CENTRAL PLAINS LTER PROJECT

Site Review: Field Day

September 8, 1993

AGENDA FOR CPER-LTER SITE REVIEW

Tuesday, September 7

6:00 PM   Pick up Review Team in lobby of University Park Holiday Inn.
6:30 PM   Meet invited participants for dinner at Jefferson Street Station

Wednesday, September 8

8:30 AM   Pick-up review team at Holiday Inn and travel to CPER

LTER Headquarters
9:30-9:45   Welcome to the CPER - Jerry Schuman

9:45-10:00   Introduction to Research Programs in the College of Natural
             Resources - Diana Freckman

10:00-10:15 Introduction to the CPER and the LTER project - Bill Lauenroth

10:15-10:45 Conceptual framework - Indy Burke

Section 21 S
11:00-11:15 Species effects on biogeochemistry - Mary Ann Vinton

11:15-11:30 Habitat use by rodents - Paul Stapp

11:30-11:45 Primary production - Bill Lauenroth

11:45-12:30 Paleoecology / paleopedology - Gene Kelly & Caroline Yonker

Section 27
1:00-1:30   Soil water and micromet station - Paul Hook & Bill Lauenroth

Section 25
1:45-2:15   Disturbances - Debra Coffin

2:15-2:45   Trace gas emissions - Arvin Mosier

Section 23E
3:00-3:30   Long-term heavy grazing - Daniel Milchunas

3:30-4:00   Landscape-scale ^{15}N experiment - Indy Burke

Section 7
4:00-5:00   Exclosure experiment - Indy Burke, John Moore, & Jim Detling

5:00-   Barbeque at LTER headquarters (Blue grama-buffalo grass experiment - Martin Aguiar)

Thursday September 9

8:30 AM   Pick up review team at the University Holiday Inn

9:00-10:00 Simulation modeling - Bill Lauenroth & Debra Coffin

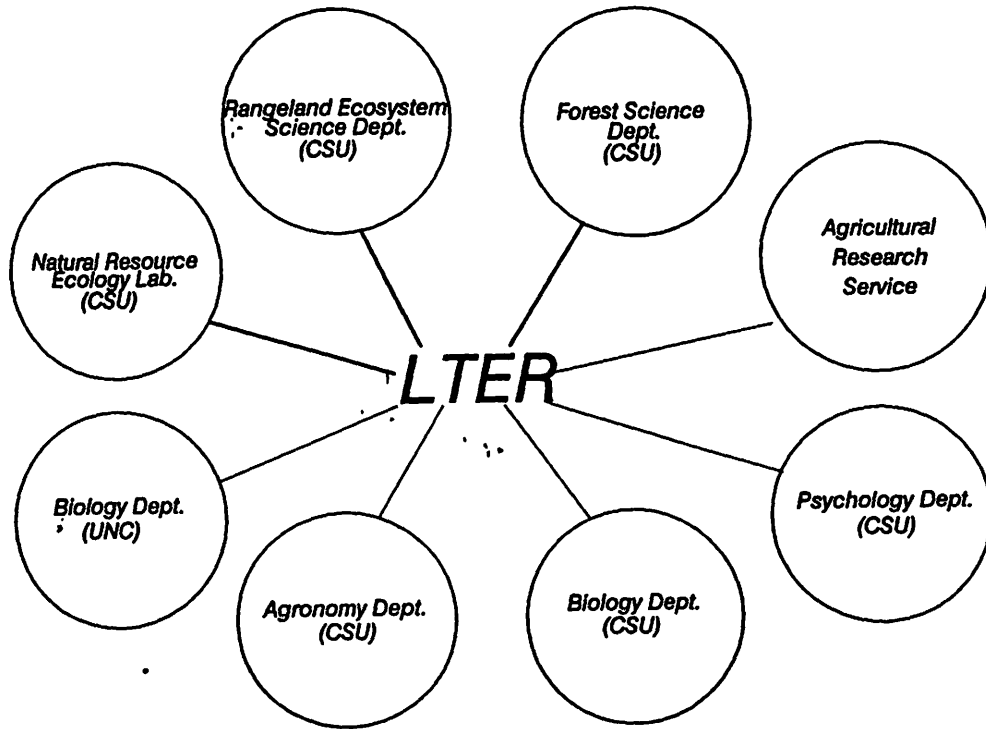10:00-10:15 Remote sensing - Roger Hoffer

10:15-11:00 Data management - Tom Kirchner

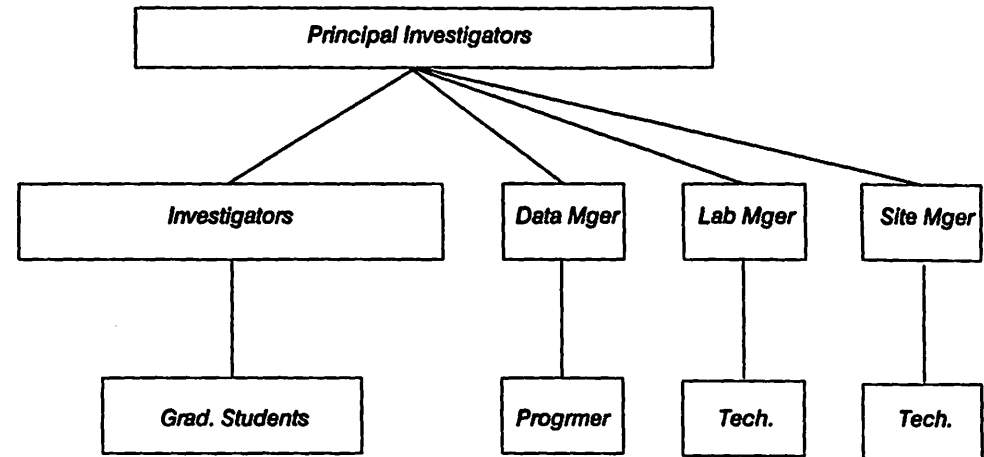11:00-12:00 GIS - Indy Burke and Martha Coleman

12:00-2:00 Lunch- Callahan & review team College of Natural Resources
            Conference Room

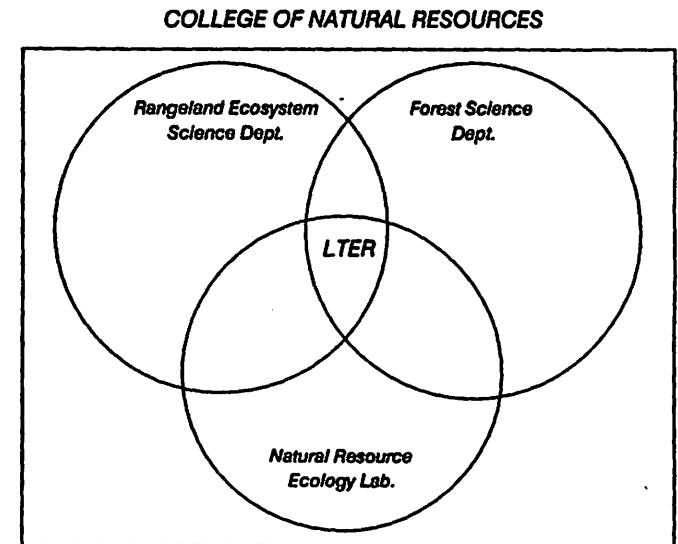2:00- 4:00 Feedback and discussion:review team and PIs

Scientific Structure

Rangeland Ecosystem Science Dept. (CSU)

Forest Science Dept. (CSU)

Natural Resource Ecology Lab. (CSU)

Agricultural Research Service

LTER

Biology Dept. (UNC)

Agronomy Dept. (CSU)

Biology Dept. (CSU)

Psychology Dept. (CSU)

Leadership Structure

Principal Investigators

Investigators | Data Mger | Lab Mger | Site Mger

Grad. Students | Progrmer | Tech. | Tech.

Administrative Structure

COLLEGE OF NATURAL RESOURCES

Rangeland Ecosystem Science Dept.

Forest Science Dept.

LTER

Natural Resource Ecology Lab.

CONCEPTUAL FRAMEWORK

I. Historical Perspective:

Our involvement in the LTER program (LTER i, 1982-86) began with spatially explicit ideas and questions about the importance of landscape structure, and particularly the classic soil catena model, in the long-term development and maintenance of shortgrass steppe ecosystems.

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

During LTER II (1987-1990), we expanded our thinking about long-term processes to include the origin and persistence of spatial patterns at a range of spatial scales. This work included substantial questioning of the catena model.

Example:

Soil catena study (Schimel et al. 1985) suggested that slope position is a major control over sol organic matter (SOM) accumulation.

Expansion to physiographic units (Yonker et al. 1988) suggests that spatial pattern in SOM is controlled by soil texture, parent material, grazing history, and slope position.

