water-use efficiencies were related less to grasstypes than to the abundance of non-grass life-forms.

Key words: Biomass – Colorado – Steppe – Water-use efficiency

The ratio of net primary production (NPP) to evapotranspiration is an expression of water-use efficiency (WUE) (Webb et al. 1978; Fisher and Turner 1978; Le Houerou 1984). Since water availability is limited in arid and semiarid regions, plant species native to these areas have evolved means of increasing water-use efficiencies (Sinclair et al. 1984). For example, plant species with high photosynthetic capacities, C_4 species, can have a WUE twice as high as C_3 species (Hsiao and Acevedo 1974) and the WUE of species with a crassulacean acid metabolism (CAM) can be 4–5 times that of C_3 or C_4 species (Kluge and Ting 1978). These large differences, however, are found only at certain times of the year. Another means by which species can increase their WUE is to limit gas exchange to a time of day or year when the air saturation deficit is low, thereby minimizing water loss per unit of carbon gain. Semiarid plant species that fit this category of water-use either grow in the spring, when temperatures and air saturation deficits are low (cool-season plants), or open stomata diurnally to

coincide with times of low air saturation deficits (Schulze et al. 1973).

The influence of WUE adaptations on annual production at the plant community level is uncertain. Species characteristics may affect the evaporation flux of the community by influencing characteristics such as the thickness of the surface litter layer, soil structure, and the degree of shading or wind protection. Dominant plant species in different grassland communities can influence community structure and can differ in water-use efficiencies, but it is uncertain to what extent different community dominants alter water-use efficiencies at the plant community level.

The object of this study was to compare the biomass and water-use efficiencies of five different kinds of plant communities that have the same macroclimate. Plant communities were selected on the basis of dominance by species of different life-forms or by species with peak vegetative growth at different times during the growing season. Fisher and Turner (1978) suggested that, other things being equal, WUE on a dry-matter basis was not greatly affected by life-form differences and was presumably even more stable within a life-form. They defined "other things being equal" as corrections among communities for differences in carbon dioxide fixation pathways, root/shoot allocations and/or transpiration rates. They indicated that WUE differences among plant communities could be attributed to these three main factors. However, if it were possible to make water-use corrections that are a direct result of dominance by a certain species or life-form, one should also be able to quantify dry matter production and WUE differences due to species or life-form. With these considerations in mind, the research question for this study was: Do steppe plant communities that are dominated by different life-forms, or by grasses with different times of peak vegetative growth, have similar biomass and similar water-use efficiencies?

Site description

The research was conducted at the Central Plains Experimental Range (CPER), a shortgrass steppe site administered by the USDA Agricultural Research Service. The CPER is located in north central Colorado, USA (40°49' N, 104°46' W) at 1,650 m elevation. Most plant communities at the CPER are dominated by *Bouteloua gracilis* (H.B.K.) Lag., but variations in topography and soil characteristics
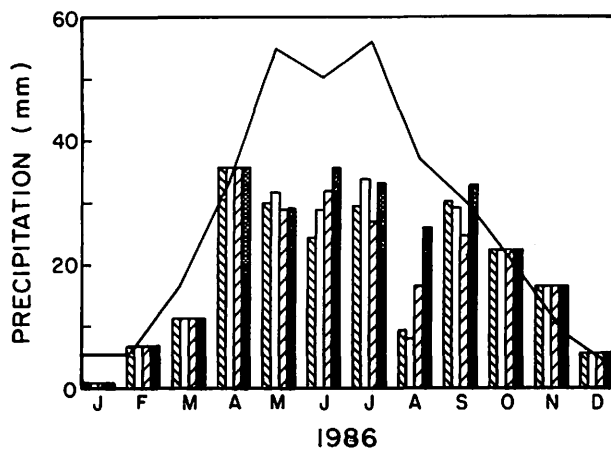
Fig. 1. Mean monthly precipitation at the Central Plains Experimental Range from 1969–1986 (line) and at the five study sites (bars). From left to right the bar graphs at each month are for: (1) sandy-loam/shrub, (2) loam/shrub and sandy-loam/pasture, (3) clay-loam/grass and (4) sandy-clay loam/half-shrub sites

Table 1. Sand, clay, organic matter and nitrogen content for five shortgrass plant communities at the Central Plains Experimental Range

	Site				
	Sandy-loam shrub	Loam shrub shrub	Clay-loam grass	Sandy-clay half-shrub	Sandy-loam pasture
Soil texture					
Sand (%)					
0– 30 cm	81	26	42	54	73
30–100 cm	76	39	27	58	68
Clay (%)					
0– 30 cm	9	27	37	24	17
30–100 cm	13	21	54	20	20
Organic matter (%)					
0– 30 cm	1.8	6.2	4.1	3.1	2.1
30–100 cm	1.8 cm	3.2	4.0	2.0	1.9
Nitrogen (%)					
0–30 cm	0.061	0.231	0.106	0.103	0.075

produce communities dominated by other species. All sites in this study were on level terrain. Mean annual precipitation at the CPER over the past 45 years was 311 mm (SD = 85 mm). Precipitation during 1986, the year the study was conducted, was 258 mm (Fig. 1). Precipitation from April to the end of July was 139 mm, 30% below the 45-year mean for this interval of 197 mm (SD = 25 mm). Approximately 70% of annual precipitation occurs from April to September, the main growing season. Mean monthly temperatures from April to September are typically in the range of 16°–31° C (maximum values) and 0°–14° C (minimum values).

The soils of the five study sites were different in terms of soil texture, organic matter and nitrogen (Table 1). Each site is labeled by a descriptive name that includes soil texture and dominant life-form. Site 1, a sandy-loam/shrub

site, is located on a lightly grazed stream terrace and is dominated by *B. gracilis*, a warm-season grass, and *Atriplex canescens* (Pursh) Nutt. shrubs. Site 2, a loam/shrub site, is located in a floodplain area protected from grazing for 17 years, is dominated by *A. canescens* and has *Agropyron smithii* Rydb. as the most common grass. The soil and vegetation characteristics of the loam/shrub site are uncommon at the CPER, but served as a sharp contrast to other sites. Site 3, a clay-loam/grass site, is located at the toeslope position of a north facing catena and is dominated by the warm-season grass *Buchloe dactyloides* (Nutt.) Engelm., but the cool-season *Carex filifolia* Nutt. and *Festuca octoflora* Walt. also occur frequently. Site 4, a sandy-clay loam/half-shrub site, is located within an exclosure protected from grazing for 17 years, is dominated by *B. gracilis*, but low-shrubs such as *Artemisia frigida* Willd. and *Eriogonum effusum* Nutt. also occur frequently. Site 5, a sandy-loam/pasture site, is a pasture plant community planted to the introduced cool-season grass *A. cristatum* (L.) Gaertn and subjected to light grazing for 20 years. Sites were either ungrazed or had wire exclosures to prevent grazing at sample points.

Materials and methods

Plant productivity and evapotranspiration must be known to calculate water-use efficiencies. Aboveground net primary production of herbs was estimated from harvest data (Singh et al. 1975) using the maximum standing crop of current year's biomass. Lauenroth et al. (1986) found this technique of estimation of aboveground net primary production to be one of the best of the eight methods evaluated. For all but the clay-loam/grass site, aboveground biomass was determined at four times of the growing season by clipping ten randomly placed 0.25 m² quadrats on 14 May, 14 June, 17 July, and 14 August 1986. Since the clay-loam/grass side had a more uniform grass cover than the other sites, biomass was estimated at this site from five randomly selected quadrats, on 14 June and 14 August. All quadrats were clipped to ground level and plant material was sorted into standing dead or current year's standing crop of warm-season grasses, cool-season grasses, forbs, succulents, and shrubs. Plant material was oven-dried at 70° C for 48 h and weighed. Ten 0.25 m² litter samples per site, collected only in May, were ashed at 550° C to separate soil from organic matter. At the two shrub sites, ten *A. canescens* branches on ten randomly selected shrubs were tagged in October 1985, and were examined in September 1986 to ascertain the portion of each shrub that was current-year's leaf and branch production. In September, the 1986 branch production of the ten banded shrubs at each site was harvested, oven dried at 70° C for 48 h, weighed, and converted to g/m² based on an estimate of the number of individual *A. canescens* shrubs at each site.

Belowground biomass was estimated by sampling ten randomly selected locations at each site. Each location was sampled to a 90-cm depth using a 5-cm diameter core. The soil was separated into 15-cm segments (6 segments per core) and washed over a 16 mesh screen to separate the roots. Roots were separated into sizes of less than or greater than 2 mm in diameter, oven dried at 70° C for 48 h, and weighed.

Actual evapotranspiration was estimated for each site by the water balance method (Rosenberg 1974). This meth-

Table 2. Total above- and belowground standing crop (g/m²) for five live and recent dead and old dead plant communities at the Central Plains Experimental Range. Aboveground biomass was sampled on 14 August and belowground biomass on 10 September

	Site				
	Sandy-loam shrub	Loam shrub	Clay-loam grass	Sandy-clay half-shrub	Sandy-loam pasture
Aboveground					
Warm-season grass	140	66	49	101	13
Cool-season grass	10	78	23	5	118
Forbs	1	9	1	4	1
Shrubs	173	1209	0	28	9
Succulents	54	0	5	14	0
Total	370	1076	77	150	142
Belowground					
0–30 cm	1362a	1948aa	1498a	1469a	1054a
30–100 cm	492a	1557aa	397a	677	305a
Roots <2 mm	1828a	3484aa	1895a	1669a	1359a
Roots >2 mm	26	21	0	477	0
Total	1854a	3505aa	1895a	2146	1359a
Aboveground: belowground ratio	0.20	0.31	0.04	0.07	0.10

BELOWGROUND BIOMASS (g/m²)

Fig. 2. Fine-root biomass (g/m²) in different soil layers on September 10 for five plant community types at the Central Plains Experimental Range

od estimates evapotranspiration by summing the precipitation input and the net change in soil water status from time 1 to time 2. Precipitation was measured at each site and soil water loss was estimated by gravimetric soil water content for the 0–30 cm depths, and by using a neutron soil moisture gauge for the 30–150 cm depths (Hazlett et al. 1988). During 1986, gravimetric and neutron gauge measurements were taken at 3-week intervals from 4 March to 15 April (3 measurements), at 2-week intervals from 8 May to 28 August (9 measurements), and on 16 September and 17 October.

Results

Among the five study sites the amount of total aboveground and belowground biomass increased in proportion to the abundance of woody perennials. The two sites with no or very few woody plants (clay-loam/grass and sandy-loam/pasture sites), had the lowest values for total aboveground and belowground biomass (Table 2). Total aboveground biomass values at the shrub sites were 2–4 times greater than at nonshrub sites. A substantial part of total aboveground biomass at the shrub sites was dead plant material (60%), while as little as 17% was dead material at the nonshrub sites. The sandy-clay loam/half-shrub site was intermediate to these sites in terms of aboveground biomass and in abundance of woody perennials. Belowground biomass values were also greater at shrub than at nonshrub sites (Table 2), but the range in values among sites was much less for belowground biomass.

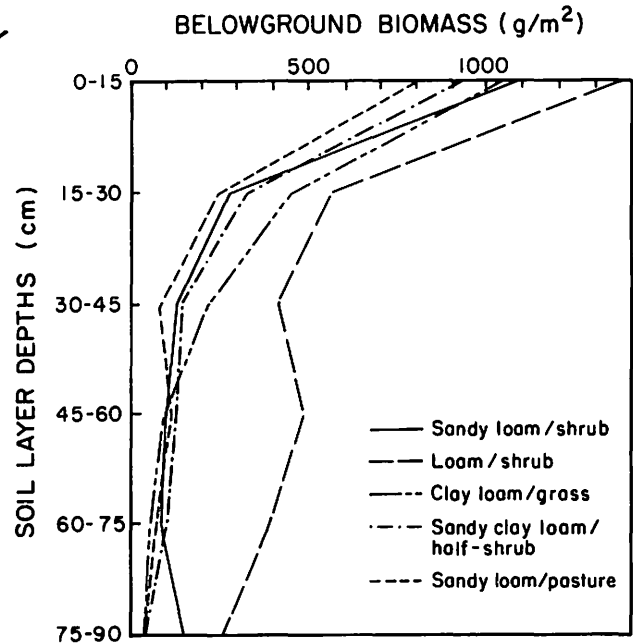For all soil layers sampled, fine-root biomass (roots <2 mm in diameter) was significantly greater (P<0.05) at

the loam/shrub site than at the other sites (Fig. 2). When total root biomass was compared among sites, including roots >2 mm in diameter, the loam/shrub site had significantly more root biomass in the 30–100 cm layers (P<0.05) than all but the sandy-clay loam/half-shrub site. A lack of significance at the sandy-clay site was probably due to the presence of approximately 140 g/m² of roots >2 mm in diameter at the 15–30 and 30–45 cm depths, while no other site had more than 10 g/m² of coarse-root biomass at these depths. No other differences in root biomass among sites were significant, but several trends were noted (Fig. 2). First, there was a sharp decline in fine-root biomass at the sandy-loam/shrub site from the 0–15 cm to the 15–30 cm depths. A greater abundance of shallow-rooted cacti at this site probably contributed to more fine roots in the 0–15 cm layer. Second, relative to other sites, only the sandy-loam/shrub site increased in fine-root biomass at the 75–90 cm depth, perhaps due to the abundance of shrubs. Finally, there were more fine roots in the 15–45 cm layer at both fine-textured sites (loam/shrub and clay-loam/grass) than in this soil layer at either sandy-loam site. Inter-site comparisons of fine-root biomass were more valid than comparisons of coarse-root biomass because large tap roots and roots below 1 m were present at the shrub sites (Alexander 1988), but were not adequately sampled.

An analysis of variance among sites of current year's aboveground biomass by different functional groups indicated significant date by site interactions for cool-season grasses, warm-season grasses and total grass biomass (F< 0.10), but not for forbs, half-shrubs, or cacti (Table 3). The absence of significant interactions for these latter groups probably relates to sampling errors of groups with low densities. The warm-season grasses had significantly less standing crop in May than by June, July, or August. The standing crop of cool-season grasses was also significantly less in May than by June, but declined in July and August. Instead of a decline in July and August, the cool-season

Table 3. Aboveground biomass (g/m²) for different components of five plant communities at the CPER. Whenever values among sites for each date and row are adjacent to two letters these values are significantly different from values by a single, identical letter and are significantly different from all other values of that date and row if followed by an asterisk ($P<0.10$)

	14 May Sites[a]					18 June Sites				
	1	2	3	4	5	1	2	3	4	5
Current season production										
Grasses										
– Cool-season	7	11	–	6	62*	9a	47aa	35aa	10a	86*
– Warm-season	28aa	4a	–	12	<1a	b58aa	27a	b44	b49	bb5a
– Both	35	16a	–	18a	63aa	67	73	78	59	90
Forbs	<1	1	–	1	2	1	9	9	5	2
Half-shrubs	13	0	–	2	2	15	0	0	11	8
Cacti	0	0	–	0	0	20	0	6	<1	0
Shrubs[b]	–	–	–	–	–	–	–	–	–	–
Aboveground dead										
Shrub	–	–	–	–	–	–	–	–	–	–
Nonshrub	124aa	121aa	–	82	59a	103aa	76	34a	69	89
Litter	49aa	211*	8a	20	22	–	–	–	–	–

	17 July Sites					14 August Sites				
	1	2	3	4	5	1	2	3	4	5
Current season production										
Grasses										
– Cool-season	22	35	–	14	64*	7a	55aa	23a	5a	83*
– Warm-season	68*	34	–	37	2	b62aa	25a	b35a	b46	bb4a
– Both	90aa	69	–	51a	65	69	80	57	51a	88aa
Forbs	3	21	–	5	3	1	9	<1	4	1
Half-shrubs	5	0	–	6	16	12	0	0	22	8
Cacti	25	0	–	21	0	54	0	5	14	0
Shrubs[b]	–	–	–	–	–	12	254	–	–	–
Aboveground dead										
Shrub	–	–	–	–	–	145	956	–	–	–
Nonshrub	191aa	149	–	97	58a	112aa	89	51a	86	59a
Litter	–	–	–	–	–	–	–	–	–	–

[a] 1 = Sandy-loam Shrub, 2 = Loam Shrub, 3 = Clay-loam Grass, 4 = Sandy-clay loam/Half-shrub 5 = Sandy-loam Pasture
[b] *Atriplex canescens* shrubs only

grass standing crop could have leveled off as production waned in July, since wind removal of mature seed and dry inflorescences of *Festuca octoflora, Sitanion hystrix* (Nutt.) J.G. Sm., and perhaps of other species, probably reduced biomass values of later sampling dates.

Aboveground biomass decreased from spring to summer at all five sites (Table 4). There was no increase in current year's biomass at the nonshrub sites (clay-loam/grass or sandy-loam/pasture sites) during the dry summer months, perhaps since these sites were dominated by, or had large amounts of, cool-season grasses. The loam/shrub site also had a considerable cool-season grass component (*Agropyron smithii*), but the abundance there of *Kochia scoparia* (L.) Schrad.), an exotic, warm-season forb, helped sustain production at this site during the summer. Increases in standing crop from spring to summer were greatest at the sandy-loam/shrub and sandy-clay loam/half-shrub sites, the only sites clearly dominated by the warm-season *Bouteloua gracilis*.

Significant differences in the amount of grass biomass among sites occurred for all the June sample dates (Table 3). At the May and August harvests, due to cool-season grass biomass, there was significantly more grass biomass at the sandy-loam/pasture site. In July, due to warm-season grass biomass, there was significantly more grass biomass at the sandy-loam/pasture site. In June, however, a time when the productivity of both warm-season and cool-season grasses were high, there were no significant differences in grass biomass among sites. When the grass production for the entire growing season was considered, grass production at different times for different sites resulted in significant seasonal differences ($P<0.05$) among sites.

Total water loss or evapotranspiration from the five study sites from 3 March to 26 August was similar, ranging from 192 to 221 mm (Table 4). Most of this amount was precipitation received between March and October. The remainder, or the net March-to-October change in soil water content in the upper meter of soil, was 21%–32% of total

Table 4. Aboveground net primary production, evapotranspiration, and water-use efficiency (WUE) at five steppe sites during the spring (3 March–30 June), summer (1 July–26 August) and entire growing season of 1986. Values in parentheses are WUE figures for grasses only for 1986

Site	Aboveground net primary production g/m²	Evapotrans- piration mm	WUE g/m²/mm
Spring			
Sandy-loam/shrub	104	144	0.7
Loam/shrub	82	173	0.5
Clay-loam/grass	93	161	0.6
Sandy-clay loam/ half-shrub	75	151	0.5
Sandy-loam/pasture	100	145	0.7
Summer			
Sandy-loam/shrub	33	53	0.6
Loam/shrub	7	48	0.1
Clay-loam/grass	–	59	–
Sandy-clay loam/ half-shrub	15	59	0.3
Sandy-loam/pasture	–	47	–
Growing Season			
Sandy-loam/shrub[a]	148	197	0.8 (0.45)
Sandy-loam/shrub[b]	137		0.7
Loam/shrub[a]	323	221	1.5 (0.36)
Loam/shrub[b]	90		0.4
Clay-loam/grass	93	220	0.4 (0.35)
Sandy-clay loam/ half-shrub	90	210	0.4 (0.27)
Sandy-loam/pasture	100	192	0.5 (0.47)

[a] Includes *Atriplex canescens* biomass
[b] Excludes *A. canescens* biomass

evapotranspiration, and represented water present in the soil before the initial March measurement. Soil water loss among sites increased as soil texture changed from coarse to fine (Hazlett et al. 1988). Soil water loss in the spring (3 March to 30 June) was 25%–35% of spring evapotranspiration, while soil water loss in the summer (30 June to 26 August), was only 8%–27% of summer evapotranspiration.

Water-use efficiencies (WUE) were calcuated for the spring, summer, and entire growing season (Table 4). During the spring, the greatest WUE values were found for the two sites on sandy soil: the *A. cristatum* sandy-loam/pasture site and the *A. canescens* sandy-loam/shrub site. During the summer, the sandy-loam/shrub site sustained its position as the site with the highest WUE values, but the sandy-loam/pasture site (no warm-season grasses) did not. During a below normal precipitation summer, 30 June to 26 August, biomass production occurred only at shrub and half-shrub sites, sites with deeper-rooted vegetation. Therefore, these were the only sites where calculations of summer WUE values were possible. When *A. canescens* biomass was excluded (Table 4), total season WUE was similar for all but the sandy-loam/shrub site. Even without *A. can-*

escens, the sandy-loam/shrub site still had the highest WUE value (0.8 g/m²/mm) of any site. When *A. canescens* biomass was included, the loam/shrub site replaced the sandy-loam/shrub site as the site with the highest WUE (1.6 g/m²). The 1.6 g/m²/mm WUE value for loam/shrub site was approximately twice that of the sandy-loam/shrub site, and was two or three times greater than the WUE of the other sites.

Discussion

Differences among sites in net aboveground biomass and WUE were related to differences in soil characteristics and to water-use adaptations of dominant life-forms. For example, during the spring both aboveground biomass and WUE were greatest at sites with coarse soil. This relationship might also have been true for the summer if one of the sandy sites, the sandy-loam/pasture site, had not been dominated by a cool-season grass. High WUE values at the sandy-loam/shrub site, even when *A. canescens* biomass was excluded, suggested several interesting possibilities. First, water utilization by shrubs may not be in strong competition with water utilization by nonshrub components of the community. Therefore, water resource partitioning among life-forms may be occurring. Second, since the inverse texture effect (Noy-Meir 1973) may help explain the increased WUE at this sandy site, biomass of the nonshrub component might have been even greater if shrubs had been absent. The inverse texture effect contrasts a relatively high productivity on sandy soils in arid regions and a relatively low productivity on sandy soils in humid regions. In this example, the low water holding capacity of the sandy soil may have facilitated deeper water penetration than occurred at other sites. This may have resulted, therefore, in less evaporation, greater transpiration, and an increase in the efficiency of water-use for production. A third possibility was that water resource partitioning among life-forms and the inverse texture effect were both contributing to the high WUE values at the sandy-loam/shrub site.

Vegetation on coarse-textured soil had the highest net primary production and WUE values, while vegetation on fine-textured soils, without *A. canescens*, had the lowest net primary production and WUE values (Table 4). Greater volumetric amounts of soil water at the clay-loam/grass site than at all other sites (Hazlett et al. 1988) did not result in high water availability to the vegetation, since clay soils hold much water that is unavailable for plants. The unavailability of soil water for plants at the clay-loam/grass site was also indicated by the high fine-root/shoot ratio of the clay-loam/grass site (Table 2), since high root/shoot ratios are an indication of soil water stress (Turner 1979).

Lauenroth (1979) analyzed data from 52 grassland sites worldwide, and estimated an average WUE of 0.5. Sala et al. (1988), using data from 100 locations in the Central Grassland region of the United States, reported an average WUE of 0.6. Our values for the growing season were between 0.6 and 2.2. Noy-Meir (1973) speculated that WUE should range between 0.5 and 2.0 for arid and semiarid regions, and our values were within this range.

Grass biomass for the entire season was not significantly different among sites and varied from 59 to 90 g/m² (Table 2). This was less variation in biomass than might be expected when comparing C_3 and C_4 grasses. The highest grass biomass was at the grass/pasture site where a C_3 grass

species was dominant. The lowest grass biomass was at the sandy-clay loam/half-shrub site where C_4 grasses were dominant. Less grass biomass at the sandy-clay site than at either shrub site suggested that competition between grasses and half-shrubs may be greater than between grasses and *A. canescens* shrubs.

The differences in community biomass for C_3 and C_4 grasses were opposite the ranking of photosynthetic capacity for C_3 and C_4 species. The photosynthetic capacity of C_4 species is potentially greater than C_3 species, but this advantage is realized only at high temperatures, and water availability. Although C_3 species may lack the maximum production capacity of C_4 species in high light and high temperature situations, this study indicated that the seasonal primary production of the C_3 and C_4 grass components in very different types of steppe communities can be similar. Ode et al. (1980), working in a North American mixed prairie, reported greater production on upland sites by C_3 compared to C_4 species. Monson et al. (1986) reported similar values of maximum photosynthetic rates for *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) at the Central Plains Experimental Range. They also found that both species reached their maximum photosynthetic rates during June.

Grass biomass among sites was similar despite differences in site fertility, soil texture, and soil water loss. Similarities in grass biomass among sites support the contention by Fisher and Turner (1978) of similar amounts of primary production within a life-form for different sites in dry regions. Fisher and Turner suggested similar primary production within and between life-forms for semiarid plant communities only after important corrections in carbon dioxide fixation pathways, root/shoot allocations and transpiration rates were considered. However, this study indicated that no such corrections were necessary to generate similar primary production values for the grasses in very different steppe communities. This statement, however, is restricted to the grass life-form. Therefore, as this study indicated, a result of this diverse mix of grass and grass-like species can be similar biomass values in structurally different plant communities. On the other hand, biomass of nongrass life-forms, especially shrubs, was dissimilar among sites and varied much more than grass biomass did in relation to soil texture and soil water status.

Since grass biomass was similar among sites, the inter-site differences in biomass and WUE values were attributed to the relative abundance of nongrass life-forms. Estimates of WUE based only upon grasses were similar among sites ranging from 0.27 to 0.47. Monson et al. (1986) reported similar values of WUE for *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) during June when photosynthetic rates for both species reached their maximum values. The positive effect of shrubs on community biomass was evident by the much higher biomass and total WUE values at the shrub sites, presumably due in part to shrub utilization of deep soil water. The high abundance of cacti at the sandy-loam/shrub site indicated the contribution of another life-form, this time with a specialized water-use from shallow roots and an efficient carbon dioxide fixation pathway (CAM), to the high biomass and WUE values of the plant communities. Although significant differences in grass biomass occurred at different points in the growing season, total season grass production among the plant communities

studied was not significantly different. Therefore, high biomass and WUE values for these steppe plant communities seemed to occur not where there was a greater mixture or dominance by C_3 and/or C_4 grass species, but rather where site characteristics favored the establishment, survival, and dominance of nongrass life-forms.

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PRIMARY PRODUCTION OF THE CENTRAL GRASSLAND REGION OF THE UNITED STATES[1,3]

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Abstract. Aboveground net primary production of grasslands is strongly influenced by the amount and distribution of annual precipitation. Analysis of data collected at 9500 sites throughout the central United States confirmed the overwhelming importance of water availability as a control on production. The regional spatial pattern of production reflected the east–west gradient in annual precipitation. Lowest values of aboveground net primary production were observed in the west and highest values in the east. This spatial pattern was shifted eastward during unfavorable years and westward during favorable years. Variability in production among years was maximum in northern New Mexico and southwestern Kansas and decreased towards the north and south. The regional pattern of production was largely accounted for by annual precipitation. Production at the site level was explained by annual precipitation, soil water-holding capacity, and an interaction term. Our results support the inverse texture hypothesis. When precipitation is <370 mm/yr, sandy soils with low water-holding capacity are more productive than loamy soils with high water-holding capacity, while the opposite pattern occurs when precipitation is >370 mm/yr.

Key words: Central Grassland region; inverse texture effect; precipitation effect; primary production; production controls; scaling; soil texture effect; spatial pattern; temporal variability; water use efficiency.

INTRODUCTION

The Central Grassland region of the United States of America extends from the deciduous forest on the east to the Rocky Mountains on the west, and from the Canadian to the Mexican borders. This region encompasses a wide variety of climatic conditions; precipitation ranges from 260 to 1200 mm and annual average temperature ranges from 3° to 22°C. Despite the large differences in climate, the potential natural vegetation of the region is largely grassland (Küchler 1964). Four types of grassland occur within the region: the northern and southern mixed prairies, the tallgrass prairie, and the shortgrass steppe (Risser et al. 1981, Singh et al. 1983).

Estimates of aboveground net primary production (ANPP) have been reported for many sites in the Central Grassland region as well as around the world (Lauenroth 1979). In each case, estimates of ANPP were from single sites. A small number of studies provide information about the temporal dynamics of productivity (Sims and Singh 1978). This paper focuses on the spatial distribution of ANPP over the entire Central Grassland region. Data collected at 9500 sites were analyzed at the individual site level, and then

grouped into major land resource areas (MLRA) (USDA, SCS 1981) and analyzed at the regional level.

We had two objectives for the analysis at the regional level. The first was to evaluate the spatial and temporal pattern of annual production for the region. While no such analysis has been attempted for the grassland region, similar analyses have been conducted for other regions (Rodin et al. 1975, Sharp et al. 1975, Sharpe 1975, Box 1978, Meentemeyer 1984). Our second objective at the regional level was to evaluate the importance of climatic variables as determinants of the pattern of primary production at the MLRA level. Rosenzweig (1968) and Lieth (1975) developed models that related primary production on a global basis to precipitation and temperature. Both models have similar structures, but Rosenzweig used actual evapotranspiration as the independent variable, while Lieth utilized annual precipitation and annual temperature. Webb et al. (1978, 1983) analyzed primary production data from three biomes in North America: forests, grasslands, and deserts. They found that precipitation and potential evapotranspiration accounted for a large fraction of the variance of ANPP in grasslands and deserts, while radiation was the most important variable in explaining forest ANPP. Lauenroth (1979) studied the controls of primary production solely for grasslands, but on a global scale. He presented a model in which primary production was explained by annual precipitation over a range from 150 to 1800 mm/yr. The model had a better fit towards the dry end of the
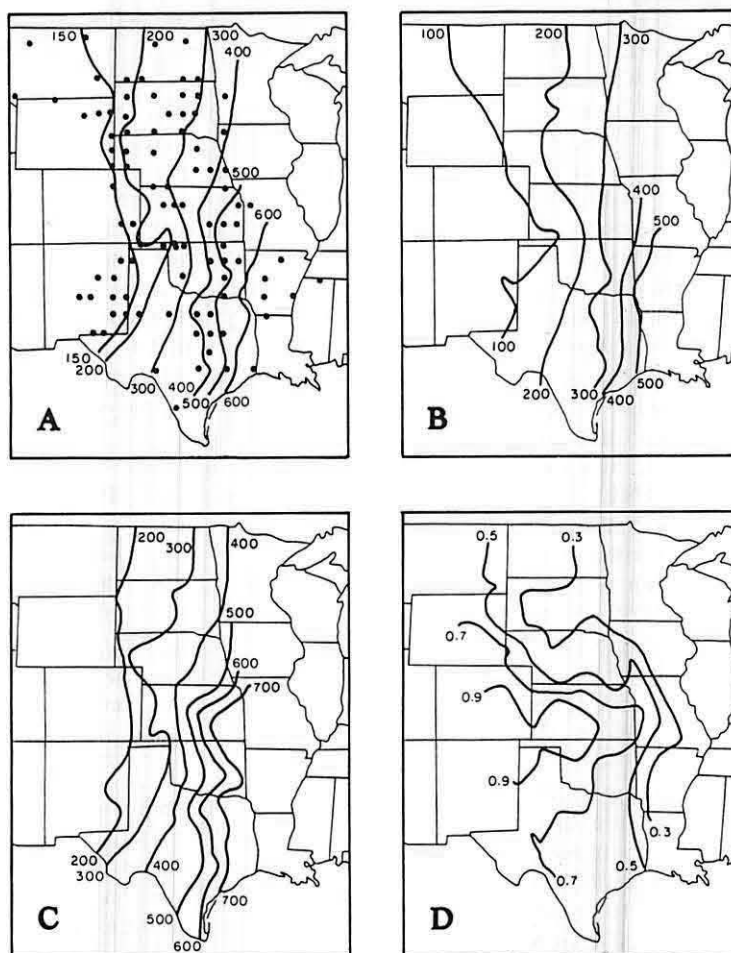
Fig. 1. Isopleths of aboveground net primary production (ANPP, g/m²) for the Central Grassland region (A) during years of average precipitation, (B) during unfavorable years, and (C) during favorable years. (D) isopleths of relative variability in production between favorable and unfavorable years estimated as

$$\frac{(\text{production favorable}) - (\text{production unfavorable})}{\text{average production}}.$$

Dots represent the location of the center of the state portions of major land resource areas (MLRA). Each state portion of the MLRA was treated as a separate unit where an MLRA crossed a state boundary.

precipitation range than towards the wet end, where water availability is less frequently the limiting factor.

Our objective for the site level analysis was to evaluate the interaction between climate and soil variables as determinants of primary production. We hypothesized that soil characteristics are important in explaining production at the site level but are overshadowed by climate at the regional level. Since primary production in grasslands is frequently limited by water availability (Lauenroth 1979), we selected water-holding capacity as the soil characteristic to explain the production pattern at the site level. Water-holding capacity along with precipitation pattern are the major determinants of soil water availability for plants (Jenny 1980). We wanted to test the inverse texture hypothesis (Noy-Meir 1973), which states that production in dry regions should be greater on coarse-texture (low water-

holding capacity) soils than on fine-texture (high water-holding capacity) soils.

METHODS

Our study was based on a data set collected by the USDA Soil Conservation Service at 9498 sites throughout the Central Grassland region of the United States (Joyce et al. 1986). For each site, the database contains estimates of primary production for favorable, unfavorable, and average years, as well as a description of the soil profile that includes texture of the A horizon.

Primary production included the aboveground parts of all plants (except mosses and lichens) produced during a single growth year, regardless of accessibility to grazing animals (USDA, SCS 1976). Primary production estimates were obtained by the double-sampling

procedure (Wilm et al. 1944). At least one plot was harvested for each seven estimated. A minimum of 10 plots and a maximum of 20 were estimated per site depending upon the spatial heterogeneity of the vegetation. Minimum plot size was 17.8 dm². An 89.2-dm² plot was used in areas where production was relatively low. Production was expressed as air-dry matter in grams per square metre. Measurements were done in sites not grazed during the current growing season.

Favorable and unfavorable years were defined based upon long-term frequency distributions of precipitation (USDA, SCS 1973). Favorable years were defined as the wettest 10% of the years in the record, and the unfavorable years were defined as the driest 10% of the years. Production was estimated for favorable, average, and unfavorable years (USDA, SCS 1976).

The regional pattern of ANPP was analyzed by grouping sites into 100 areas that represent the major land resource areas (MLRA) within each state, as defined by the Soil Conservation Service (USDA, SCS 1981). The average of the ANPP of all the sites within a state's MLRA determined its ANPP. Long-term averages of monthly temperature and precipitation were retrieved for locations near the geographical center (Fig. 1A) of each MLRA (United States Weather Bureau 1964). Using this information, we calculated annual and growing-season values of potential evapotranspiration (Linacre 1977), temperature, precipitation, and the precipitation/potential evapotranspiration ratio.

We constructed isopleths of production using MLRA data, with a contour interval of 100 g/m² for favorable, average, and unfavorable years. The importance of climatic variables as determinants of the pattern of primary production at the MLRA level was evaluated by multiple regression analysis between ANPP and different climatic variables. Soil water-holding capacity for each of the 9498 sites was estimated from soil texture information (A. J. Erickson, *personal communication*). Soil water-holding capacity depends foremost on the texture of a soil (Jenny 1980). The controls of primary production at the site level were evaluated by multiple regression analysis between ANPP estimates and soil water-holding capacity and climatic variables.

RESULTS AND DISCUSSION

The spatial pattern of average aboveground net primary production for the Central Grassland region has a dominant east–west gradient (Fig. 1A). This pattern of production is very similar to the isohyet pattern (Borchert 1950). In the northern portion of the region, the 200 g/m² isopleth runs in a north–south direction. We observed that west of this isopleth production increases towards the north. In contrast, east of this line production decreases northward. We speculate that in the humid portion, decreasing temperatures and length of growing season limit production. In the dry portion, decreasing temperatures result in a reduction of evapotranspiration and an increase in available water. Dur-

ing average years, ANPP ranges from 150 g/m² in the west to 600 g/m² in the southeastern portion of the region.

Production during unfavorable years is characterized by an eastward shift in the spatial pattern (Fig. 1B). The 200 g/m² isopleth shifts ≈2° longitude in unfavorable years compared to average years. Production during favorable years is characterized by a westward shift in the spatial pattern (Fig. 1C). The 200 g/m² isopleth shifts to the west, following the eastern edge of the Rocky Mountains, and the range in production increases compared to average years. From unfavorable to favorable years the ANPP isopleths shift from east to west, but their shape remains approximately the same.

Unfavorable years correspond to drought years, which are associated with a decrease in the normal flow of air from the Gulf of Mexico during the summer months and a predominance of westerlies throughout the year. Because droughts are the consequence of changes in the large-scale pattern of atmospheric circulation, they affect the entire grassland region (Borchert 1950).

The variability in production among years, estimated as the relative difference between favorable and unfavorable years $\dfrac{(\text{favorable} - \text{unfavorable})}{\text{average}}$, has a distinct regional pattern (Fig. 1D). Isopleths of variability have the approximate shape of concentric wedges with the center in southwest Kansas. Maximum variability occurs in the region that extends from northern New Mexico to southwestern Kansas. Variability decreases towards the north and south of this area. The shape of the area where variability is higher than 80% coincides with Borchert's (1950) wedge of spring and summer rainfall deficiency, characteristic of major drought years across the Central United States. His analysis showed the occurrence of this wedge-shaped area in which precipitation rapidly decreased towards the center during drought years. Outside the wedge, precipitation tended to be near or above normal during these years.