YONKER ET AL: PATTERNS OF ORGANIC CARBON ACCUMULATION IN A SEMIARID SHORTGRASS STEPPE   479

Fig. 1. Three-dimensional projection of Central Plains Exp. Range (10 x vertical exaggeration).

Expansion to the Central Grasslands region (Burke et al. 1989) suggested that SOM is most closely related to mean annual temperature and precipitation, modified by soil texture and landuse history.

What controls ecosystem structure and function across scales? What are the rules for generalizing spatial pattern among scales? Can we use rules based on spatial variation to make predictions about temporal variaion?
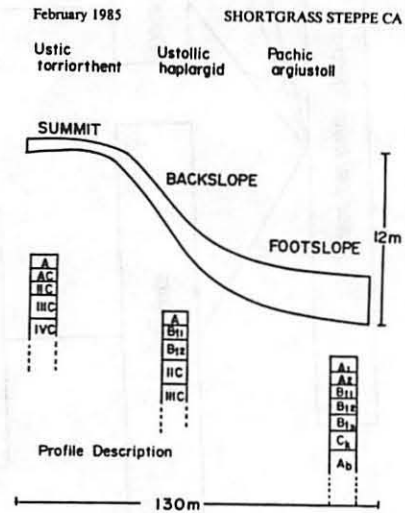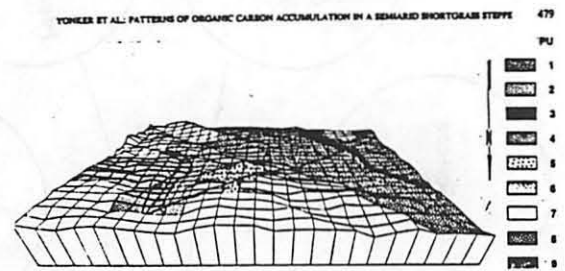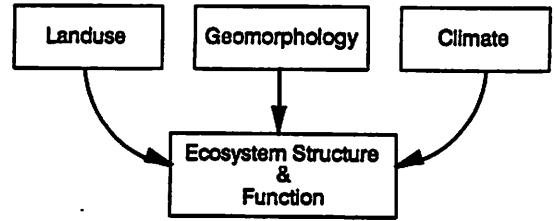
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II. The Conceptual Framework:

The major controls over ecosystem structure and function are climate, geomorphology, and landuse management. Each has important spatial and temporal heterogeneity across a range of scales, and exerts its influence at a particular combination of levels.

All biological processes in this system are fundamentally controlled by these variables.

Landuse	Geomorphology	Climate

Ecosystem Structure & Function

A. Climate:

Temporal Control (annual):
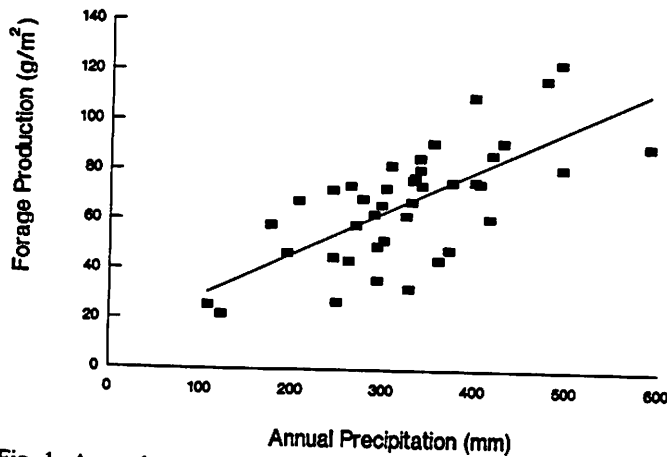
EXTRAPOLATING LTER RESULTS

Fig. 1. Annual precipitation vs. forage production estimated at the Central Plains Experimental Range (CPER) from 1939 to 1990. The regression equation is: Forage production = $13 + 0.172 \times$ (annual precipitation), $P < 0.001$ (both slope and equation). Data from Lauenroth and Sala (1992).
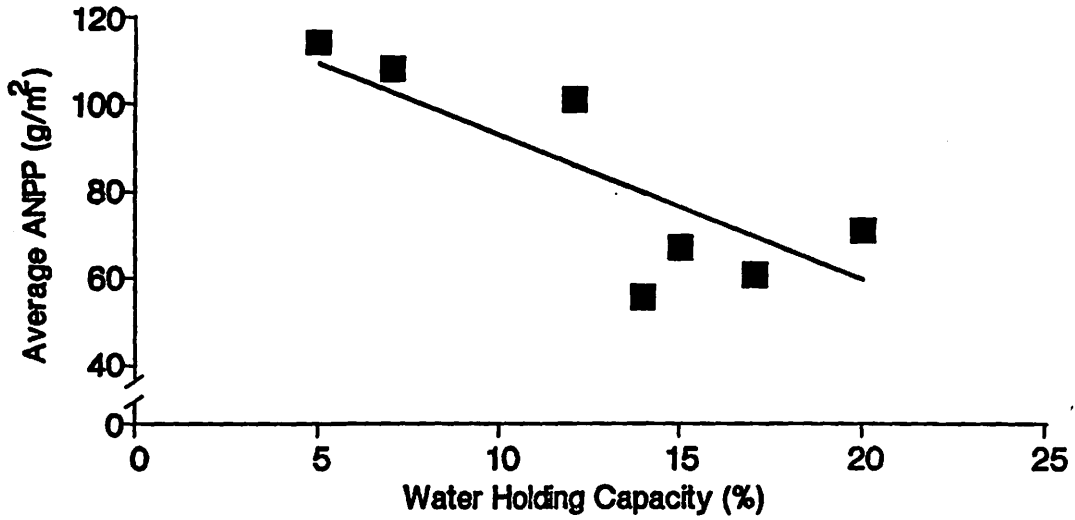
B. Geomorphology:

Figure 2.14 ANPP on sites representing a gradient in soil texture from Soil Conservation Service MLRA database for NE Colorado. Textures were converted to water holding capacities.

(a)

SEEDS(U) = exp (-0.349 * %CLAY + 7.65)
r^2 = 0.94

SEEDS(G) = exp (-0.064 * %CLAY + 2.37)
r^2 = 0.22

(b)

SEEDS(U) = exp (-0.279 * %CLAY + 9.83)
r^2 = 0.91

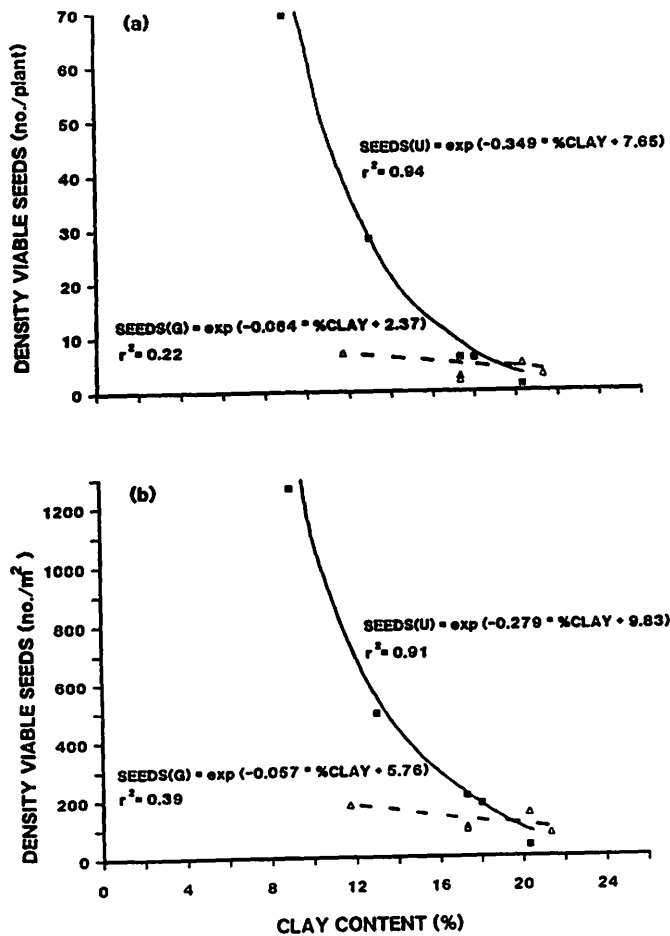SEEDS(G) = exp (-0.057 * %CLAY + 5.76)
r^2 = 0.39

Fig. 3. Relationship between percentage clay content and density of viable seeds for two grazing intensities: ungrazed (squares) and grazed (triangles) (a) viable seeds/plant (b) viable seeds/m².

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C. Landuse:

GRAZED   UNGRAZED

Aboveground

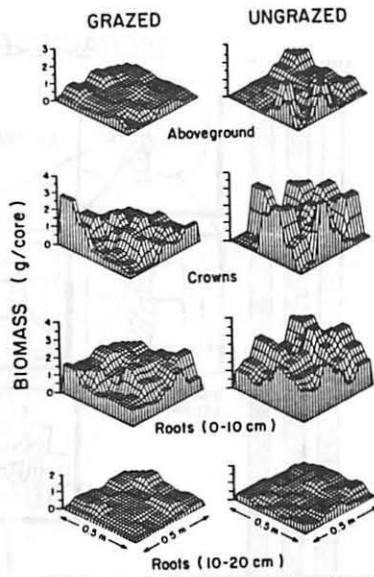BIOMASS (g/core)

Crowns

Roots (0-10 cm)

Roots (10-20 cm)

Fig. 2. Horizontal and vertical distributions of plant biomass for one representative replicate of the 0.25-m² plots from grazed and ungrazed uplands.

MAT 13
CLAY

RANGE

CULTIVATED

MAT 13
LOAM

MAT 13
SANDY LOAM

SOIL ORGANIC CARBON (kg/m²)
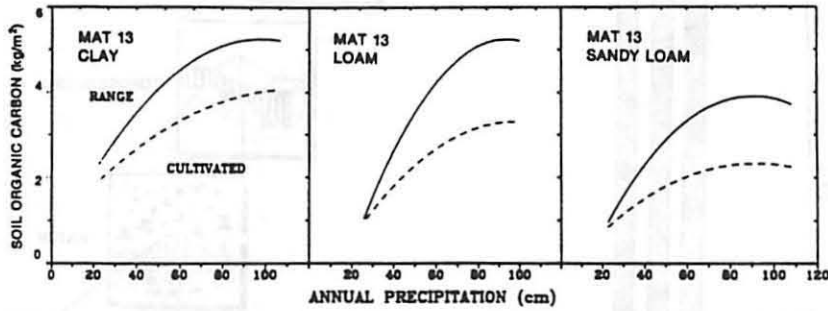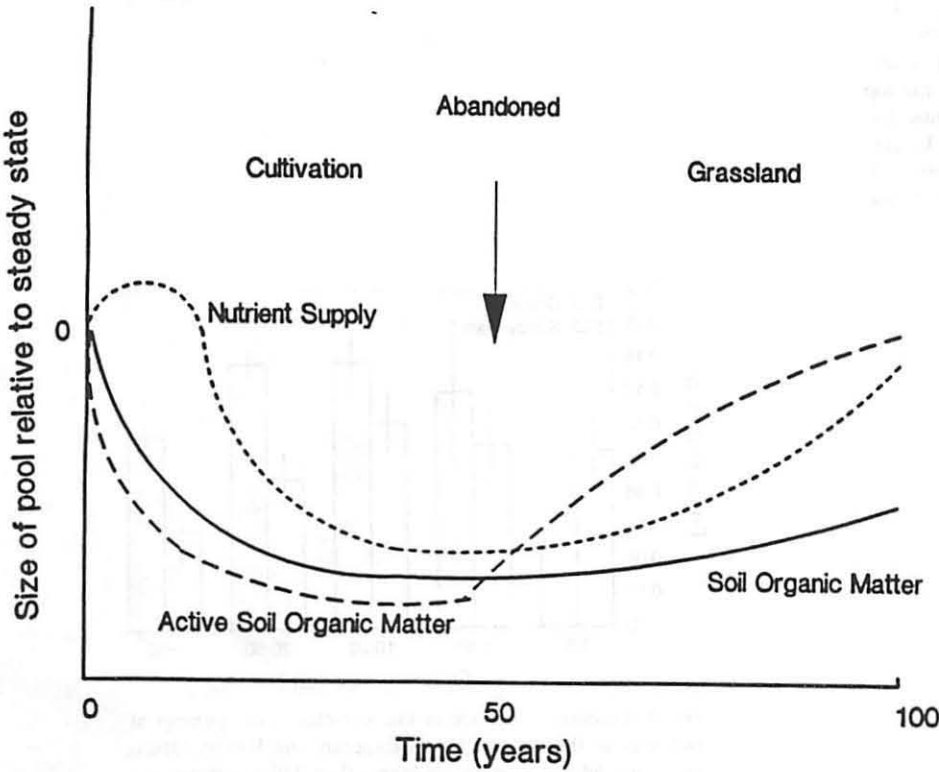
ANNUAL PRECIPITATION (cm)

Fig. 2. Predicted relationship between soil organic carbon and annual precipitation at a set temperature in clay (50% clay, 20% silt), loam (20% clay, 40% silt), and sandy loam (10% clay, 30% silt) soils. The difference between the range and cultivated organic C represents the predicted absolute soil organic C loss due to cultivation.

Abandoned

Cultivation   Grassland

Nutrient Supply

Active Soil Organic Matter

Soil Organic Matter

Size of pool relative to steady state
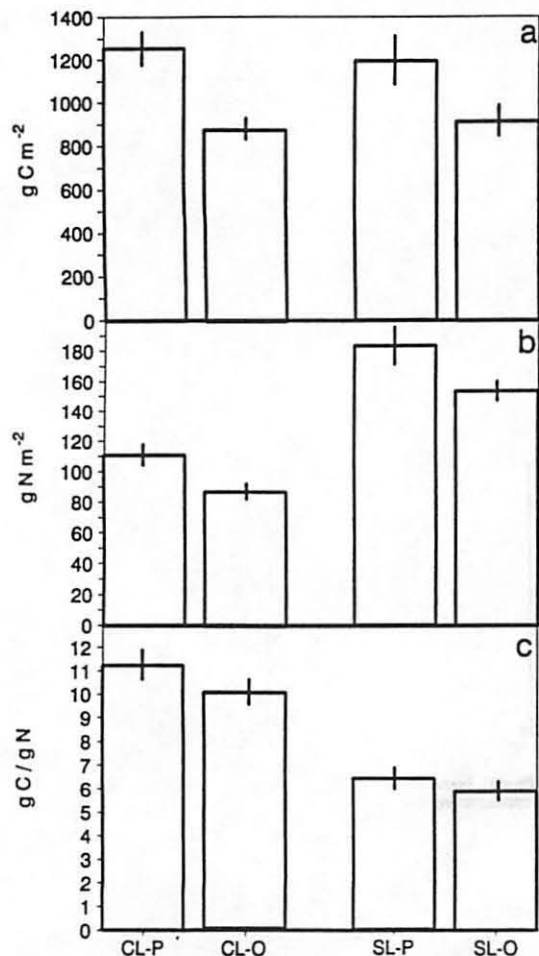
0   50   100

Time (years)

7

Fig. 2. Standing stocks of soil organic carbon (TOC) (a) and total nitrogen (TN) (b) and mass ratio of C to N in the top 0.05 m of soil (c) at two sites at the Central Plains Experimental Range. Site and microsite codes are: CL, clay loam site; SL, sandy loam site; P, plant-covered microsite; O, opening. Error *bars* represent ±1 standard error of the mean.

HIERACHICAL LEVEL

CENTRAL GRASSLAND REGION

CENTRAL GREAT PLAINS

SHORTGRASS STEPPE

CENTRAL PLAINS EXPERIMENTAL I
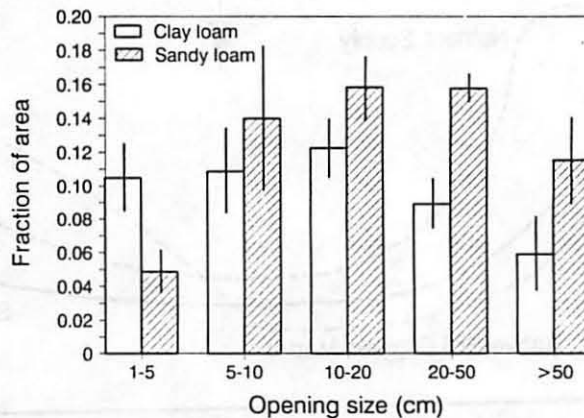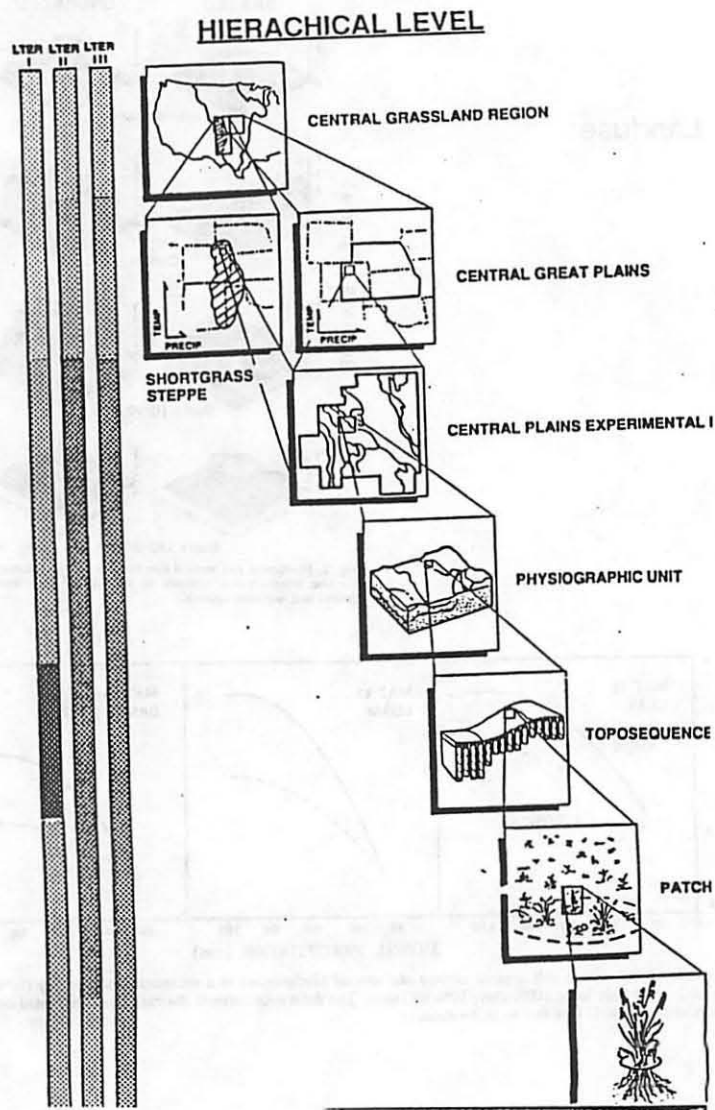
PHYSIOGRAPHIC UNIT