The pattern of production at the MLRA level is largely accounted for by annual precipitation (Fig. 2). For average years the model is ANPP = −34 + 0.6·APPT, $r^2 = 0.90$; $F_{1,98} = 935$, $P < .01$, where ANPP is annual aboveground net primary production in grams per square metre and APPT is annual precipitation in millimetres. Addition of other climatic variables such as potential evapotranspiration, temperature, or the precipitation: potential evapotranspiration ratio for the growing season or the entire year did not improve the model. None of the more complicated models accounted for >90% of the variance in production. Our simple model can be written in the form of Noy-Meir's (1973) model:

$$\text{ANPP} = 0.6 \cdot (\text{APPT} - 56),$$

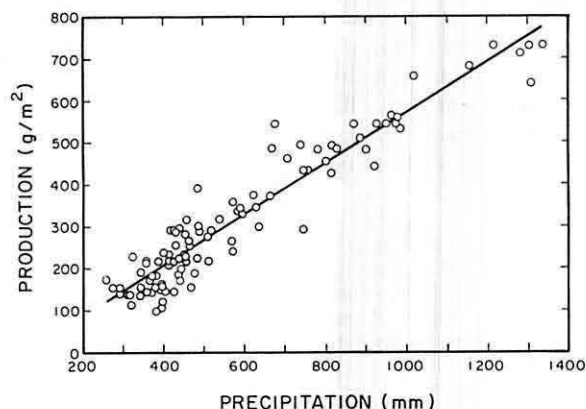where 0.6 represents the average water-use efficiency

FIG. 2. Relationship between mean annual precipitation and mean aboveground net primary production (ANPP) for 100 major land resource areas across the Central Grassland region. $ANPP = -34 + 0.6 \cdot APPT$; $r^2 = 0.90$.

of the community (dry matter: $g \cdot m^{-2} \cdot mm^{-1}$ of precipitation) and 56 (mm/yr) is the "ineffective precipitation," or "zero-yield intercept." Our efficiency value for the Central Grassland region lies within the range originally proposed by Noy-Meir (1973) $(0.5-2 \ g \cdot m^{-2} \cdot mm^{-1})$ and closely agrees with the efficiency reported by other authors (Lauenroth 1979, Rutherford 1980, Le Houérou 1984). Our value for ineffective precipitation is higher than Lauenroth's (1979) (29 mm/yr) but lies within the range proposed by Noy-Meir (1973) (25–75 mm/yr). Some of the previous models implicitly set an upper limit on production (Whittaker 1970, Lieth 1975, Webb et al. 1978). For our production data, which ranged between 100 and 700 g/m^2, inclusion of an upper limit did not improve the fit of the model (Fig. 2). We expect that our simple model will not be useful for regions with a higher precipitation regime, where production is mostly limited by light or nutrients.

Production at the site level was analyzed using information from the 9498 sites. Variability in production of sites was accounted for by annual precipitation and soil water-holding capacity. Our models are

Average years:

$$ANPP = 32 + (0.45 \cdot APPT) - (352 \cdot WHC) + (0.95 \cdot WHC \cdot APPT),$$
$$R^2 = 0.67; \quad F_{3, \ 9483} = 6630; \quad P < .01;$$

Favorable years:

$$ANPP = 80 + (0.51 \cdot APPT) - (327 \cdot WHC) + (0.94 \cdot WHC \cdot APPT),$$
$$R^2 = 0.60; \quad F_{3, \ 9483} = 4746; \quad P < .01;$$

Unfavorable years:

$$ANPP = -7.2 + (0.38 \cdot APPT) - (415 \cdot WHC) + (1.01 \cdot WHC \cdot APPT),$$
$$R^2 = 0.68; \quad F_{3, \ 9483} = 6705; \quad P < .01,$$

where WHC is soil water-holding capacity, which ranges

from 0.05 to 0.2 water as a proportion of soil dry mass. The three models show that production increases with precipitation and that soil water-holding capacity can have a positive or negative slope depending upon the precipitation value. The model for average years predicts that, when annual precipitation is <370 mm, sandy soils with low water-holding capacity will be more productive than loamy soils with high water-holding capacity (Fig. 3). When precipitation is >370 mm, the model predicts that sandy soils will be less productive than loamy soils. The relationship between the values observed and predicted by the model gives an indication of the spread of the raw data (Fig. 4). Data points were uniformly distributed and no characteristic departure from the model was observed.

Our data and models support the inverse texture hypothesis (Noy-Meir 1973) and yield and estimation of the point at which there is no texture effect. This is the first data set that is broad enough to test this hypothesis for grasslands. Gaines et al. (1954) reported increased forage production from deep sands to clayey soils for a site near the more humid end of our range. Le Houérou (1984) found that with precipitation <300 mm/yr, olive yield in the arid zone of Tunisia was higher on sandy soils than on silty soils. The opposite pattern was found when precipitation was higher than 300 mm/yr.

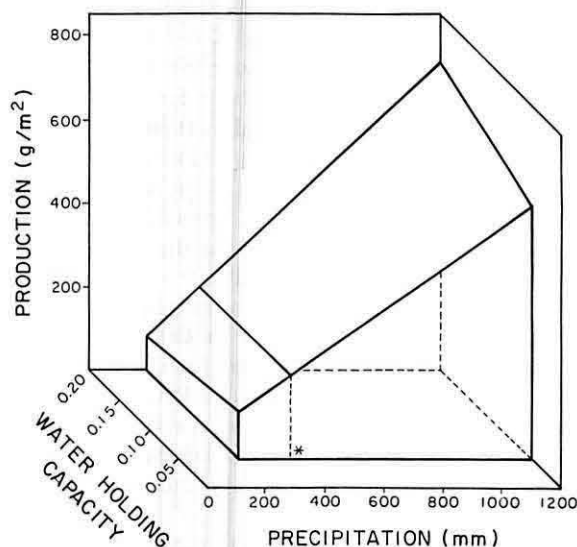The explanation for the interaction between precip-

FIG. 3. Relationship between aboveground net primary production (ANPP) during average years, soil water-holding capacity (WHC, as a proportion of soil dry mass), and mean annual precipitation for 9498 sites across the Central Grassland region. At 370 mm of precipitation (∗), soil water-holding capacity does not modify primary production. Above this value, primary production increases with increasing water-holding capacity. Below 370 mm of precipitation, primary production decreases with increasing water-holding capacity. $ANPP = 32 + 0.45 \cdot APPT - 352 \cdot WHC + 0.95 \cdot WHC \cdot APPT$; $R^2 = 0.67$.
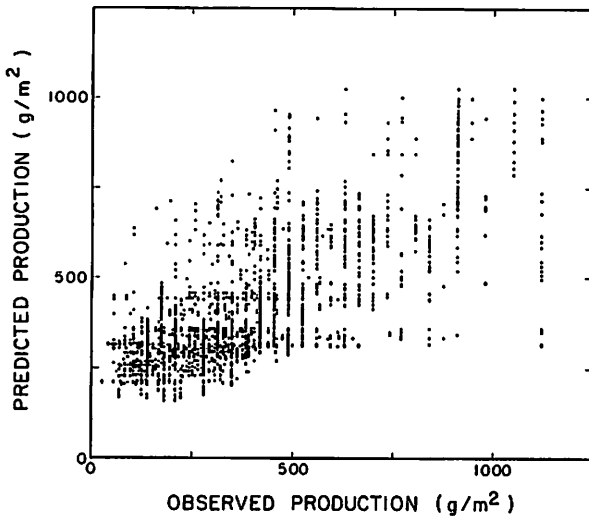
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FIG. 4. Relationship between the observed values of production and the values predicted by the site level model for average years.

itation and soil water-holding capacity is related mainly to the dynamics of soil water. In dry regions, major losses of soil water occur via bare soil evaporation. However, where sandy soils occur, bare soil evaporation is lower than in loamy soils because water penetrates deeper into the soil. Runoff also is lower in sandy soils than in loamy soils (Buckman and Brady 1960). In more humid regions, substantial water losses occur via deep percolation, which is reduced in soils with high water-holding capacity (Noy-Meir 1973). Therefore, in dry regions, sandy soils with low water-holding capacity have more water available for plant growth than soils with higher water-holding capacity. The opposite pattern occurs in more humid regions.

The variability in production at the site level was accounted for by two variables, annual precipitation and soil water-holding capacity. At the MLRA level only one variable (annual precipitation) was necessary to explain a large fraction of the variability in production. The better fit of a simpler model at the coarse scale was not the result of a reduction in variance, as the variance of production at the MLRA level was not statistically different ($P > .05$) from the variance at the site level. The same response in variance due to grouping was observed for favorable, average, and unfavorable years.

We suggest that for a constant frame of reference, in our case the Central Grassland region, as the scale of analysis becomes finer, a model will need to include a larger number of variables to account for the pattern of the same process. This principle, which emerged empirically from our work, can be deduced from hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986). Consequently, it should be applicable to processes other than production. The pattern of a process at a coarse scale constrains the pattern at a finer scale.

Therefore, variability at the fine scale will be accounted for by factors at this scale plus the factors that determine the pattern at the coarse scale. In the case of production, at scales finer than the individual site it will be necessary to account for additional variables such as plant species composition and grazing history.

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SEX RATIOS OF BUCHLOE DACTYLOIDES (NUTT.) ENGELM. ALONG CATENAS ON THE SHORTGRASS STEPPE

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The sex ratios in naturally occurring populations of *Buchloe dactyloides* (buffalograss) were evaluated along 20 catenas in the northern part of the shortgrass steppe. A male : female : mixed sex ratio of 0.92 : 1.00 : 0.83 was found and did not differ significantly from unity. Overall density of male and female clones averaged ca. 5,500 and 6,000 clones/ha, respectively. Mixed clones were the result of the stolons of male and female individuals intertwining and does not imply monoecy. *Buchloe dactyloides* was not segregated spatially aboveground along the catenas by slope position; however, there was considerable variation between ratios by slope aspect. North- and south-facing slopes averaged significantly more clones/ ha than did the east- and west-facing slopes. We suggest that dioecy in this genus may not be exclusively the result of ecological differentiation to reduce intrasexual competition but is an adaptation for colonizing disturbed areas.

Introduction

Dioecy occurs in 5% of angiosperm genera (YAMPOLSKY and YAMPOLSKY 1922) and is an uncommon adaptation that has arisen independently in many unrelated plant groups. At least 75% of angiosperm families have dioecious species (YAMPOLSKY and YAMPOLSKY 1922; WESTERGAARD 1958), and, assuming a conservative estimate of 600 genera in the Poaceae, dioecy occurs in ca. 3.3% of the genera.

The monotypic genus, *Buchloe,* is the most widespread North American dioecious taxon within the Chlorideae. *Buchloe dactyloides* (Nutt.) Engelm. (buffalograss) is a perennial, stoloniferous species occurring from southern Canada to central Mexico (BEETLE 1950; HITCHCOCK 1951). Staminate plants typically bear one to several short spicate inflorescence branches that are well exserted above the leafy portion of the plant, whereas pistillate plants have several spikelets enclosed in a capitate, burlike cluster restricted to the basal portion of the plant (GOULD and SHAW 1984). Occasionally a plant is monoecious (PLANK 1892; HITCHCOCK 1895), and rarely a plant occurs with perfect florets among the staminate spikelets (HENSEL 1938; WENGER 1940).

Ecologically, *B. dactyloides* is a codominant with *Bouteloua gracilis* Lag. ex Steud. (blue grama) over much of the shortgrass steppe (WENGER 1943; W. K. LAUENROTH and D. G. MILCHUNAS, unpublished). Although *B. dactyloides* occurs on many different soil types, it most commonly is found on heavy clay soils and is absent from very sandy soils (BEETLE 1950). REEDER (1971) and STEBBINS (1975)

suggested that *Buchloe* originated in central Mexico and that the species developed from the Madro-Tertiary geoflora. The tetraploid and hexaploid populations underwent minor genetic modifications while migrating into northern Mexico and subsequently the Great Plains.

The primary objectives of this study were (1) to describe the sex ratio of *Buchloe* in naturally occurring populations, and (2) to determine whether the sex ratio varies in relation to slope position and aspect of catenas common to the northern part of the shortgrass steppe.

Material and methods

This study was conducted at the Central Plains Experimental Range (CPER), managed by the Agricultural Research Service, USDA. CPER is located 12 km north of Nunn, Weld County, Colorado at lat. 40° 48′ N, long. 104° 45′ W. Average precipitation at CPER is 310 mm/yr, and April through July are the wettest months. Mean annual temperature is 18 C, ranging from −5 C in January to 20 C in July (SCHIMEL et al. 1985). The region has been classified as semiarid (TREWARTHA 1968), and the climate is typical of a midcontinental temperate area where precipitation tends to coincide with maximum temperatures (LAUENROTH and MILCHUNAS, unpublished). Average elevation at CPER is 1,650 m, and topography rolls slightly. The landscape is a topographic series sequence (i.e., catenas), and slopes range from 1% to 10%.

The vegetation at CPER is typical of the shortgrass steppe and is dominated by the C_4 species *Buchloe dactyloides* and *Bouteloua gracilis*. Ground cover can vary on a catena from 90% to 100% on the footslope to 30% or 40% on the summit (STILLWELL 1983). *Opuntia polyacantha* Haw. (plains pricklepear), *Aristida longiseta* Steud. (red threeawn), and *B. gracilis* dominate the summit and backslope along the catena, while the footslope is

dominated by *B. dactyloides, B. gracilis,* and *Carex filifolia* Nutt. (threadleaf sedge).

Catenas sampled at CPER were separated into four slope positions: summit, backslope, footslope, and toeslope (RUHE and WALKER 1968). Sites designated as summit positions occurred at the apex of the slope. The linear portion below the summit delineated the backslope. This area was followed by a concave portion (footslope) that merged with the lower terrain. Beyond the footslope was an area of deposition that extended beyond the base, the toeslope. All slopes were at an inclination between 5% and 10%. A total of 20 slopes were sampled (seven north-, five south-, four east-, and four west-facing). Thirty 0.5-m randomly placed circular plots were situated along transect lines at each slope position. A total of 2,400 plots were evaluated for the number of male (staminate), female (pistillate), and mixed *B. dactyloides* clones. Clones were identified to sex during peak flowering (July to mid-August 1984). Because of the stoloniferous nature of *B. dactyloides,* when it was impossible to verify where clones with both sexes originated, they were classified as mixed (SCHAFFNER 1920). The χ^2 analysis tested the significance of ratio differences among male, female, and mixed clones at different slope positions and slope aspects (CONNOR 1984; WASER 1984). The expected ratio used for comparison was 1:1:1 (FISHER 1930; CONNOR 1984).

Results and discussion

The overall male:female:mixed sex ratio was 0.92:1.00:0.83 and did not differ significantly from unity ($P < .05$). This ratio agreed with the "Fisher principle" that states a sex ratio is in equilibrium (1:1) when the effort spent producing the two sexes is equal (FISHER 1930; HAMILTON 1976). Our results are similar to those in other studies in which sex ratios were determined from *Buchloe* seeds (WEBB 1941; WU et al. 1984), though slight female-biased sex ratios also have been reported for *Buchloe* (WENGER 1940; VOIGT et al. 1975; QUINN and ENGEL 1986). Varying ratios have been found in other grass species: near unity—*Spinifex sericeus* R. Br. (CONNOR 1984), *Distichlis spicata* (L.) Greene var. *stricta* (FREEMAN et al. 1976); slightly male-biased—*Leucopoa kingii* (S. Wats.) W. A. Weber (FOX and HARRISON 1981); and slightly female-biased—*Bouteloua chondrosioides* (H.B.K.) Benth. ex S. Wats. (REEDER and REEDER 1966). WILLSON (1979) noted that a biased adult sex ratio may reflect differential mortality, length of reproductive life, and/or differences in vegetative growth.

Clones designated as mixed included intertwining male and female plants, which does not imply monoecy. Only one monoecious plant was found during sampling, and it had male and female inflorescences alternating at the nodes. The monoecious character of *Buchloe* is well documented

(BURR 1951; HITCHCOCK 1895), but there is little information that describes the survival and continuation of monoecy as well as if *Buchloe* has the ability to alter sexual expression or sex ratio in response to differing environments under natural conditions.

Overall, there was little variation in sex ratios within slopes (fig. 1). Regardless of slope position, the male clones were evenly distributed along the catenas and averaged ca. 5,500 clones/ha. Slightly more variation occurred in the female and mixed components. Female clones were more numerous at the backslope and summit. Average density of female clones over all slope positions was ca. 6,000 clones/ha. The mixed component did not differ significantly at the toeslope, footslope, and backslope ($P < .05$) but was reduced significantly at the summit ($P > .05$). *Buchloe* clones were smaller and less intertwined at the summit, which would account for the fewer mixed clones recorded at this position.

Though there was little variation in the sex ratio within slopes (fig. 1), there was deviation from unity with slope aspect (fig. 2A–2D). The north- and south-facing slopes were comparable and not statistically different in male : female : mixed ratios (fig. 2A, 2B, $P < .05$). North slopes had an overall ratio of 0.95:1.00:0.95, while south slopes had a ratio of 0.94:1.00:0.90. North-facing slopes had nearly 9,000 more clones/ha than did south-facing slopes ($P > .05$). The male clones were distributed evenly on the slopes except for higher values at the footslope on the south-facing slopes and the summit on the north-facing slopes. There was no discernible pattern in the female component along the gradients. The mixed component was greatest on the toeslopes and least at the summit ($P > .05$).
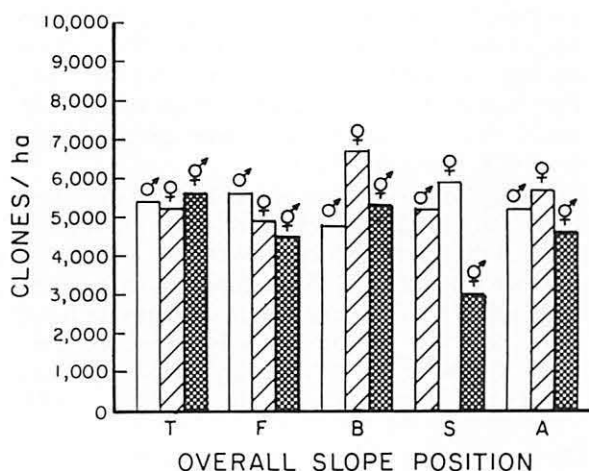

FIG. 1.—Overall density of males, females, and mixed clones (clones/ha) of *Buchloe* by slope position. T = toeslope, F = footslope, B = backslope, S = summit, A = average of the four slope positions.
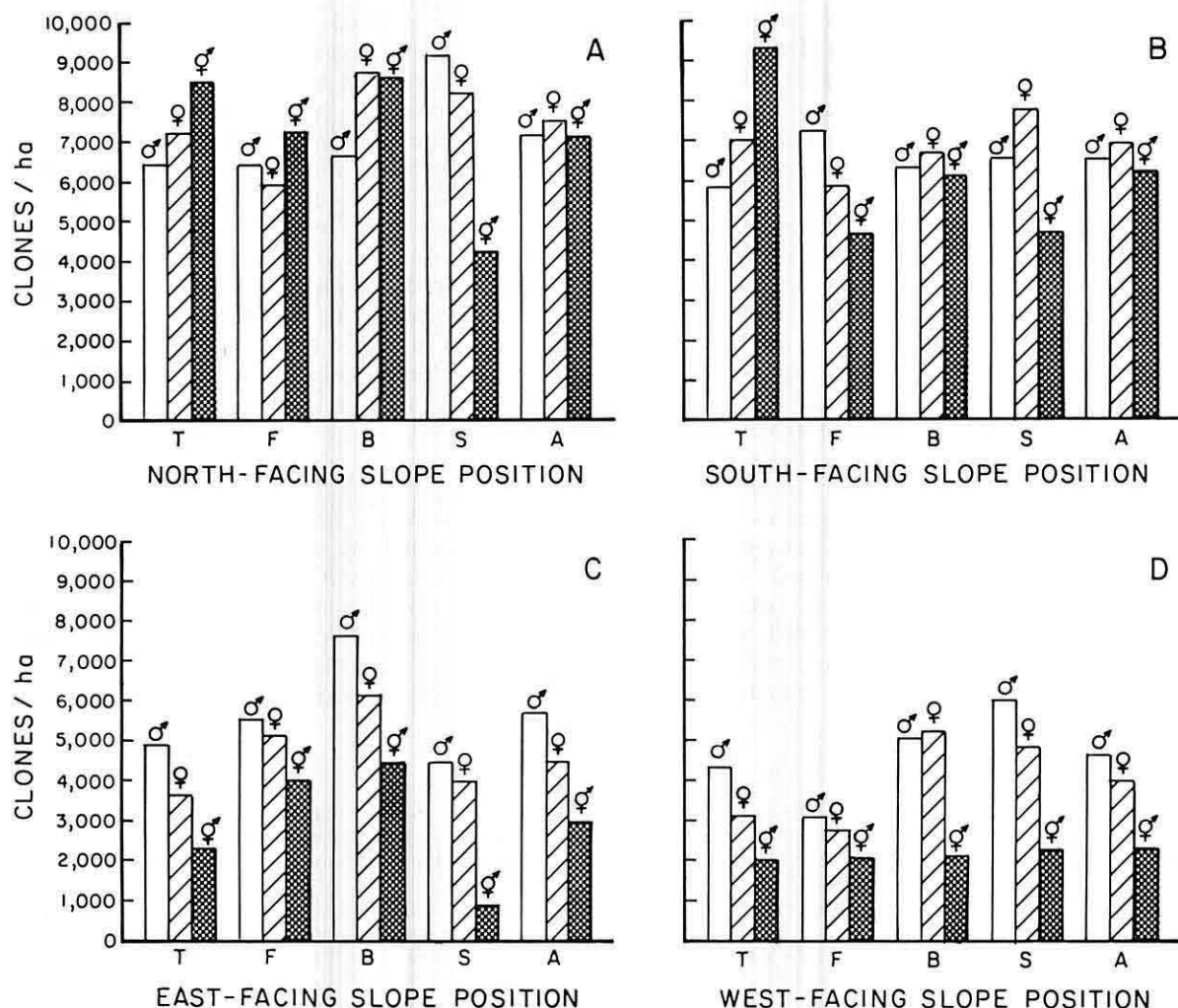
FIG. 2.—Density of males, females, and mixed clones (clones/ha) of *Buchloe* by slope aspect. *A–D*, North-, south-, east-, and west-facing, respectively. *T* = toeslope, *F* = footslope, *B* = backslope, *S* = summit, *A* = average of the four slope positions by aspect.

East- and west-facing slopes had comparable trends (fig. 2*C*, 2*D*). Both slopes had slightly different male-biased sex ratios, but these differences were not significant ($P < .05$). The overall sex ratio was 1.00:0.86:0.46 on west-facing slopes and 1.00:0.79:0.52 on east-facing slopes. Again, the male clones were distributed evenly on east- and west-facing slopes except for the backslope position of the east-facing slope that had a significantly higher number of clones ($P > .05$). Also, male clones were greater in number at all slope positions except the west-facing backslope (fig. 2*C*, 2*D*), whereas female clones dominated five of the eight slope positions on north- and south-facing slopes (fig. 2*A*, 2*B*). Female clones on west- and east-facing slopes were consistent in number except for the lower slope positions on west-facing slopes. Mixed clones were the lowest component at all slope positions.

Because sexual segregation was seen between slopes but not within a slope, spatial segregation appears to be the result of multiple physical and environmental factors. Differences in soil depth, texture, nutrients, and a resulting change in above- and belowground phytobiomass as well as percentage of cover have been reported for a catena at CPER (STILLWELL 1983; SCHIMEL et al. 1985). These differences may not have been great enough to cause a segregation of the sexual morphs within a slope; however, when coupled with the influences of aspect, they may have caused the segregation found among the aspects.

Sexual reproduction and a greater chance for outcrossing between nonrelated plants may be ensured because of the multiseeded burs produced on female plants of *Buchloe*. QUINN and ENGEL (1986) noted that one to five caryopses are found within burs and that there is a 50% probability that both sexes will be present. Also, there is differential germination of caryopses within a single bur so that

there are multiple opportunities for germination and establishment at a given location. The bur of *Buchloe* protects, anchors, and acts as a dispersal unit and, as QUINN (1984) suggested, may minimize desiccation of the establishing seedling.

Sexual segregation may give *Buchloe* an adaptive advantage during colonization of an area by facilitating outcrossing and by increasing resource allocations to vegetative growth. Vegetative proliferation allows the individual genet to scatter ramets throughout an area. *Buchloe* has two forms of vegetative growth: "phallanx" and "guerilla" (LOVETT-DOUST 1981). The first type is a consolidated growth form; conversely, the latter is an exploratory type that is often responsive to environmental conditions (DAUBENMIRE 1960; KERSHAW 1964). Though a colonizing syndrome is not readily applicable to most dioecious species (WILLSON 1979), there is a propensity for dioecious species with aggressive vegetative growth in the Chlorideae, Aeluropodeae, and Paniceae. Because 26 of 30 dioecious grass species examined were either stoloniferous or rhizomatous, there may be a correlation among dioecy, vegetative reproduction, and the ability to establish in disturbed sites.

Thus, it seems possible that dioecy in *Buchloe* may have developed as a colonizing mechanism. This mechanism may have been in response to the increasingly arid environments following the rise of the Rocky Mountains in the early Tertiary (AXELROD 1958). This would have enabled *Buchloe* to take advantage of the more arid environments made available during and after the last Pleistocene glaciation. Indeed, *Buchloe*, along with several species of *Bouteloua*, are the most successful members of the Chlorideae in North America, and they have been able to spread their influence far from their centers of origin in central Mexico.

Acknowledgments

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THE EFFECTS OF DISTURBANCE SIZE AND FREQUENCY
ON A SHORTGRASS PLANT COMMUNITY[1]

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Abstract. We examined the effects of small, patch-producing disturbances on a short-grass plant community dominated by the perennial grass blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths). Size distributions and rates of occurrence were determined from field data and from the literature for *B. gracilis* plants and for three disturbance types: cattle fecal pats, western harvester ant mounds, and small animal burrows. A spatially explicit simulation model was then used to determine the effects of each disturbance. The average turnover rates (percent affected per year) of the basal cover and density of *B. gracilis* plants in the simulated plots were calculated for three topographic positions and three grazing intensities.

Disturbance size relative to the size of *B. gracilis* plants distinguished two classes of disturbances. Ant mounds and animal burrows were significantly larger than *B. gracilis* plants, while fecal pats were comparable in size to *B. gracilis* plants. The frequency of occurrence of a disturbance was found to be a good predictor of the amount of basal cover and the number of plants killed each year by each disturbance type. The fastest turnover rates for basal cover were associated with the smallest and most frequent disturbance type (fecal pats). The effects of these disturbances were found to be dependent on topographic position and grazing intensity, especially the former. Slopes and lowlands had faster turn-over rates than uplands.

Our results suggest that the recovery of *B. gracilis* is dependent on the spatial scale of the disturbance.

Key words: animal burrows; ant mounds; Bouteloua gracilis; *disturbance frequency; disturbance size; gap turnover; grassland; grazing; patch dynamics; simulation model.*

INTRODUCTION

The disturbance regime of most plant communities includes a number of kinds of disturbances that collectively operate over a wide range of spatial and temporal scales. The importance of the characteristics of a disturbance to its effects on community structure has been recognized for many different plant communities (Sousa 1984, Pickett and White 1985). Two characteristics of particular importance are size and frequency of occurrence (Denslow 1980, Miller 1982). The relationship between size and frequency is typically inverse. Recent studies in grasslands have suggested the importance of within-community patch-producing disturbances on spatial pattern, and on the persistence of species able to utilize small, relatively short-lived patches (Platt 1975, King 1977, Hobbs and Mooney 1985, Loucks et al. 1985). The objective of this study was to evaluate the role of patch-producing processes on the dynamics of a semi-arid grassland in Colorado.

The shortgrass steppe in northcentral Colorado is dominated by the perennial grass blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths; nomenclature follows McGregor [1986]). *Bouteloua gracilis* accounts

for 75–90% of net primary production on most sites, so the processes that reduce *B. gracilis* cover or abundance have the largest effects on community structure. Therefore, we focused on disturbances that reduce either the number of tillers of *B. gracilis* (basal cover) or the density of *B. gracilis* plants (number). Recolonization by *B. gracilis* is a relatively slow process that differs depending on the spatial extent of the patch. Disturbances smaller than an individual plant reduce *B. gracilis* cover by killing tillers. Recolonization is primarily by tiller replacement from the damaged plant. As patch size increases, and entire *B. gracilis* plants are killed, recolonization is through seedling establishment.

Disturbance types operating over a wide range of spatial scales influence the biomass of this community. In this study, we examined three types of disturbances: cattle fecal pats, western harvester ant mounds, and burrows from small animals. Each disturbance type has an associated size distribution and frequency of occurrence that can be used to evaluate its effects on a *B. gracilis* population; both size and frequency may vary as a result of different topographic positions and grazing regimes. Field estimates were combined with information available in the literature to determine the size and frequency distributions of these three disturbance types, and the size distributions and cover of *B. gracilis* plants. We then used simulation modeling to

calculate a set of summary variables (plant cover killed, number of plants killed, and turnover rates) to compare the impacts of these disturbances on *B. gracilis*.

SITE DESCRIPTION

All data were collected at the Central Plains Experimental Range (CPER) of the United States Department of Agriculture-Agricultural Research Service located in northcentral Colorado ≈60 km northeast of Fort Collins (40°49′ N, 107°47′ W). Mean (± SD) annual precipitation is 311 ± 79 mm, and mean monthly temperatures range from −5°C in January to 22° in July. The topography consists of flat uplands and lowlands connected by gentle slopes. The vegetation is typical of the shortgrass steppe. Basal cover of all plants ranges from 25 to 40% of which 85-90% is *Bouteloua gracilis*. A number of grasses, succulents, half-shrubs, and forbs account for the remainder. Moderate grazing by cattle occurs throughout the site. Lightly (1.4 ha·yearling⁻¹·month⁻¹), moderately (1.1 ha·yearling⁻¹·month⁻¹), and heavily (0.7 ha·yearling⁻¹·month⁻¹) grazed pastures have been maintained since 1939. These average stocking rates represent an average of 20, 40, and 60% removal, respectively, of the standing crop over a 6-mo period during the growing season (Klipple and Costello 1960).

METHODS

The effects of disturbance size and frequency on *Bouteloua gracilis*–dominated plots were evaluated using a spatially explicit simulation model. Plots were simulated for each combination of three topographic positions (uplands, slopes, and lowlands) and three grazing intensities (light, moderate, and heavy). The disturbance types included were cattle fecal pats, western harvester ant mounds (*Pogonomyrex occidentalis* [Cresson]), and burrows of small animals (including skunks, badgers, and pocket gophers). Although the specific disturbance agents associated with these disturbance types differ, each produces a patch in which *B. gracilis* tillers are killed. The low stature of *B. gracilis* plants guarantees that the portion of the plant beneath a fecal pat is unlikely to survive. Western harvester ants remove all of the vegetation from their mound, and small burrowing animals produce a mound of soil at the surface that covers and kills the vegetation.

Bouteloua gracilis *size distributions and cover*

The sizes of individual *B. gracilis* plants were measured in five 4-m² quadrats randomly located in each of the three topographic positions in a heavily grazed pasture. An individual *B. gracilis* plant was defined as all tillers currently connected by a crown. Topographic position was expected to have a greater effect on plant size than was grazing regime: cattle behavior patterns within a grazing regime, and hence the potential effects of grazing on plant size, have been found to be strongly related to topographic position (Senft et al. 1985), and

estimates of grazing intensity (reflected in fecal pat deposition rates, see Table 1) based on stocking rates and cattle behavior patterns were more similar among grazing treatments within a topographic position than among topographic positions within grazing treatments (Klipple and Costello 1960, Schwartz 1977, Senft 1983). Therefore, we assumed that the size distributions of *B. gracilis* in each topographic position were similar in the lightly and moderately grazed pastures to those in the same topographic position in the heavily grazed pasture. The average *B. gracilis* cover for each topographic position in the heavily grazed pasture was calculated by averaging the cover values of the field quadrats. Cover values were calculated for the lightly and moderately grazed pastures from comparable data from Gill (1985) for similar sites in the same three pastures.

Determination of disturbance sizes and frequencies

Fecal pats were measured in randomly located quadrats in the heavily grazed pasture from the same sites in which plant size was measured. We assumed that ≈300 pats would be necessary to describe adequately each size distribution; therefore, the number of 400-m² quadrats required depended on the density of pats in each topographic position. We assumed that size distributions were similar in a particular topographic position in all three grazing treatments. The frequencies of fecal pat deposition were estimated in each topographic position under each grazing regime using average stocking rates (Klipple and Costello 1960) and data on excretion rates, behavior patterns, and time spent in each topographic position (Schwartz 1977, Senft 1983). We assumed that cattle behavior patterns and excretion rates were comparable among grazing treatments.

The size distribution of western harvester ant mounds was obtained by measuring all full-size mounds in a 2.5-ha lightly grazed upland. Size distributions were assumed to be similar for all topographic positions and grazing treatments since a previous study had found that average mound size was not affected significantly by grazing treatment (Rogers and Lavigne 1974), and field observations indicated similar mound sizes among topographic positions within each grazing treatment. The total number of mounds at different stages of development in the lightly grazed upland pasture was used to estimate the frequency of occurrence. Mound construction involves three stages in which the size of the mound increases through time until the full-size stage is reached (Cole 1932). An analysis based on the number of mounds in each stage and the approximate length of time a mound will remain in each stage was used to estimate the number of new mounds, initiated each year, that would become full-size mounds. Relative frequencies of occurrence for the moderately and heavily grazed pastures were estimated using density data for these pastures from Rogers and Lavigne (1974)

by assuming stable mound densities through time. The frequencies of occurrence of ant mounds were assumed to be similar for each topographic position within each grazing treatment since the density data from Rogers and Lavigne (1974) were obtained by pooling across topographic positions, and field observations indicated similar frequencies of occurrence of mounds among topographic positions within each grazing treatment.

Due to the relatively infrequent occurrence of small animal burrows, the size distribution was obtained by measuring burrows in the three grazing treatment pastures and pooling across treatments and topographic positions. The number of burrows produced over a 2-yr period on a 2.5-ha moderately grazed upland was used to estimate the frequency of occurrence of burrows. Field observations indicated that soil texture, not grazing treatment or topographic position, may be the most important factor determining the size and location of a burrow.

Construction of simulations

Fifteen replicate plots were simulated for each of the nine grazing regime–topographic position combinations. Each 9-m² plot was simulated by a 101 × 101 point grid (a distance of 3 cm between points). *Bouteloua gracilis* plants were randomly selected from one of the field-estimated size class distributions. Seven size classes of rectangular plants from 18 to 648 cm² were used in the simulation. The use of size classes of plants resulted in the model being relatively insensitive to the assumption of similar plant size distributions across grazing treatments within a given topographic position, since large differences in the field-estimated size distributions would be necessary for the distributions to be represented by significantly different size class distributions, and for a significant effect on the results. Each plant was assigned to a set of contiguous points. For example, a 648-cm² plant consisted of a set of 7 × 13 points, that is, an 18 × 36 cm rectangle. Plants were randomly positioned in the simulated plot with two restrictions: the entire plant must be contained within the plot, and the plant must not overlap other plants. Plants were added to each plot until a critical cover value was reached. Critical cover values were drawn from normal distributions with the means and standard deviations estimated as described above.

Each disturbance was represented by a square of contiguous points whose size was randomly selected from the sizes of disturbances of that type measured in the field. Although only one ant mound or animal burrow constituted an event, more than one fecal pat was possible for each excretion event. Each disturbance event was positioned randomly within the plot, except that overlap was not allowed between disturbance types or events except for the potential overlap of pats within one event.

The amount of each *B. gracilis* plant covered by each disturbance event was determined. The number of plants killed was estimated by assuming that 100% of the plant must be hit for the plant to be killed; an indirect hit merely reduced its size. This assumption is supported by field observations of fecal pats of a variety of ages. The cover was reduced by the portion of the plant under the disturbance. The total amount of cover lost and number of plants killed in the plot were calculated. The average amount of disturbed area and the average number of plants killed were calculated after 100 events for each disturbance type on each plot. The 100 events represent simulations ranging from 400 to 6700 yr (fecal pats), 69 000 to 716 800 yr (ant mounds), and 222 200 yr (burrows). The values were then averaged over the 15 plots for each of the nine locations.

Relative turnover rates (in percent per year) were calculated as: the percentage basal cover affected per year and the percentage of the number of plants killed per year. Turnover rate is therefore very closely related to the relative area affected by disturbances (i.e., the relative amount of disturbed area). These two variables will not take identical values due to the variation introduced by the simulation model. The relative area affected by disturbances will also differ from the turnover rate of plants (but not the turnover rate of cover) for another reason. For a given area affected by disturbances, the smaller the size of each disturbance event, the fewer the plants that will be killed: as disturbance size decreases, the ratio of perimeter length to surface area increases, resulting in more plants that are only partially covered and therefore will survive. At one extreme, some fecal pats may cover no plants completely, and result in no deaths.