TOPOSEQUENCE

PATCH

Fig. 1. Fraction of surface in five size-classes of openings at two sites at the Central Plains Experimental Range. Openings were defined as segments longer than 0.01 m without live plant cover on line transects. Error *bars* represent ±1 standard error of the mean.

III. How large an area does our site represent:

We believe that key questions for LTER sites should be "how representative is our site of this ecosystem type? To what area may we extrapolate our results?"

We draw upon our conceptual framework to address these questions. In a recent analysis, we tested the shortgrass steppe region to assess the area that our site may be considered to represent.
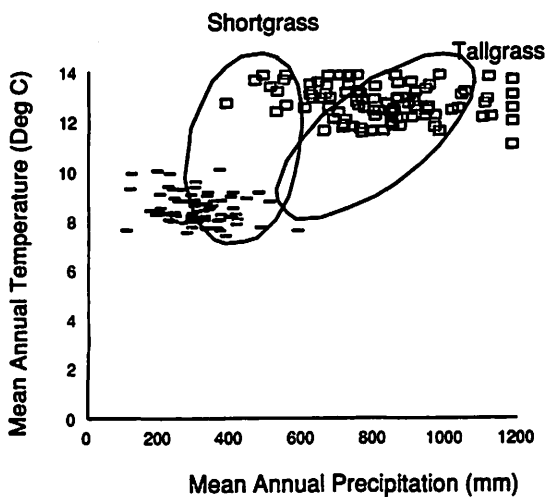
Fig. 4. Mean annual temperature and precipitation fields for shortgrass and tallgrass prairie, derived from overlaying vegetation and average climate maps for the central Great Plains and adjacent Central Lowlands. The bars represent annual data from the Central Plains Experimental Range (CPER) LTER site, and the squares represent annual data from the Konza Prairie Research Natural Area LTER site.
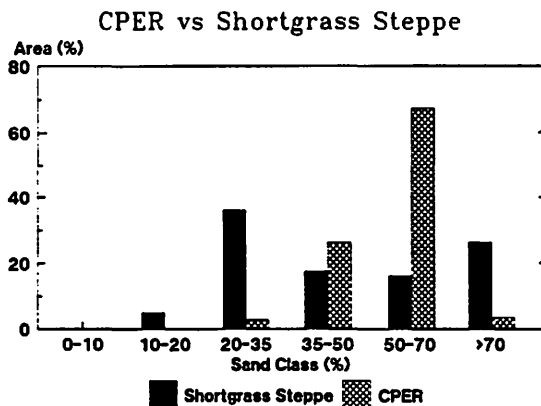

Fig. 7. Distribution of soil textures (as sand class) at the Central Plains Experimental Range (CPER) LTER site, compared with the distribution in the shortgrass steppe. Data for the shortgrass steppe were derived by overlaying soil maps (USDA Soil Conservation Service, 1989) with a map of the shortgrass steppe (Kuchler, 1964).
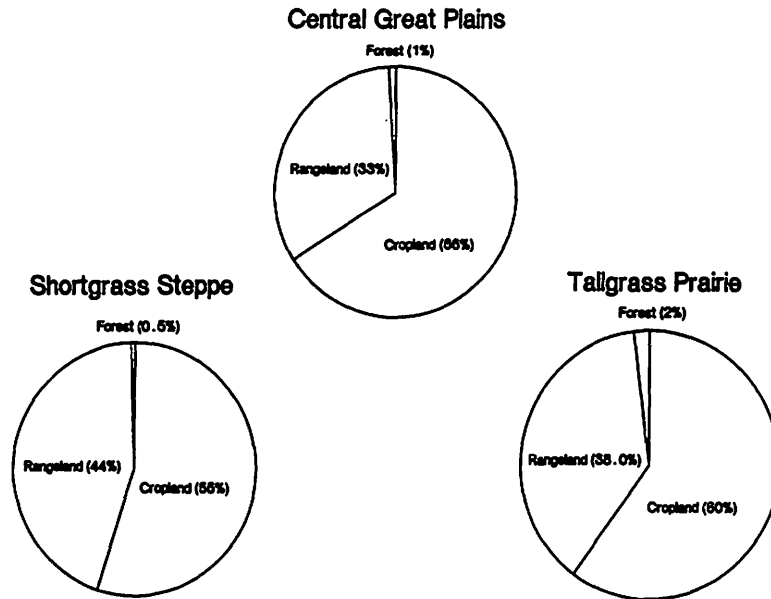
Fig. 9. Proportion of area in rangeland, cropland, and forest in (a) the central Great Plains and adjacent Central Lowlands, (b) the shortgrass steppe within (a), and (c) the tallgrass prairie within (a). Data were derived from landuse maps of the area (USDI U.S. Geological Survey, 1986).

Fig. 10. Map of the area within the central Great Plains and adjacent Central Lowlands that may be considered to be represented by the Central Plains Experimental Range (CPER) LTER site with respect to soils, climate, and landuse (see text for description of analysis).

Plant-Soil Interactions on Previously Watered and Fertilized Shortgrass Steppe

Questions:

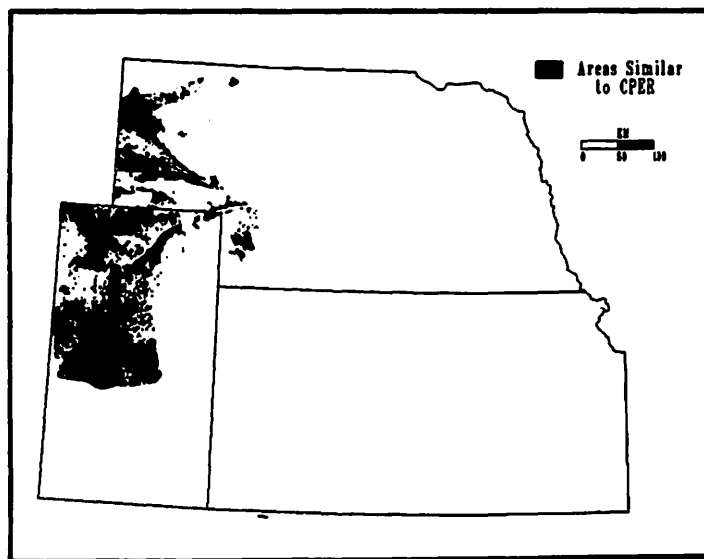♦ Our central question is:

How do plants, by virtue of their presence or their identity, affect local and ecosystem patterns in soil carbon and nitrogen cycling?

♦ In addition, we used this site to examine the effects of the historical addition of water and nitrogen from 1970-1974 on current plant and soil properties.

Approach and Experimental Design:

♦ We measured above and belowground standing biomass and tissue chemistry of several common plant species on each of the historical treatment plots.

♦ We sampled soils both under and between canopies of these plant species, and measured carbon and nitrogen pool sizes and turnover rates.
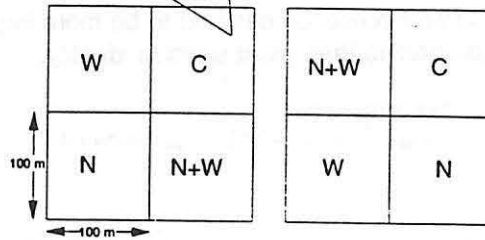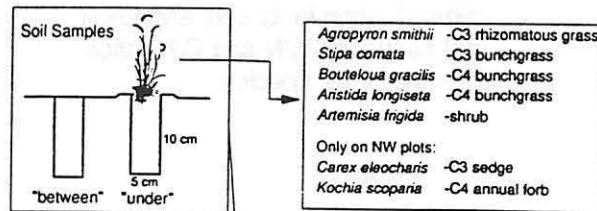
Major Results:

♦ The historical N+W plots had higher total carbon and nitrogen, probably due to the production increase that occurred on the plots 20 years ago.