RESULTS

Size distributions and occurrence

Size distributions of *B. gracilis* plants were similar for the three topographic positions (Fig. 1). Average plant sizes were 134 cm² (uplands, $n = 360$), 118 cm² (slopes, $n = 288$), and 142 cm² (lowlands, $n = 344$). The highest cover value for each grazing treatment was found in the lowlands, with no differences between treatments, while the lowest value occurred in the uplands under the heavy grazing regime (Table 1).

Average sizes of fecal pats were 134 cm² (uplands, $n = 329$), 167 cm² (slopes, $n = 295$), and 190 cm² (lowlands, $n = 432$), overlapping the size range of *B. gracilis* plants (Fig. 1). Within each grazing treatment, cattle tend to spend more time in lowlands than on slopes or uplands (Schwartz 1977, Senft 1983), which is reflected in the estimated numbers of fecal pats at each topographic position within a grazing treatment (Table 1). The number of fecal pats also increased as grazing intensity increased.

Ant mounds and animal burrows were always larger than *B. gracilis* plants. The sizes of mature ant mounds were approximately normally distributed (mean ± SD
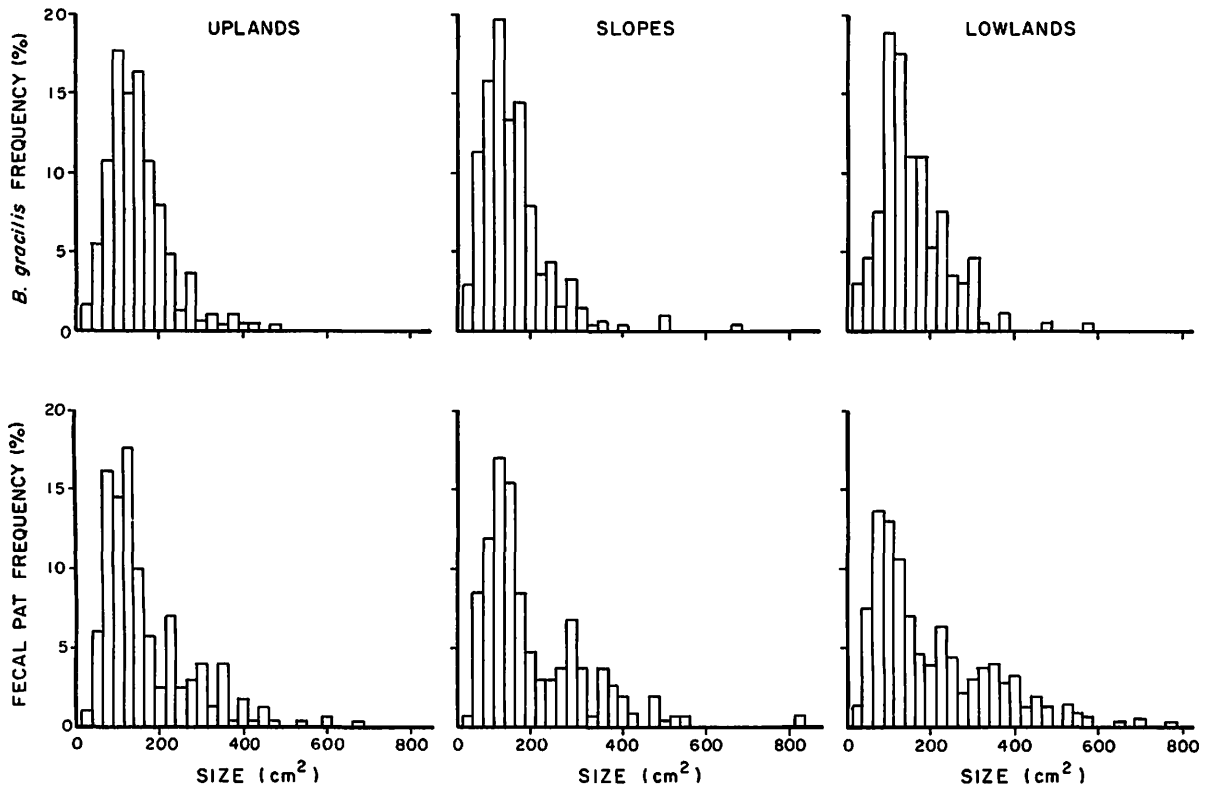
FIG. 1. Size distributions for *Bouteloua gracilis* and fecal pats for uplands, slopes, and lowlands in a heavily grazed pasture.

$= 1.4 \pm 0.28$ m², $n = 62$). The frequency of mound occurrence varies with grazing treatment: 0.16 (heavy), 1.5 (light), and 1.6 mounds·ha⁻¹·yr⁻¹ (moderate) (Rogers and Lavigne 1974). The sizes of animal burrows were approximately uniformly distributed between 1.0 and 2.0 m² ($n = 10$) with a frequency of 0.5 burrows· ha⁻¹·yr⁻¹.

Effects of disturbances

The relative importance of disturbance type to turnover rates was related to disturbance size and topographic position. The smallest disturbance type (fecal pats) affected the largest area each year in most sites because fecal pats were so abundant. However, the plant turnover rates for a given amount of area affected were always less for fecal pats than for mounds or burrows because fecal pats were smaller and so were less likely to cover plants entirely (see Methods).

The effect of fecal pats and ant mounds on the turnover rate of *B. gracilis* populations was primarily a function of frequency of occurrence, since the measured size distributions of fecal pats were similar across topographic positions and were assumed to be similar across grazing treatments, and ant mounds were assumed to have a constant size distribution (Figs. 2 and 3). Estimated reductions in plant cover ranged from a low of 0.0429 m²·ha⁻¹·yr⁻¹ due to ant mounds under conditions of heavy grazing to a high of 6.3 m²·ha⁻¹· yr⁻¹ due to fecal pats in heavily grazed lowlands. The

corresponding turnover rates were 0.00002–0.00205%/ yr. The estimated average number of plants killed per year per hectare ranged from 2.8 (ant mounds) to 95.2 (fecal pats), resulting in turnover rates for plants of 0.00002–0.00047%/yr. Animal burrows were assumed to have a constant frequency of occurrence and a constant size; their effect therefore varied only with plant cover. On the average, animal burrows reduced plant cover by 0.20 m²·ha⁻¹·yr⁻¹ and killed 13.5 plants·ha⁻¹· yr⁻¹. Average turnover rates due to animal burrows were 0.00008%/yr (cover) and 0.00006%/yr (number).

The number of plants killed by each disturbance type is a conservative estimate based on the assumption that the entire plant must be hit for the plant to be

TABLE 1. Average percent cover of *Bouteloua gracilis* and estimated frequencies of occurrence of fecal pats for three topographic positions and three grazing intensities.

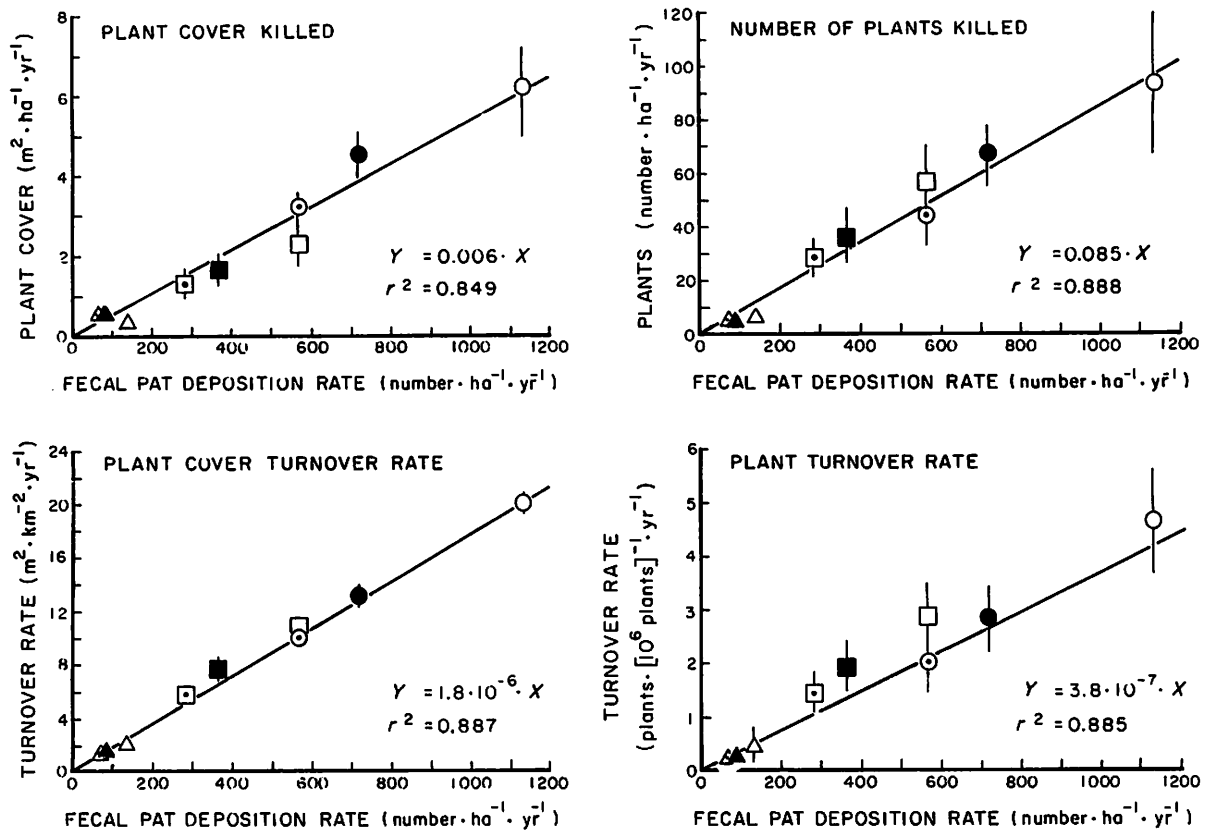| Grazing intensity	Topographic position		
	Uplands	Slopes	Lowlands
Average *B. gracilis* basal cover (%)			
Light	27	23	30
Moderate	27	23	34
Heavy	19	23	31
Estimated fecal pat deposition rate (pats·ha⁻¹·yr⁻¹)			
Light	67	284	569
Moderate	84	360	724
Heavy	133	567	1138

FIG. 2. Amount of basal cover and number of *Bouteloua gracilis* plants killed per year as a function of fecal pat deposition rate with corresponding turnover rates. Symbols represent the average value of the 15 replicate plots and the associated lines represent the range in values. (Location by grazing intensity and topographic position: Heavy: O lowlands, □ slopes, △ uplands; Moderate: ● lowlands, ■ slopes, ▲ uplands; Light: ⊙ lowlands, ⊡ slopes, △ uplands). Regressions are based on 135 points (15 replicates of each of the nine grazing intensity–topographic position combinations).

killed. The level of coverage required to kill a *B. gracilis* plant most likely depends on the environmental conditions following the disturbance since a given reduction in size probably causes a larger increase in the probability of death when conditions are adverse. Incorporating the death of partially disturbed plants would increase the estimated turnover rates, especially for fecal pats. Most of the time, pats only partially covered *B. gracilis* plants while ant mounds and animal burrows completely covered most of the plants they hit.

The number of plants killed may also be affected by the assumption of similar plant size distributions among grazing treatments within each topographic position. If the sizes were significantly smaller than used in the simulations then more plants would be killed, while if the sizes were significantly larger then fewer plants would be killed than were killed in the simulations.

The turnover rates for the three disturbances were combined to estimate the total turnover rate for the plot (Fig. 4). The average estimated turnover rates for plant cover ranged from 0.00028 to 0.00213%/yr; turnover rates for number of plants were 0.00011 to 0.00051%/yr. Turnover rates would decrease if disturbances were allowed to overlap within a simulated

plot, although the effect of overlap is not expected to change the results significantly.

Relative importance of disturbance types

As described above, the three types of disturbances differed in size distributions and in frequency, and in some cases differences in these characteristics were found or estimated among topographic positions and among grazing treatments for a particular type of disturbance. The effects of these differences are summarized by the estimated turnover rates (Fig. 5). In all but upland sites, fecal pats were responsible for the largest part of the total turnover of cover, and a substantial part of the turnover of individual plants.

Topographic position was more important than grazing intensity in determining the effects of these three types of disturbances (Fig. 5). The rates of plant cover turnover were higher on lowlands and slopes than on uplands. The heavily grazed pasture had the lowest plant turnover rates in the uplands; grazing regime did not have a large effect elsewhere. The relatively small turnover rates of the heavily grazed uplands is the result of the low occurrences of ant mounds
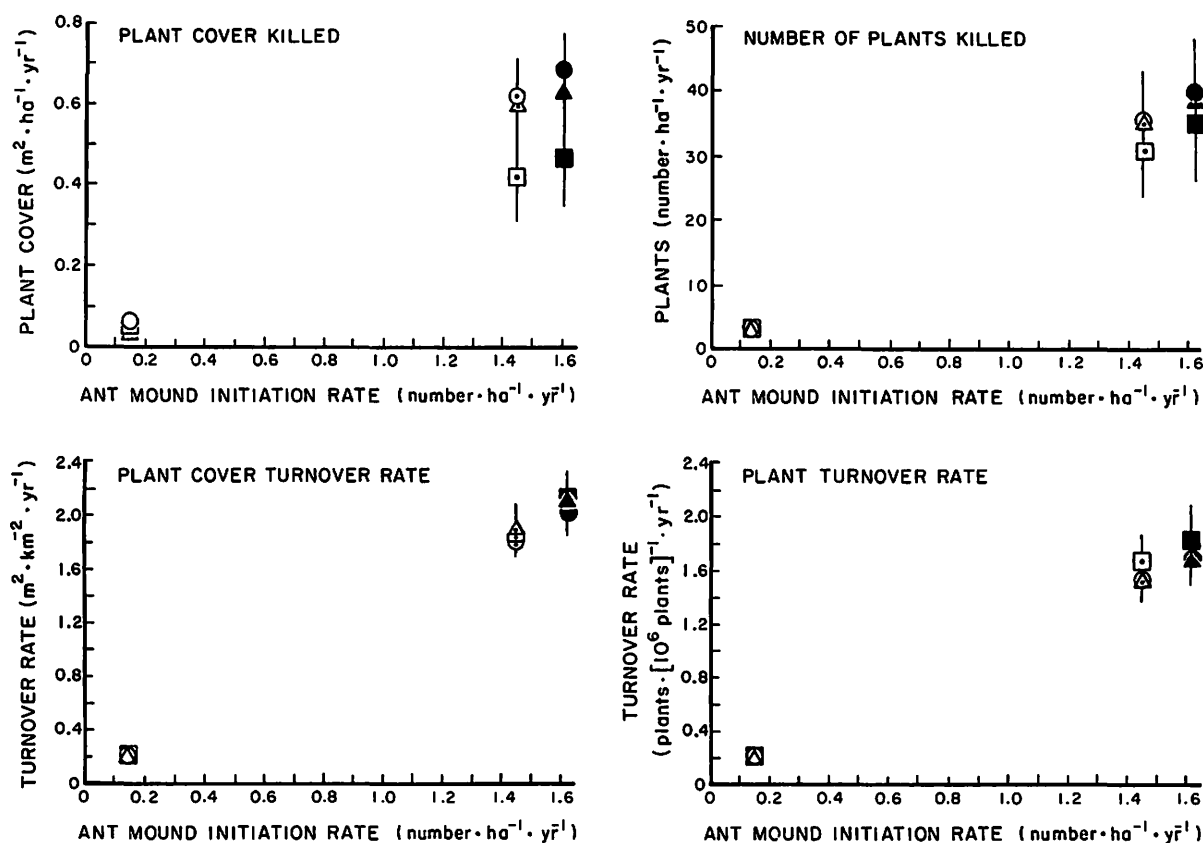
FIG. 3. Amount of basal cover and number of *Bouteloua gracilis* plants killed per year as a function of the rate of initiation of western harvester ant mounds, with corresponding turnover rates. Symbols as in Fig. 2.

in the heavily grazed pasture and of fecal pats in upland positions.

The importance of topographic position rather than grazing treatment on the contribution of fecal pats to the total turnover rates was a result of the different frequencies of occurrence of pats among topographic positions within a grazing treatment rather than the effects of pat size; the measured size distributions were similar across topographic positions and were assumed to be similar across grazing treatments. The greater contribution by ant mounds and animal burrows in uplands relative to other locations is an indirect result of the relatively infrequent occurrence of fecal pats in upland sites; the size distributions of mounds and burrows were assumed to be constant while the frequencies of occurrence of mounds and burrows were assumed to be similar for all topographic positions within a grazing treatment.

DISCUSSION

An important characteristic for a disturbance in the shortgrass steppe is its size in relation to the average size of a *Bouteloua gracilis* plant. Disturbances equal to or larger than the average size of a *B. gracilis* plant will have a larger impact per disturbance than smaller disturbances because they will kill plants as well as reduce cover. Furthermore, bigger disturbances have

relatively less perimeter length than surface area, and will kill more plants for the same total area affected (see Methods: Construction of Simulations). Therefore, the effects of a given set of disturbances on cover and on plant numbers are not equivalent (Fig. 5).

The total impact of a disturbance type depends upon its frequency as well as its size, and frequency tends to be inversely related to size. The effect of these small-scale disturbances on the cover and abundance of *B. gracilis* plants was primarily a function of their frequency of occurrence. Size and frequency together determine the total area affected by disturbances.

Disturbance size relative to the size of *B. gracilis* plants distinguished two classes of disturbances: fecal pats were similar in size to *B. gracilis* plants; ant mounds and animal burrows were always larger than *B. gracilis* plants. Neither class of disturbance was consistently more important than the other (Fig. 5). Topographic position was more important than grazing intensity in determining relative turnover rates and the relative effects of the different disturbances on *B. gracilis* cover and abundance.

Factors not included in this study may be important in determining the frequency and effects of ant mounds and animal burrows. Localized concentrations of mounds and burrows are known to occur, most likely as a result of local environmental conditions related to
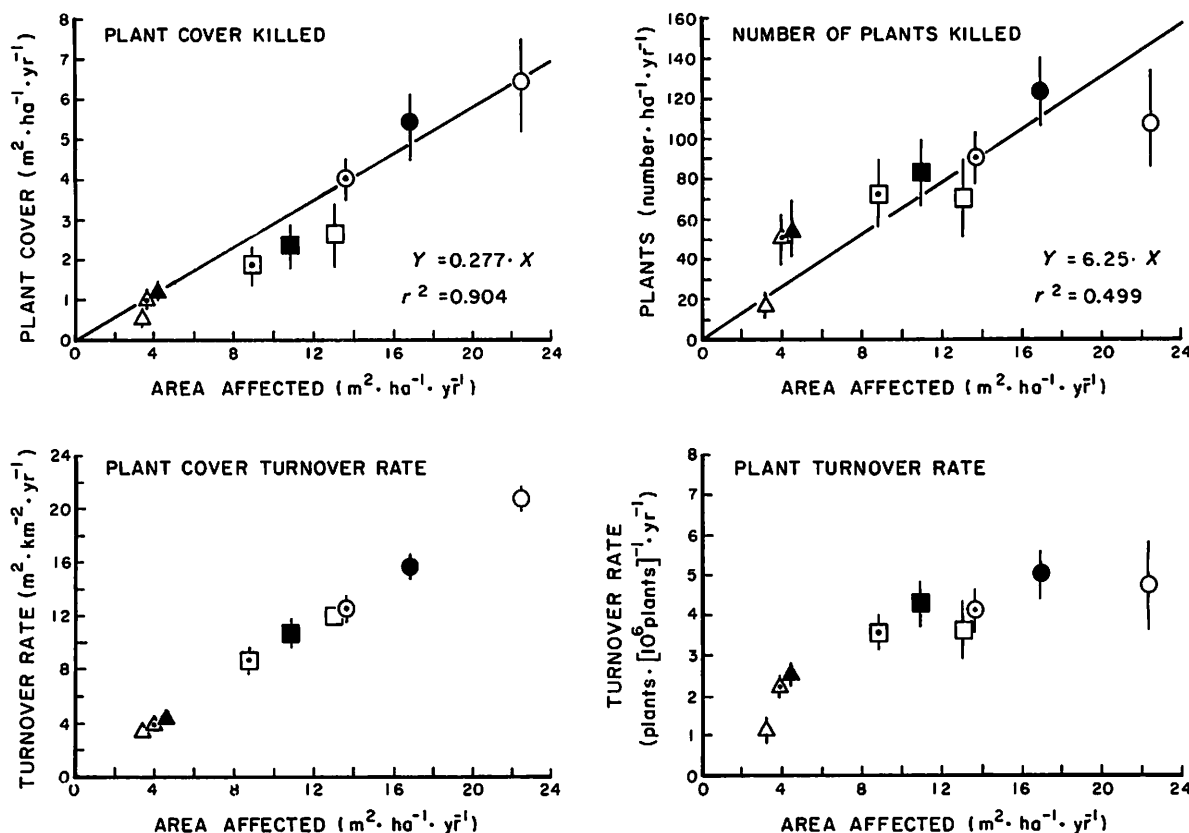
FIG. 4. Amount of basal cover and number of *Bouteloua gracilis* plants killed per year by fecal pats, ant mounds, and animal burrows combined as a function of the total area affected per year, with corresponding turnover rates. Symbols and regression basis as in Fig. 2.

soil texture. A field study conducted at the CPER in several locations of high pocket gopher densities reported that a much larger area was affected by the mounds (6%/yr: Grant et al. 1980) than was estimated in this study (0.0084%/yr). The effects on the vegetation would be more pronounced in these areas resulting in larger turnover rates than those determined from our conservative estimates of numbers of burrows.

Most of the information about responses to and recovery from disturbances in the shortgrass steppe region of North America is based on large disturbances, such as abandoned agricultural fields (Savage and Runyon 1937, Judd and Jackson 1939, Costello 1944, Judd 1974, Reichhardt 1982). These studies suggest that reestablishment of *B. gracilis* occurs very slowly after a disturbance or not at all (Riegel 1941, Hyder et al. 1971, Briske and Wilson 1977), and that a large-scale *B. gracilis* establishment event has not occurred in the past 50 yr (Reichhardt 1982).

It has therefore been suggested that *B. gracilis* may have become established under a previous climatic regime in which environmental conditions frequently favored the germination and establishment of seedlings. Alternatively, it has been hypothesized that infrequent, large-scale *B. gracilis* establishment events occur with

a sufficiently high frequency to enable the population to maintain its dominance through time. Studies have indicated that a restrictive set of environmental conditions based on soil water and temperature must be present for *B. gracilis* seedling germination and establishment (Briske and Wilson 1977, 1978, Wilson and Briske 1979). Under these hypotheses, *B. gracilis* dominance must be maintained by frequencies of disturbance that are very low.

If either of the above hypotheses were correct, *B. gracilis* cover should decrease each year as the effects of disturbances accumulate. In the first case the decrease in *B. gracilis* cover would be uninterrupted, and in the latter case *B. gracilis* cover would increase only after a rare establishment event. In addition, the effects of disturbances on the *B. gracilis* population should be dependent on disturbance rate. For example, in lowland sites the loss of cover should be faster where stocking rates are higher, since disturbance rates are higher there (Fig. 5). Calculations of the area disturbed by the three small disturbances included in this study (fecal pats, ant mounds, and animal burrows) indicate that the basal cover of *B. gracilis* should have declined by 3% during the past 48 yr in lowlands under heavy grazing. However, recent data suggest that basal cover
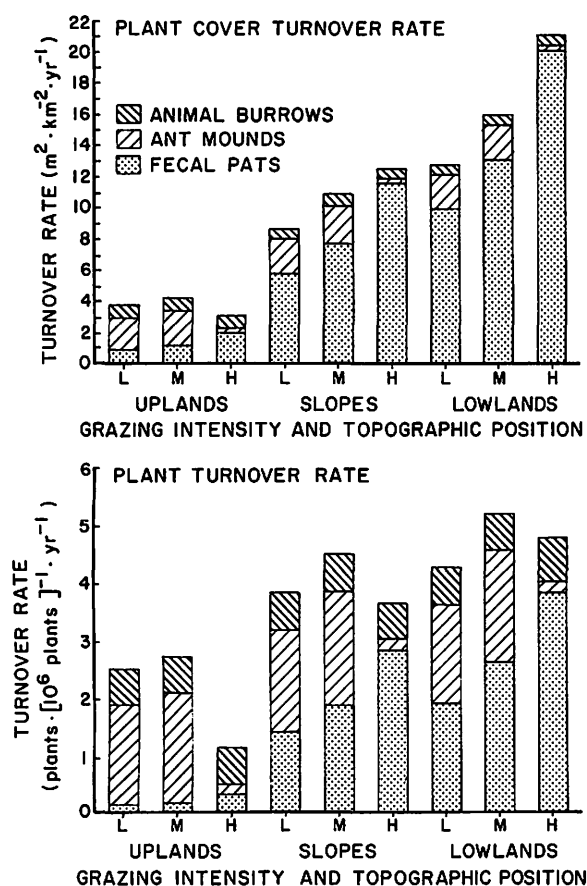
FIG. 5. Average contribution to turnover rates of basal cover and number of *Bouteloua gracilis* plants by each disturbance type for nine locations, by grazing intensity and topographic position. (Grazing intensity: L = light, M = moderate, H = heavy).

is significantly ($P < .05$) higher in grazed lowlands than on adjacent ungrazed lowlands, although ungrazed lowlands receive no fecal pats (the major form of disturbance in grazed swales). The average difference in basal cover between grazed and ungrazed lowlands was 10% (D. G. Milchunas et al. *personal communication*). It is unlikely that tillering alone could account for the observed difference in cover. Therefore, these results suggest that the recolonization potential of *B. gracilis* may differ for different sizes of disturbances. Although infrequent, large-scale establishment events may be necessary for the return of *B. gracilis* after large, infrequent disturbances, the continued dominance of *B. gracilis* indicates that it routinely revegetates smaller disturbances.

Watt (1947) suggested that the removal of a mature individual of the dominant species from a plant community initiated successional processes that he collectively called gap-phase dynamics. If these processes operate in shortgrass plant communities, the removal of an entire *B. gracilis* plant will result in a gap in the resource space and initiate gap-phase dynamics. Patch-producing disturbances that are always larger than *B.*

gracilis plants tend to occur less frequently than disturbances comparable in size to *B. gracilis* plants, although they may have a longer lasting effect because they always require the establishment of new *B. gracilis* individuals.

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A GENERALIZED MODEL OF THE EFFECTS OF GRAZING BY LARGE HERBIVORES ON GRASSLAND COMMUNITY STRUCTURE

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Why are certain plant communities very sensitive to grazing by large generalist herbivores and others not? Current models that relate predation, competition, or disturbance to community structure do not always answer this question or provide predictions consistent with data from grazing studies. A key element missing from current models is the evolutionary history of plant-herbivore interactions. The evolutionary history of grazing has had a large impact on the physiognomy of grasslands and on their ability to support grazing (Mack and Thompson 1982). The evolutionary history of grazing is not, however, a good single explanatory variable for the response of grassland communities to grazing. Very different, even opposite, responses to grazing occur within communities with either short or long evolutionary histories of grazing. We develop a model based on environmental moisture and the evolutionary history of grazing that explains grazer-grassland interactions over a wide range of communities.

The current models that do not adequately explain the response of grassland plant communities to grazing by large generalist herbivores are the predation hypothesis (Paine 1966, 1971), the intermediate-disturbance hypothesis (Grime 1973; Horn 1975; Connell 1978; Fox 1979), and the Huston hypothesis (1979, 1985). The predation hypothesis suggests that local prey diversity increases when predators prevent dominant species from monopolizing resources. The intermediate-disturbance hypothesis proposes a bell-shaped response of species importance along a stress gradient. Diversity is limited by stress at one extreme and by competitive exclusion at the other. Huston's model adds the important component of the reaction to, or recovery from, the disturbing force. Species diversity is related to "the dynamic balance . . . between the rate of competitive displacement and the frequency of population reduction," or population growth rates and disturbance intensity (Huston 1979, p. 97). The action and the reaction thus define the dimension of a window of relaxed competitive interactions after disturbance.

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The problems associated with applying the Huston model to grazing are twofold. First, numerous, very different types of disturbances are lumped together on a single axis. Grazing may or may not be a disturbance for a plant community depending on its evolutionary history. Thus, Huston's disturbance axis must be redefined as one proceeds along an evolutionary-time axis. Second, we show that interactions occur along gradients of environmental moisture and of the evolutionary history of grazing. These interactions influence not only the window of relaxed competition but also the manner in which the competitive relationships are expressed.

We first define terms and set bounds on the model. Second, we briefly review the state of knowledge of the effects of grazing on community structure and integrate these within the context of the gradients of moisture and of the evolutionary history of grazing. Third, we present a model of the effect of grazing on grassland community structure and present quantitative evidence that supports the model. Finally, we discuss the relationship of our model to other hypotheses.

<center>DEFINITIONS AND BOUNDS OF THE MODEL</center>

Grasslands can be categorized as climatically determined, successional, or agricultural (Lauenroth 1979). Climatically determined grasslands occur in areas having a period during the year when the availability of soil water falls below the requirements for forests yet is sufficient to sustain grasses (Poaceae) as the dominant or major component of vegetation. Here we consider savanna and shrub steppe (or the ecotone between grassland and forest) as climatically determined grassland. This category encompasses the potential natural vegetation of 25% of the earth's land surface (Shantz 1954); these areas receive 250–1000 mm of annual precipitation and have mean annual temperatures between 0° and 26°C (Lauenroth 1979). Successional and agricultural grassland, which often result from the removal of the original forest vegetation, are maintained by agronomic or other management practices. Most of the grasslands in Great Britain, Europe, Japan, eastern North America, and areas of Australia and Asia are successional or agricultural grasslands.

We constrain our model to climatically determined, nonanthropogenic grasslands because (1) the model is concerned with global-regional areas rather than small, isolated grasslands; (2) anomalies to the model may result from various management practices that override or mask the usual plant-animal interactions; and (3) the interactions that we describe between environmental moisture and the evolutionary history of grazing depend on the relationship between aboveground net primary production (ANPP) and measures of environmental moisture such as mean annual precipitation (Lauenroth 1979; Sala et al. 1988) or actual evapotranspiration (Rosenzweig 1968; Webb et al. 1978). The environmental-moisture axis of our model is thus interchangeable with ANPP. We speak primarily in terms of environmental moisture because we are concerned with plant adaptations. We term grasslands at the low end of the environmental-moisture range as *semiarid* and those at the high end as *subhumid*.

The effect that an herbivore has on plant community structure depends in part

on its level of diet selectivity. Plant community structure can be affected quite differently by generalist herbivores and by specialist herbivores, depending on whether the specialist consumes competitively dominant or competitively inferior species (Lubchenco 1978). Our model applies to generalist herbivores. We examine studies across a wide range of grasslands where grazing by a large generalist ungulate or an assemblage of several more-specialized ungulates exerts a relatively uniform grazing pressure across plant species. The effects of these large ungulates are addressed conceptually in terms of herbivory, not in terms of the effects that they may have on community structure through other activities such as wallowing, trampling, and urine or fecal deposition.

Definitions of disturbance have been based on alterations in the level of competitive interactions (Grime 1973; Connell 1978; Huston 1979), changes in species composition (Sousa 1984; Loucks et al. 1985), forces counter to past selection pressures, or equilibrium–domain-of-attraction models (Holling 1973). All definitions of disturbance are wrought with ambiguities and complexities and lack objectivity (Connell and Sousa 1983; Sousa 1984). The model that we present raises questions about using the above definitions in the context of grazing, and it raises questions in addition to those presented by Connell and Sousa (1983) and Sousa (1984). We present part of our model in a form analogous to the Huston model and to the intermediate-disturbance hypothesis for three reasons: (1) these models are widely used; (2) gradients in level of disturbance or level of grazing are intuitively appealing; and (3) contrasting our model of grazing with disturbance models raises further questions about a proper definition of disturbance in terms of grazing. In the context of these models, we must temporarily adopt the definition of disturbance presented in Sousa: "[A] disturbance is a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established" (1984, p. 356).

GRADIENTS OF MOISTURE AND OF THE EVOLUTIONARY HISTORY OF GRAZING: THE EFFECT ON GRASSLANDS' RESPONSE TO GRAZING

Convergent and Divergent Selection

The origin of nonanthropogenic grasslands is associated with regional climatic shifts toward aridity (Singh et al. 1983). Increasing specialization and adaptations to dry conditions among grasses occurred simultaneously with the development and radiation of large ungulate grazers (Stebbins 1972, 1981; Raven and Axelrod 1974). Consequently, ascertaining the original adaptive values of the traits is difficult (Gould and Lewontin 1979). Regardless of their origin, adaptations that enhance survival in semiarid environments may promote tolerance or avoidance of grazing. Coughenour (1985) discussed how basal meristems, small stature, high shoot density, deciduous shoots (high turnover), belowground nutrient reserves, and rapid growth allow grasses to evade or to tolerate both semiarid conditions and grazing.

Water stress and grazing stress are similar in that both periodically result in

partial or total loss of organs. Tolerance to one necessarily includes tolerance to the other. Both drought and herbivory provide selection pressures to minimize the impact of the loss of individual plant organs (Orians and Solbrig 1977; Mooney and Gulmon 1982; Coughenour 1985). With respect to avoidance, the same characteristic that enables a plant to evade grazing can act to conserve or more effectively use moisture. For example, basal meristems, protected by basal sheaths, may better withstand drought as well as avoid grazing (Stebbins 1972; Barlow et al. 1980; Coughenour 1985). Expression of these characteristics increases with decreasing moisture and with an increasingly long evolutionary history of grazing, and there is an interaction of environmental moisture with grazing history. Thus, selection pressures in semiarid grasslands that have coevolved with large ungulate grazers are convergent. In this context, a convergent selection pressure is one that results in complementary effects on the plants' water-use efficiency and on response to herbivory.

In contrast, adaptations to grazing are divergent from other adaptations for survival that have evolved in species of subhumid grasslands. The moisture gradient from shortgrass steppe to mixed-grass prairie to tallgrass prairie in North America concurrently traverses gradients of low to high productivity, of short to tall stature in grasses, and of sparse to dense canopies with low to high competition for light. Tall growth forms, with relatively greater investment in aboveground rather than belowground production (Sims and Singh 1978), are adaptations that enhance the grasses' competitiveness for light but make them more vulnerable to grazing by large herbivores.

Competition and Regrowth

Current models predict an increase in diversity at intermediate levels of disturbance as a result of a reduction in competitive exclusion. However, plants respond to grazing in ways that may not necessarily decrease competition. In addition to reducing competition, grazing can change the relative importance of the mode of competition and can influence the longevity of the change in competitive relationships after the grazing event. These responses include regrowth and horizontal tillering or spread by rhizomes and stolons. Increased tiller numbers and regrowth of a grazed tiller have different effects on community structure, the subsequent mode of competitive relationships, and a plant's subsequent susceptibility to further herbivory.

Tillering response to grazing depends on the growth form and the grazing history of the species. Stimulated tillering or activation of rhizomes is more likely to occur among short-statured species (McNaughton et al. 1983; McNaughton 1984; Coughenour et al. 1985a). Rhizomatous or stoloniferous grasses are more prevalent in grasslands with long evolutionary histories of grazing (Mack and Thompson 1982). Unlike intermediate-height grasses and tallgrasses with a short grazing history, those with a long history of grazing may, however, produce many new tillers in response to defoliation (Caldwell et al. 1981; Hodgkinson et al. 1985). The total basal cover of grasslands grazed over a long period may increase or remain unchanged compared with basal cover in adjacent exclosures (Weaver and Albertson 1936; Costello and Turner 1941; Ellison 1960; Vogel and Van Dyne

1966; Pieper 1968; Thornton 1971; Holechek and Stephenson 1983; McNaughton 1984).

Competition need not be decreased by intermediate levels of grazing. In the shortgrass steppe and in the Serengeti, grazing increases tillering and spread by rhizomes and stolons, which does not result in reduced competition (McNaughton 1983b, 1984; Lauenroth and Milchunas, unpubl. data). Thus, grazing may not change competition for soil resources in communities with grazing-tolerant species, or it may shift the mode of competition from canopy resources to soil resources, depending on the intensity of grazing and on the proportions of tall, intermediate-height, and short grasses and of tolerant and intolerant grasses in the community. In contrast, tillering responses to grazing in communities of grazing-intolerant species are less well developed, rhizomatous and stoloniferous species are not prevalent, and defoliation results in reduced competitive interactions.

The capacity for regrowth after grazing results, in many cases, from mechanisms that increase the relative availability of resources such as water, nutrients, and light to remaining plants or tissues (McNaughton 1979b, 1983a; Dyer et al. 1982; Deregibus et al. 1985; Sterner 1986). This indicates the presence of a temporal window of relaxed competitive interactions. The degree and rate of regrowth influences the degree and longevity of competitive relaxation. Slower regrowth means that a given level of disturbance creates a longer temporal window (Huston 1979). Therefore, less frequent or lower levels of defoliation are necessary to achieve a given change in a slowly regrowing community, and the opportunity for establishment of invader species is greater. The degree and rate of regrowth is relatively greater in short species and in grazing-tolerant species (McNaughton et al. 1983; Wallace et al. 1984; Coughenour et al. 1985a,b; Richards and Caldwell 1985).