♦ In general, soil under plants had higher carbon and nitrogen pool sizes and turnover rates than soil between plants. However, the historical W plots had less or reversed plant canopy-induced variation in soils than the plots that did not receive water. This is probably a result of the large turnover in plants that occurred on these W plots, due to increased mortality of native plants and increased recruitment of new plants, especially those with an annual lifespan.
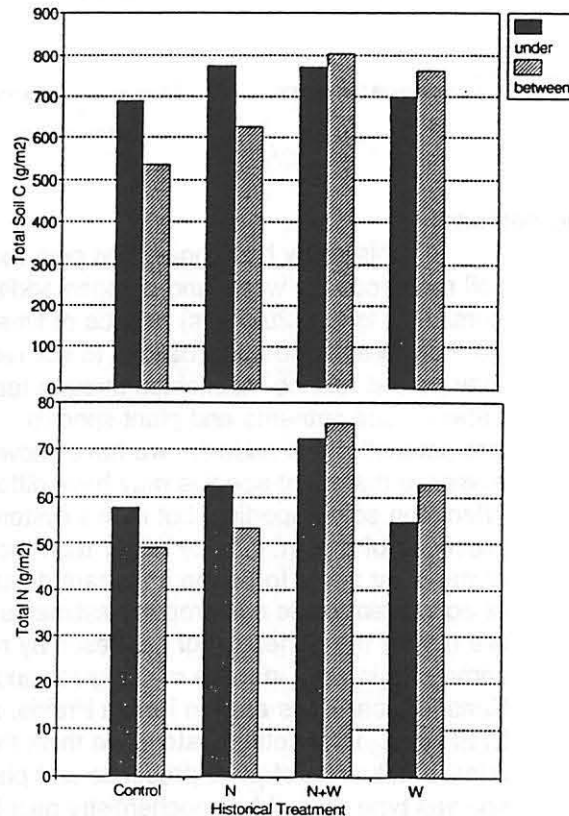
♦ The bunchgrasses had higher rates of C mineralization in soils under their canopies than the non-bunchgrasses, except the annual invasive species *Kochia scoparia*. Also, the bunchgrasses had more canopy-induced heterogeneity in C mineralization than the non-bunchgrasses.
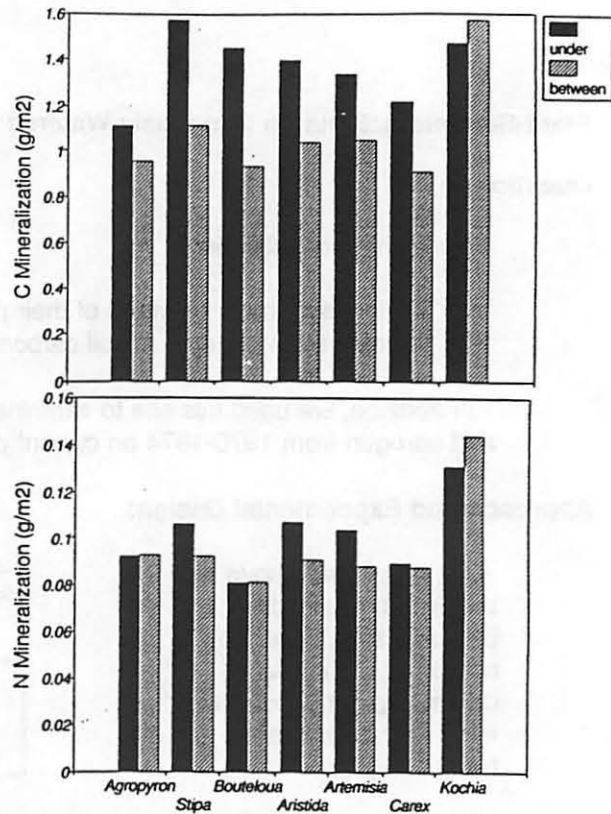
♦ The invasive annual species in the NW plots, *Kochia scoparia*, had less canopy-induced heterogeneity in carbon mineralization rates, greater rates of potential net N mineralization in its soil, and lower root tissue lignin/N and C/N ratios than the other species.

♦ Plant presence seemed to be more important to ecosystem-scale estimates of soil properties than plant species identity.

1.
$$\frac{\overline{X} \text{ "bare ground" soil property}}{\overline{X} \text{ bare ground cover}} \longrightarrow \text{assume 1.0}$$
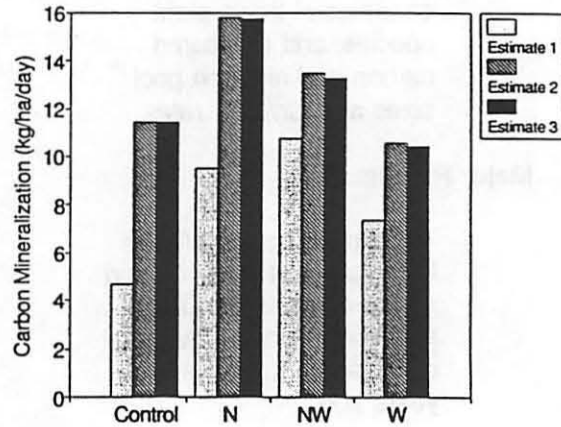
2.
$$\frac{\overline{X} \text{ "under plant" soil property}}{\overline{X} \text{ plant cover}} + \frac{\overline{X} \text{ "bare ground" soil property}}{\text{bare ground cover}}$$

3.
$$\sum_i \left(\frac{\overline{X} \text{ "under species}_i \text{" soil property}}{\overline{X} \text{ species}_i \text{ cover}} \right) + \frac{\overline{X} \text{ "bare ground" soil property}}{\text{bare ground cover}}$$

Conclusion:

This study has shown that perturbations in soil resources via water and nitrogen additions can persist for long (>20 years) periods of time. Furthermore, these perturbations to soil resources may persist and be maintained through feedbacks between soil nutrients and plant species characteristics. In addition, we have shown some evidence that plant species may have differential effects on soil properties, but in this system the presence of a plant canopy rather than the identity of the plant seem to be the important determinant of ecosystem-scale soil property estimates. We are testing the generality of this result by repeating some of this work in more mesic grasslands in Kansas, near Hays and on Konza Prairie, another LTER site. In a wetter system, we think the relative influence of plant presence and plant species type on soil biogeochemistry might be reversed.

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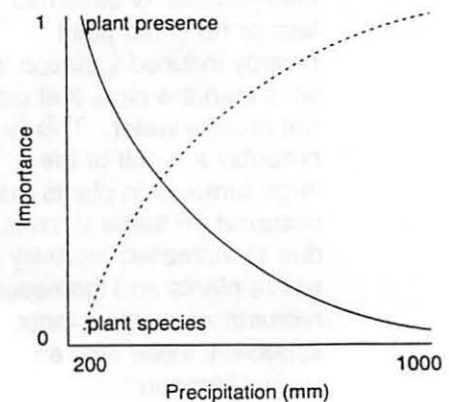
HABITAT USE, MOVEMEMENTS, AND BEHAVIORAL INTERACTIONS AMONG NOCTURNAL RODENTS ON THE COLORADO SHORTGRASS PRAIRIE

Investigator: Paul Stapp, Program for Ecological Studies and Department of Biology, Colorado State University.

Research Advisor: Beatrice Van Horne, Department of Biology, Colorado State University.

I currently am finishing my first complete field season of doctoral research on the Central Plains Experimental Range (CPER). This work has been supported by the Shortgrass Steppe Long-Term Ecological Research project and by a grant from the American Museum of Natural History. The general objectives of my research are to describe the patterns of habitat use and movement of nocturnal rodents on the shortgrass prairie, and to elucidate mechanisms (e.g. habitat heterogeneity, interspecific interactions, distribution of prey) that may be responsible for these patterns. Currently, my efforts are focused on three aspects of the biology of two common rodents on the CPER, the northern grasshopper mouse (*Onychomys leucogaster*) and the deer mouse (*Peromyscus maniculatus*).

1) Factors affecting surface activity and habitat use of northern grasshopper mice.

Although grasshopper mice are one of the most common rodents on shortgrass prairie, relatively little is known of their activities under natural conditions. Grasshopper mice are insectivorous, wide-ranging, and occur at relatively low population densities. My preliminary studies on the CPER suggest that grasshopper mice prefer open areas with patches of bare soil and that, unlike many quadrupedal rodents, do not concentrate their activity near shrubs. During both winter and summer field seasons, I will conduct a more detailed examination of their movements and surface activity using fluorescent powder tracking and radiotelemetry to describe patterns of habitat use across a range of spatio-temporal scales. These results will be compared to similar habitat use data collected concurrently from deer mice. Deer mice are similar in size and form to grasshopper mice but are omnivorous and ubiquitous in distribution. Comparisons between deer mice and grasshopper mice may reveal insights into correlates of habitat and diet specialization.