<div align="center">THE MODEL</div>

Selection pressures resulting from grazing and from environmental moisture through evolutionary time are two important forces that have shaped the present structure (composition and physiognomy) of grasslands and their relative abilities to withstand grazing (fig. 1). The action of grazing results in both injury to individual plants and changes in community physiognomy. The community reacts to the grazing event directly by death or by regrowth in response to injury and indirectly by a regrowth response to the altered physiognomy. The mode and magnitude of the grazing action and of the community reaction are functions of the past history of the community; these actions and reactions feed back to become part of the history of the community (fig. 1).

Environmental moisture and the evolutionary history of grazing are continuous variables that intersect to form a two-dimensional space exemplified by four extreme cases. The response of plant communities to grazing is mediated through an interaction of convergent or divergent selection pressures along the moisture gradient and factors relating to a tolerance or an intolerance of grazing along the evolutionary-history-of-grazing gradient.

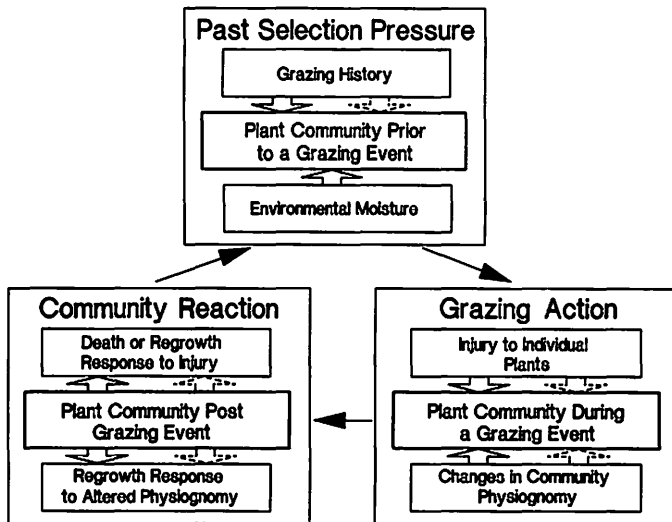We have chosen data sets from areas representing the four boundary cases of

Past Selection Pressure

| Grazing History |

| Plant Community Prior to a Grazing Event |

| Environmental Moisture |

Community Reaction

| Death or Regrowth Response to Injury |

| Plant Community Post Grazing Event |

| Regrowth Response to Altered Physiognomy |

Grazing Action

| Injury to Individual Plants |

| Plant Community During a Grazing Event |

| Changes in Community Physiognomy |

FIG. 1.—Illustration of past selection pressures that shape grassland community structure, the effect of grazing during a grazing event, and the plant community response to the grazing event. The force of the grazing actions and the community reactions can be strong (*solid arrow*) or weak (*dashed arrow*) or a mixture of strong and weak within a box, depending on where the community lies along the axes of environmental moisture and of evolutionary history of grazing. The four boundary cases are examined in the text and illustrated in figures 2 and 3.

the moisture gradient and the evolutionary-history-of-grazing gradient. Examples of the response of plant communities to grazing by large generalist herbivores in grasslands with long evolutionary histories of grazing are examined for the semiarid North American shortgrass steppe and the subhumid grasslands of Africa (table 1). The bunchgrass steppe region of the northwestern United States and the Patagonian steppe represent the semiarid grasslands with short histories of grazing, and the pampa region of Argentina the subhumid grasslands (table 1). We present the model and the experimental evidence for each of the four boundary cases. Finally, we suggest how the model behaves for grasslands between these four boundary cases, and we examine the response to grazing of a grassland that falls outside the definitions of the model.

Semiarid grassland communities with a long history of grazing are dominated by relatively short grasses that have developed in response to the convergent selection pressures of herbivory and semiaridity (fig. 2). Competition is mainly for soil resources. Occupancy of aboveground space is maximized horizontally rather than vertically. Grazing has relatively small effects on community composition and physiognomy because (1) changes in canopy structure are usually insignificant and there is no shift in competitive interactions between soil and canopy resources; and (2) grazing pressures have selected for rapid regrowth following defoliation, thus ensuring a short duration in the relaxation of competitive interactions. The lack of competitive release from the established dominants in the

TABLE 1

CHARACTERISTICS OF GRASSLANDS REPRESENTING THE FOUR BOUNDARY CASES ALONG GRADIENTS OF THE
EVOLUTIONARY HISTORY OF GRAZING AND OF MOISTURE

Grassland Type	Site	Evolutionary History of Grazing Reference	Precipitation ($\bar{x}$ annual, mm)	Above-ground NPP* (g/m^2)	Canopy Height (cm)	Experimental Grazing Intensity†	Years of Treatment	Study
Long history Semiarid	Colorado shortgrass steppe	Stebbins 1981; Mack & Thompson 1982; Coughenour 1985	310	103 ± 23	grazed, 3–5 ungrazed, 5–10	heavy (60%) moderate (40%) light (20%) none	14 24 31 45	Klipple & Costello 1960 Hyder et al. 1966 Hyder et al. 1975 Milchunas & Lauenroth, MS
Long history Subhumid	Serengeti	Raven & Axelrod 1974; Sinclair 1983; Coughenour 1985	500–1000[a]	400–1200[a]	shortgrass[b] grazed, 2 ($\bar{x}$), 3 (max); ungrazed, 12 ($\bar{x}$), 39 (max) mid-height grazed, 9 ($\bar{x}$), 45 (max); ungrazed, 21 ($\bar{x}$), 58 (max)	none ?	12	McNaughton 1979a, 1983b
	Uganda Themeda/ Heteropogon		714	?				Thornton 1971
	Uganda Sporobolus/ Setaria		?	?		none ?	3 24	Spence & Angus 1970 Hatton & Smart 1984
Short history Semiarid	Washington bunchgrass steppe	Osborne 1953; Daubenmire 1970	250	50–70 live biomass		none moderate	4	Rickard 1985
	Oregon bunchgrass steppe	Mack & Thompson 1982; Markgraf 1985		100[c]		none ?	36	Sneva et al. 1984
	Argentina Patagonian arid steppe		138	66		none light heavy	20	Schlichter et al. 1978
Short history Subhumid	Argentina flooding pampa	Stebbins 1981; Markgraf 1985	924	532		none moderate	4	Sala et al. 1986

SOURCE.—a, McNaughton 1985; b, McNaughton 1984; c, Lauenroth 1979.

* Net primary production.

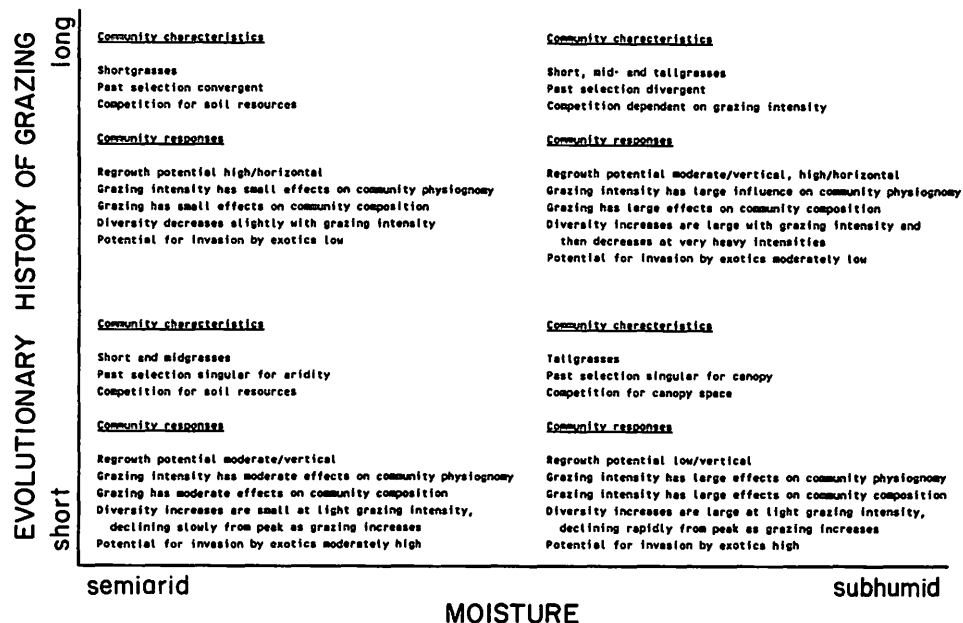† The experimental grazing intensities apply to all studies at each site.

FIG. 2.—Grassland community characteristics and responses to grazing along gradients of moisture and of evolutionary history of grazing.

community reduces the capacity for invasion by exotics. Therefore, the function describing diversity with increasing grazing intensity is linear with a small negative slope (fig. 3). Rare species that are less tolerant of grazing are eliminated as grazing intensity increases, but the major components of the plant community do not shift.

The semiarid shortgrass steppe of the North American Great Plains is dominated by *Bouteloua gracilis* and *Buchloe dactyloides*, two clonal species that are tolerant of drought and grazing and grow to an average height of only 3–10 cm. Long-term controlled-grazing experiments (table 1) were established in north-central Colorado at the Central Plains Experimental Range in 1939 on areas that were not previously overgrazed (Klipple and Costello 1960). No grazing or light-, moderate-, or heavy-grazing treatments did not differ in community composition in 1940–1942, 1946–1948, 1952–1953, or 1962–1963 (Klipple and Costello 1960; Hyder et al. 1966). Sampling from 1964 to 1966 continued to reveal no significant effects of grazing, with only minor alterations detected in 1967–1970 (Hyder et al. 1975). These studies suggest that grazing did not affect plant community composition. Our recent studies of these grazing treatments indicate that subtle changes in community composition are still occurring after 45 years. Basal cover of the dominant grasses and total vegetation increased, whereas those of forbs decreased with heavy grazing. The increase of grasses with grazing was not all at the expense of a decrease in cover of other species because total cover increased. McNaughton (1979a) termed these other grass species *grazophiles*. Diversity (H')
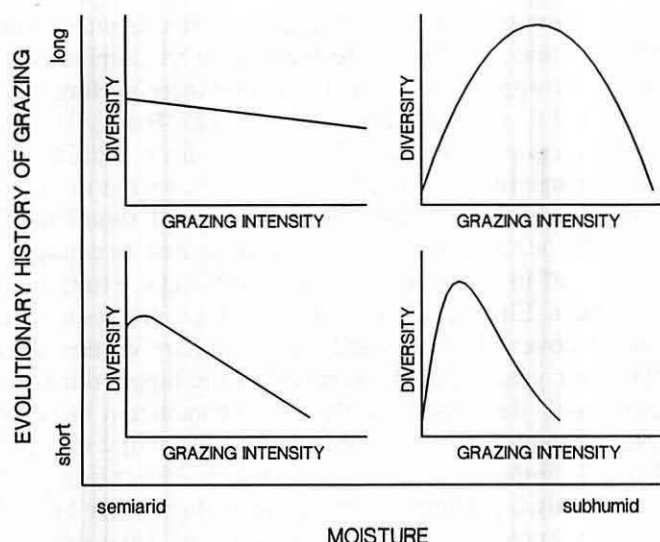
Fig. 3.—Plant diversity of grassland communities in relation to grazing intensity along gradients of moisture and of evolutionary history of grazing. Increments in the diversity axis are equal in all cases, but equal specific values are not implied; that is, relative response, not absolute diversity, is implied.

increased as grazing intensity decreased as a result of both decreased dominance and increased richness.

Subhumid grasslands with a long history of grazing are composed of intermediate-height, short, and tall grasses as a result of divergent past selection for grazing tolerance and canopy dominance (fig. 2). In the absence of grazing, a few tall species dominate the community. Moderate grazing creates a mosaic pattern, with shortgrasses predominating in relatively heavily grazed patches, mixtures of grasses in moderately grazed patches, and tallgrasses where ungrazed growth deters grazing because of high ratios of stem tissues to leaf tissues or dead to live tissues. The mixture of shortgrasses and tallgrasses and, therefore, of canopy structure, regrowth potential, and mode of regrowth by horizontal spread or vertical reestablishment results in a mosaic pattern in the duration of competitive relaxation, in the mode or mixtures of modes of competitive interactions, and in the potential for the establishment of exotics. Diversity is low at low grazing intensities because a few species dominate the canopy (fig. 3). Diversity is high at moderate grazing intensities because of the mosaic of growth forms. With increasingly heavy grazing, diversity declines as shortgrasses dominate a greater proportion of the community.

Changes in community physiognomy and species composition inside and outside grazing exclosures in African grasslands differ from those observed in the shortgrass steppe of North America. McNaughton (1979a, 1983b) assessed vegetation inside and outside 12-yr exclosures in several communities of the Serengeti grasslands and observed that organization and structural properties had changed radically because of protection; in some cases, species composition had changed

almost completely. Low-growing prostrate and short caespitose species domi-
nated heavily grazed areas, whereas protected areas were dominated by "stemmy
species capable of overtopping less erect species and thereby eliminating the latter
by competition for light" (McNaughton 1979*a*, p. 62). Belsky (1986*b*) observed
that mats of *Andropogon greenwayi* disappeared from within an exclosure,
whereas *Pennisetum stramineum* tallgrass, which was sparse in the grazed com-
munity, made up nearly 50% of the cover. The rapid switching from plants
maximizing horizontal occupation of space near the ground to canopy competitors
has also been reported in other African grasslands. The extermination of hip-
popotamuses in Queen Elizabeth National Park, Uganda, resulted in large de-
creases in the basal cover of grasses and increased bare ground after only 1 yr
(Thornton 1971). Four years after the removal of the hippopotamuses the basal
cover of "carpet grass" decreased greatly with a concurrent increase in bunch-
grass cover. Large changes in species composition and canopy structure have also
been reported for *Sporobolus-Setaria* grasslands in Murchison Falls National
Park, Uganda, after only 2 yr (Spence and Angus 1970) or after 24 yr (Hatton and
Smart 1984) of exclosure from grazing. Working in *Themeda* grasslands of
Uganda, Kenya, and Tanzania, Heady (1966) observed that dominance by inter-
mediate-height, tall, or short grasses was not closely related to soils or climate but
was primarily a result of grazing intensity. Tall *Themeda* plants were present and
abundant in parts of each study area, and conversely, even thick stands of
tallgrasses usually contained a few shortgrass individuals. Belsky, however, con-
cluded that "although moisture, grazing, and soil were the major determinants of
vegetational composition at the regional and catenary scales in the Serengeti
ecosystem, termite activity and growth habits of the plants were dominant lo-
cally" (1983, p. 150).

Differences in plant diversity inside and outside of exclosures were observed
for several community types in the Serengeti (McNaughton 1983*b*; Belsky 1986*c*).
Diversity declined in all exclosures. Equitability dropped sharply, although
species richness was not significantly different. McNaughton attributed this to
replacement by tall species in ungrazed areas formerly dominated by short species
when the area had been grazed. Pattern diversity, rather than point diversity, was
found to be the major contributor to stand diversity.

The response of subhumid African grasslands to changes in grazing intensity
contrasts with the response observed in the shortgrass steppe of North America.
Large changes in species composition and community physiognomy occur rapidly
after changes in grazing regimes in African grasslands, whereas changes in the
shortgrass steppe are slow and subtle. In these two grasslands with their long
histories of grazing, grazing has resulted in opposite changes in diversity.

Belsky (1986*a*) raised questions concerning the effects of grazing on compensa-
tory growth of plants. Our model is not based on absolute overcompensation;
rather, it is based on relative differences in rates and modes of regrowth and the
influence of these on competitive relationships among plants. It demonstrates the
difficulty of generalizing along single gradients of environmental moisture or of the
evolutionary history of grazing.

Although often considered semiarid, the driest grasslands of the Serengeti have

nearly double the precipitation and four times the ANPP of the shortgrass steppe (table 1). The shortgrass region of the Serengeti falls between mixed-grass and tallgrass prairies in North America in terms of ANPP and precipitation (see the table; Sims and Singh 1978; Sims et al. 1978), suggesting that this region of the Serengeti would support tall growth forms in the absence of heavy grazing. We have temporarily lumped the Serengeti grasslands (500–1000 mm of precipitation) for the general comparison with the shortgrass steppe, even though we would expect different responses to grazing within Serengeti grasslands. We address this when we describe intermediate locations along the axes of figures 2 and 3.

Semiarid grasslands with a short history of grazing are dominated by short-grasses and intermediate-height grasses that have been selected for their tolerance to drought. Semiaridity limits development of full canopy structure; therefore, grazing has moderate effects on community physiognomy. Since adaptations for drought tolerance also confer some degree of grazing resistance, but regrowth potential is low and does not occur through horizontal spread, changes in commu-nity composition with grazing are moderate. We term changes in physiognomy and composition moderate in this community because they are less than what occurs in the subhumid type with a short evolutionary history of grazing but greater than what occurs in semiarid grasslands with a long history of grazing (figs. 2, 3). The potential for invasion by exotics is moderately high because of the relatively low rate of regrowth by dominants. This community type exhibits a small increase in diversity at low grazing intensities, declining slowly from the peak as grazing intensity increases.

The semiarid regions of the northwestern United States and southwestern Canada are grasslands with a short evolutionary history of grazing (table 1). Before the introduction of cattle, these grasslands were dominated by caespitose grasses and contained few rhizomatous grasses (Tisdale 1947; Daubenmire 1970). The inability of these grasses to cope with heavy grazing allowed the invasion and eventual dominance of many areas by Eurasian weeds (Daubenmire 1940, 1970; Ellison 1960; Mack 1981; Mack and Thompson 1982).

Heavy grazing of the bunchgrass steppe of western North America was exten-sive during the early 1900s. Few areas remained in a relatively undisturbed condition. Community composition in one such undisturbed grassland after 4 yr of moderate grazing was not significantly altered (Rickard 1985). The invasion of exotics occurred only in areas around watering tanks that were heavily grazed and trampled. After 36 yr of moderate grazing and grazing-exclosure treatment in *Artemisia-Agropyron* habitat in eastern Oregon, species composition inside and outside the exclosures showed parallel temporal changes (Sneva et al. 1984). Although these grasslands can be invaded by exotics if heavily grazed, moderate grazing does not produce the large, immediate effects on community composition or physiognomy that are observed in subhumid grasslands. Changes in community structure are, however, much greater than those that occur in semiarid grasslands with long evolutionary histories of grazing.

Changes in diversity with grazing intensity were not reported for studies in the northwestern United States. However, the Patagonian steppe in southern Argen-tina is another example of a semiarid grassland with a short evolutionary history

of grazing (Markgraf 1985). Comparison between 20-yr-old exclosures and areas subjected to light and heavy grazing showed a clear decrease in species number, species diversity, and equitability with grazing intensity (Schlichter et al. 1978).

Subhumid grasslands with a short evolutionary history of grazing have the greatest potential for being altered by grazing (fig. 2). These communities are composed of tallgrasses that do not tolerate well grazing or aridity. In the past, there was primarily a single selection pressure for canopy dominance, but grazing significantly affects canopy structure. Slow rates of regrowth and a lack of flexibility in the modes of regrowth following defoliation result in a high potential for invasion by exotics. The response of inferior canopy competitors to canopy removal and the increase in exotics produce large increases in diversity at relatively low grazing intensities (fig. 3). Diversity declines rapidly thereafter as grazing mortality becomes a relatively greater force than the relaxation of competitive interactions in shaping community composition.

The flooding pampa of Argentina is representative of subhumid grasslands with a short evolutionary history of grazing (table 1). Grazing in this system resulted in a relatively small reduction in total leaf area, whereas the largest response was observed in the distribution of leaves in the canopy (Sala et al. 1986). In the grazed areas, most of the green material was concentrated in the 0–5-cm layer, but in the ungrazed treatments, the largest portion of the leaf area was in the 10–30-cm layer. Many small tussocks characteristic of the grazed areas were replaced by a few large ones in the ungrazed areas. These changes in canopy structure resulted in changes in the microenvironment. The quantity of light reaching the soil surface increased by 50% (Deregibus et al. 1985). The effect of grazing on leaf area and basal cover was accounted for by changes in species composition and in the structure of existing species. After 4 yr of exclosure, cover of grasses and sedges increased, dicot and monocot annuals were replaced by perennials, and exotic species were greatly reduced. Grazed areas had higher diversity than ungrazed areas, primarily because of the greater numbers of forbs. In contrast, reduced dominance by grasses and increased number of forb species were the primary reasons for the greater diversity of ungrazed areas of the shortgrass steppe.

Figures 2 and 3 represent the boundary cases of moisture and grazing history for climatically determined grasslands. Many grasslands are at intermediate locations along the environmental-moisture axis or the axis of the evolutionary history of grazing. Smooth or punctuated, linear or nonlinear transitions from one case, through the intermediate zones of the model axes, to the other case are possible. Changes in plant community response to grazing with increasing environmental moisture are based on the increasing importance of competition for light, the greater potential for a grazing event to alter community physiognomy and for plants to respond to this alteration, and the relatively greater intolerance of grazing by many tallgrasses. The change in model conditions from semiarid to subhumid can be described as a function of canopy development with increasing moisture. We envision this function as a sigmoid curve. Increasing moisture from semiarid conditions would at first involve increases in both basal cover and canopy height. A region of moisture would be reached where small increases would have relatively large effects on light intensity within the canopy. When light

compensation points are reached, additional increments in moisture influence only the length of time in which light within the canopy is below the compensation point. Therefore, the expected rate of change in model conditions from semiarid to subhumid would be parabolic.

In our discussion of African grasslands, we temporarily lumped Serengeti grasslands receiving 500–1000 mm of precipitation for the purpose of general comparison with the boundary case of the semiarid shortgrass steppe. The drier regions of the Serengeti were described as comparable to productive mixed-grass prairies of North America in terms of ANPP and precipitation. In exclosures on shortgrass Serengeti grasslands, canopy heights lie between those for shortgrass steppe and tallgrass Serengeti grasslands (table 1). Greater diversity in grazed areas compared with exclosures has been reported for both shortgrass Serengeti grasslands (McNaughton 1983b; Belsky 1986c) and the mixed-grass prairie of North America (Collins and Barber 1985). Data comparing the response of vegetation to levels of grazing within these grasslands, or between grasslands of different environmental moisture, are not available. On the basis of our model, we predict a diversity curve with a peak that is lower and left-skewed compared with that for the subhumid case with a long history of grazing described in figure 3, and we predict differences in changes in community composition and physiognomy that are intermediate between those described for semiarid and subhumid grasslands with long histories of grazing in figure 2.

The transition in responses to grazing across the evolutionary-history-of-grazing axis in figures 2 or 3 are not easily described. In a review of theoretical models, Roughgarden (1983) examined some of the many factors that may determine the rate and outcome of coevolution in the context of the effect of coevolution on traits that determine how populations interact and on the abundance and distribution of the interacting populations. Roughgarden concluded that "there is a glaring shortage, even absence, of good models for many kinds of coevolutionary situations, including the plant-herbivore and plant-pollinator interactions" (1983, p. 64). Experimental evidence is also lacking. This would require controlled, consistent, multi-intensity grazing experiments across a range of levels of environmental moisture and evolutionary history of grazing. Our inability to predict transitions across the evolutionary-history-of-grazing axis is a weakness of our current model.

Are there examples of climatically determined grasslands that do not respond according to the predictions of our model? Although we do not know of any, two situations are possible. In the first situation, factors other than environmental moisture may operate with the evolutionary history of grazing to determine the response of the plant community to grazing. The exclosure of grazing animals from sugar-limestone outcrops on a plateau summit in England did not result in substantial changes in community structure, even though precipitation is high (Elkington 1981). The sandy, mineral-nutrient-poor soil and low temperatures were the factors contributing to the lack of change in exclosures. This edaphically controlled, isolated grassland occurs in an area that climatically would not be grassland (see Walter 1979). It is possible that the combined effects of semiaridity and a severe mineral-nutrient deficiency in the soil could result in a sparsely

populated community in which competitive exclusion would not occur even in the absence of disturbance. However, substantial evidence indicates that competition among plants is both common and strong enough to be readily detected in dry grassland and even deserts (Fowler 1986). Furthermore, we are not comparing the importance of competition across a moisture gradient. Rather, we are comparing the relative importance of the modes of competition within a community and then comparing this across a moisture gradient. In the second situation, frequent fires or other disturbances may maintain a plant community at its potentially peak diversity. The additional effect of grazing would decrease diversity by causing a shift toward population reduction.

RELATIONSHIP TO OTHER HYPOTHESES

Disturbance Models

The Huston, predation, and intermediate-disturbance hypotheses of species diversity predict the occurrence of a frequency of disturbance at which diversity is greatest. Our model is consistent with this prediction. However, it is difficult to define grazing as a disturbance across communities with different histories of grazing or within communities having a long evolutionary history of grazing. If the lack of grazing is considered a disturbance in a community that has evolved with grazing, then diversity should increase when grazing is reduced from the nominal. Although this is true for the shortgrass steppe, it is not for the Serengeti. However, if grazing is considered a disturbance in a community that has evolved with grazing, then current disturbance hypotheses do not accurately predict the responses of the shortgrass steppe to grazing. Disturbance hypotheses predict an increase in diversity at a level of disturbance that is predicated on a decrease in competitive exclusion. Grazing may not always decrease competition.

In the Serengeti, diversity declines with the exclusion of grazing. Removal experiments show that grazing does not eliminate competition between plant species (McNaughton 1983b); however, although intermediate levels of grazing may not reduce the overall level of competition, they may alter the modes of competition. Even though grazing is a disturbance to an individual grass plant, it is not a disturbance at the community level, because negative effects on tallgrasses are compensated for by positive effects on shortgrasses, and competitive interactions are not eliminated. Many of the species colonizing areas of human disturbance in the Serengeti were ruderals or weeds that rarely grew where natural disturbances had occurred, even when these occurred only a few meters from a seed source (Belsky 1987). The difference between this situation and that predicted by the Huston hypothesis is that the rapid regrowth and lack of a relaxation in competitive exclusion result in major, not minor, changes in community composition and diversity.

In the shortgrass steppe, diversity declines with increasing grazing intensity. Disturbance hypotheses predict that grazing initially decreases competitive exclusion and increases diversity. The increase in density of dominants and of total basal cover with grazing suggests that competitive interactions may not be low-

ered. Disturbance species occur at low densities on both the grazed and ungrazed treatments but in large numbers on small-mammal diggings, on ant mounds, around water-tank areas, and along roadsides. The opportunity exists for increases in disturbance species, but these species do not significantly contribute to the community composition of grazed or ungrazed areas.

Thus, moderate grazing may not be a disturbance on either the Serengeti or the shortgrass steppe, because neither the rapid switching capabilities of grasses on the Serengeti nor the increases in the heavily grazed dominants of the shortgrass steppe reduce competitive interactions. Alternatively, moderate grazing may be considered a disturbance in the Serengeti but not on the shortgrass steppe because semiaridity and adaptation to grazing are complementary selection pressures, but grazing and competition for light in subhumid communities are divergent selection pressures. In any case, defining grazing as a disturbance in different communities is a problem inherent in applying disturbance models to large-herbivore grazing of grasslands, but it is not inconsistent with our model. Our model is not a disturbance model but a grazing model. Contrasting it with disturbance models emphasizes the difficulty in defining grazing as a disturbance using even more liberal, safe definitions, such as changes in species composition or altered competitive relationships. Equilibrium–domain-of-attraction models suffer from the lack of objectivity in defining a threshold at which a periodicity becomes a disturbance (Karr and Freemark 1984; Sousa 1984). There is the additional problem of how the force interacts with the selection pressures that have shaped the community. That is, given two communities subjected to the same level, frequency, and duration of a particular force, the resulting adaptations and the manner in which the communities respond to an alteration of the force depend on the degree of convergent, neutral, or divergent adaptations to the particular force arising from the many other forces operating on the communities.

Predator-Mediated Coexistence Models

Caswell (1978) reviewed studies that failed to demonstrate predator-mediated coexistence or actually showed a decrease in the number of coexisting species under the impact of predation (Harper 1969; Paine and Vadas 1969; Hurlbert et al. 1972; Adicott 1974; Janzen 1976). Caswell developed and made comparisons between an open-cell, nonequilibrium model and a closed-cell, equilibrium model that explain these anomalies. Nonequilibrium models rely on the temporary action of predation. New cells are opened for colonization and then released from predation pressure to allow nonequilibrium population growth. If the predation pressure does not disappear periodically, the nonequilibrium effect will not be seen. Instead, within the cell, a new equilibrium is established, having no more and perhaps fewer species than occur in the absence of predation. As one example, Caswell used the situation in which grazing herbivores are in enclosed pastures. At high densities of grazers, the entire pasture is treated as a single cell, receiving uniformly high predation pressure, which results in a negative effect on coexistence.

Is the decline in diversity with grazing intensity on the shortgrass-steppe grazing treatments simply a result of a single-cell equilibrium effect? The lightly,

medium-, and heavily grazed pastures are each 130 ha. Even in the heavily grazed pastures, large differences occur in grazing pressure between and within topographical position. Furthermore, grazing intensities on swales and ridgetops shift seasonally (Senft et al. 1985). These pastures can hardly be described as a single-cell equilibrium system.

SUMMARY

Current disturbance models do not adequately account for the wide range of responses by grassland plant communities to grazing by large generalist herbivores. The evolutionary history of grazing, an important factor in the response of grasslands to grazing, has not been explicitly addressed. Grazing history alone, however, is not a good predictor of plant-herbivore interactions. Interactions occur along gradients of convergent to divergent selection pressures with increasing environmental moisture and of intolerance to tolerance of grazing with increasingly long evolutionary histories of grazing.

We suggest that feedback mechanisms between plants and grazing animals are well developed in grasslands with long evolutionary histories of grazing. Feedback mechanisms are manifest in the rapid switching capabilities (of plant species and modes of competition) of subhumid grasslands with long evolutionary histories of grazing and divergent selection pressures. Switching capabilities do not exist in semiarid grasslands with long evolutionary histories of grazing and convergent selection pressures. Rather, for heavily grazed dominant species dominance increases. Feedback mechanisms are not well developed in systems with short evolutionary histories of grazing. In these cases, the differences in response to grazing by semiarid and subhumid situations arise primarily from differences in the grazing tolerance of plants adapted to semiaridity or of plants adapted to competition for light and from the different effects of grazing on canopy structure.

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Large Herbivore Foraging and Ecological Hierarchies

Landscape ecology can enhance traditional foraging theory

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Applications of optimal foraging theory (Pyke 1984, Schoener 1971) to large herbivores have been problematic (Owen-Smith and Novellie 1981, Westoby 1974), partly because optimal foraging theory has been developed for predators and nectar feeders rather than large herbivores. Predators generally seek spatially scattered prey of nearly constant and high nutritional value. Large herbivores, on the other hand, confront an apparent food surplus, which is of low and highly variable nutritive quality (Belovsky 1984, Westoby 1978). Compared with the prey consumed by predatory animals, the food of large herbivores is much more likely to be widely dispersed over the landscape, rather than concentrated in discrete patches.

Large herbivores interact with forage resources at several levels of ecological resolution. The animals confront a series of interrelated foraging problems, each on a different tempo-

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> While predators seek scattered prey of high nutritional quality, large herbivores confront widely dispersed, lower quality food

ral and spatial scale. The fundamentally spatial nature of this problem suggests that landscape ecology, the science that studies the development and dynamics of spatial heterogeneity in ecosystems (Risser et al. 1984), may be a very useful tool.

We have found that many of the problems of applying traditional optimal foraging theory to large herbivores, including ruminant and nonruminant ungulates (Artiodactyla, Perissodactyla, and Proboscidea) and marsupials (Macropodidae), can be solved by blending elements of foraging theory, landscape ecology, and hierarchy theory. Our approach is different from traditional optimal foraging theory in that we are more concerned with behavioral processes and patterns than with theoretical or evolutionary outcomes. Our conceptual framework spans patch to regional levels of ecological resolution. We invoke hierarchy theory to integrate foraging decisions at different spatio-temporal scales. In this article, we present hypotheses pertaining to the different scales in this ecological hierarchy.

Ecological hierarchies

Food resources of large generalist herbivores can be considered to be micropatches (or feeding stations or plants), plant communities, landscapes, and regional systems (Figure 1). Boundaries between the subunits within each hierarchical scale must be defined ultimately by animal perceptions and foraging responses.

While ecologists usually define such plant communities by species composition or physiognomy (McNaughton 1983, Whittaker 1971), these criteria do not necessarily coincide with an animal's ecological requirements or perceptions of resource pattern (Wiens 1976). We posit that animals often perceive relatively consistent assemblages of plant populations that are clustered in conjunction with soils or patterns of disturbance.

Communities, in turn, cluster in conjunction with geomorphic features to form landscape systems (Forman and Godron 1981). Regional systems are large-scale assemblages of landscapes (Rowe 1961). Boundaries of a home range or of a fenced pasture often delineate a landscape system, while the annual range of migration of wild herbivores can define a regional system.

A basic postulate of hierarchy theory is that functional parameters, the frequencies and rates of activities, are often more useful for defining hierarchical scales than are physical structures (Allen and Starr 1982). Scales in an ecological hierarchy are separated by identifying frequencies or rates of pertinent processes (Table 1). Ungu-
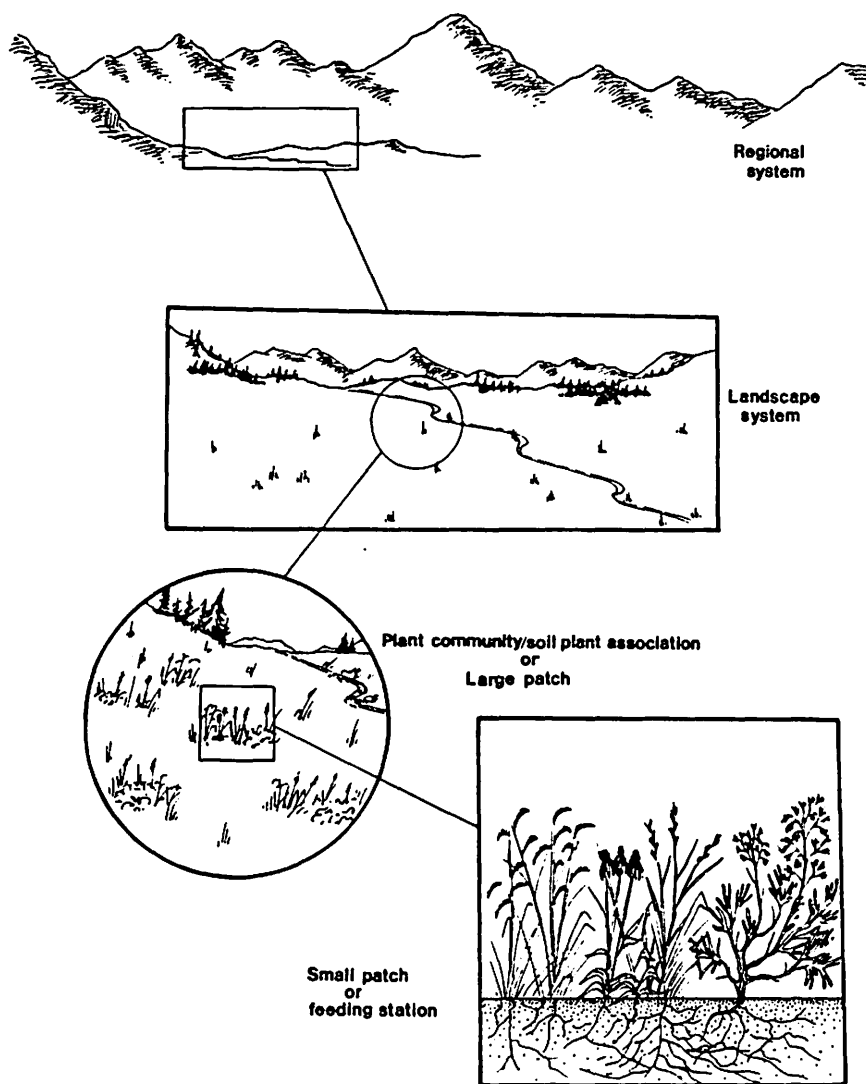
Figure 1. An ecological hierarchy encountered by large herbivores while foraging. Scales are defined by rates of foraging processes and ecosystem processes. Boundaries between units at each scale are defined by animal behavior.

lates eat approximately 10^7 bites/yr (Chacon et al. 1976), and each bite represents a decision about what plant or plant part to eat. Large herbivores cross plant-community boundaries as many as 50 times/day,[1] which implies a decision frequency of 10^4/yr. At the regional scale, animals switch among landscape systems as often as several times per year or as seldom as once in several years.

Foraging patterns

Different foraging response patterns are displayed at different scales (Table 1). In a manner analogous to the emergence of deterministic gas laws

[1]R. L. Senft, 1981. Unpublished data.

from large numbers of stochastic molecular interactions, molar foraging patterns are the aggregate results of many individual molecular foraging decisions (Staddon 1983). The type of behavior that is observed depends upon the relationship between frequency of observation and frequency of the behavior (Allen and Starr 1982). Diet selection decisions, for example, often occur at such high frequency that only molar patterns are generally measured. On the other hand, regional-scale movements occur at such low frequency that molecular decisions are easily observed.

There are three basic molar response patterns: matching, overmatching, and undermatching (Staddon 1983). Matching occurs when an

animal adjusts its foraging behavior in proportion to changing dietary rewards (Herrnstein 1970, Staddon 1983). Overmatching results from a disproportionately large foraging response to a change in reward; undermatching from a disproportionately small response.