Documentation of patterns of habitat use will reveal potential underlying mechanisms that can be further examined with experimentation. For example, during spring and summer, I sample terrestrial arthropods in different cover types on my study sites to determine whether prey availability and distribution affects microhabitat use of grasshopper mice. Manipulation of the distribution of patches of bare ground should influence movement patterns if these areas are important to grasshopper mice.

2) Behavioral and ecological interactions between grasshopper mice and deer mice.

Grasshopper mice prey upon deer mice under laboratory conditions, and may compete with deer mice for food. This predator-competitor relationship is unusual in rodent communities, and the intensity of this interaction likely varies with seasonal variation in resource availability. Grasshopper mice influence microhabitat use of kangaroo rats (*Dipodomys ordii*; Conley and Rebar 1983; Ecology 64:984-988) and I predict that deer mice would similarly avoid grasshopper mice because of their similarities in size and food habits. I will remove grasshopper mice from replicated study plots on the CPER and compare movements, habitat use, and diet of deer mice to those on control plots to detect possible shifts in these parameters.

Because olfactory communication is important in maintaining small mammal community structure, I hypothesized that deer mice would avoid areas containing odors of grasshopper mice. In June and July 1993, I presented free-living deer mice with traps baited with odors of grasshopper mice and harvest mice, and with clean traps to test this prediction. Contrary to my expectations, no avoidance was observed. This experiment will be repeated during Winter 1993-94 because grasshopper mice may prey more heavily upon other rodents when arthropods are scarce.

3) Movements of deer mice in response to the distribution of shrub cover.

In arid environments, quadrupedal rodents such as deer mice restrict their activities to shrub microhabitats, presumably to reduce exposure to predators. My research during Winter 1993 revealed that, on shortgrass prairie, deer mice respond to shrub cover at different spatial scales. Population densities were highest on plots with a large proportion of shrubs, and deer mice restricted their movements largely to areas where shrub cover was abundant. Whereas small-scale movements were relatively linear on shrub-dominated areas, mice moved more tortuously on plots where shrubs are more widely-spaced, and therefore may have oriented toward these shrubs. Despite inter-plot differences in the dispersion of shrubs, deer mice apparently responded similarly to shrub cover by remaining approximately as close to shrubs as possible given differences in shrub spacing.

Preliminary analyses of tracking conducted in Summer 1993 confirm the results from the previous winter's fieldwork. I will continue to track deer mice in areas that differ in shrub distribution to further document this pattern. I hope to support these results with simulation modelling, which will allow me to predict movements and population characteristics of deer mice for a given distribution of shrubs in the field.

PRESENTATIONS/PUBLICATIONS TO DATE:

Stapp, P., L. Ennis, and B. Van Horne. Microhabitat use and movements of *Peromyscus maniculatus* on the Colorado shortgrass prairie: responses to the availability of shrub cover. *Paper presented at 1993 Meeting of the American Society of Mammalogists, June 19-23, Bellingham, WA.*

Stapp, P. Response of deer mice (*Peromyscus maniculatus*) to traps containing odors of northern grasshopper mice (*Onychomys leucogaster*). *Paper to be presented at the 1993 Meeting of the Guild of Rocky Mountain Population Biologists, October 1-3, Abiquiu, NM.*

Stapp, P., J.K. Young, and S. VandeWoude. An evaluation of the pathological effects of fluorescent powder on deer mice (*Peromyscus maniculatus*). *Submitted September 1993 to Journal of Mammalogy.*

Stapp, P., and B. Van Horne. Effect of odors of northern grasshopper mice (*Onychomys leucogaster*) on the trap response of deer mice (*Peromyscus maniculatus*). *In preparation, to be completed Winter 1993-94.*

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Aboveground

LTER Data

Four locations at the CPER have been sampled for ANPP since 1982; five since 1986. Three of the locations were selected to represent topographic positions (summit, backslope, and swale) in conjunction with sampling of soilwater. The fourth site was selected because we had previous data from the US IBP Grassland Biome project. The final site was selected because it was on an extreme soil texture (sand).
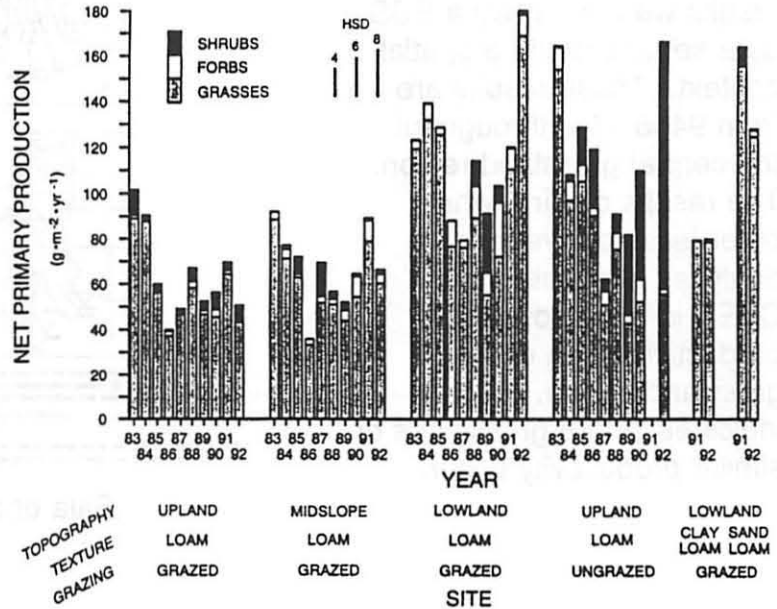
Lauenroth and Milchunas (unpublished)

Long-term ARS Data

When the CPER was established in 1939 the Forest Service began sampling annual forage production. When the ARS assumed responsibility for the site in 1952 they continued collecting these data. Despite the fact that the methods and sampling locations varied over the years and these data have been extremely valuable in providing us with a context for our LTER results.
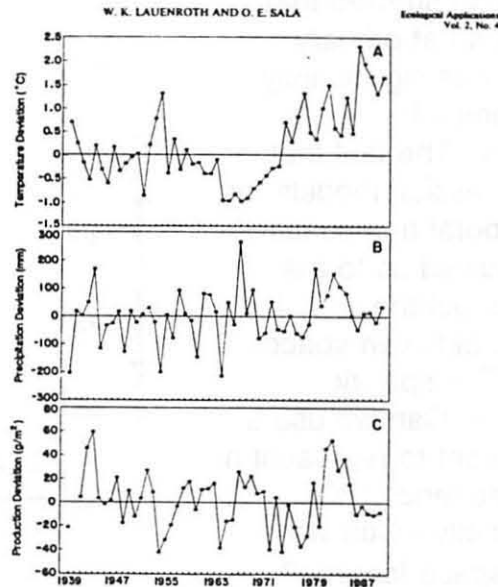
Lauenroth and Sala (1992)

Soil Conservation Service Data

In addition to being able to use ARS to provide a temporal context for our results we have used a SCS data set to provide a spatial context. These results are from 9498 sites throughout the central grassland region. The results confirm what other less comprehensive analyses suggested; the CPER is in the lowest productivity area of the grassland region. It also indicates where grasslands of similar productivity occur.
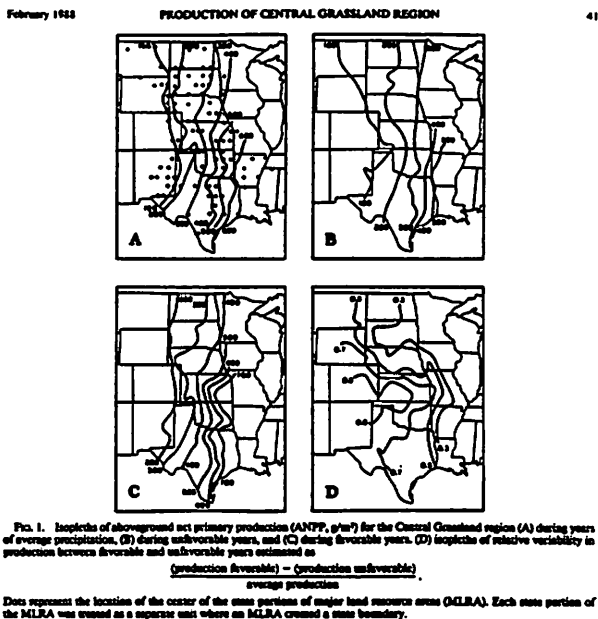

Fig. 1. Isopleths of aboveground net primary production (ANPP, g/m²) for the Central Grassland region (A) during years of average precipitation, (B) during unfavorable years, and (C) during favorable years. (D) Isopleths of relative variability in production between favorable and unfavorable years estimated 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.