Community scale. Overmatching is the pattern most prominent when a large herbivore selects plants either from a community or from locations within a community (i.e., micropatches) (Table 1). To maximize nutrient intake (Belovsky 1984), the generalist herbivore employs tactics in which preferences are nonlinearly related to forage abundance and quality. Diet selection is based in part on palatability, the aggregate sensory image of a potential food. However, palatability is only weakly correlated with nutritive quality and may be modified by plant physical characteristics, presence of secondary compounds, and prior feeding experience (Arnold and Hill 1972, Cooper and Owen-Smith 1986).

Where the sensory cues for forage selection reinforce each other, relative preference (the ratio of the proportion of an item in the diet to the proportion of available herbage) may be a positive exponential function of relative nutritive quality (Senft 1984) (Figure 2a). Conversely, negative exponential relationships may arise between preference and negative reinforcements, such as phytochemical deterrents (Bryant and Kuropat 1980, Reichardt et al. 1987). Both these conditions produce overmatching.

Landscape scale. Matching is the prominent pattern when large herbivores interact with landscape systems by selecting plant communities and other landscape components for feeding (Table 1). Animals' relative preference for plant communities (the ratio of the proportion of total feeding time to the proportion of home range area) is generally a linear function of the relative abundance and/or nutritive quality of the preferred plants in the communities (Figure 2b). A wide array of herbivores exhibit landscape-scale matching, including domestic sheep and cattle, mule deer, wapiti, feral horses, North American bison, eastern grey kangaroos, and walla-

roos (Coppock et al. 1983, Duncan 1983, Hanley 1984, Hunter 1962, Senft et al. 1985, Taylor 1984).

Selection of feeding areas is modified from a pure matching pattern by several factors, including topography and proximity to water or salt licks (Valentine 1947). Because watering points and salt licks act as attractants, foraging intensity nearby is not affected by declining forage availability. Escape from insect harassment and selection of favorable microclimates further modify the basic matching pattern. Animals may avoid otherwise attractive feeding areas to escape discomfort.

Regional scale. If animals or human herders switch among landscapes on the basis of forage availability, then the regional molar response pattern will be matching. Thus, we hypothesize that in the absence of overriding constraints, foraging behavior should produce a landscape stocking rate that is a linear function of landscape productivity (Figure 2c).

Regional-scale foraging tactics include migration, transhumance, nomadism, and home-range behavior (Table 1). Transhumance is a repeatable, patterned response to predictable seasonal shortages in forage availability (Breman et al. 1978, Gulliver 1955, Tucker 1986). In contrast, nomadism, whether natural or caused by human herders, is an adaptation to unpredictable forage production (Baker 1978, Dyson-Hudson and Dyson-Hudson 1980).

In the Serengeti regional ecosystem, nomadic herds opportunistically follow spatially distributed rainfall-related production pulses (McNaughton 1985, Pennycuick 1975, Sinclair 1985). Thus, ungulate herds move among landscape units on a contingency basis, as forage distributions vary. A similar regional response pattern has been suggested for the North American bison (England and DeVos 1969). Under unfenced, unherded conditions, domestic livestock also move to new grazing areas when forage intake or availability decreases to some critical threshold (Squires 1982).

Home-range behavior is the regional-scale response wherein subpopulations restrict their movements to a subset of the potentially available range. Ungulate home ranges are centered on best foraging habitat and watering areas (Hunter 1964). Although carrying capacities of home ranges are directly related to proportions of higher-quality plant communities, responses may deviate from that shown in Figure 2c. Where animal numbers are increasing, more favorable home ranges are often occupied first (Hunter 1964). Low-status animals and juvenile herds may be forced onto low-quality ranges, resulting in densities higher than expected from forage availability (Van Horne 1983); conversely, when populations are depressed, the lowest-quality home ranges may be abandoned first (Arnold and Dudzinski 1978).

Foraging mechanisms

Community scale. Foraging ungulates must solve two problems at the plant community scale: which plants or plant parts should be selected from the array of immediately available material (diet selection) and how they should move through the community (location selection). Direct application of optimal foraging theory mod-

Table 1. Summary of a conceptual model of large herbivore foraging in an ecological hierarchy.

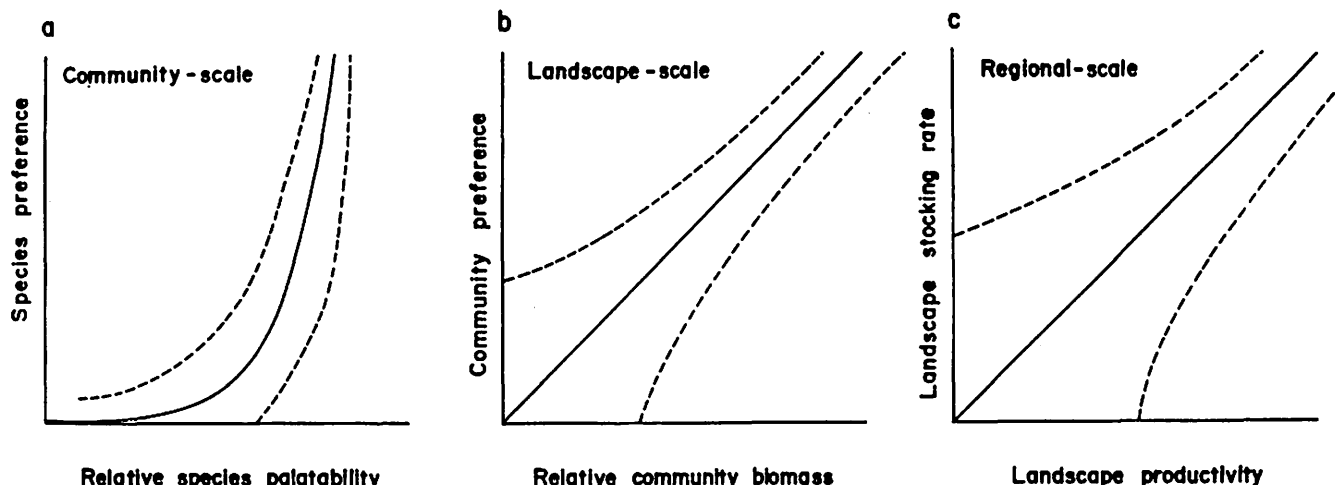| Foraging Component	Scale in Ecological Hierarchy		
	Plant Communities	Landscape	Region
Units of selection	Plants, feeding stations, or micropatches	Communities or large patches	landscape
Foraging behavior	Diet selection	Feeding-area selection	Migration Nomadism Transhumance Home range
Behavior frequency (decisions/yr)	10^7	10^4	10^{-1}–10^1
Aggregate response pattern	Overmatching	Matching	Matching
Alternative hypothetical foraging mechanisms	Momentary maximization Feeding station processes Micropatch-level processes	Turning frequency Boundary contrast Transit rate Patch-selection processes	Boundary contrast Calculated migration Noncalculated migration Genetically programmed migration
Hypothetical foraging goals	Nutrient maximization Toxin minimization Nutrient balance	Optimize foraging efficiency	Maintain intake Avoid physical stressor
Interactive factors	Forage biomass Nutritive quality Plant morphology	Forage biomass Nutritive quality	Forage biomass
Noninteractive factors	Microsite variables	Substrate Topography Water location Microclimate	Geomorphology Regional climate Physical barriers Water location

Figure 2. Foraging response patterns observed at three hierarchical scales. a. Community scale. Species preference equals a plant's percentage in the animal's diet divided by the plant's percentage in the community. Relative species palatability is a measure of the desirability of a given species with respect to the average desirability of all the species available. b. Landscape scale. Community preference equals percentage of total grazing time spent in a community. Relative community biomass is community biomass divided by the area-weighted mean community biomass. c. Regional scale. Landscape stocking rate equals animal numbers times duration divided by landscape area. Landscape productivity is mass per unit area. Theoretical confidence bands (——) have been drawn to be broader at larger scales where nonforage factors have more importance. These confidence bands become narrower as rewards and responses increase.

els to field situations may encounter several major problems (Pyke 1984).

Optimal foraging theory models predict outcomes of processes on an evolutionary time scale and assume the existence of appropriate decision-making mechanisms on a behavioral time scale. Thus, optimal foraging theory predicts molar behavioral patterns that ought to evolve, but operational molecular mechanisms remain poorly conceptualized. Optimal foraging theory must necessarily assume either that animals integrate formidable amounts of information about forage resource distributions, or it must assume natural selection for simple behavioral rules-of-thumb that yield approximately optimal solutions, but require far less cognitive function (Cowie and Krebs 1979, Janetos and Cole 1981, Krebs and McCleery 1984). Unfortunately, very few studies either support or distinguish between these two assumptions (Pyke 1984).

Diet selection by large herbivores requires the solution of two opposing problems: obtaining maximal quality and adequate quantity. Since the vast majority of an herbivore's available food material is of low nutritive value, selection for quality is at the expense of quantity. Additionally, herbivores' diet selection is constrained by body size, gut type and capacity,

ability to prehend forage, and available feeding time (Belovsky 1984, Demment 1982, Hanley 1982, Owen-Smith 1982).

Herbivores may utilize momentary maximization to solve the quality-quantity problem. Momentary maximization dictates sequential acceptance of the most palatable items encountered at each feeding location until palatability decreases to some threshold level (Staddon 1983). Threshold of acceptance is presumably conditioned by recent experience. Each encounter with a high-quality item raises the threshold, while encounters with low-quality items lower the acceptance level. However, the herbivore must consume some items regardless of quality to maintain total intake and to sample for temporal changes in relative palatability (Westoby 1974). Therefore, there is usually a low, nonzero probability that any item will be consumed. This probability need not be constant but may vary with level of satiation (Ellis et al. 1976, Ivlev 1966).

Movement through the community, or selection of a grazing location within it, can be explained in a variety of ways. Perhaps the most parsimonious is to assume that the grazing animal selects a diet by momentary maximization from a sensorially de-

fined (Arnold 1966a,b) array of plants larger than it can reach without moving. Selection of the best available plant from those sensed will eventually require that the animal move forward to obtain it. Once the animal has changed location and the boundary of the array under consideration has changed, further movement is possible. A single mechanism—diet selection by momentary maximization—thus solves the diet-selection and location problems simultaneously.

Alternative hypotheses explaining foraging behavior within a plant community can be erected but require adding to the spatial hierarchy an additional level intermediate between the plant and the plant community. One such hypothesis assumes that ungulates feed at a series of "feeding stations," consisting of the forage immediately available when the forefeet are stationary (Novellie 1978). Diet selection proceeds at that station by momentary maximization, as before. In this case, however, no movement results from the diet-selection decision process, and an additional rule must be postulated. The simplest rule is a simple giving-up rule. When the best remaining item at the station is below some threshold, or when the rate of forage acquisition at that station falls below a threshold, the ani-

Large herbivores may determine their own foraging strategies or be directed by humans. A giraffe grazing on a tree in the Serengeti Plain. Zebras graze on the Serengeti Plain. A Turkana herdsboy watches over his livestock in Kenya. Photos: M. Coughenour.
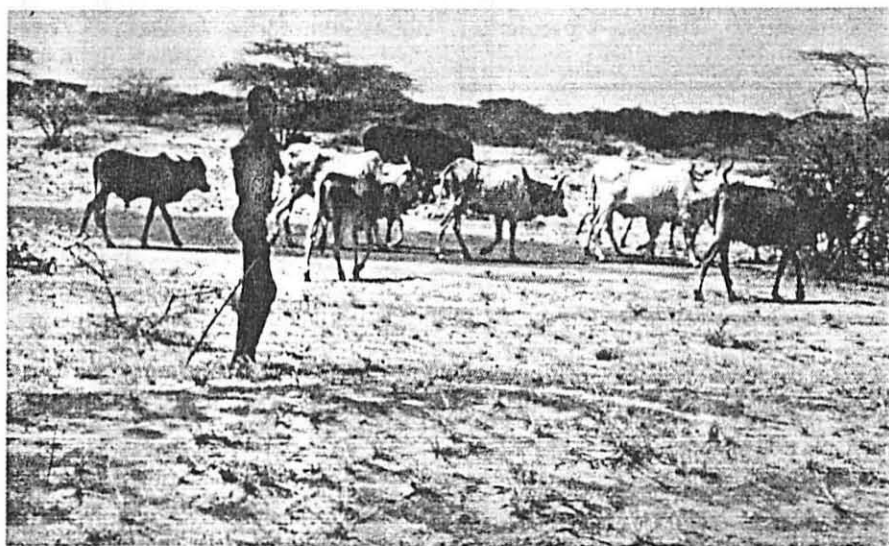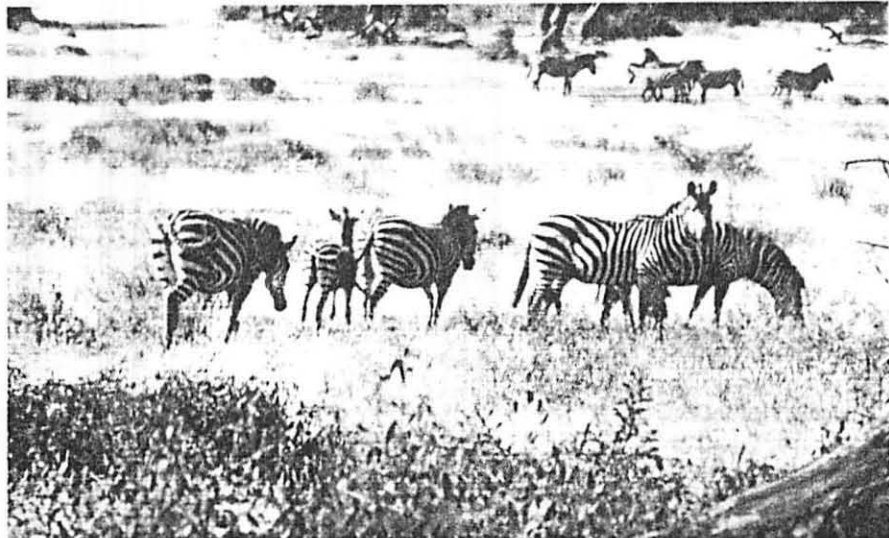
mal moves forward, establishing a new feeding station at which diet selection again proceeds.

Rather than introduce feeding stations as the intermediate scale, one may consider that the plant community consists of an array of patches, rather than individual plants, that are sensed by the grazing animal. Within a patch, diet selection is again a process of momentary maximization but movement among patches must be accomplished by assessing the "marginal value" of the patch relative to all others (Charnov 1976).

The decision to leave a patch and to select a new patch may be based on the rate of forage intake at the present patch, the expected rate at other patches, and the cost of moving to a new patch. Foragers should remain in a patch until forage is depleted below some threshold, until a certain amount of forage has been taken, until a certain time has passed in the patch (Charnov 1976), until a certain time has passed since a food item has been procured (McNair 1982), or un-

til intake rate falls to some level (Cowie and Krebs 1979). Thresholds are reached more quickly in poor patches than in rich ones. Thus, patch residence times will be proportional to relative food availability, resulting in a matching pattern.

Landscape scale. Landscape matching may be a simple outcome of community-scale foraging. Some biologists have hypothesized that ungulates move through a community from plant to nearest plant, or from patch to nearest patch, changing direction with each move. The animals may turn more frequently when foraging in more productive and more diverse communities (Crawley 1983). Thus, animals will stay longer in communities with higher densities of preferred forage. On the other hand, animals would turn less frequently in poor

stands, resulting in faster transit.

The turning-frequency hypothesis is in conflict with some features of observed ungulate behavior. Animals often follow topographic contours when feeding, with little evidence of zigzagging (Arnold and Dudzinski 1978). In addition, gregarious species may form grazing fronts (McNaughton 1984, Sinclair 1985), which would be disrupted by random-walk behavior of individual animals. Browsing animals (e.g., deer) often follow established trails, physical boundaries, and topographic contour lines. Finally, empirical and computer-simulation studies of foraging directionality have indicated that animals should and actually do tend to maintain foraging direction (Pyke 1978).

Alternatively, landscape matching could result from ungulate herds

moving more slowly across more productive, nutrient-rich communities. This behavior also can be modeled from simple community-level feeding-station processes. If time spent at each station is positively related to biomass (Ruyle and Dwyer 1985), then foragers will move slowly across rich communities and rapidly across poor ones. This model is attractive because it does not assume behaviors, such as frequent changes of foraging direction, that conflict with observed ungulate behavior.

In a third scenario, animals evaluate the relative attractiveness of vegetation types at community boundaries. The probability of animals' returning to a given type is proportional to community richness. A prediction of the boundary-contrast model is that animals would frequently reverse direction of movement when moving from a high-quality to a low-quality community. However, animals rarely reverse direction of grazing after crossing community boundaries.[2] The boundary-contrast model may require sharp boundaries between communities, a condition that is uncommon for most large herbivore habitats; otherwise, it would require animals to have the capacity to recognize gradual changes in community composition.

Regional scale. Regional-scale foraging behavior is the result of a wide array of tactics and movement cues. Movements are more likely to be dictated by factors beyond the scope of simple optimization. For example, animals may be forced to move during dry periods or when forage is buried by snow. Thus, there is a greater likelihood that herbivores obey landscape-departure rather than landscape-selection rules. Further, genetically coded responses to nonforage cues, such as photoperiod, may trigger long-range migrations in some species that do not have direct information about distant resources.

Hypothetical regional mechanisms parallel landscape-level mechanisms, but with important distinctions. Not all landscape-level mechanisms are appropriate at the regional level. Migratory and nomadic ungulates exhibit landscape switching, an all-or-

[2]See footnote 1 above.

nothing response triggered by a cue (Murdoch 1969). Turning frequency and rate-of-transit rules acting at the landscape level cannot generate a switching response; boundary-contrast and marginal value-based decisions among landscapes could, however. Regional moves of nomadic and migratory herds may stem from a simple dissatisfaction rule; however, there is evidence that some species sample areas outside the habitual range in anticipation of a move (Franklin et al. 1975).

Information gained by sampling allows implementation of powerful selection rules. Baker (1978) distinguished "noncalculated" migration, in which there is no information about alternative landscapes, from "calculated" migration, in which some regional knowledge is assumed. Noncalculated switches require only a departure decision, whereas calculated migration also requires selection. Ungulates employ a number of mechanisms that may increase the ratio of calculated to noncalculated migration, including contact among adjacent social groups and exploratory migration.

Foraging goals

Proximal foraging goals arise within two systems: natural selection acting over generations (Krebs and McCleery 1984, Mayr 1983) and new rules or strategies that an animal learns within its lifetime. Evolution of rule-based behavior can be numerically simulated by staging "contests" between alternative rules (Holland 1986), provided there is a mechanism for selection based on contest results. The scales of such contests may range from individual foraging events to the fate of a population over generations.

Decision-making goals at different scales in the ecological hierarchy relate to specific aspects of the overall problem of obtaining an adequate and balanced diet (Table 1). The immediate goals of one scale differ from those of another because resource distributions, foraging costs, and risks vary with scale. Decision making at larger spatial scales occurs less frequently than decision making at smaller scales. However, the consequences of each individual decision for the animal are likely to be more

significant at larger spatial and longer temporal scales.

A proximal goal of diet selection is to maximize dietary nutrient concentration (Belovsky 1984, Pyke 1984). Nutrient maximization is a very efficacious goal at the community scale, because nutrient concentrations of individual plants and plant parts vary greatly (Mattson 1980). Rate of protein intake is generally more important for large herbivores than rate of digestible-energy intake (Belovsky 1984). However, the degree to which energy or protein is maximized depends upon body size and digestive physiology (Demment 1982, Janis 1976).

Landscape-scale decision-making goals are less easily defined. While there may be differences in nutrient content of diets selected from different communities, these may in some circumstances be overshadowed by the time and energy costs of travel. Further, significant amounts of foraging time may be lost if animals do not feed in some suboptimal habitats while moving among watering, feeding, and sheltering sites. Thus, a goal of dietary maximization cannot suffice at the landscape scale because the importance of other, nondietary goals has increased. Available time must be used efficiently to satisfy multiple objectives.

Regional-scale decision making is invoked when forage intake cannot be maintained or when climatic stress becomes limiting. Minimal dissatisfaction can suffice as the goal of a landscape departure rule, whereas minimization of travel costs relative to gain is a more prudent goal for a landscape-selection rule.

Although ecological scales appear somewhat discrete (Allen and Starr 1982), interactions among foraging goals at different scales may be important. For example, when different food items are differentially distributed among communities, goals of diet selection interact with, and even become synonymous with, goals of landscape use.

Another example is central-place foraging from water or shelter, where nonfood resources such as water, shelter, salt licks, and protection from predators are highly localized on landscapes, but forage resources are dispersed. Water is often concentrated

at discrete locations, and selection for watering points occurs less frequently than does diet or community selection. Thus, community- and landscape-scale foraging goals can be nested within goals of seeking water, and water becomes a major constraint on regional movement.

Interactive versus noninteractive resources

The degree to which a foraging animal is capable of modifying its behavior in response to foraging-induced environmental change depends on the scale of change. Animals tend to interact more with resource systems at low to intermediate scales than at larger scales (Figure 3). Animals have the largest effects on resource variables that change at rates similar to their own behavioral frequencies (Allen and Starr 1982).

In direct contrast, factors with slower rates of change act as constraints upon environments of faster processes. These noninteractive factors are essentially driving variables, as they affect forage resources, but are not affected by forage use. An analogous distinction between interactive and noninteractive plant herbivore systems (Caughley 1976) addresses controls on population dynamics rather than controls on foraging behavior.

While localized forage removal produces variability, which then affects animals' subsequent foraging decisions, it is also important to consider plants' active responses, such as regrowth. At the plant scale, maximal growth is achieved at low to intermediate grazing intensities (Coughenour 1984, McNaughton 1979). At community and landscape scales, ungulate herds may actively maintain specific areas of short, rapidly growing plants in otherwise tall coarse vegetation (grazing lawns) and thereby actually facilitate rates of resource renewal greater than those in ungrazed or lightly grazed areas (McNaughton 1984).

Interaction strength may also depend upon the way herbivore mobility compares with rates of plant processes. At the level of diet selection, plants cannot respond before animals move to the next plant or small patch. Significant plant responses do occur
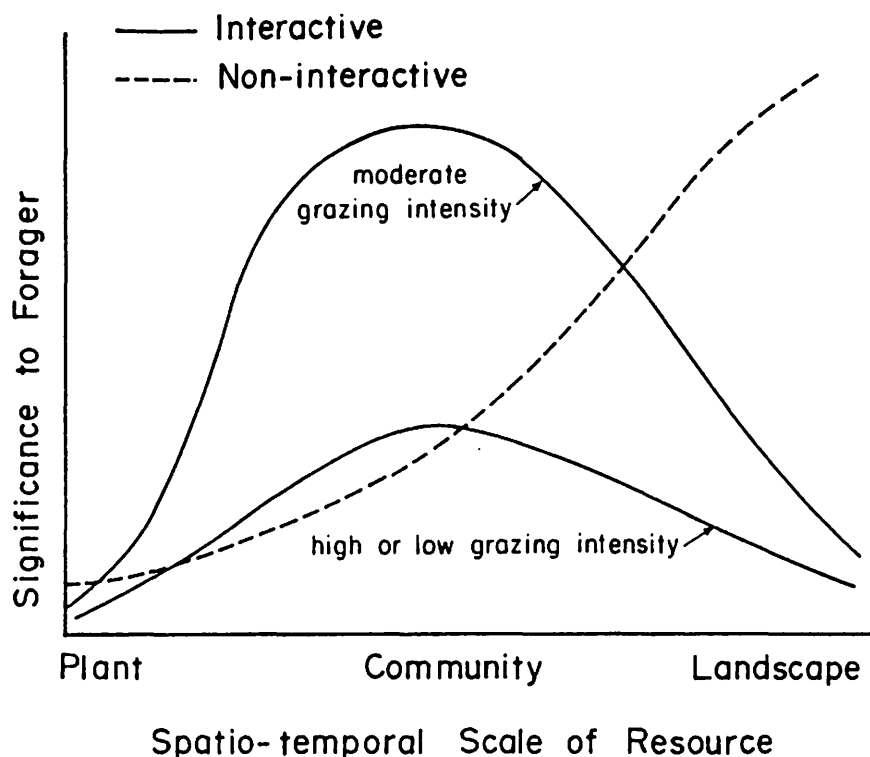

Figure 3. Conceptual model of the way the significance of interactive and noninteractive variables change with scale and grazing intensity. "Significance" refers to the extent to which foraging decisions are influenced by plant, community, and landscape or regional-scale variability. Interactions between foragers and resources prevail at smaller scales; noninteractive constraints, such as of topography and macroclimate, dominate at larger scales. Interactions are stronger at moderate grazing intensities than at low or high intensities.

over a time scale comparable with that of movements among landscapes. In some ecosystems herbivores may induce a shifting mosaic of patches (Ring et al. 1985). Regionally, however, herbivore movements occur over a timespan similar to, or slightly greater than, a single plant-growth cycle, so interactive effects are still present but weak.

Plant-herbivore interactions decline in relative importance at very large scales, as foraging decisions increasingly involve tradeoffs with nonforaging decisions. Variations in these factors may also dictate the form and strength of interactive processes (Coughenour 1984, 1985). With increasing spatial scale, the frequencies of animal decisions become less similar to the frequency of environmental changes (Allen and Starr 1982). Consequently, we suggest that the confidence bands around relationships between forage factors and animal response should become increasingly wide as the spatial scale increases (Figure 2).

Conclusions

A theory of large herbivore foraging must first be based on actual decision-making mechanisms. Decision making is governed by specific rules, which can be postulated and tested. To approach foraging optimality (Janetos and Cole 1981, Pyke 1984), learning or natural selection must act upon these mechanisms. Second, a useful foraging theory must explain how foraging behavior varies with ecological scale. We have proposed that an ecological hierarchy be used as a framework for such investigation. Third, the theory must invoke realistic goals applicable to various ecological scales in order to explain the objectives of foraging behavior. Fourth, a mechanism for goal evolution must be provided. Finally, the theory needs to be put into an ecosystem context, by considering the responses of plants on the various ecological and evolutionary time scales and identifying how the relative significance of interactive and noninter-

active processes varies.

We also have presented alternative hypotheses for foraging decision-making rules. Critical experimentation is necessary to select among these possibilities.

Acknowledgments

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ABSTRACT

Organic C accumulation was measured along an 8-km transect at a site in the semiarid shortgrass steppe of northeastern Colorado. Specific objectives of the study were to (i) measure the quantity and distribution of organic C across toposequences, (ii) test the hypothesis that a disproportionate amount of soil organic C resides in the lowlands (as defined herein), and (iii) assess the role of geomorphic history as a determinant of contemporary rates of biogeochemical organic C transformations. Results of the study showed the surface (A) horizon organic C concentration did not vary systematically among slope positions of a given toposequence. Similarly, the mass of organic C within the surface meter of soil often did not increase with decreasing elevation across a toposequence. Mass of organic C was found to range from 2.5 kg m^{-3} on terrace escarpments to 10.7 kg m^{-3} on sandy uplands. The mass of organic C, as calculated to the BCk horizon, was highest in the lowlands. The mass of buried organic C, as calculated uniformly for a 50-cm thickness of material, represents 17% of the total organic C estimate for the site. In spite of buried soils, lowlands did not contain a disproportionate amount of total landscape organic C.

Additional Index Words: Toposequence, Biogeochemistry, Buried soils, Geomorphic history.

PATTERNS OF SOIL organic C accumulation within the soil profile and along toposequences are functions of both pedogenic and geomorphic processes. These processes are driven primarily by water as it moves both vertically and laterally through and over the soil in response to topographic gradients. A plausible model of soil organic C accumulation, based on water movement alone, predicts an increase in organic C with decreasing elevation along the toposequence. This gradient results from changes in production, organic matter decomposition, and humus formation as affected by run-on, increased water holding capacity from the deposition of eroded fines, and the simple addition of eroded organic matter. Indeed, several studies have demonstrated systematic patterns of organic C variation across toposequences (Kleiss, 1970; Malo et al., 1974; Schimel et al., 1985a, b; Aguilar, 1984). Such findings brought the concept of the catena to general acceptance, wherein such parameters as A horizon thickness, solum depth, and degree of soil development all increase from the convex portion of the toposequence to its base as a function of water movement.

This model of organic C accumulation assumes extended periods of normal water erosion without major perturbations to the system from episodic accelerated water erosion or wind erosion. Landscape characterization data and soil data previously collected at a shortgrass steppe site in Colorado showed little evidence of current water erosion (Paroussis, 1984). Data did, however, indicate that episodes of accelerated erosion and deposition had occurred in the region since the end of the Pleistocene period (D.O. Doehring, 1986, personal communication). The extent to which systematic patterns of soil organic C developed across toposequences in water-limiting environments or in landscapes of geomorphic instability has not been fully explored.

This paper analyzes soil organic C accumulation across topographic gradients, and presents the distribution of organic C mass for a semiarid shortgrass steppe site in Colorado. We chose to study distributions of organic C because organic matter is a key constituent of soils and ecosystems (Paul, 1984; Anderson and Coleman, 1985), and because organic C quantity and distribution are sensitive to many properties that may vary with landscape position (Schimel et al., 1985a; Campbell and Souster, 1982; Jenny, 1941). Specific objectives were to (i) measure the quantity and distribution of organic C across selected landscape segments, (ii) test the hypothesis that a disproportionate amount of soil organic C resides at the lowland position, and (iii) assess the role of geomorphic history as a determinant of contemporary rates of biogeochemical organic C transformations.

METHODS

The Central Plains Exp. Range (CPER) is located near the western border of the Great Plains region in northeastern Colorado, approximately 40-km south and east of Cheyenne, WY. Mean annual precipitation at CPER is approximately 31 cm, 70% of which occurs during the May through September growing season. The natural vegetation of the area is dominated by blue grama (*Bouteloua gracilis*). The major species associated with blue grama include fringed sagewort (*Artemisia frigida*), plains prickly pear (*Opuntia polycantha*), and buffalograss (*Buchloe dactyloides*).

The topography of the 6500-ha site is characterized by gently rolling hills, broad ephemeral stream courses, and low flat-topped terraces. The region is underlain by late Cretaceous shales and interbedded sandstones of the Laramie Formation. Parent materials were derived with rare exception from surficial deposits of alluvium composed of material derived from Front Range (Colorado Rockies) sources. Soils of the CPER are of four predominant subgroups: Aridic Argiustolls, Ustollic Haplargids, Ustic Torriorthents, and Ustic Torrifluvents. Soils and their associated landforms are listed in Table 1.

An inventory of the soils and geology, conducted before initiation of this study, showed an unexpectedly high degree of spatial heterogeneity with respect to soils, geologic substrates, and landforms. This heterogeneity results from a complex geomorphic history. Four different types and ages of alluvium, three different types and ages of eolian materials, and colluvium produced from the reworking of these materials by slope processes were identified within the CPER. Superimposed on a minimum of three terrace levels were deflation hollows and occasional vegetated dunes (D.O. Doehring, 1986, personal communication). Because of this variability an attempt was made to identify patterns in the
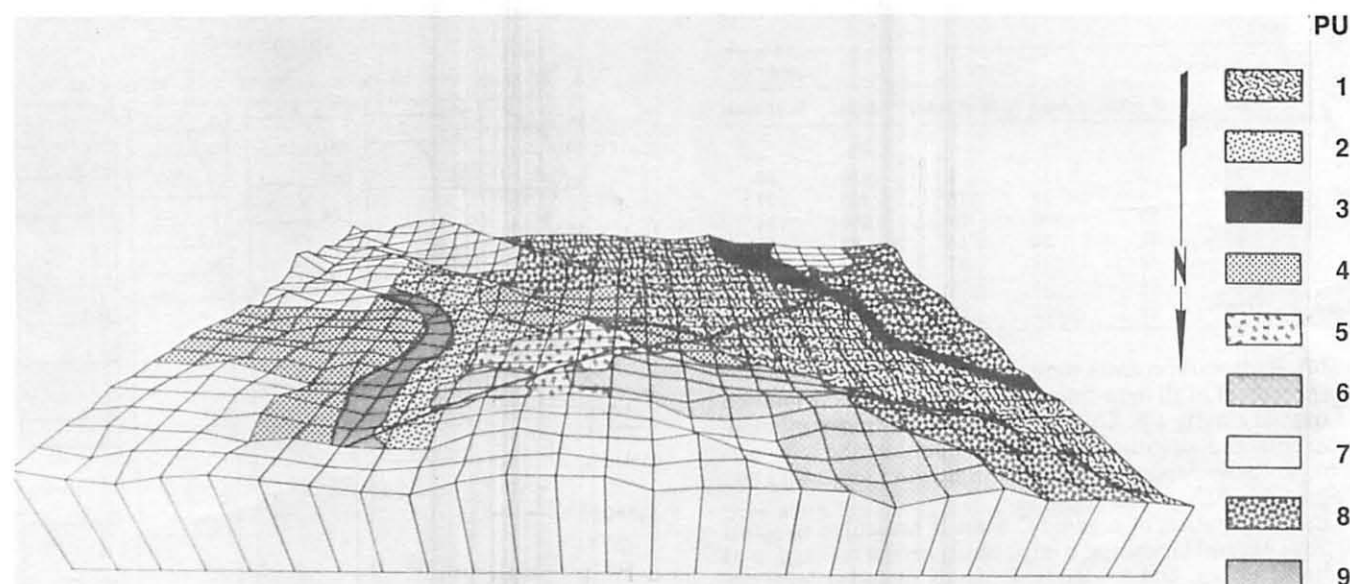
Fig. 1. Three-dimensional projection of Central Plains Exp. Range (10 × vertical exaggeration).

occurrence of soils and landforms. Nine physiographic units (PUs) were identified on the basis of similarity of topographic features and surface geology (Fig. 1, Table 1). The soil patterns across hillslopes and plains were more similar within, than between, PUs.

Pedons and their corresponding topography were described along an 8-km transect, oriented normal to the major drainages, which traversed a number of PUs. A total of 161 pedons representing 24 toposequences and seven plains segments were characterized. Sampling sites were selected within toposequences according to slope position (summit, shoulder, backslope, footslope, toeslope). Sites occurring within topographically uniform upland and lowland plains were sampled at approximate intervals of 100 m. Pedons were sampled to as great a depth as equipment and soil conditions permitted and at least to the BCk horizon.

Samples corresponding to genetic horizons were collected from 5.1-cm-diam soil cores taken at each of the 161 sites. Soil organic C was determined by a modified Walkley-Black procedure (Nelson and Sommers, 1975), using H_2SO_4 and potassium dichromate. Particle size analysis was done by the hydrometer method (Day, 1965).

Organic C quantities (kg m^{-2}) were calculated to the BCk horizon and to 1 m. In buried soils, kilograms per square meter organic C was calculated for a constant thickness of 50 cm to obtain estimates of buried C mass. A constant depth was used instead of actual buried solum thickness because the latter frequently could not be measured in the field because of soil hardness. Fifty centimeters was chosen based on the mean thickness of buried horizons whose depth could be measured. Soil bulk density was calculated, using particle size and organic C data (Rawls, 1983). Organic C concentrations and bulk densities of genetic horizons in buried soils were not statistically different across PUs; therefore, an average organic C concentration of 2.5 g kg^{-1} and bulk density of 1.5 g cm^{-3} was used for buried horizons in all PUs. Organic C was not measured in BCk (formerly Cca) or C horizons because previous studies at CPER have shown organic C concentrations typically to be quite low (<1.5 g kg^{-1}) (Schimel et al., 1985b; Paroussis, 1984; Gould et al.,

Table 1. Description of PUs at the CPER.

Physiographic unit	Topography	Landform	Subgroup	Surficial deposit	Bedrock geology†	Ha
1	Nearly level to gently sloping	Uplands	Ustollic Haplargids Aridic Argiustolls	Alluvium and eolian	--	1898
2	Nearly level to moderately sloping	Uplands	Aridic Argiustolls	Alluvium and eolian	--	530
3	Gently to strongly sloping	Dissected uplands	Ustollic Harlargids	Alluvium, gravelly alluvium	--	353
4	Moderately sloping	Upland hills Ridges Sideslopes	Aridic Argiustolls Ustic Torriorthents Ustollic Haplargids	Alluvium	Shale	1472
5	Nearly level to gently sloping	Upland hills Ridges Sideslopes	Aridic Argiustolls Ustic Torriorthents Ustollic Haplargids	Alluvium	Shale	171
6	Moderately sloping	Upland hills Ridges Sideslopes	Ustollic Haplargids Ustic Torriorthents Ustollic Haplargids	Alluvium	Sandstone, shale	872
7	Nearly level	Floodplain	Ustic Torrifluvents	Silty alluvium	--	130
8	Gently to strongly sloping	Uplands	Ustollic Haplargids Aridic Argiustolls Ustollic Calciorthids	Alluvium, gravelly alluvium	--	1028
9	Nearly level	Floodplain	Ustic Torrifluvents	Alluvium	--	206
						6660

† Noted only if influential on soil development or behavior.

Table 2. Areal extent of PUs, and percentage of CPER occupied by each.