Sala et al. (1988)

Spatial vs Temporal Results

Analyses of the ARS and SCS both showed that aboveground net primary production was significantly related to annual precipitation. The fact that we had regression models for both a temporal and spatial data set allowed us to ask questions about the relationship between space and time. The specific question was: Can we use a spatial data set to represent a temporal sequence? Or more succinctly - Can we substitute space for time?
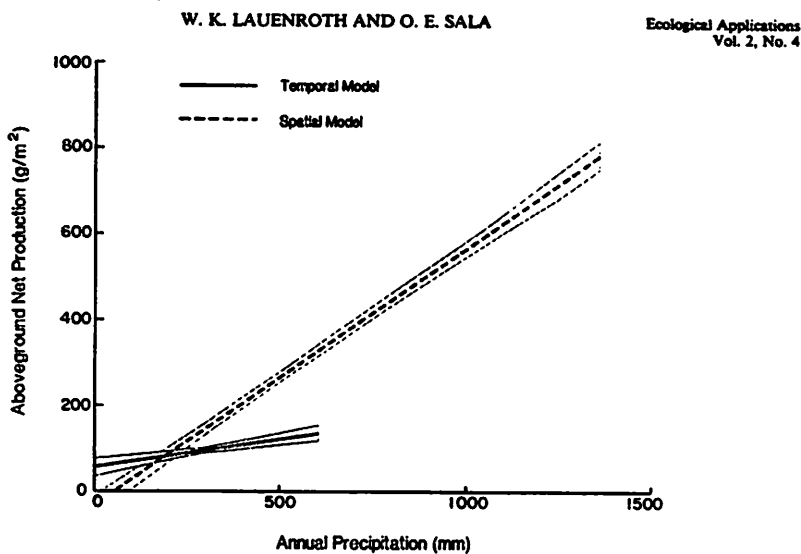
Lauenroth and Sala (1992)

Belowground

Results from a ^{14}C labelling experiment begun in 1985 have completely revised our assessment of the magnitude of belowground net primary production. Estimates based upon harvest data suggested that the ratio of BNPP/ANPP was in the range of 5-20. Estimates from ^{14}C turnover suggest that the ratio should be in the range of 1-3.
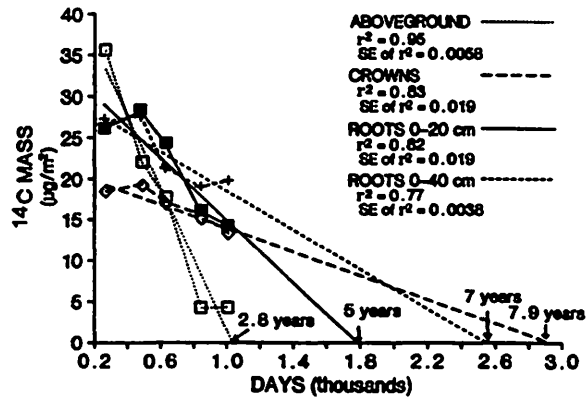

FIG. 8. Regression of ^{14}C mass on time, and extrapolations to time of complete turnover of ^{14}C, in plant components. Sample points are from long-term plots after stabilization of labile ^{14}C, i.e., 1986–1988, not including 1985.

Milchunas and Lauenroth (1992)

TABLE 4. Net primary production (NPP) and aboveground to belowground NPP ratios obtained by the ^{14}C turnover method for the Central Plains Experimental Range.

	NPP by ^{14}C turnover ($g \cdot m^{-2} \cdot yr^{-1}$)					
	1985*	1986*	1986†	1987†	1988†	Mean
Aboveground	159	111	94	93	87	109
Crown	74	52	60	53	47	57
Root (0–20 cm)	188	180	185	165	158	175
Root (0–40 cm)	145	160	143	149	157	151
	Aboveground : belowground ratios					
0–20 cm with crowns‡	1.24	0.91	0.83	0.88	0.85	0.95
0–20 cm without crowns	0.86	0.62	0.51	0.56	0.55	0.62
0–40 cm with crowns‡	1.61	1.02	1.08	0.98	0.85	1.10
0–40 cm without crowns	1.10	0.69	0.66	0.62	0.55	0.73

* Mean biomass from short-term experiment plots divided by number of years for complete turnover.
† Mean biomass from long-term experiment plots divided by number of years for complete turnover.
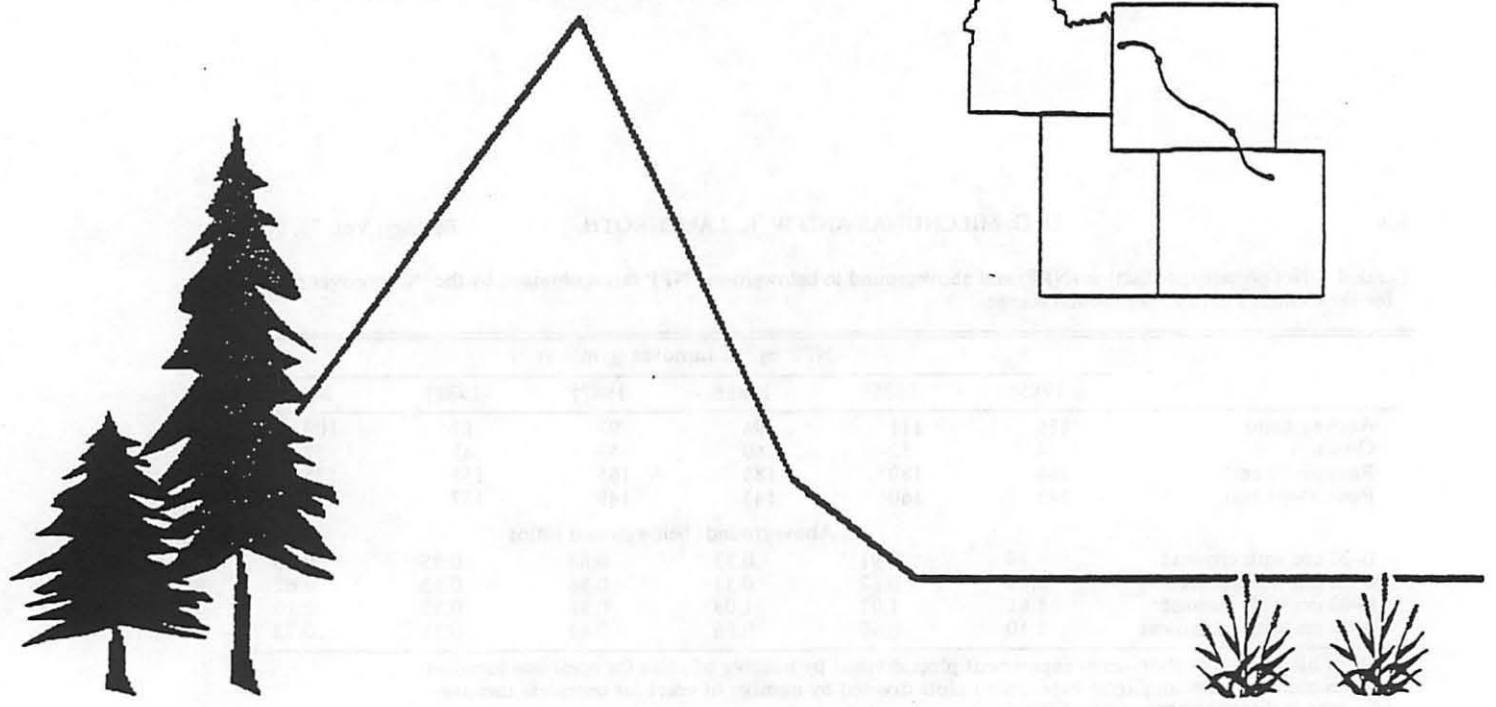‡ Crowns included in aboveground fraction.