PU	Lowland		Slope		Upland	
	Area	% of total	Area	% of total	Area	% of total
	ha		ha		ha	
1	38	2	171	9	1689	89
2	27	5	95	18	408	77
4	471	32	795	54	206	14
5	53	31	24	14	94	55
6	375	43	323	37	174	20
9	152	74	54	26	0	0
Total	1116	22	1462	28	2571	50

1979). Radiocarbon dates were determined for two paleosols after removal of all light-fraction material in an NaI solution of specific gravity 1.8. This was assumed to remove all modern roots and detritus. No further fractionation was performed. Radiocarbon age was determined by Geochron Lab., Cambridge, MA.

The distribution of organic C mass is presented in terms of three general landscape components, herein referred to as uplands, slopes, and lowlands. Uplands included level upland plains and the summit portion of toposequences; slopes included the area between the shoulder and footslope portions of toposequences and terrace escarpments; and lowlands included toeslopes, broad ephemeral stream courses, and other level, low-lying areas.

An electronic distance measure (EDM) was used to obtain the distance between sites and across physiographic units. These data were used to estimate proportions of uplands, slopes and lowlands within each unique PU (Table 2). The area within each PU was estimated using a dot grid overlay of a 1:24 000 map, at a resolution of 10 dots cm^{-2}. Hectares of uplands, slopes, and lowlands were derived for each PU from the latter two estimates by multiplying the proportion of each position along the transect by the total area of the PU.

RESULTS AND DISCUSSION

Patterns of Organic Carbon Concentrations

Organic C concentrations in surface horizons of CPER soils averaged 9.8 g kg^{-1}, with minimum, maximum, and standard deviations (SD) of 1.3, 35.9, and 3.2, respectively. Some variation was due to slope position, although differences between positions of a given toposequence may not be striking (Fig. 2). Typically, surface (A) horizon organic C concentration did not vary systematically among positions of a given toposequence. Although toeslopes nearly always had higher concentrations than corresponding summits, organic C concentration did not decrease at the shoulder or increase systematically downslope in most cases (Table 3). Similarly, surface horizon texture and thickness were not well differentiated across toposequences. These results are in contrast to other findings (Aan-
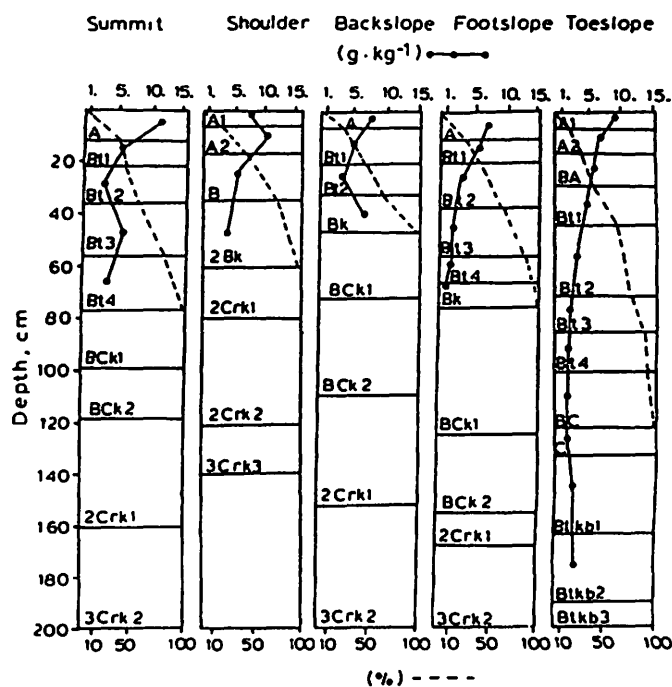
Fig. 2. Organic C concentration and cumulative percent of organic C mass as a function of depth for a selected toposequence.

dahl, 1948; Aguilar, 1984; Kleiss, 1970; Malo et al., 1974) and suggest that the role of water as the agent of differentiation is minimized in the present-day environment. Further evidence for the importance of eolian processes within the shortgrass steppe was presented in Schimel et al. (1985b), where the increase in fines downslope was found to result from the combined effect of an eolian footslope deposit and a recently denuded summit. Although some flow downslope apparently occurred at that site, wind was the overall dominant process in determining soil distribution.

The decrease in organic C concentration with solum depth (Fig. 2) was uniform except where perturbed by recent eolian deposition, buried soils, or lithologic discontinuities. All of these conditions were common at the shortgrass steppe site; two were reflected in the soils of Fig. 2. The A1 horizon at the shoulder contained less organic C and more sand than the A2, suggesting a more recent deposit, which has not accumulated an organic C concentration comparable with that of the A2. Although not dramatic in this example, the increase in organic C concentrations in the Btkb1, Btkb2, and Btkb3 horizons of the toeslope soil reflects the influence of buried horizons, which were often found relatively deep in the profile. Organic C concentrations in buried horizons were typically higher

Table 3. A horizon organic carbon (OC), sand content, and horizon thickness by slope position for each physiographic unit sampled.

PU	Summit			Shoulder			Backslope			Footslope			Toeslope		
	OC	Sand	Thickness	OC	Sand	Thickness	OC	Sand	Thickness	OC	Sand	Thickness	OC	Sand	Thickness
	g kg^{-1}	%	cm	g kg^{-1}	%	cm	g kg^{-1}	%	cm	g kg^{-1}	%	cm	g kg^{-1}	%	cm
1	7±2 (7)	74±5	9±3	7±2 (7)	71±2	9±5	9±3 (7)	71±7	15±14	9±2 (7)	63±13	8±6	13±5 (6)	54±18	9±6
2	7±2 (2)	69±13	13±11	10±3 (2)	60±17	14±1	8±1 (2)	58±14	10±6	11±3 (2)	61±2	12±4	19±14(2)	52±22	10±8
4	8±2 (4)	68±7	9±5	8±1 (5)	66±6	10±4	8±2 (5)	64±9	12±4	9±4 (5)	69±3	12±3	12±5 (5)	60±8	17±7
5	15±4 (2)	57±4	9±4	10±3 (2)	67±2	14±2	8±0 (2)	65±6	9±2	7±2 (2)	70±4	14±5	8±2 (2)	68±4	14±3
6	8±2 (5)	58±16	11±11	6±3 (6)	60±15	12±8	8±3 (6)	55±17	10±4	7±1 (6)	60±7	8±2	10±4 (6)	52±8	8±1
9	8 (1)	61	7	8±3 (2)	66±5	9±6	7±1 (2)	64±10	5±1	7±7 (2)	62±7	7±4	11±8 (2)	57±15	6±3

than those in C horizons, often reaching levels comparable with those of B horizons in the younger surface soils. The increase in organic C concentration in the Bk horizon of the backslope was an apparent anomaly, as neither its color, texture, nor structure were indicative of a buried horizon.

In the shortgrass steppe approximately 60% of the root mass resided in the surface 10 cm (Schimel et al., 1986); however, surface horizons did not contain a similarly disproportionate amount of the soil organic C. As evident in the soils of Fig. 2, organic C in the A horizons represented 25% or less of the total quantity in the solum.

Distribution of Organic Carbon Mass

Distinctive patterns in organic C distribution emerged when viewed on a mass basis to a constant depth (Table 4). The quantity of organic C accumulated to 1 m varied as a function of both physiographic unit and slope position. Averaged across all PUs and slope positions, the mean value was 6.4 kg organic C m⁻³. Average values for lowlands, slopes, and uplands, across PUs, were 7.3, 5.2, and 6.6 kg m⁻³, respectively. Quantities ranged from 2.5 kg m⁻³ on the terrace escarpments of PU 9, to 10.7 kg m⁻³ on the uplands of PU 6. Estimates of mean soil organic C for the shortgrass steppe reported in the literature include 7.6 kg m⁻³ (Post et al., 1982) and 5 to 10 kg m⁻³ (Franzmeier et al., 1985).

Quantities of accumulated organic C would typically be expected to increase with decreasing elevation along a toposequence. This expectation is particularly true in semiarid environments, where many landscapes act as closed drainages because of insufficient energy to remove soil material from the watershed. The mean values for toposequences of PUs 1, 2, and 4 followed this trend, wherein the lowlands contained more organic C (1-m depth) than the slopes, and the slopes contain more than the uplands (Table 3). The pattern was different for the average toposequence data of PUs 5 and 6, where the highest quantity of organic C resided in the uplands and the lowest in the slopes. The latter pattern suggests an open system composed of stable uplands, eroded slopes, and lowlands, whereas material was removed from temporary storage zones almost as quickly as it was accumulated.

Our 1-m data do not support the hypothesis that lowlands contain a disproportionate amount of organic C. Lowlands contributed 25% of the total landscape organic C, as compared with 48% for the uplands. The PUs displaying highly dissected topography and having a greater potential for runoff and material redistribution should have a disproportionate amount of organic C in depositional sites. Physiographic units 4, 5, and 6, which were more dissected than the others, did not indicate that this pattern generally occurs within the shortgrass steppe. Contribution of the lowlands to total land area and total quantity of organic C for these PUs was 32 and 40, 31 and 29, and 43 and 41, respectively. Lowlands contributed 25% of total organic C and 22% of total area, averaged over the entire CPER, showing a slight tendency towards disproportionate organic C accumulation.

Organic C Storage in Active vs. Inactive Pools

We define active organic C as that which is present within the microbiologically more active part of the soil, thereby excluding organic C in BCk (formerly

Table 4. Total quantities of organic carbon (OC) to 1 m, calculated according to areal extent of each slope position within each PU sampled.

PU	Lowland			Slope			Upland			PU total
	OC	OC	% of PU total	OC	OC	% of PU total	OC	OC	% of PU total	OC
	kg m⁻³	kg 10³		kg m⁻³	kg 10³		kg m⁻³	kg 10³		kg 10³
1	8 ± 1 (4)	2 850	2	6 ± 1 (5)	10 260	8	6 ± 2 (4)	108 096	90	121 206
2	8 ± 4 (2)	2 106	8	6 (1)	5 700	20	5 ± 1 (5)	19 992	72	27 798
4	9 ± 2 (5)	42 861	40	7 ± 1 (3)	54 855	52	4 (1)	9 064	8	106 780
5	6 ± 2 (2)	3 180	29	5 (1)	1 104	10	7 ± 1 (2)	6 580	61	10 864
6	6 ± 2 (4)	24 375	41	5 (1)	16 796	28	11 (1)	18 618	31	59 789
9	7 (1)	10 640	89	2 (1)	1 350	11				11 990
x̄	7.3			5.2			6.6			
Totals		86 012			90 065			162 350		338 427
% of grand total		25			27			48		

Table 5. Total quantities of organic carbon (OC) to the BCk horizon calculated according to areal extent of each slope position within each PU sampled.

PU	Lowland			Slope			Upland			PU total
	OC	OC	% of PU total	OC	OC	% of PU total	OC	OC	% of PU total	OC
	kg m⁻³	kg 10³		kg m⁻³	kg 10³		kg m⁻³	kg 10³		kg 10³
1	9 ± 3 (6)	3 344	4	4 ± 1 (7)	7 695	10	4 ± 2 (23)	69 249	86	80 288
2	12 ± 4 (2)	3 132	13	4 ± 3 (2)	3 420	14	4 ± 2 (7)	17 952	73	24 504
4	10 ± 1 (5)	46 629	41	8 ± 3 (5)	60 420	52	4 ± 1 (4)	7 828	7	114 877
5	5 ± 1 (5)	2 650	26	5 ± 1 (2)	1 104	11	7 ± 2 (8)	6 298	63	10 052
6	6 ± 2 (6)	24 000	66	3 ± 1 (6)	9 367	26	2 ± 1 (5)	2 958	8	36 325
9	6 ± 2 (3)	8 512	87	2 ± 1 (2)	1 296	13				9 808
x̄	7.8			4.3			4.1			
Totals		88 267			83 302			104 285		275 854
% of grand total		32			30			38		

Table 6. Summary of buried organic C (inactive organic C) vs. active organic C (mass calculated to BCk horizon).

PU	Buried organic C		Active organic C	Buried + active organic C
	Lowland	Upland		
			kg × 10³	
1		31 289	80 288	111 577
2		7 558	24 504	32 062
4	8 725		114 877	113 062
5	982		10 052	11 034
6	6 947		36 325	43 272
9	2 816		9 808	12 624
Totals	19 470	38 847	275 854	334 171

Cca) and C horizons. We define inactive organic C as that which resides in buried horizons below the C horizon of the surface soil, or below the zone of pedogenesis. Therefore, we define active and inactive organic C pools with respect to pedogenesis, and not as fractions of varying residence time within a given horizon, in the sense of Jansson (1958) or Paul and Juma (1981).

Buried soils are common at CPER. They occupy all slope positions with the exception of shoulders. Of the 161 pedons described, 50 had buried horizons; of these 50, the majority reside in either the uplands of PUs 1 and 2, where they were overlain by loess, or the lowlands of PUs 4, 5, 6, and 9, where they have been overlain by alluvium. Buried soils were also frequently encountered within the solum of the overlying soil and therefore contributed to the active C pool. The distribution of active organic C showed more significant effects of both PU and slope position than did 1 m of organic C (Table 5). The mass of active organic C was closely tied to solum depth. With few exceptions, solum depth increased steadily from the shoulder to the toeslope of a given toposequence. This finding corresponds with the results of Aandahl (1948), Kleiss (1970), and Malo et al. (1974). Solum depth reflected more rapid rates of pedogenesis in the often more moist and productive lowlands (Schimel et al., 1986). Solum depth and, hence, active organic C accumulation reflected the steady effects of normal pedogenic and erosional processes, rather than the more episodic effects of wind erosion.

On the basis of active C mass, lowlands contained somewhat more organic C per unit area than did the slopes and uplands, having 32% of total organic C in 22% of the total area. Active organic C comprised 103% of 1 m of organic C in lowlands as compared with 92 and 64% of 1 m of organic C for slopes and uplands, respectively. This suggests that 1 m of organic C is an underestimate of organic C for the lowlands, because none of 1-m lowland organic C was found in BCk and C horizons, in contrast to 8 and 36% for slopes and uplands, respectively. If we assume similar ratios of active to BCk and C horizon organic C for the lowlands as were found in the uplands, then lowlands might contain a disproportionate amount of total organic C. Our data do not allow us to make a quantitative estimate of BCk and C horizon organic C in lowlands.

Our estimate indicated that significant amounts of organic C were stored in buried horizons (Table 6). Buried horizon organic C mass was 58 317 kg, cal-

culated for a 50 cm thickness, or 17% of the total organic C estimate for the entire site. Much of this buried organic C (67%) was found in upland positions under eolian deposits as a result of intense and probably episodic wind erosion events, while the remainder was found in lowlands under alluvial deposits. The accumulation of C in buried horizons may have been an artifact of the postglacial history of the site. Alternately, periods of intense erosion and deposition may have occurred with contemporary fluctuations in climate.

The residence time of organic C in buried soils greatly exceeded those reported for humic fractions in surface horizons (~1200 yr) (Martel and Paul, 1974). We dated two paleosols at 8390 ± 332 yr before present (BP) (SD = 42 yr) and 3995 ± 240 yr BP (SD = 700 yr). The former was beneath an alluvial deposit and the latter was beneath an eolian deposit. Extensive C dating will be required to assess the frequency of soil burial.

CONCLUSIONS

Gradients in soil organic C accumulation on an active basis (as defined herein) are suggestive of extended time periods wherein the effects of water and its redistribution are expressed. Had such time periods gone uninterrupted, such gradients would still be expressed in surface horizon characteristics as well. Departure from systematic patterns has been due to the slow rate at which surface wash, soil creep, solution, and other water-driven processes function in the semiarid steppe relative to the effects of episodic wind erosion. The effects of episodic wind erosion on the spatial distribution of soil properties, particularly in this water-limited environment, should not be overlooked. The extent to which current soil distributions reflect contemporary, as opposed to post-Pleistocene climatic fluctuations, cannot be assessed without further data. Establishing the expected frequency of drought severe enough to induce large scale eolian soil movement will be essential in developing long-term management plans for the shortgrass steppe.

Uplands occupy the largest area and contained the greatest amount of active organic C at CPER. Uplands also contained 67% of inactive organic C buried beneath eolian deposits. Burial of organic C under eolian deposits was a large potential sink in the shortgrass steppe. Cultivation and other practices that increase wind erosion may lead to increased long-term storage of organic C in buried soils.

This study indicates that contemporary and historical geomorphic processes exert a significant impact on contemporary rates of biogeochemical organic C transformations in the shortgrass steppe. The long-term accumulation of organic C in surface and deep soil layers and in buried horizons has been influenced by periods of normal erosion and by episodes of intense wind erosion. Patterns of organic C accumulation with topographic position and depth are, in turn, valuable indicators of the geomorphic history of the site. Better understanding of the potential impacts of geomorphology on biogeochemistry will be essential to future management of erosion-prone regions.

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BIOGEOCHEMISTRY OF C, N, AND P IN A SOIL CATENA OF THE SHORTGRASS STEPPE[1]

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Abstract. Measurements of carbon, nitrogen, and phosphorus content were carried out in the soils of a hillslope of shortgrass steppe. Plant biomass, soil morphology, and soil physical properties were also measured. Soil morphology indicated that the site had undergone several cycles of rapid erosion and deposition. Total mass of C, N, and P increased downslope, following a trend in soil depth, but the summit A horizon had higher C, N, and organic P concentrations than the backslope, reflecting a higher clay content. Laboratory and field incubations showed that N availability increased downslope, while relative N mineralization (N mineralized : total N) decreased. Organic matter content and mineralization rate were closely coupled to physical properties of the soil, which reflect the geomorphic history of the site.

Key words: carbon; erosion; geomorphology; nitrogen; nutrient availability; phosphorus; shortgrass steppe; soil chemistry.

INTRODUCTION

The content of nitrogen and organic matter in soil changes systematically down hillslopes or "toposequences" (Jenny 1980). Lower slope positions and depressions typically have higher levels of N and organic matter than slopes or ridgetops, although this pattern may be reversed in sandhills topography (Barnes and Harrison 1983) and in areas affected by wind erosion. Aandahl (1948) found that N contents along a hillside increased downslope, although the cause of the increase was not determined. Similar trends with elevation have been shown for total organic matter (Malo et al. 1974, Kliess 1977). It is difficult to determine the cause of C and N accumulations in soils, since these elements can be either moved downslope or fixed in situ. Phosphorus has no gaseous pathway and so is a more conservative tracer than C or N. Phosphorus may move downslope as soluble P (Smeck and Runge 1971), organic P, or P-enriched sediment (Sharpley 1980). Smeck (1973) used the distribution of P along hillslopes as an indicator of both movement between soils and movement within a profile.

Few studies have looked at the correlation of C and nutrients among sites as a function of topographic position. The amount of P and fine clays along hillslopes would be expected to influence the in situ turnover and steady-state levels of C and N. A large body of literature discussing the influence of P concentration on the tendency of C and N to accumulate has been recently reviewed by Cole and Heil (1981). Evidence from chronosequences of soils and from fertilizer additions suggests that C and N accumulate as P increases in the soil (Donald and Williams 1954, Walker 1958, Walker et al. 1959, Griffith 1978). In this paper we examine the correlation of C, N, and P concentrations down hillsides where P has been redistributed.

Clay-sized particles are segregated along hillsides; fine particles are moved selectively downslope or downwind (Ruhe and Walker 1968). Clay particles appear to influence the accumulation and mineralization of C and N in soils, so gradients of clay content and mineralogy may be related to gradients of nutrient turnover (Jenkinson 1977, Monreal et al. 1981, Sørensen 1981). Clay appears to increase the retention of soil organic matter as well as to retard the rate of N mineralization (Monreal et al. 1981). Clay-sized particles often have higher P concentrations than bulk soil because organic P and $PO_4^=$ are absorbed by clays (Sharpley 1980, Dong et al. 1983). Erosional processes that cause deposition of clays may also lead to accumulation of P (Dong et al. 1983). Thus, the effects of clay and phosphorus on carbon and nutrients are often confounded.

In this study, we measured soil nutrients, organic matter, and nutrient mineralization along a soil catena of the shortgrass steppe of eastern Colorado. The topography of the northern Colorado Piedmont and Western High Plains is characterized by rolling hills, 10 to 30 m high (Thornbury 1965, Schumm et al. 1980). The region is underlain by the Laramie formation, which is composed of shale with interbedded sandstones. Much of the region is covered with a thin veneer of ancient alluvium, containing igneous and metamorphic material typical of Front Range (Colorado Rockies) lithology. Deep deposits of fine-textured sediments are found in the smaller valleys. In the larger valleys, material removed from hillslopes is spread more thinly, resulting in shallow alluvial horizons that may be removed periodically by ephemeral streamflow. Extensive wind reworking of soils has occurred, resulting in local aeolian deposits. Closed drainages or "playas"

Ustic   Ustollic   Pachic
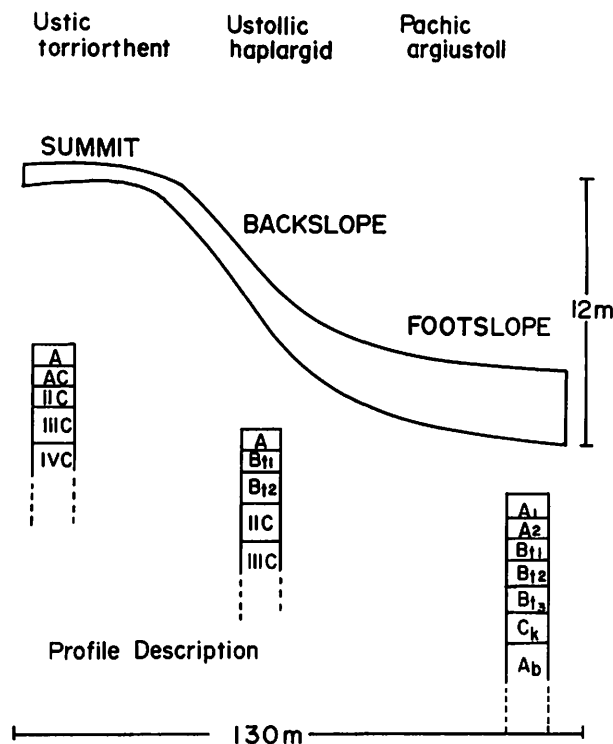torriorthent   haplargid   argiustoll

SUMMIT

FIG. 1. Horizonation of soils and topography of a shortgrass steppe catena.

are also found. These are generally saline or sodic and have distinctive vegetation. Large variations in soils occur along shortgrass steppe catenas, with as many as six soil series and three soil orders occurring along 120–130 m slopes. Sorting of particles often occurs along catenas, with sandy soils on ridgetops and clay loams in lower slope positions, although aeolian deposits frequently complicate this pattern. The area is ideal for studies of biogeochemical cycles in a landscape context.

The objectives of this study were (1) to describe the nutrient and organic matter content of soils in relation to topographic position, and (2) to identify the mechanisms through which erosion and runoff affect nutrients and organic matter.

MATERIALS AND METHODS

Study site

All studies were conducted at the United States Department of Agriculture–Agricultural Research Service Central Plains Experimental Range (CPER). CPER is located north of Nunn, Colorado, in Weld County (latitude 40°48′23″N, longitude 104°45′15″W). Average precipitation is 310 mm/yr and mean monthly temperatures range from −5°C in January to 22° in July. The site chosen was a north-facing hillside near the head of a narrow drainage located in Range 66W, Township 10N, Section 26. The base elevation of the

hillslope was 1641 m, with 12 m relief from base to summit. The slope was 130 m long. The site was fenced to exclude cattle in May 1980.

Three soils were found along the hillside (Fig. 1). The summit was a Ustic torriorthent formed in ancient coarse alluvium. The backslope was a Ustollic haplargid, also formed in ancient coarse alluvium. The footslope was a Pachic argiustoll, formed in recent fine-textured alluvium. Terminology for slope morphology follows Ruhe and Walker (1968).

The vegetation also varied along the catenary sequence (Stillwell 1983). Percent ground cover ranged from 90–100% on the footslope to 30–40% on the ridge-top. The perennial vegetation on the ridgetop was dominated by *Opuntia polyacantha* (starvation cactus), *Aristida longisetum* (red three-awn), and *Bouteloua gracilis* (blue grama). Patches of *Muhlenbergia torreyi* (ring muhley) and *Stipa comata* (needle-and-thread) also occurred. The backslope was dominated by *Opuntia, Bouteloua,* and *Buchloe dactyloides* (buffalo grass). The dwarf shrub *Guterrezia sarothrae* (snakeweed) also occurred. The footslope was dominated by intermixed stands of *Buchloe* and *Bouteloua,* with large amounts of *Carex filifolia.* An unusual growth of the biennial forb *Thelosperma filifolia* occurred on the ridgetop and backslope sites but was not found in the footslope.

Soil and vegetation sampling and analysis

Aboveground live and dead vegetation on three 180 cm diameter circular plots was clipped on 26 June 1980 for aboveground biomass determination on each of three slope positions. Roots and detritus were removed from three 10 cm diameter, 20 cm deep cores per plot by repeated flotation and filtration through a 1-mm mesh screen. This depth increment included >90% of total root mass. We did not attempt to separate live from dead roots.

Three replicate 5.1 cm diameter soil cores spaced 20 m apart were taken for chemical and physical analysis from each of three slope positions. Cores were subdivided by genetic horizon as distinguished in the field, and were taken to as great a depth as could be obtained.

Total N in soil and plant samples was determined following Kjeldahl digestion using a block digestor (Nelson and Sommers 1980). Digests were analyzed for NH_3^0 colorimetrically. Organic P was determined by the method of Saunders and Williams (1955), in which paired samples are extracted with 1 mol/L H_2SO_4. One of the pair is ashed at 400°C prior to extraction, and the difference between the two is organic P. Total P was determined by NaOH fusion (Smith and Bain 1982). Available P was estimated using an $NaHCO_3$ extract (Olsen et al. 1954). After removal of carbonates with H_2SO_4, soil organic carbon was determined by wet oxidation with $K_2Cr_2O_7$ in a concentrated H_2SO_4–H_3PO_4 mixture in sealed culture tubes containing an alkaline CO_2 trap (2 mol/L NaOH). The wet oxidation

TABLE 1. Physical properties of catena soils. Data are means ± SD.

Horizon	Bottom depth (cm)	Bulk density (g/cm³)	>2-mm fragments (%)	% sand	% silt	% clay	Depth to lime* (cm)
Footslope							
A1	8	1.29 ± 0.2	0.0 ± 0.0	39.5 ± 2.2	32.3 ± 0.1	28.2 ± 2.3	72 ± 2
A2	15	1.56 ± 0.1	0.0 ± 0.0	55.7 ± 2.0	18.8 ± 1.4	25.1 ± 0.8	
B₁	35	1.32 ± 0.1	0.0 ± 0.0	43.8 ± 3.0	21.4 ± 3.0	34.8 ± 2.7	
B₂	55	1.60 ± 0.2	0.0 ± 0.0	41.8 ± 6.6	14.7 ± 1.6	43.5 ± 6.3	
B₃	71	1.39 ± 0.3	0.0 ± 0.0	28.2 ± 7.5	19.7 ± 1.2	52.0 ± 7.8	
Bₖ + Cₖ	85	1.60 ± 0.1	0.0 ± 0.0	44.7 ± 11.0	17.6 ± 4.2	36.7 ± 8.5	
Aᵦ	⋯	1.50 ± 0.2	0.0 ± 0.0	60.3 ± 7.8	12.2 ± 0.0	21.9 ± 1.9	
Backslope							
A1	15	1.36 ± 0.3	11.3 ± 2.0	72.5 ± 0.6	12.5 ± 2.1	15.0 ± 1.6	60 ± 3
B₁	31	1.26 ± 0.2	3.0 ± 1.0	69.9 ± 2.1	12.3 ± 0.4	17.7 ± 2.0	
B₂	55	1.30 ± 0.1	0.0 ± 0.0	65.7 ± 1.2	10.6 ± 1.3	23.7 ± 2.5	
IIC	68	1.24 ± 0.1	0.0 ± 0.0	64.0 ± 1.4	15.2 ± 0.3	21.7 ± 1.1	
IIIC	⋯	1.45 ± 0.1	0.0 ± 0.0	63.6 ± 2.7	14.8 ± 2.2	21.6 ± 0.5	
Summit							
A	10	1.44 ± 0.1	7.0 ± 0.9	66.5 ± 5.1	13.4 ± 2.8	20.1 ± 2.4	9 ± 2
ACₖ	20	1.35 ± 0.2	1.3 ± 0.2	67.6 ± 6.6	8.3 ± 1.0	24.0 ± 6.4	
IIC	43	1.56 ± 0.2	2.8 ± 0.8	72.1 ± 3.6	6.9 ± 2.1	20.9 ± 2.8	
IIIC	53	1.72 ± 0.3	0.0 ± 0.0	70.4 ± 9.3	7.4 ± 2.9	22.2 ± 6.4	
IVC	⋯	1.87 ± 0.3	15.8 ± 2.3	68.2 ± 5.2	11.9 ± 5.2	20.0 ± 10.1	

* Free carbonates, principally $CaCO_3$.

was cross-checked against a Coleman Carbon Analyzer (Nelson and Sommers 1982) on representative samples. Similar results were obtained using either method. Sand, silt, and clay in the <2 mm fraction were determined by the hydrometer method (Day 1965) after removal of organic matter with H_2O_2.

Statistical analyses were performed using the SPSS MANOVA package (Hull and Nie 1981); single-degree-of-freedom contrasts were used to test for pairwise differences. Except where noted otherwise, significance was assumed whenever $P \leq .10$.

Nitrogen mineralization

Nitrogen mineralization was measured using the buried bag technique (Eno 1960). Five soil samples from the 0–10 cm depth were collected randomly at 1-mo intervals from each site along the catena. To calculate relative N mineralization, soil samples were collected for determination of total N in the same depth increment. Samples were sieved through a 2-mm mesh screen to remove coarse root fragments. This was essential, given the high root density in surface soils. Half of each sample was placed in a large polyethylene bag and immediately returned to the soil and buried at the 0–10 cm depth. The other half of the sample was extracted with 2 mol/L KCl, with 5 mg/kg phenyl-mercuric acetate (PMA) added to inhibit microbial activity. Gravimetric moisture content was also determined by drying the soil at 105° for at least 48 h. Soils were extracted and moisture determined within 8 h after sampling. The bags were allowed to incubate for 1 mo before collection. Bags were set out each month for 10 mo. The incubated samples were handled as described for the initial samples. The 2 mol/L KCl–PMA extracts

were analyzed for NH_4^+ and $NO_3^- + NO_2^-$ colorimetrically with a modified Technicon I (D. S. Bigelow et al., *personal communication*).

Laboratory incubations were made in cylinders 20 cm tall and 5 cm in diameter, which were packed with air-dry soil. Sufficient water was added to bring them to near field capacity. Water was added weekly to maintain the soil moisture levels. Three replicate cores from each of the three sites were analyzed destructively for NH_4^+ and $NO_3^- + NO_2^-$, initially and at 2, 4, and 6 wk thereafter.

In the statistical analyses of mineralization studies, the same procedures and significance levels were used as in the analyses of soil and vegetation samples.

RESULTS AND DISCUSSION

Erosional history and pedogenesis

The soils of the site reflect several intense episodes of erosion and deposition rather than a gradual sorting of materials down the hillslope. The summit (Ustic torriorthent) and backslope (Ustollic haplargid) soils were formed in coarse ancient alluvium over sandstone. Pebbles found in these two soils are granitic and streamworn, indicating that they probably originated in the Rocky Mountains. Four lines of evidence suggest that significant erosion has recently occurred from the summit. First, pebbles were a larger fraction of the soil in the surface than in the immediate subsurface horizons of the summit soil, indicating the removal of fines from this soil (Table 1). Second, free carbonates appeared at an unusually shallow depth (9 cm) in the summit soil, indicating that erosion has been more rapid than leaching. Third, the clay content of the sum-

TABLE 2.   C, N, and P contents of catena soils. Data are means (±SD) of three replicate soil cores at each slope position.

Horizon	Bottom depth (cm)	$C_{organic}$ (kg/ha)	$N_{organic}$ (kg/ha)	P_{total} (kg/ha)	$P_{organic}$ (kg/ha)	$NaHCO_3$-P (kg/ha)	C:N	$C:P_{organic}$
Footslope								
A1	8	21 050 ± 1650	1998 ± 284	489 ± 88	212 ± 63	29.0 ± 5.0	10.5 ± 1.5	99.3 ± 18.0
A2	15	10 050 ± 874	1020 ± 88	464 ± 31	199 ± 15	29.0 ± 2.2	9.8 ± 0.8	50.5 ± 4.0
B,1	35	19 270 ± 185	2390 ± 203	1090 ± 106	472 ± 155	65.0 ± 13.5	8.1 ± 0.7	40.8 ± 6.5
B,2	55	13 760 ± 2240	2270 ± 1690	1427 ± 115	291 ± 89	106.0 ± 45.8	5.1 ± 2.3	47.3 ± 10.9
B,3	71	7340 ± 917	990 ± 320	826 ± 17	206 ± 49	20.0 ± 6.3	7.4 ± 1.5	35.6 ± 6.5
B_K + C_K	85	8280 ± 448	1050 ± 160	1040 ± 123	179 ± 36	24.0 ± 5.6	7.9 ± 0.8	46.2 ± 6.0
A_b	...	...	...	...	...	...	7.6 ± 0.5	...
Total or average		79 750 ± 6314	10 168 ± 2745	4510 ± 480	1559 ± 407	267 ± 68.4	7.8 ± 1.4	51.1 ± 8.4
Backslope								
A	15	11 630 ± 816	1360 ± 188	475 ± 43	133 ± 3.5	24.0 ± 0.6	8.6 ± 0.6	87.4 ± 14.0
B,1	31	9276 ± 1008	1210 ± 93	532 ± 46	227 ± 46	7.0 ± 1.0	7.7 ± 0.7	40.8 ± 6.1
B,2	55	12 160 ± 312	1700 ± 125	786 ± 44	303 ± 81	7.0 ± 0.6	7.1 ± 0.3	40.1 ± 5.9
IIC	68	4990 ± 806	750 ± 106	559 ± 99	185 ± 6	4.0 ± 0.9	6.6 ± 1.0	34.2 ± 3.2
IIIC	...	...	...	...	...	...	6.6 ± 0.7	34.2 ± 0.0
Total or average		38 050 ± 2942	5020 ± 514	2352 ± 279	848 ± 166	42 ± 6.0	7.6 ± 0.7	44.9 ± 4.0
Summit								
A	10	9930 ± 1296	1330 ± 140	341 ± 10	178 ± 36	6.0 ± 2.0	7.5 ± 1.3	55.8 ± 8.4
AC	20	7020 ± 945	990 ± 174	390 ± 16	174 ± 4	3.0 ± 0.3	7.1 ± 1.1	40.3 ± 4.0
IIC	43	5270 ± 1217	820 ± 95	371 ± 0.0	65 ± 4	2.0 ± 0.4	6.4 ± 1.1	81.1 ± 7.3
IIIC	53	3610 ± 344	520 ± 203	473 ± 14	172 ± 4	2.0 ± 0.2	6.9 ± 1.4	20.9 ± 1.2
IVC	...	...	...	...	...	...	7.6 ± 1.0	19.3 ± 2.0
Total or average		25 830 ± 3802	3660 ± 612	1575 ± 40	589 ± 48	13 ± 3.0	7.1 ± 1.1	43.8 ± 4.8

mit A horizon was higher than that of the backslope and was similar to that of the backslope B horizon (Table 1), suggesting recent removal of the original eluvial A horizon. Fourth, the $C:P_{organic}$ ratio of the summit soil A horizon was significantly lower ($P <$ .05) than those of the back and footslope A horizons and was similar to those in subsurface horizons (Table 2). The clay content and $C:P_{organic}$ ratios both suggest that the original A horizon was removed and that the new surface horizon has properties that are intermediate between A and B horizons. The carbonate, clay, and $C:P_{organic}$ ratio together suggest that comparatively little pedogenesis has occurred since the original A horizon was removed, although the soil has accumulated significant amounts of C, N, and $P_{organic}$.

The footslope soil (Pachic Argiustoll) is a depositional soil. It is extremely well sorted, containing no pebbles or coarse sand in the solum. It may thus be either an aeolian or alluvial deposit. A buried A horizon was found at 85 cm overlain by either a weakly developed B_K or a C_K. The A_b does not contain free carbonates although the overlying horizon (B_K or C_K) does. The abrupt transition from the B_K/C_K horizon to the A_b suggests that the overlying material may have been deposited relatively rapidly, with no time for pedogenesis during the depositional event. The depositional event must have occurred before the summit was denuded, since the overlying depositional soil is quite well developed, in contrast to that of the summit.

The deposition may have occurred during the altithermal (5000–8000 yr BP), a period of dry weather and widespread erosion. A buried horizon <2 km from this site is dated between 6000 and 7000 yr BP (Gould et al. 1979).

Nutrient availability

Relative availability of N and P increased down the hillslope. Annual nitrogen mineralization measured in situ increased from 30 kg/ha at the summit to 55 kg/ha at the footslope (Table 3). These values are slightly less than estimates of net annual plant uptake, which range from 53 to 83 kg/ha (Bokhari and Singh 1975). Measurements of mineralization potential, carried out

TABLE 3.   Laboratory and in situ N mineralization rates in the surface 10 cm of catena soils.

Position	N mineralized in situ (kg·ha·yr⁻¹)	% total N mineralized in situ	Lab incubation N mineralized (kg·ha⁻¹·6 wk⁻¹)	% total N mineralized in lab incubation
Summit	30 a*	4.2 a	47 a	6.5 a
Backslope	41 b	5.0 a	30 b	3.7 b
Footslope	55 c	1.8 b	58 c	1.9 c

* Values within a column with the same letter are not significantly different ($P \geq$ .10, MANOVA single-degree-of-freedom contrasts).

TABLE 4. Ash-free dry biomass and organic-N content of above- and belowground vegetation components of a shortgrass steppe catena in 1981. Data are means ± SD.

	Ridgetop		Backslope		Footslope	
	Grasses	Forbs	Grasses	Forbs	Grasses	Sedges
Aboveground biomass (kg/ha)	702 ± 110	1270 ± 958	859 ± 110	1427 ± 1629	1160 ± 338	425 ± 117
N (%)	1.1 ± 0.1	1.1 ± 0.3	1.2 ± 0.1	1.0 ± 0.5	1.3 ± 0.1	1.7 ± 0.2
N (kg/ha)	7.7 ± 0.9	14.0 ± 7.2	10.3 ± 4.3	14.3 ± 11.7	15.1 ± 2.8	7.2 ± 1.4
Roots* + detritus (kg/ha)	19 160 ± 5640		18 460 ± 5210		27 390 ± 7760	
N (%)	1.9 ± 0.1		1.9 ± 0.3		1.7 ± 0.2	
N (kg/ha)	364 ± 63.1		350 ± 77.0		465 ± 93.2	

* Grasses, forbs, and sedges were not separated.

under optimal conditions to eliminate effects of the different moisture and temperature regimes that occur under field conditions, showed the footslope to be highest, followed by the summit (Table 3). Mineralization expressed as percent of total N (relative N mineralization) showed a different pattern, indicating differences in organic matter quality. Values for the footslope were lowest both in the laboratory and in situ. Relative N mineralization in the upper slope positions was higher in both lab and field incubations (Table 3). Thus, nitrogen availability to the vegetation increased downslope, while turnover of N decreased. Evidence from a fertilizer study on this site (Stillwell 1983) suggests that in moist years the footslope is N-limited, while the other sites are water-limited. Thus, at least in wet years, the footslope must receive some runoff. This transition from water- to N-limitation across a moisture gradient is analogous to the situation described for the Sahel (Breman and de Wit 1983), where a transition from water- to nitrogen-limitation occurs at a precipitation level of 300 mm/yr, which is about the same amount of precipitation as the CPER receives.

Phosphorus availability, measured as $NaHCO_3$-extractable $PO_4^=$, increased downslope from 13 to 267 kg/ha (Table 2). Available P as a percentage of total P increased downslope, in contrast to available N as a percentage of total N, regardless of whether the ratio was computed as $NaHCO_3$-P : total P (0.8–5.9%) or as $NaHCO_3$-P : $P_{inorganic}$ (1.3–9.0%).

Vegetation

Perennial aboveground and total belowground biomass increased from the upper slope positions to the footslope (Table 4). Annual or biennial forbs contributed significantly to biomass in 1981, when sampling occurred, but were not observed in any other year between 1979 and 1983. The estimate of perennial biomass may thus be a more accurate indicator of the typical pattern of biomass along the catena. Nitrogen mass in the aboveground perennial biomass followed the same patterns as biomass. Although there was no downslope increase in aboveground biomass if forbs were considered, an increase in belowground biomass occurred even though forb roots were included. Soil organic matter may be primarily derived from root detritus in this ecosystem, given the relative magnitudes of the above- and belowground biomass pools.

The estimate of belowground biomass includes both live and dead roots of all species. Nitrogen content of belowground material ranged from 1.7 to 1.9%, including both N in live roots and N immobilized in dead roots. Live roots typically have an N content of 1.1%, whereas detrital and senescent roots have N contents of ≈2.5% (Clark 1977). Values of root N content in our study suggest either an increase in the ratio of live to dead roots or a reduction in the N content of dead roots between the upslope and footslope sites.

Organic matter accumulation and turnover

Organic C, N, and P, as well as total P mass, increased downslope (Table 2). The increase was the result of changes in both soil depth and element concentration; the footslope was much deeper and higher in element concentration than the upper slope sites. The B_K/C_K horizon, which has been least altered from the original sediment, is high in both P and clay (Tables 1 and 2), which is consistent with observations that fine particles are often enriched in P relative to whole soils (Sharpley 1980). The parent material for the footslope was produced by selective deposition of fines from nearby sites. This soil is enriched in clay-associated P, even though the parent material may have

TABLE 5. C, N, and $P_{organic}$ concentrations in catena soil surface horizons. Data are means ± SD.

Slope position	Horizon	Concentration (mg/kg)		
		$C_{organic}$	$N_{organic}$	$P_{organic}$
Summit	A	6 900 ± 800	921 ± 97	124 ± 25
Backslope	A	5 700 ± 400	665 ± 92	65 ± 16
Footslope	A_1	20 400 ± 1500	1 937 ± 275	206 ± 61

originated from the same alluvium and sandstone that formed the upslope sites. If so, accumulation of C and N following the depositional event may have been influenced by high P levels (Cole and Heil 1981).

Two additional factors control soil organic C, N, and P accumulation. First, the increase in soil carbon downslope reflects trends in carbon input to the soil, indicated in this study by biomass estimates. Production increases downslope reflect increases in nutrient availability and, possibly, soil water. Second, clay content may increase soil carbon concentration in a given horizon by adsorption and aggregation. This effect can be seen by comparing the summit and backslope. The summit A horizon (Table 1) was higher in clay than the backslope. Although values for the mass of soil C and N in the A horizon increased from the summit to the backslope (Table 2), the concentrations of C and N increased from backslope to summit (Table 5), following the trend in clay content. The reduction in relative mineralization of organic N down the hillslope may also result from the two factors discussed above. Increasing the input of C to the system may result in higher N immobilization, thus reducing relative N mineralization. The increase in soil C:N ratio downslope (Table 2) might be an indicator of this phenomenon, with larger C:N ratios indicating that N availability for decomposers is not as favorable as when C:N ratios are small. The correlation between soil C:N ratio (Table 2) and percent total N mineralized in the laboratory incubation (Table 3) supports this hypothesis. Clay may also directly reduce turnover of N in organic matter, either by adsorption or incorporation into stable aggregates (Tisdale and Oades 1982). $NaHCO_3$-P does not follow the same pattern, as it is largely controlled by inorganic processes. The effect of topographic position on organic P mineralization, not measured in this study, would be expected to be similar to N mineralization.

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Analysis of Factors Controlling Soil Organic Matter Levels in Great Plains Grasslands[1]

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ABSTRACT

We analyzed climatic and textural controls of soil organic C and N for soils of the U.S. Great Plains. We used a model of soil organic matter (SOM) quantity and composition to simulate steady-state organic matter levels for 24 grassland locations in the Great Plains. The model was able to simulate the effects of climatic gradients on SOM and productivity. Soil texture was also a major control over organic matter dynamics. The model adequately predicted aboveground plant production and soil C and N levels across soil textures (sandy, medium, and fine); however, the model tended to overestimate soil C and N levels for fine textured soil by 10 to 15%. The impact of grazing on the system was simulated and showed that steady-state soil C and N levels were sensitive to the grazing intensity, with soil C and N levels decreasing with increased grazing rates. Regional trends in SOM can be predicted using four site-specific variables, temperature, moisture, soil texture, and plant lignin content. Nitrogen inputs must also be known. Grazing intensity during soil development is also a significant control over steady-state levels of SOM, and since few data are available on presettlement grazing, some uncertainty is inherent in the model predictions.

Additional Index Words: grazing, *simulation modeling, soil texture,* mineralization, immobilization.

A BUNDANT INFORMATION is available in the soils literature on organic matter and the cycling of C, N, S, and P through organic matter (Stevenson, 1986). Incorporation of concepts of organic matter formation and turnover into simulation models is an excellent means of integrating this information. We have developed a model of rangeland and cropland ecosystems that is designed to simulate the effects of macroenvironmental gradients as a first step toward simulating the effects of climatic change. The model includes the effects of management and soil and plant properties over long periods of time (ca. 50–2000 yr). The model simulates primary productivity, soil nutrient dynamics, and soil water, but focuses on changes in soil organic matter. We focus on organic matter because it integrates changes in production and decomposition over time. Organic matter is central to the cycling of plant nutrients, influences water relations and erosion potential, and is a key factor in soil structure (Tisdale and Oades, 1982). The model simulates both the labile (rapid turnover) and stabilized (slow turnover) fractions, thus simulating the nu-

trient-supplying capacity of the soil organic matter as well as the absolute quantity.

The modeling exercise had several objectives. The first was to simulate the effects of climatic gradients on productivity and soil organic matter over large areas, which is a first step in modeling the effects of climate change. The second was to identify key soil properties that would allow us to simulate differences between soils within a single climatic zone.

A variety of different types of models have been used to represent long-term changes in soil organic N and C. Jenny (1941) used a single-state variable model form to represent the decline of organic C and N in cultivated soils. Campbell et al. (1978) improved upon this approach by dividing soil organic matter (SOM) into two different compartments, which included stable organic matter and labile organic matter with turnover rates ($1/k$) of 53 and 1429 yr, respectively. Paul and Van Veen (1978) and Van Veen and Paul (1981) made further improvements in the SOM models by dividing the plant residue into recalcitrant and decomposable fractions and introducing the concept of physically protected soil organic matter. A critical assumption in their model was that physically protected organic matter has a much lower decomposition rate than nonphysically protected organic matter.

Our soil organic matter formation model (the Century model) incorporates multiple SOM compartments (Anderson, 1979; Jenkinson and Rayner, 1977), simulates decomposition rates that vary as a function of monthly soil temperature and precipitation, and includes both N and C flows. The structure and concepts used in our model are similar to those used by Paul and Van Veen (1978); however, we do not explicitly use the concept of physically protected and nonphysically protected organic matter. In recent years, Pastor and Post (1986) and Aber et al. (1982) have used a modeling approach similar to ours for representing soil C and N dynamics in forest systems.

We estimated as many of the parameters as possible directly from published data using a nonlinear data-fitting procedure (Powell, 1965). We validated the model by comparing simulated soil C and N and aboveground plant production to mapped values at 24 sites on the Great Plains, which span the overall moisture and temperature gradients in this region.

MODEL DESCRIPTION

Soil and Decomposition Submodel

The SOM submodel contains three soil organic matter (SOM) fractions (Fig. 1). They constitute (i) an active fraction (active SOM) of soil C and N consisting of live microbes and microbial products, along with soil organic matter with a short turnover time (1–5 yr); (ii) a pool of C and N (slow SOM) that is physically protected and/or in chemical forms
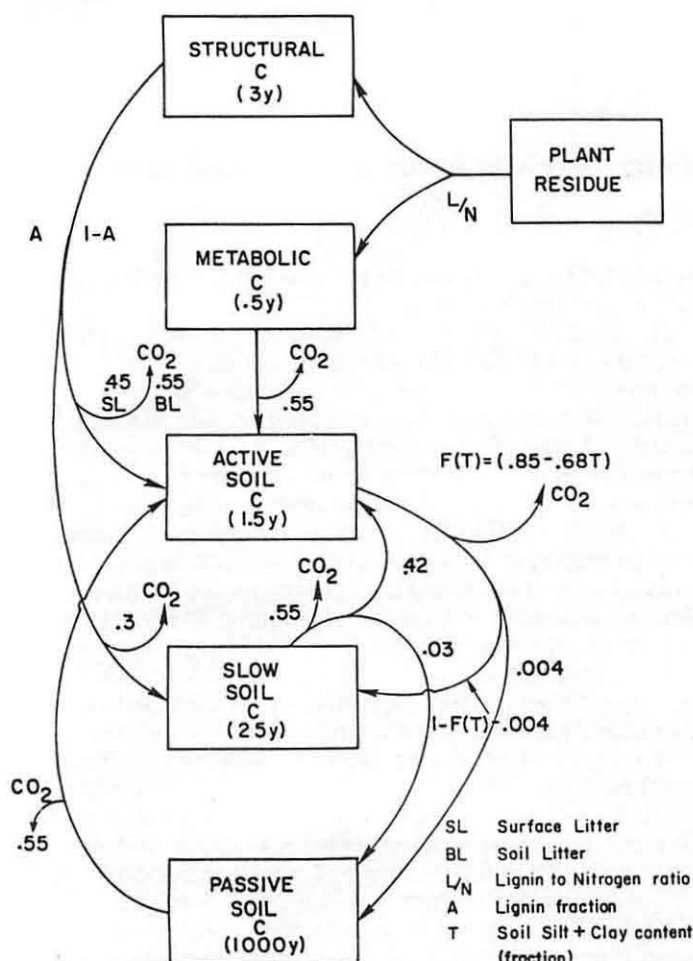
Fig. 1. Flow diagram for the C flows in the Century model.

Fig. 2. The effect of soil temperature (T_d) and moisture (M_d) on monthly decomposition rates.

with more biological resistance to decomposition, with an intermediate turnover time (20–40 yr); and (iii) a fraction that is chemically recalcitrant (passive SOM) and that may also be physically protected, with the longest turnover time (200–1500 yr). Plant residue (shoot and root plant biomass) is divided into structural pools that have 1- to 5-yr turnover times and metabolic pools that have 0.1- to 1-yr turnover times (based on McGill et al., 1981) prior to transfer into SOM pools.

We assume that the lignin-to-N ratio controls the split of plant residue into structural and metabolic material and that all of the plant residual lignin flows into the structural compartment. We also assume that the decay rate of structural material is a function of its lignin content and that the lignin fraction is incorporated into the slow soil pool. This direct flow of lignin into slow soil organic matter is based on data from laboratory incubation of labeled lignin-type material (Stott et al., 1983), which show that very little (<2%) of the lignin is found in microbial biomass, with most (70%) being stabilized in the soil. The release of lignin at a rate that is proportional to its concentration in structural material is based on the assumption that lignin is distributed fairly uniformly through the structural material and is released as the microbes decompose the more labile components of the structural material (e.g., hemicellulose and cellulose).

Decomposition of each of the state variables is calculated using the following equation:

$$dC_i/dt = K_i \cdot M_d \cdot T_d \cdot C_i, \qquad [1]$$

where C_i = the carbon in the state variable; i = 1, 2, 3, 4, 5, 6, and 7 for structural and metabolic soil surface litter,

structural and metabolic soil litter, and active, slow and passive soil fractions; K_i = the maximum decomposition rate parameter (per week) for the ith state variable (K_i = 0.076, 0.28, 0.094, 0.35, 0.14, 0.0038, and 0.00013); M_d = the effect of the ratio of monthly precipitation (PPT) to potential evapotranspiration rate (PET) on decomposition (see Fig. 2b); and T_d = the effect of monthly average soil temperature on decomposition (see Fig. 2a).

The effect of soil temperature on decomposition was determined by using a nonlinear data-filling procedure (Powell, 1965) to determine the parameter value for an equation (generalized Poisson function) that represented the effect of soil temperature on decomposition of labeled cellulose at three different temperatures (10, 20, and 30°C) for a 90-d incubation [data derived from Sørenson (1981)]. The average monthly soil temperature was calculated by averaging the average monthly maximum and minimum soil-surface temperatures, which were calculated as a function of the observed averaged monthly maximum and minimum air temperatures (2 m) and the standing crop plant biomass, using an equation developed by Parton (1984). The effect of the ratio of PPT to PET on decomposition was calculated using daily water budget (Parton, 1978) and soil temperature (Parton, 1984) models and a daily decomposition model to simulate monthly average decomposition rate for a 34-yr simulation run. We then evaluated the best fit curve to represent the effect of the ratio of monthly PPT to PET on monthly decomposition rates. The monthly decay rate was assumed to be proportional to the product of a soil temperature term (see Fig. 2a) and a moisture term (see Fig. 2b).

All of the decomposition rate parameters (K_i) for the state variables were constant except for the structural decay rate (K_1^a and K_3^a), which is a function of the lignin content of the structural material, and the active SOM decay rate (K_3^a), which is a function of the soil texture. Also note that decay rates for the soil surface litter are 20% lower than the soil litter.

This is based on the assumption that soil moisture content will be less optimal for decomposition near the soil surface (Holland and Coleman, 1987).

The model assumes that all C decomposition flows are a result of microbial activity and that microbial respiration is associated with each of these flows. The model assumes (see Fig. 1) that 55% of the C decomposition flow for soil non-lignin structural C, metabolic C, and slow and passive soil SOM is lost as microbial respiration. Nonlignin surface structural litter has a low respiration loss (45%), since fungi are the primary decomposers of surface litter and more efficiently stabilize C into microbial biomass (Holland and Coleman, in press). Stabilizing lignin into slow SOM is a fairly efficient process with only 30% lost as respiration loss (Stott et al., 1983). The efficiency of stabilizing active SOM into slow SOM is assumed to be a function of soil texture, with sandy soils being less efficient than fine-textured soils (see discussion below).

Twelve 1-yr plant residue incubations in subsoil (Pinck et al., 1950) were used to estimate the effect of the lignin (L) to N ratio on the split plant residue into structural and metabolic components and decay rates for soil structural and metabolic litter $(K_3$ and $K_4)$. The L content of incubated plant residue ranged from $<5\%$ for bluegrass $(Poa\ pratensis$ L.) to 17% for corn $(Zea\ mays$ L.) stover, whereas N content ranged from 4.3% for bluegrass to 0.7, 0.6, and 0.4%, respectively, for oak $(Quercus$ sp.) leaves, wheat $(Triticum\ aestivum$ L.) straw, and corn stover. To evaluate the parameters, we used a simplified version of the model, where we dropped the passive SOM pool and assumed that the loss of slow C was minimal in a 1-yr incubation, and then evaluated the fit for the specific parameters. Note that the decay rate for active SOM and the efficiency of creating slow SOM from active SOM were determined by an independent data-fitting process. A comparison of the Pinck et al. (1950) data with more recent soil incubation data (Ladd et al., 1981) shows similar results and suggests that controls over decomposition are similar in subsoil and surface horizon soils.

A comparison of the observed and simulated C remaining vs. time for five different plant incubations (Fig. 3a) showed high C losses during the first 8 weeks and low C losses at the end of the incubation. The high-N and low-lignin residues (oats and millet, $Avena\ sativa$ L. and $Panicum\ miliaceum$ L.) decomposed more rapidly than the high-lignin and low-N residue. In general, the difference between the observed data and simulated results was small $(<3\%)$.

The split of plant residue into metabolic and structural components is determined as a function of the L/N ratio of the residue, using the following equation:

$$F_M = 0.85 - 0.018 \cdot L/N,\qquad [2]$$

where F_M = the fraction of residue that is metabolic and F_S = fraction of residue that is structural $(F_S = 1 - F_M)$. This equation predicts that as the L/N ratio gets larger, F_M decreases while F_S increases. This is consistent with data presented by Melillo et al. (1984), who showed that decomposition of leaf litter was inversely related to the initial L/N ratio of the plant material. The split between structural and metabolic material occurs when the plant residue is transferred into surface or soil litter material. We assume that fractions of the soil mineral N (0.05 and 0.10 for surface and soil litter, respectively) are immobilized and, in effect, modify the L/N ratio. This can stimulate the decomposition of low-N plant residue (Pinck et al., 1950). Uptake of N from the soil does not occur if the C/N ratio is <10 (Pinck et al., 1950). The decomposition rate for surface and soil structural material $(K_1^q$ and $K_3^q)$ are calculated as a function of fraction of structural material that is lignin (L_s) and the maximum decay rates (K_1, K_3), using the following equations:

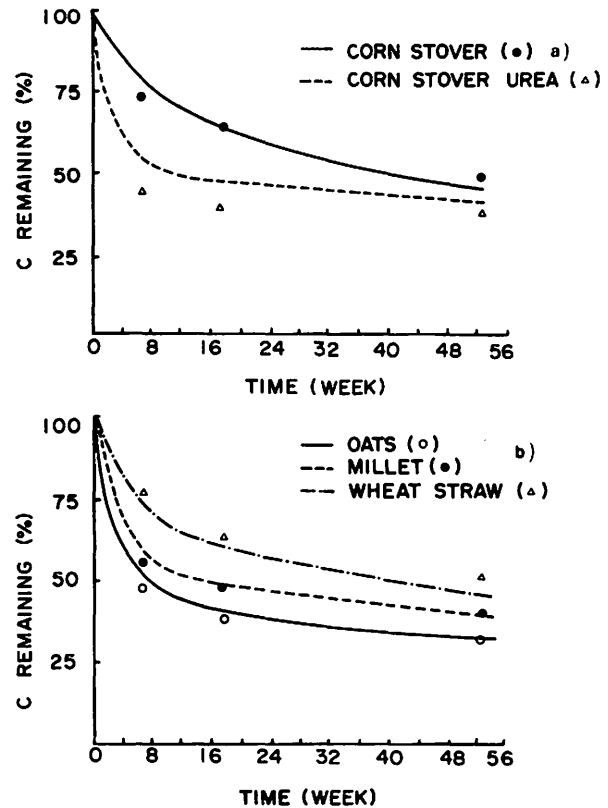$$K_1^q = K_1 \cdot \exp(-3.0 \times L_S),\qquad [3]$$

Fig. 3. A comparison of observed and simulated C remaining vs. time for 1-yr incubations of different types of (a) plant material and (b) wheat straw in a sandy and a clayey soil [data from Pinck et al. (1950].

$$K_3^q = K_3 \cdot \exp(-3.0 \times L_S).\qquad [4]$$

These equations cause the structural decay rates to decrease as the lignin content increases and are based on the assumption that as the lignin content increases, the ability of the microbes to decompose the more readily decomposable substrates (cellulose, hemicellulose, etc.) decreases rapidly (Melillo et al., 1982, 1984). The estimated parameter values in Eq. [2], [3], and [4] and the value for K_3 and K_4 were determined by fitting the model to the observed laboratory incubation data (Fig. 3a), whereas values for K_1 and K_2 were determined by assuming that surface residue decomposes $\sim20\%$ slower than incorporated soil residue.

The model assumes that the lignin content of dead-root biomass (L_R) and dead aboveground plant material (L_a) changes as a function of the annual precipitation $(L_a = 2 + 0.12 \cdot \text{PPT}, L_R = 26 - 0.15 \cdot \text{PPT};$ PPT in cm). The lignin values are based on grassland plant lignin data from the Great Plains (unpublished data from the USIBP Grassland Biome). Shifts in lignin content with precipitation may result from within-species responses and from changes in plant-community composition. Since the model does not explicitly include species characteristics, it does not distinguish between these two types of effects.

The model assumes that soil texture influences the decomposition rate of active SOM (K_9^q) and efficiency of stabilizing active SOM into slow SOM $(E_S =$ fraction of C lost as CO_2 when active SOM is decomposed and stabilized into slow SOM). The effect of soil texture was determined by fitting the model to Sørensen's (1981) laboratory incubation data of cellulose in soils with different textures. Equation [5] shows the effect of the soil silt plus clay fraction (T) on the decay rate of active SOM (K_9^q), and Eq. [6] shows the effect of T on the efficiency of stabilizing active SOM into slow SOM (E_S)

$$K_s^q = K_s \cdot (1 - 0.75 \cdot T), \qquad [5]$$

$$E_S = (0.85 - 0.68\ T). \qquad [6]$$

Equation [5] shows that the decay rate of active SOM decreases as the silt plus clay content increases. Many other studies show that microbial turnover rates are similarly related to texture (Ladd et al., 1981; Schimel et al., 1985a, b; Schimel, 1986). The E_S decreases as the silt plus clay content increases, with a resulting increase in the amount of C stabilized in slow SOM for fine-textured soils (high silt and clay content). This model for the stabilization of active SOM into slow SOM has been independently validated using wheat straw (see Fig. 3b) laboratory incubation data (Pinck et al., 1950) and glucose laboratory incubation data (Van Veen et al., 1984).

The decay rate for the slow SOM pool ($K_6 = 0.0038$ week^{-1}) was assumed to be equal to the decay rate at the end of (day 360 to day 1600) Sørenson's (1981) long-term cellulose incubation. His data also show that the decay rate at the end of the incubation is the same for different soil textures in spite of the fact that the C level in the sandy soil was 50% lower than the C level in the high-clay soil.

The flows that control the formation of passive SOM and its decay rate (K_7) could not be estimated using existing laboratory incubation data because of the long turnover time of passive SOM. The stabilization of active SOM into passive SOM and the stabilization of slow SOM into passive SOM are the flows into passive SOM, and were set equal to 0.4% of the C flow out of active SOM and 3% of the C flow out of slow SOM. The decay rates of passive SOM and the fraction of total SOM in the passive fraction are based on soil carbon-dating data from Martel and Paul (1974), which show that C dates of older soil organic fractions ranged from 800 to 1600 yr and that the old SOM fraction comprises >50% of the total SOM. The actual value of K_7 and the parameters that control the formation of passive SOM were determined by a systematic model-tuning procedure, where the parameters were adjusted to fit observed total SOM levels for several sites ranging from Colorado to eastern Kansas.

Plant Submodel

The plant production flow model simulates the monthly dynamics of C and N in the live and dead aboveground plant material, live roots, and structural and metabolic surface and soil residue pools. Maximum annual aboveground (P_{max} = g biomass m^{-2}) and belowground production (R_{max} = g biomass m^{-2}) without nutrient limitations are calculated as a function of annual precipitation (APPT in cm), using the following equations:

$$P_{max} = -40 + 7.7 \cdot APPT, \qquad [7]$$

$$R_{max} = 100 + 7.0 \cdot APPT. \qquad [8]$$

The equation for aboveground production is based on data of Dodd and Lauenroth (1978) and Owensby et al. (1970); root production is based on data from Sims and Singh (1978). The monthly maximum plant production during the growing season (May–September) is equal to annual maximum production divided by the length of the growing season (30 weeks) and is then reduced if there is insufficient mineral N. The C/N ratio of plant material is allowed to float between a maximum value (C_{max}) and a minimum value (C_{min}). The value of C_{max} and C_{min} change as a function of the APPT, using the following equations, which were estimated using plant-N data from grasslands in the Great Plains (unpublished data from the U.S. IBP Grassland Biome):

$$C_{max} = 44 + 0.2 \times APPT, \qquad [9]$$

$$C_{min} = 39 + 0.2 \times APPT. \qquad [10]$$

Plant production is reduced if mineral N is insufficient to produce plant material with a C/N ratio less than or equal to C_{max}, and uptake of N will be restricted so that the C/N ratio will not be less than C_{min}. Changes in C_{max} and C_{min} result from both within-species growth responses and changes in species composition, which are not modeled explicitly. Plant lignin content was determined as described in the previous section.

Death of live shoots occur at a base rate of 6% per 30 d, but at plant senescence, 98% of the biomass dies. Dead shoots are transferred to standing-dead material which is transferred to surface litter at a rate of 10% per 30 d. Live root biomass dies at the rate of 4% per 30 d and is transferred directly into soil residue. When standing-dead biomass is transferred to surface litter and live roots die, the residue is split into structural and metabolic material as a function of its initial L/N ratio (see Eq. [2]). Nitrogen flows for the plant model are calculated as functions of the C flows and are equal to the product of C flow times the N/C ratio of the source pool.

Nitrogen Submodel

The nitrogen model (Fig. 4) has the same structure as the carbon-flow diagram and we assume that most N is bonded to C. We assume that the C/N ratio of structural (150), active (8), slow (11), and passive (11) fractions remains fixed. The C/N ratio for the active SOM is based on typical C/N ratios for microbes and microbial products; the element ratios of structural material were based on results in McGill et al. (1981). The N content of the metabolic pool is allowed to vary as a function of the N content of the incoming plant material, with the plant N not needed to create structural material (C/N of 150) going to the metabolic-N pool.

The N flows were assumed to be stoichiometrically related to C flows and were equal to the product of the C flow rate and the fixed N/C ratio of the state variables receiving the C. Either mineralization or immobilization of N (see Fig. 4) can result from C flow, depending on the initial C/N ratio of material, the C/N ratio of pools receiving the C, and the fraction of the C flow lost as CO_2 respiration (30–80% of the total C flow).

The model also simulates N inputs due to atmospheric deposition (N_a — g N m^{-2} yr^{-1}) and symbiotic plus nonsymbiotic N$_2$ fixation (N_F — g N m^{-2} yr^{-1}) by using Eq. [11] and [12], respectively, which assumes that N inputs are controlled by the annual precipitation

$$N_a = 0.21 + 0.0028 \cdot APPT, \qquad [11]$$

$$N_F = -0.18 + 0.014 \cdot APPT. \qquad [12]$$

Equation [11] is based on annual wetfall atmospheric N deposition data (NO$_3^-$ + NH$_4^+$) from the National Atmospheric Deposition sites in the Great Plains from 1979 to 1984. The soil plus plant N$_2$ fixation equation (Eq. [12]) was determined by a model-tuning procedure that used observed plant production data from sites in Colorado and Kansas.

Nitrogen loss from grasslands occurs as a result of NH$_3$ volatilization (Schimel et al., 1986), leaching, and volatilization of the N$_2$O and N$_2$ resulting from nitrification and denitrification (Mosier et al., 1983). In the model it is assumed that N will be lost as a result of volatilization of N products (N$_2$, N$_2$O, and NH$_3$) and removal of N by cattle (*Bos taurus*) grazing. Leaching is assumed to be negligible for undisturbed grasslands. Volatilization losses are estimated by assuming that 5% of the sum of the N mineralization flows will be lost to the atmosphere, so that N volatilization rates were proportional to gross N-mineralization rates.

Losses of N due to large ungulate grazing are assumed to be equal to 20% of the N uptake by the cattle and include loss via NH$_3$ volatilization from feces and urine, and N removed by the cattle. We assume that N returned to the
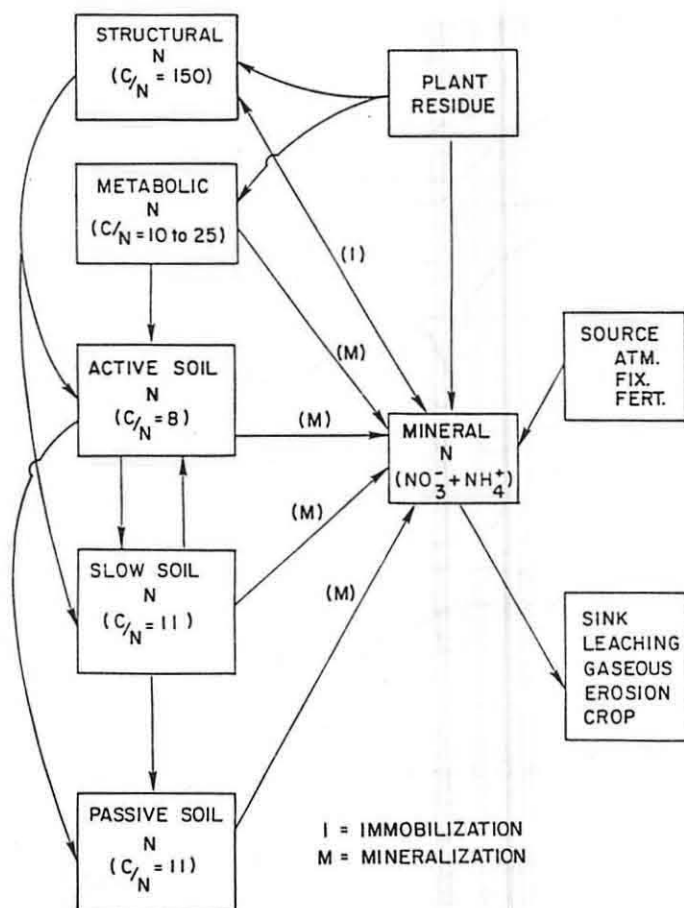
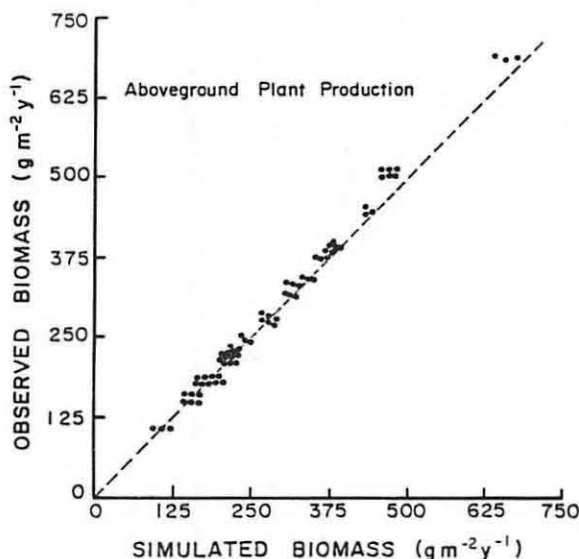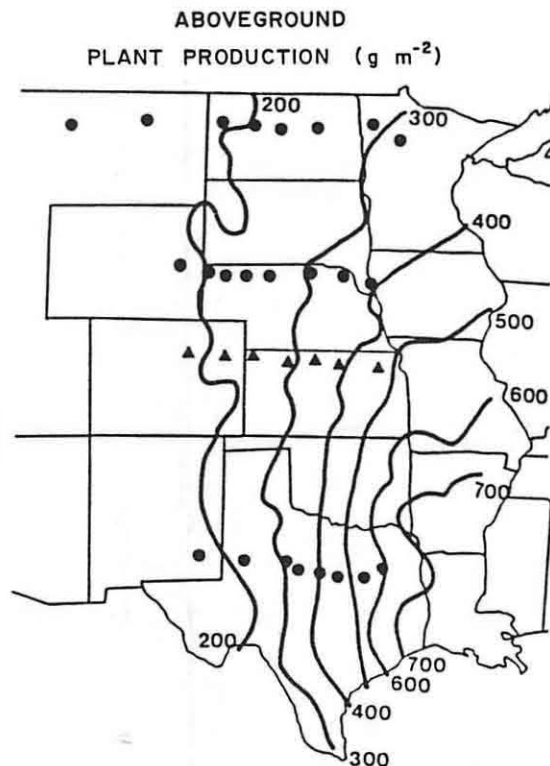Fig. 4. Flow diagram for the N submodel of the Century model.

Fig. 5. (a) Mapped aboveground grassland plant production for the Great Plains, and (b) comparison of mapped and simulated aboveground plant production for the 24 validation sites. The dots on plant production maps show the location of validation sites. The triangles show the parameterization sites.

system is equally split between urine and feces and that 30% of the C consumed by the cattle is returned to the system with a 25% lignin content (Schimel et al., 1986).

Model Validation

The model was validated by simulating steady-state soil C and N levels and aboveground plant production for 24 sites in the Great Plains and comparing the simulated values with mapped plant production and soil C and N levels for fine- (25% sand, 30% clay), medium- (50% sand, 22% clay), and sandy- (75% sand, 10% clay) textured soils at these sites. The sites were selected along three east-west transects (see Fig. 5a). Data from a transect from Colorado to eastern Kansas were used to estimate some of the parameters in the model (Fig. 5).

The model was run using the observed maximum and minimum monthly temperature and monthly precipitation as inputs for the model. We further assumed that the grasslands had been grazed during their development at a moderate level, with 16 and 8%, respectively, of the live and standing-dead biomass removed per 30 d from April through September (45% removal of animal aboveground production). Steady-state SOM, C, and N levels were very sensitive to grazing levels, with SOM level dropping by 40% as the simulated grazing level increased from zero to 50% of annual production. The model's sensitivity to changes in the grazing intensity is supported by data from Bauer et al. (in press), which show that preventing grazing for 80 yr caused soil C levels to increase 0.4 to 0.6 kg m^{-2}.

Plant production maps (Fig. 5b) and soil C maps for sandy and fine-textured soils (Fig. 6) are shown. The plant production (PROD) map was based on range production data

collected by the Soil Conservation Service at 9500 sites in the Great Plains and was generated using a regression equation (PROD = $-34 + 6 \times$ APPT, $r^2 = 0.9$) to predict plant production at 400 sites in the Great Plains as a function of annual precipitation, and a contouring routine from the S package (Bell Labs, Murray Hill, NJ, USA) to generate the maps.

A similar approach was used to generate the soil C and N maps. We developed regression equations ($r^2 = 0.49$ for C and $r^2 = 0.42$ for N; $n = 560$) to predict soil C and N levels as functions of soil texture (silt and clay content) and climatic factors (growing season [April–September] precip-
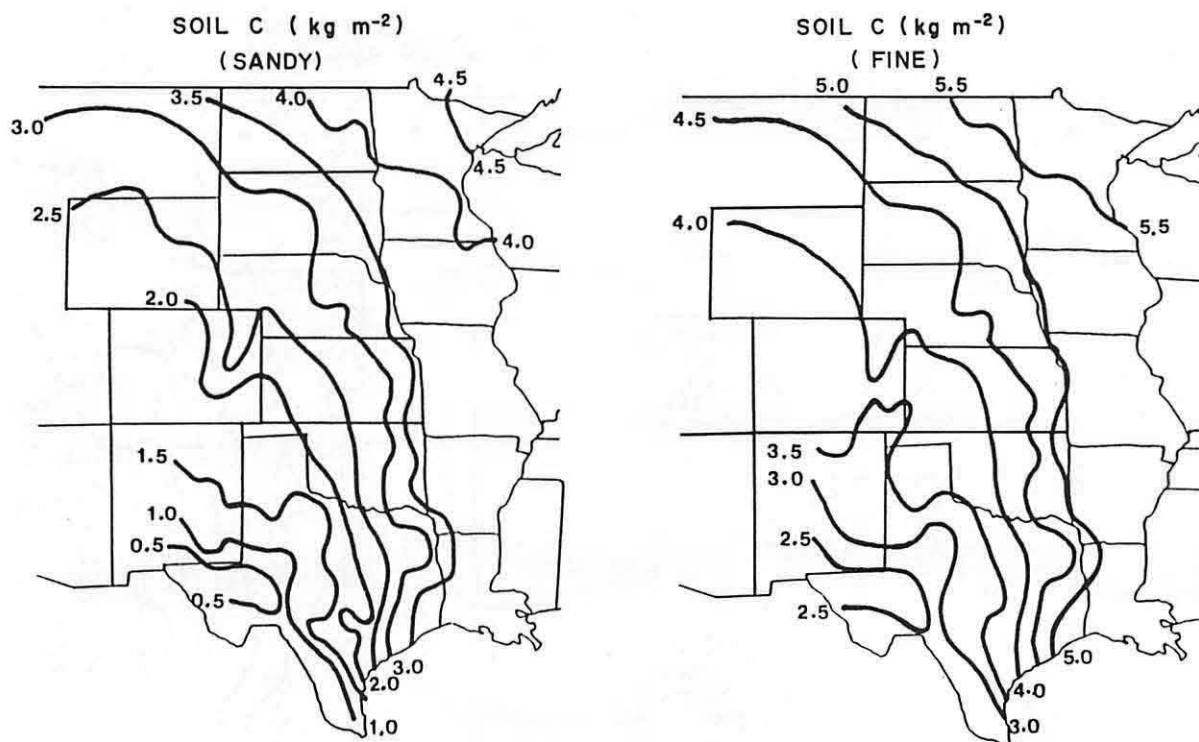
Fig. 6. Soil C levels (0–20 cm) (a) for sandy and (b) fine-textured soils of the Great Plains. Contours are based on regression analysis of SCS pedon data and are potential values for soils of specified textures.

itation and potential evapotranspiration rate, and mean annual temperature) by using soil C and N data from 560 soil pedons in the Great Plains (unpublished data). This equation was used to predict potential soil C and N levels at three soil textures for 400 sites in the Great Plains, which were then used to generate the maps. Figure 7 compares mapped and simulated soil C and N levels for all 24 validation sites and shows regression lines for each soil texture. The model tends to overestimate the soil C and N levels for the fine-textured soils, underestimates the values for sandy soils with the higher C and N levels (i.e., in the more mesic parts of the Great Plains), and does an excellent job of fitting the medium-textured soil. The results show that the model adequately represents the effect of soil texture and climate on soil C and N levels in the Great Plains. The significance of the discrepancies in some soils are unclear because of problems with the equation used to calculate bulk density and, hence, in converting C and N on a mass basis to a volume basis. A major uncertainty is associated with Rawls's (1983) bulk density equation, since it substantially overestimated (5–30%) bulk density in the surface soils (0–20 cm layer). Limited bulk density data from Bauer et al. (1987) showed that the apparent error is a function of soil texture (error is highest for the sandy soils) and was used to modify the Rawl's (1983) bulk density equation.

The model did an excellent job of simulating aboveground plant production (Fig. 5b). The fit is a result of the facts that simulated plant production is highly correlated to simulated N inputs, that N inputs in the model are direct functions of annual precipitation, and that observed plant production was highly correlated with annual precipitation.

DISCUSSION

This analysis demonstrates that broad regional trends in productivity and organic matter can be adequately modeled using a small set of driving variables. In the current model, only four driving variables are required to characterize a site. Annual precipita-

tion affects the decomposition and production submodels and controls N inputs. Temperature is a control over the decomposition submodel directly and through estimates of PET. Soil texture is a control over the formation and turnover rates of the active and slow soil organic matter pools. Plant lignin content is an important control over decomposition rate and varies for above- and belowground material as a function of climate. The model represents regional trends in organic matter content with an overall error of about 15% using this set of driving variables. Site-specific data on climate, soil texture, and plant lignin content are readily obtained over large areas, and so the applicability of the model, at least within the Great Plains, is not limited by data availability. Pastor and Post (1986) used the same set of driving variables in a model of forest C and N cycles, suggesting that the utility of this approach is not restricted to grasslands.

The model's ability to predict SOM levels is limited by its sensitivity to several factors for which data is difficult or impossible to obtain. Grazing intensity and N input during soil development exert an important influence over contemporary organic matter levels. There are no sources of data from which to estimate the history of presettlement grazing intensity or N input rate by region within the Great Plains. Although we used reasonable assumptions, uncertainty resulting from site history cannot be eliminated. Pastor and Post (1986) reached similar conclusions about the effects of site history (past forestry practices) on model uncertainty in their model of forest nutrient cycling. These uncertainties set a limit on the precision that may be expected from the Century model's regional predictions. This uncertainty is not unacceptable, given our objectives.
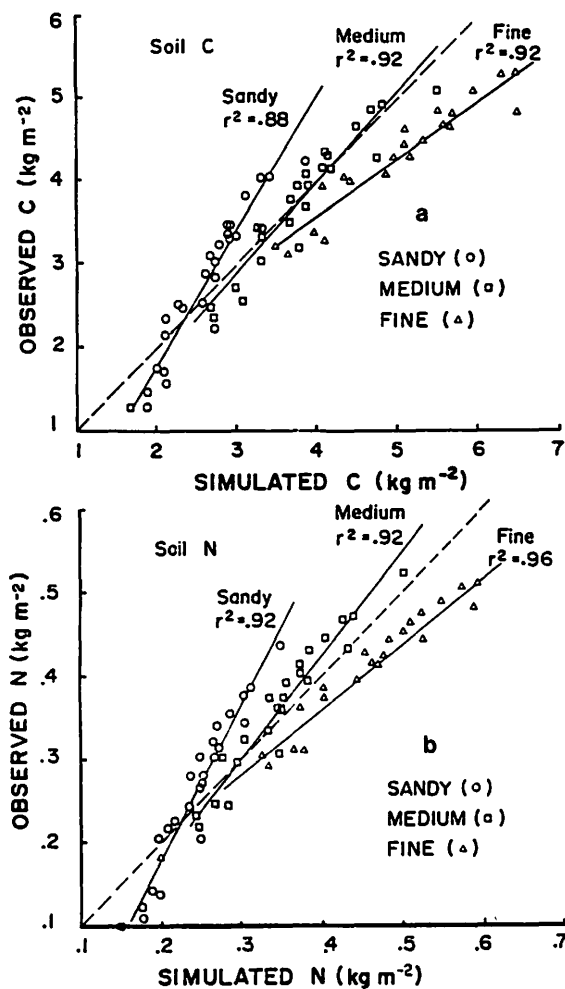
Fig. 7. Comparison of mapped and simulated (a) soil C and (b) N levels for the sandy, medium, and fine-textured soils. The regression lines for each soil texture (solid line) are included on the graphs. The equality line (1:1) is shown as a dashed line.

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Disturbances and gap dynamics in a semiarid grassland: A landscape-level approach

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Abstract

We developed a spatially-explicit gap dynamics simulation model to evaluate the effects of disturbances at the scale of a landscape for a semiarid grassland in northcentral Colorado, USA. The model simulates the establishment, growth, and death of individual plants on a small plot through time at an annual time step. Long-term successional dynamics on individual plots (single gaps) and on a landscape composed of a grid of plots were evaluated. Landscapes were simulated as either a collection of independent plots or as a collection of interacting plots where processes on one plot were influenced by processes on adjacent plots. Because we were interested in the recovery of the dominant plant species, the perennial grass blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths) after disturbances, we focused on scale-dependent processes, such as seed dispersal, that are important to the recruitment of individuals of *B. gracilis*.

The type of simulated landscape was important to the recovery time of *B. gracilis* after a disturbance. Landscapes composed of independent plots recovered more rapidly following a disturbance than landscapes composed of interacting plots in which the recovery time was dependent on the spatial scale of the disturbance.

Introduction

Disturbances operate over a wide range of spatial scales (Pickett and White 1985). The recolonization of disturbed areas may be dependent on the size of the disturbance since different physical and biological processes may be important at different spatial scales (Delcourt *et al.* 1983). Disturbances, viewed in the context of a landscape, produce a patch in the background matrix (Forman and Godron 1981, 1986). Understanding the relationship among disturbance size, degree of interaction among disturbed and undisturbed patches, and pattern of recolonization is one of the most important issues to be addressed in the development of landscape ecology.

Successional studies in the shortgrass steppe region of North America have focused on large-scale disturbances, such as abandoned agricultural fields (Savage and Runyon 1937; Judd and Jackson 1939; Costello 1944; Jud 1974; Reichhardt 1982). An important conclusion from these studies is that the dominant plant species, blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths (Nomenclature follows McGregor (1986))) recovers very slowly after a disturbance or not at all because of climatic constraints on seed germination and seedling establishment (Riegel 1941; Hyder *et al.* 1971; Briske and Wilson 1977).

A recent study of small-scale disturbances indicated that conclusions reached about the inability of *Bouteloua gracilis* to recolonize large disturb-

may not hold for all disturbances, and in particular, small disturbances

ances that occur frequently (Coffin and Lauenroth 1988). Results from a simulation model based on a gap dynamics conceptualization of succession in shortgrass communities suggested that the availability of seeds may be a more limiting factor in the recovery of *B. gracilis* than climatic constraints on seed germination and seedling establishment, and furthermore that the availability of seeds may be a function of the spatial scale of the disturbance (Coffin and Laurenroth unpublished).

The availability of seeds of *Bouteloua gracilis* at a particular point on a landscape depends on several factors, including the production, dispersal, and storage of seeds in the soil. The production and dispersal of seeds of *B. gracilis* each year may be particularly important since a field study found relatively few seeds of *B. gracilis* stored in the soil (54 seeds/m² averaged over a two-year sampling period) with a large variability in the number of seeds stored through time (Coffin and Lauenroth 1989). Seeds of *B. gracilis* are primarily wind dispersed; therefore the recovery of *B. gracilis* may depend on the spatial scale of the disturbance relative to the dispersal distance of the seeds.

Our objective in this analysis was to evaluate the effects of disturbance size and the spatially-explicit process of seed dispersal on the recovery of *Bouteloua gracilis* after disturbances. Our approach was to incorporate spatial structure into the gap dynamics simulation model for a semiarid grassland (Coffin and Lauenroth unpublished) by conceptualizing the landscape as a grid of plots in which either processes on one plot may affect processes on other plots (Fig. 1a) or processes on one plot are independent of processes on other plots (Fig. 1b).

Site description

All data were collected at the Central Plains Experimental Range (CPER) in northcentral Colorado approximately 60 km northeast of Fort Collins (40° 49′ N latitude, 107° 47′ W longitude). The CPER is administered by the USDA Agricultural Service. Mean annual precipitation is 311 mm (sd = 79 m) and mean monthly temperatures range from −5° C in January to 22° C in July. The topog-

raphy consists of relatively flat uplands and lowlands connected by gentle slopes. The vegetation is typical of the shortgrass steppe in that most sites are dominated by the perennial grass *Bouteloua gracilis*. Moderate grazing by cattle occurs throughout the area.

Model description

The effects of spatially-explicit processes on the recovery of *Bouteloua gracilis* after disturbances was evaluated using a modification of a gap dynamics simulation model developed for a semiarid grassland (Coffin and Lauenroth unpublished). The gap model is similar to models developed for forests (Botkin *et al.* 1972; Shugart 1984), and simulates the establishment, growth, and death of individual plants on a small plot (0.12 m²) through time at an annual time step. The establishment and mortality of plants are modeled as stochastic processes: there is a probability associated with each species that establishment of plants will occur each year either as seedlings or vegetative propagules, while the probability of mortality for an individual each year is based on the disturbance rate, the longevity of the species, and the greater risk of death associated with slow-growing individuals than with plants of average growth rates (Shugart 1984). Plant growth is based on the importance of belowground processes associated with the acquisition of soil water resources, since soil water is the most frequent control on plant growth and community structure in semiarid grasslands (Noy-Meir 1973; Lauenroth *et al.* 1978) and belowground net primary production contributes approximately 85% to total net primary production (Sims and Singh 1978). Details of the model can be found in Coffin (1988) and Coffin and Lauenroth (unpublished).

Spatial structure was incorporated into the model by considering the landscape to consist of a grid of plots in which processes on one plot could affect processes on other plots. Because we were interested in the recovery of *Bouteloua gracilis* after disturbances, we were concerned with processes important to the recruitment of individuals of *B. gracilis*
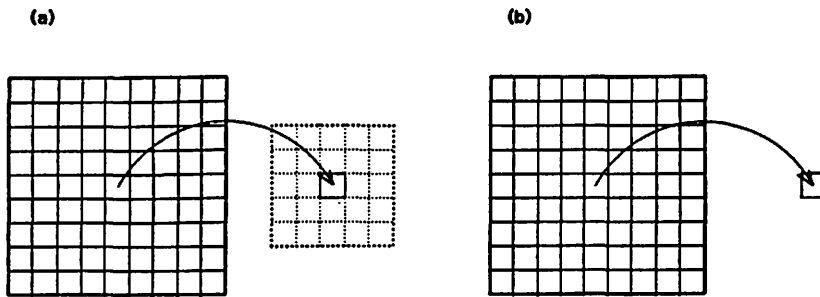
Fig. 1. Two conceptualizations of a landscape (a) a grid of plots in which processes on one plot may affect processes on other plots (b) a grid of plots in which processes on one plot are independent of processes on other plots.

onto each plot. Three general processes were included with at least one probability associated with each process:

1. The probability (0.125) that the microenvironmental conditions required for the germination and establishment of *B. gracilis* seedlings would occur each year was based on the timing of precipitation and temperature, and the effects of soil texture from Briske and Wilson (1977) and Laurenroth *et al.* (1987).

2. The availability of seeds of *B. gracilis* to each plot was based on probabilities associated with the production and dispersal of seeds of *B. gracilis*. The probability of seeds being produced was a function of the amount of aboveground biomass of *B. gracilis* and the amount of precipitation received in the previous year, since seeds of *B. gracilis* produced in the fall of one year are available to germinate in the spring of the following year (Dickinson and Dodd 1976; Coffin and Lauenroth 1989). We assumed that 49 g/m², or 50% of the maximum biomass of *B. gracilis*, was necessary for seeds to be produced. Therefore, the probability was calulated as:

$$P_b = 1.0 \quad \text{if BIOMASS} >= 49 \text{ g/m}^2 \quad (1)$$

$$P_b = 0.0 \quad \text{if BIOMASS} < 49 \text{ g/m}^2 \quad (2)$$

where P_b is the probability that seeds of *B. gracilis* were produced and BIOMASS is the biomass of *B. gracilis* on the plot.

If the biomass of *B. gracilis* was sufficient for seed production, then the probability associated with annual precipitation was calculated by the function:

$$P_s = 1.0 - 0.99*\exp(-0.0018953*(\text{LYPPT-105})) \quad (3)$$

where P_s is the probability of seeds of *B. gracilis* being present on the plot and LYPPT is the amount of precipitation in the previous year. The values of P_s range from 0.01 in the dryest year (LYPPT = 105 mm) to 0.55 in the wettest year (LYPPT = 520 mm). We assumed that even in the wettest year the probability of seeds being present is small since few seeds of *B. gracilis* persist in the soil through time (Coffin and Lauenroth 1989); thus the production of seeds in one year does not necessarily result in seeds being available the following year.

3. The probability of seeds dispersing to a plot was a function of the distance from the source of seeds, the height of the inflorescence, the average wind speed, and the aerodynamics of the seeds. We assumed the distribution of seeds dispersing from a parent plant was described by a negative exponential function (Werner 1975):

$$P_d = \exp(-\text{RATE}*\text{DIST}) \quad (4)$$

where P_d is the probability that at least one seed will disperse to a distance of DIST from the parent plant, and RATE is a measure of the dispersability of the seeds. The value of RATE (3.78) was calculated by assuming $P_d = 0.005$ at the maximum distance (MAXD) that seeds of *B. gracilis* can travel under field conditions. MAXD was estimated using an equation for winddispersed seeds (Greene and Johnson 1986):

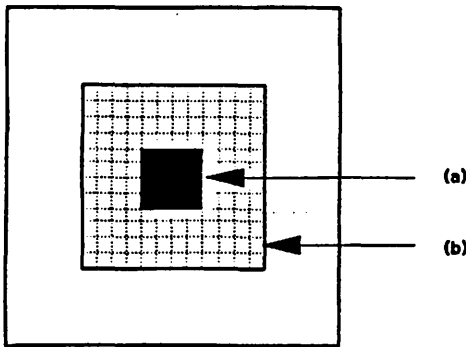$$\text{MAXD} = (H * V_w) / V_t \quad (5)$$

Fig. 2. A simulated landscape consists of a grid of plots that contains (a) the disturbed plots (b) the plots surrounding the disturbance within the maximum dispersal distance of *Bouteloua gracilis* seeds (MAXD).

where H is the average release height of the inflorescences (30 cm), V_w is the mean horizontal wind speed (500 cm/sec), and V_t is the average sinking velocity of the seeds (100 cm/sec). H and V_w were estimated from field data from the CPER, and V_t was estimated using data from wind-dispersed grassland species with similar seed aerodynamics as seeds of *B. gracilis* from Rabinowitz & Rapp (1981). The value of MAXD used in the model (1.4 m) was based on an even number (4) of 35 cm × 35 cm square plots.

Experimental simulations

The effects of five disturbance sizes (2, 8, 18, 31, and 49 m²) on the recovery of *Bouteloua gracilis* were evaluated for landscapes consisting of a grid of plots. The corresponding number of 0.12 m² plots in each square disturbance was: 16, 64, 144, 256, and 400. Each 100-year simulation began by 3 initializing each plot in the grid with plants. The species composition on each plot was based on the proportion of plots in a steady-state landscape with a given species composition from Coffin & Lauenroth (unpublished). A disturbance was then positioned within the grid of plots with the restriction that the entire disturbance and the surrounding plots within the maximum dispersal distance of seeds of *B. gracilis* (MAXD) were included inside the grid (Fig. 2). We assumed all plants on the plots

in the disturbance were killed. The simulations were conducted in two ways: (1) the landscape was considered a collection of interacting plots in which the recovery of *B. gracilis* on a single plot was a function of the dynamics of *B. gracilis* on that plot as well as on surrounding plots within the dispersal distance of seeds of *B. gracilis* (dependent landscapes) (Fig. 1a); (2) the landscape was considered a collection of independent plots in which the recovery of *B. gracilis* on a single plot was only a function of the dynamics of *B. gracilis* on that plot (independent landscapes) (Fig. 1b).

In the case of the dependent landscapes, each disturbance was considered a separate unit; therefore 25 replicate landscapes, or disturbance events, were simulated for each disturbance size. For each disturbance event, there was a probability of the microenvironmental conditions occurring for seed germination and seedling establishment, and a probability that annual precipitation was sufficient to allow the production of seeds. The probability of seeds of *Bouteloua gracilis* being available to each plot in the disturbed area was then a function of the distance from the plot to the nearest plot with sufficient biomass for seeds to be produced. For the independent landscapes, each plot represented a separate unit; therefore one disturbance event was simulated for each disturbance size. Each plot was simulated independently of the other plots in the grid and the probabilities associated with seedling establishment were calculated for each plot separately. We assumed the only constraint on seed availability to these plots was the effect of precipitation on the production of seeds.

The average aboveground biomass of *Bouteloua gracilis* for the dependent landscapes for each time step was found by averaging the biomass on all plots contained within each disturbed area. Those values were then averaged for the 25 replicates for each disturbance size. The 95% confidence intervals for the average biomass values were calculated based on the standard deviations among the 25 replicates. The average aboveground biomass of *B. gracilis* for the independent landscapes was based on the biomass for all plots within the disturbed area for each size. The 95% confidence intervals for the average biomass values were calculated based
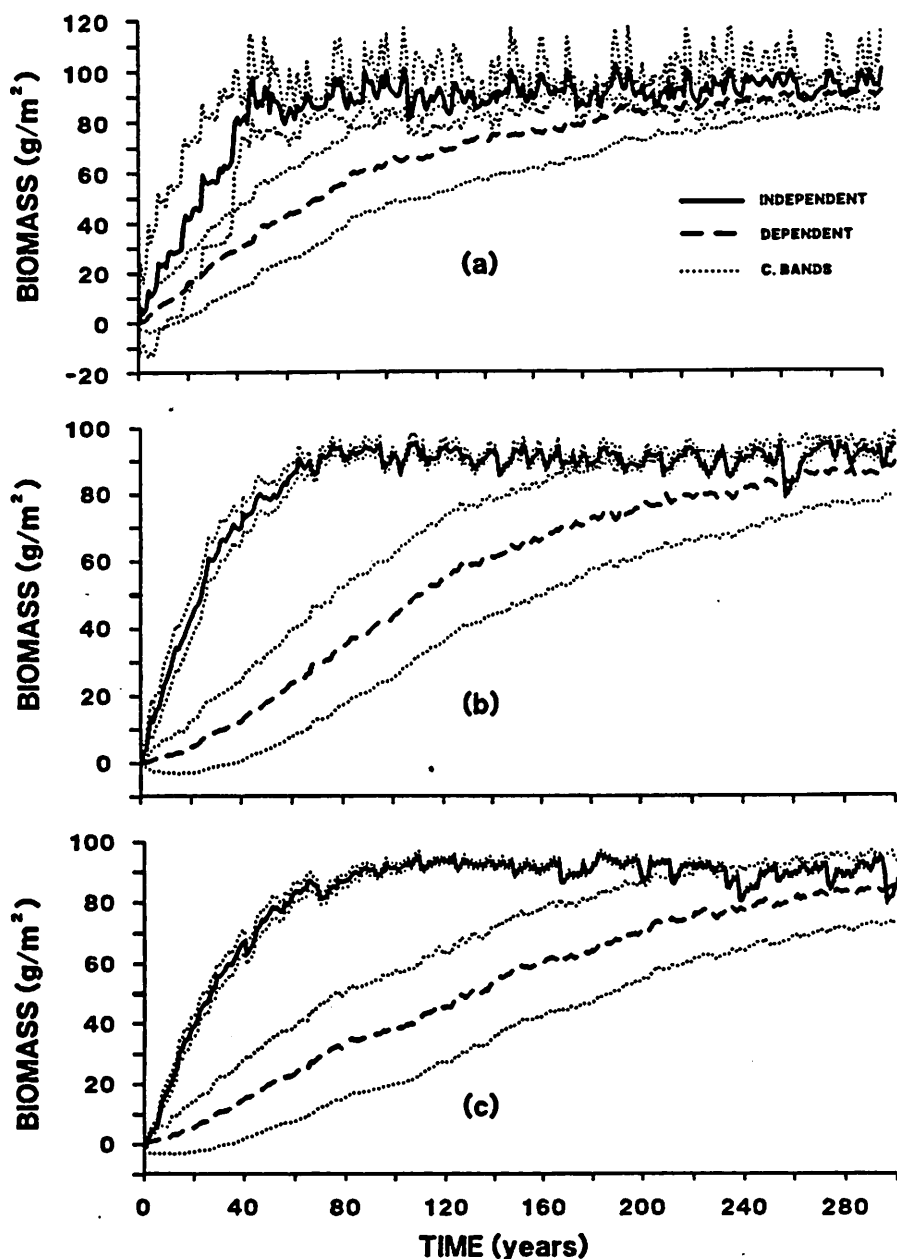
on the standard deviations among the plots.

For both types of landscapes and each disturbance size, the recovery time of *Bouteloua gracilis* was defined as the time at which the five year running average of the upper 95% confidence interval of biomass of *B. gracilis* reached steady-state (89 g/m²). The recovery times were calculated as an average for all plots in each disturbance and as an average for different types of plots. Plot type was based on the distance from a plot in the disturbance to the first row of plots bordering the disturbance. Each plot in the disturbance was identified based on the number of maximum seed dispersal distances of *B. gracilis* between the plot and the border plots
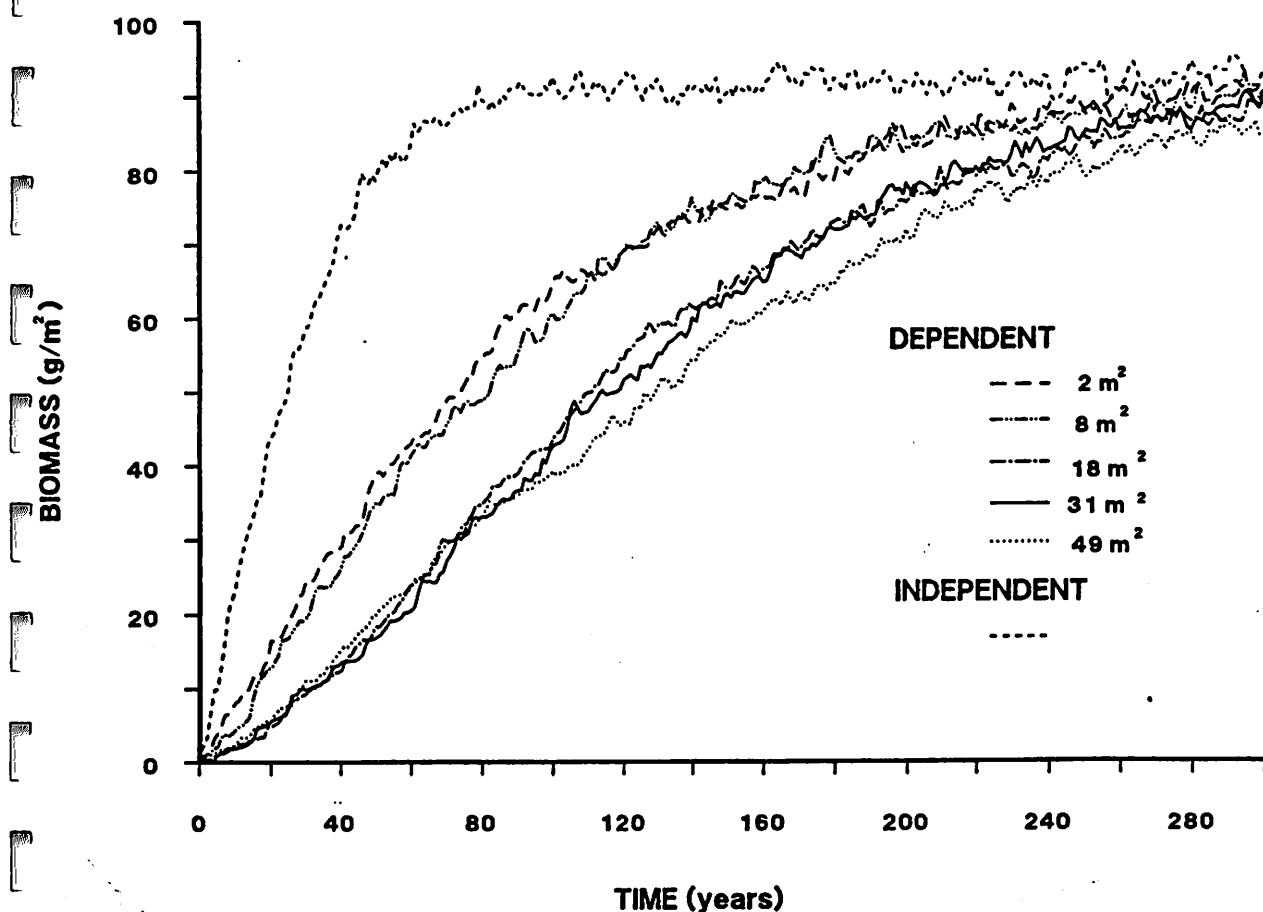
Fig. 4. Average aboveground biomass of *Bouteloua gracilis* for 300 years for two landscape types and five disturbance sizes. The average of the five sizes is shown for the landscapes consisting of independent plots.

(plot type 1 = 1*MAXD, plot type 2 = 2*MAXD, and plot type 3 = 3*MAXD).

Results and discussion

The recovery of *Bouteloua gracilis* after a disturbance was affected by the degree of interaction between plots making up the landscape, and the size of the disturbance. Landscapes consisting of a collection of interacting, dependent plots had smaller average aboveground biomass of *B. gracilis* through time and longer recovery times for all disturbance sizes than landscapes consisting of independent plots (Fig. 3). Although the results are only shown for the smallest-, intermediate-, and largest-sized disturbances, the results for the re-

maining two disturbance sizes (8 and 31 m²) were similar. The variability in biomass, as indicated by the width of the confidence bands, was less for the independent than for the dependent landscapes for all five disturbance sizes. The decrease in the variability of biomass of *B. gracilis* as the disturbance size increased for the independent landscapes was a result of the increase in the number of plots averaged to obtain the mean (from 16 for the 2 m² to 400 for the 49 m² disturbance size). The similar variability for all disturbance sizes for the dependent landscapes was a result of averaging across the 25 disturbance events for each size.

The average aboveground biomass of *Bouteloua gracilis* on the five disturbance sizes for the dependent landscapes were smaller through time than for the overall average of the five sizes for the indepen-

dent landscapes (Fig. 4). The overall average biomass for each time step is shown for the independent landscapes since the values were not significantly different. Two classes of curves are distinguishable for the dependent landscapes based on the size of the disturbance relative to the maximum dispersal distance of seeds of *B. gracilis*. Biomass on the two smallest disturbance sizes were similar and larger through time until steady-state was reached than biomass values on the three largest disturbance sizes. All plots within the two smallest sizes were within the maximum dispersal distance of seeds of *B. gracilis* from plots surrounding the disturbance; therefore all plots were accessible to seeds of *B. gracilis* at the start of each simulation. In contrast, plots in the center of the three largest disturbance sizes were beyond the maximum dispersal distance of seeds of *B. gracilis* from the surrounding undisturbed plots; therefore plots within the disturbed area that were accessible to seeds of *B. gracilis* from the undisturbed plots had to be recolonized by *B. gracilis* before seeds were available to the center plots and recolonization could begin.

The average time required for *Bouteloua gracilis* to reach steady-state and dominate the biomass on a disturbance was less for the landscapes consisting of independent plots for each disturbance size than for the landscapes of dependent plots (Fig. 5a). Recovery time increased as disturbance size increased for the dependent plots while similar values were found for all disturbance sizes for the independent plots.

The average recovery times of *Bouteloua gracilis* (136–206 years) associated with the landscapes that incorporated the spatially-explicit process of seed dispersal (dependent plots) were more similar to recovery times reported from experimental studies than the average recovery times for the independent plots (34–65 years). Most successional studies in the shortgrass steppe of North America have been conducted on abandoned agricultural fields where a shortgrass community dominated by *B. gracilis* has been suggested to occur after greater than 50 years of plant recovery (Hyder *et al.* 1971; Reichhardt 1982), although the recovery of *B. gracilis* has not actually been monitored for this length of time.

Most fields were abandoned in the 1930's and currently *B. gracilis* is a minor component of the plant communities (Hyder *et al.* 1971); *B. gracilis* frequency values of 2% were recently recorded (Reichhardt 1982).

The model results indicate that *Bouteloua gracilis* achieved 20–50% of its average biomass on the dependent plots 50–60 years after a disturbance (Fig. 4). Because of the important effects of disturbance size on the recovery of *B. gracilis* for the dependent plots, the simulation of sizes comparable to abandoned fields (> 1 ha) is expected to result in longer recovery times than for the largest size evaluated in this study (49 m²). Therefore, the recovery times that include the dispersal of *B. gracilis* seeds as a spatially-explicit process are still faster than those observed experimentally. It is possible that other processes important to the recovery of *B. gracilis* are scale-dependent, such as the occurrence of the microenvironmental conditions required for the germination and establishment of seedlings of *B. gracilis*, or that seeds of *B. gracilis* are present on disturbed areas less frequently than used in the simulations. Long-term experimental studies on a range of disturbance sizes are necessary to evaluate the recovery of *B. gracilis* after disturbances. Recently a study was initiated to evaluate successional dynamics on disturbances, such as western harvester ant mounds (*Pogonomyrex occidentalis* (Cresson)), that are comparable in size to the smallest size simulated (2 m²) (Coffin 1988).

The distance from a disturbed plot to the plots bordering the disturbance, as distinguished by plot type, had a more important effect on the recovery time of *Bouteloua gracilis* than the size of the disturbance (Fig. 5b). Plots closest to the edge of the disturbance (type 1) had the fastest recovery times with an average for the five disturbance sizes of 162 years. Plots located at two dispersal distances of seeds of *B. gracilis* (type 2) had an intermediate average recovery time (243 years) while plots at three dispersal distances (type 3) had the longest average recovery time (289 years).

The similar recovery times of *Bouteloua gracilis* for each disturbance size for plots at comparable seed dispersal distances from the edge of the disturbance indicate that recovery time will increase as
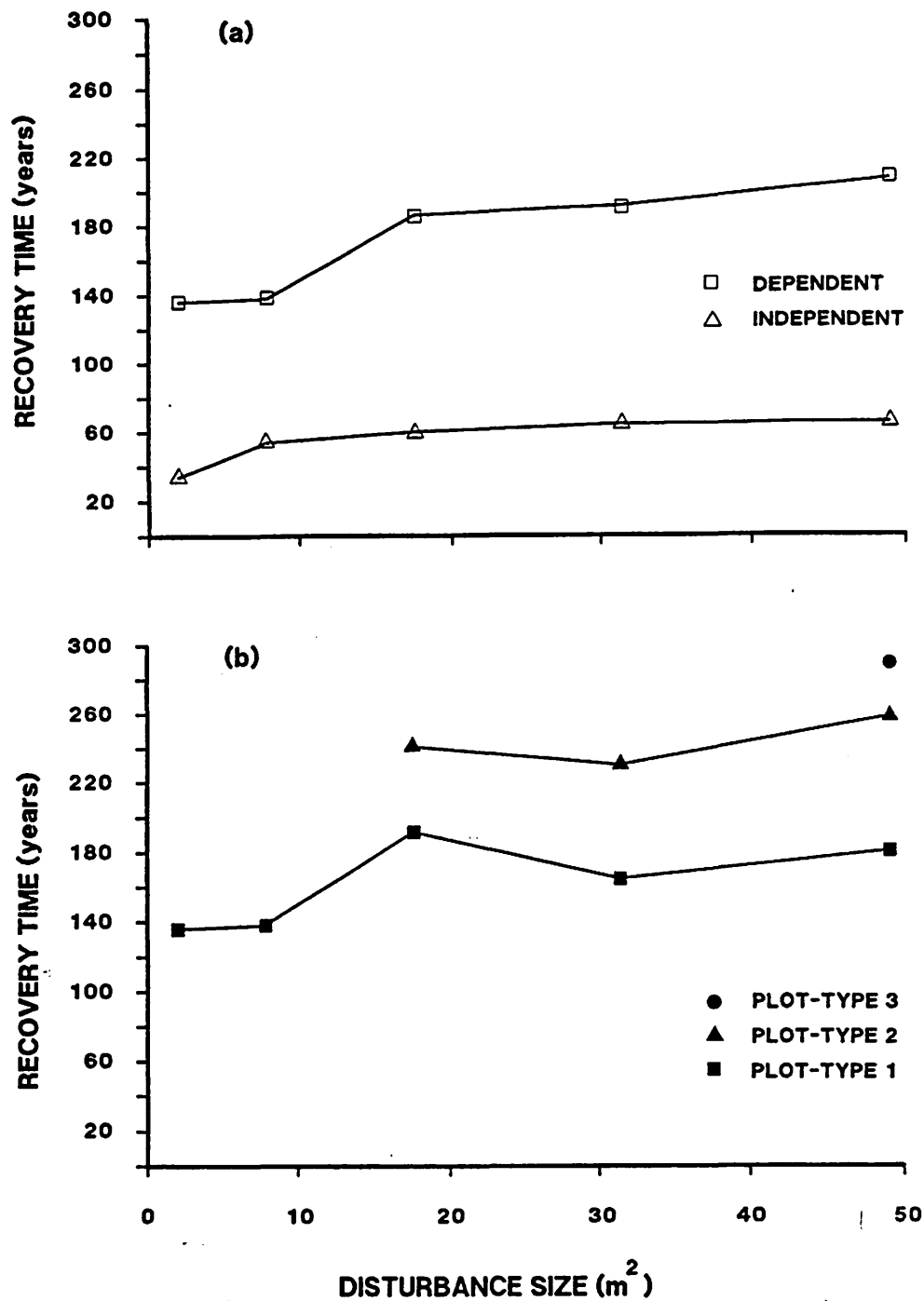
Fig. 5. Average time required for *Bouteloua gracilis* to dominate the biomass on a disturbance for two landscape types and five disturbance sizes (a) average of three plot types (b) average for each plot type.

the number of different types of plots contained in a disturbed area increases rather than as disturbance size increases; disturbances of different sizes yet with the same number of plot types will have similar recovery times. The incorporation of other factors into the model, such as spatial heterogeneity in soil texture, may result in different recovery times for plots of the same type, and different

recovery times for disturbances with the same number of plot types yet of different sizes.

Acknowledgements

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