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this chapter taken from:

Kelly, E. F., and C. M. Yonker (eds). 1991. Field guide, American Society
of Agronomy soils-geomorphology pre-meeting tour. Denver, Colorado.
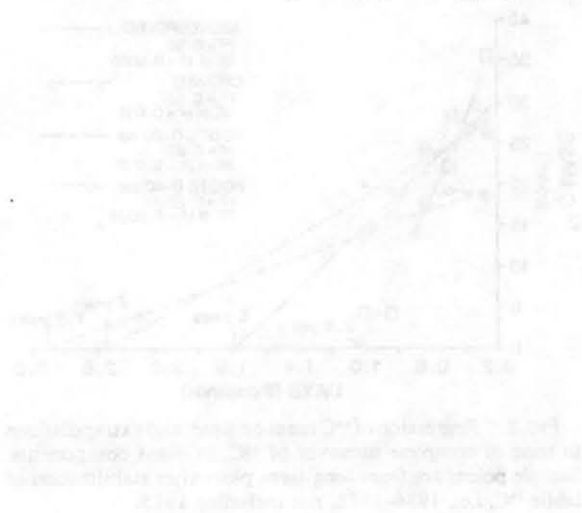
1991 ASA Soils-Geomorphology Pre-Meeting Tour

Edited by E.F Kelly and C.M. Yonker

LANDFORMS AND HOLOCENE SOIL EVOLUTION OF THE SHORTGRASS STEPPE (CENTRAL PLAINS EXPERIMENTAL RANGE)

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INTRODUCTION

The CPER is located in the Colorado Piedmont section of the Great Plains, between the southern Rocky Mountain section to the west and the High Plains section to the east (Thornbury, 1965). The post-Pleistocene history of the area includes three soil forming periods separated by periods of drought. Five types and ages of alluvium and two types and ages of eolian material have been identified (Davidson, 1988). Superimposed on four terrace levels are deflation basins and vegetated dunes, suggesting the importance of eolian processes in shaping the contemporary landscape. Buried soils are common; eight radiocarbon dates concur with proposed soil forming intervals. (Gould et al., 1979; Yonker et al., 1988) The goal of our research has been a reconstruction of the Holocene evolution of the site including reconstruction of paleosurfaces. To that end, a number of paleoenvironmental investigations have been initiated, including mapping of buried soils, determination of the stable isotope composition of soil organic matter, phytoliths and $CaCO_3$ in buried profiles, and radiocarbon dating of charcoal and organic matter. The tour will focus primarily on the upper Owl Creek drainage (Figure 1).

REGIONAL SITE DESCRIPTION

The Central Plains Experimental Range (CPER), a USDA-ARS facility, is located near the border of the Great Plains region in northeastern Colorado, approximately 40 km south and east of Cheyenne, WY. Mean annual precipitation at the CPER is approximately 31 cm, 70% of which occurs between May and September. Mean annual precipitation in northeastern Colorado reaches a maximum of approximately 47 cm at its eastern boundary. Long term monthly temperatures at the CPER range from below 0°C in
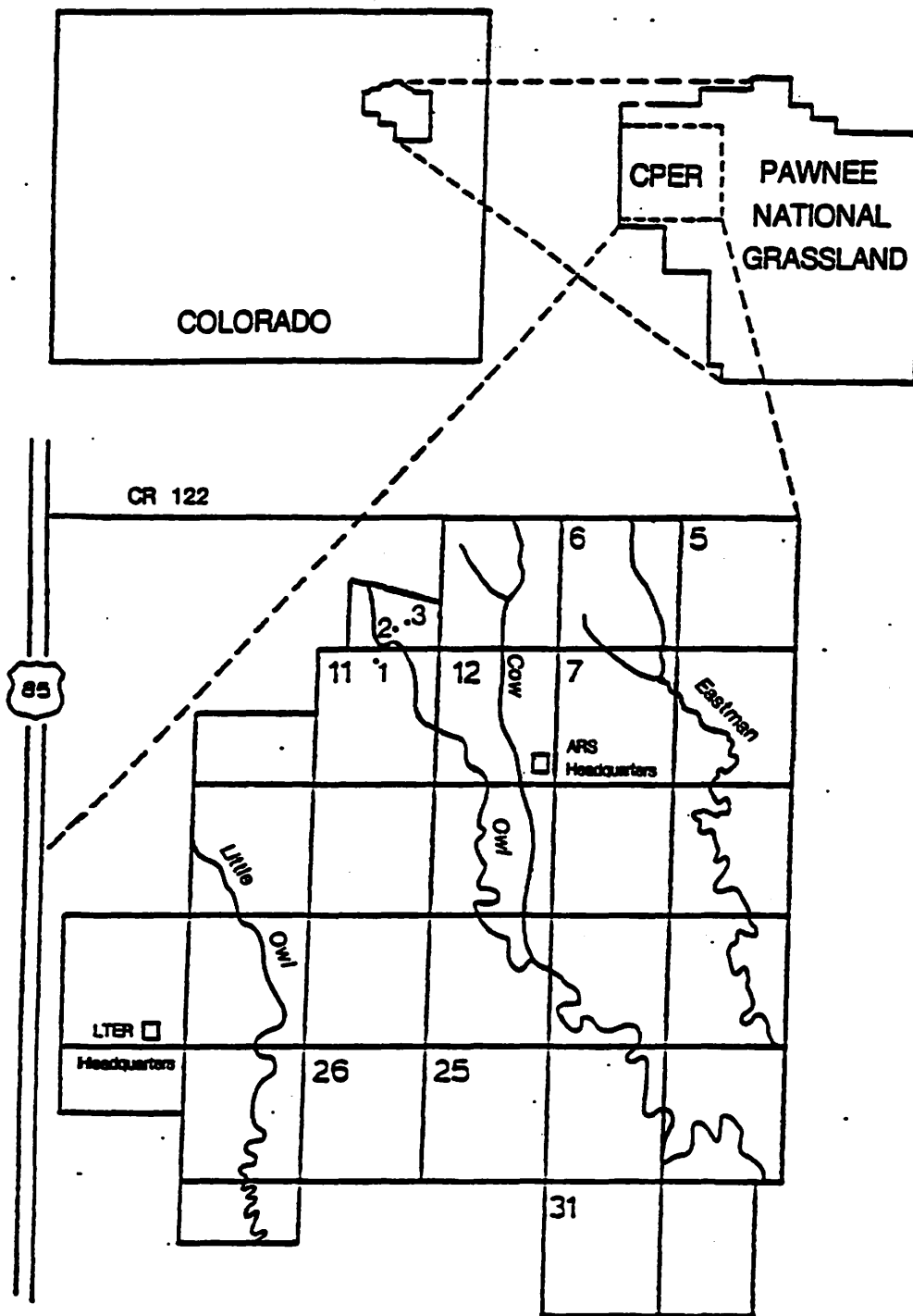
Figure 1. Location of Central Plains Experimental Range (CPER) and tour stops 1, 2, 3.

December to 22°C in July. The average elevation is 1650 m. The natural vegetation of the area is characteristic of much of the shortgrass steppe and is dominantly blue grama (Bouteloua gracilis) grassland with mixed low and half shrubs. Major associated species include fringed sagewort (Artemesia frigida), plains prickly pear (Opuntia polycantha) and buffalograss (Buchloe dactyloides).

The CPER is underlain by the Laramie Formation. Deposited in the late Cretaceous, the Laramie is approximately 3200 feet of interbedded sandstones and shales, with some coal, dipping 12-15° to the east. Looking north, from the CPER, the Chalk Bluffs (Brule Formation) are visible. They are part of the White River Group, deposited during the Tertiary as the Rocky Mountains were uplifted and streams subsequently carried heavy loads of silt, sand and gravel eastward. The Arikaree and Ogallala Formations are present north and east of the site and are the upper geologic units of the High Plains section of northeastern Colorado. These Tertiary sediments are not present in the Colorado Piedmont, as they were eroded from the region by the South Platte and its tributaries. Consequently, the Piedmont is several hundred feet lower in elevation than the High Plains to the north and east.

There are two curious physiographic phenomena common to northeastern Colorado and parts of the surrounding Great Plains region. First, there is a strong northeast-southwest alignment of the drainages when in many cases the slope of the regional terrain is to the east or north. Second, there are innumerable closed depressions (or deflation basins) scattered across the landscape whose alignment is generally in the same direction. Because their orientation parallels that of the Quaternary prevailing wind direction (Muhs, 1985) eolian processes are generally cited as the probable cause.

The soils of northeastern Colorado are dominantly Aridic Arguistolls and Ustollic Haplargids which have formed in calcareous alluvium derived from Front Range (Colorado Rockies) sources, wind reworked alluvium and some loess. Large areas of Ustic Torripsamments are found south and east of the CPER in the Greeley dune field, south of the Platte River in the Fort Morgan dune field and east along the Colorado-Kansas-Nebraska junction in the Wray dune field. These soils have formed in wind deposited sand and wind reworked sandy alluvium. Ustic Torriorthents occur in patches along the Colorado-Wyoming border where they have formed in silty materials derived from the Brule Formation.

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CPER SITE GEOLOGY AND GEOMORPHOLOGY

As we approach the CPER site, we drop in both elevation and stratigraphic section from the Wyoming border. The CPER is within the Cretaceous-age Laramie Formation. Little, if any evidence remains of the large Tertiary "rampart" with its long eastern gradient extending from the Rocky Mountains to the High Plains. Both surface topography and stream drainage are oriented northwest-southeast with gradients to the southeast. Examination of topographic maps from large segments of Weld County illustrates a series of large, dissected alluvial fans whose structures comprise the majority of this region. In this part of the Colorado Piedmont there are at least 2 major fans, each with its source for fan debouchment; one from the northwest and one directly from the north.
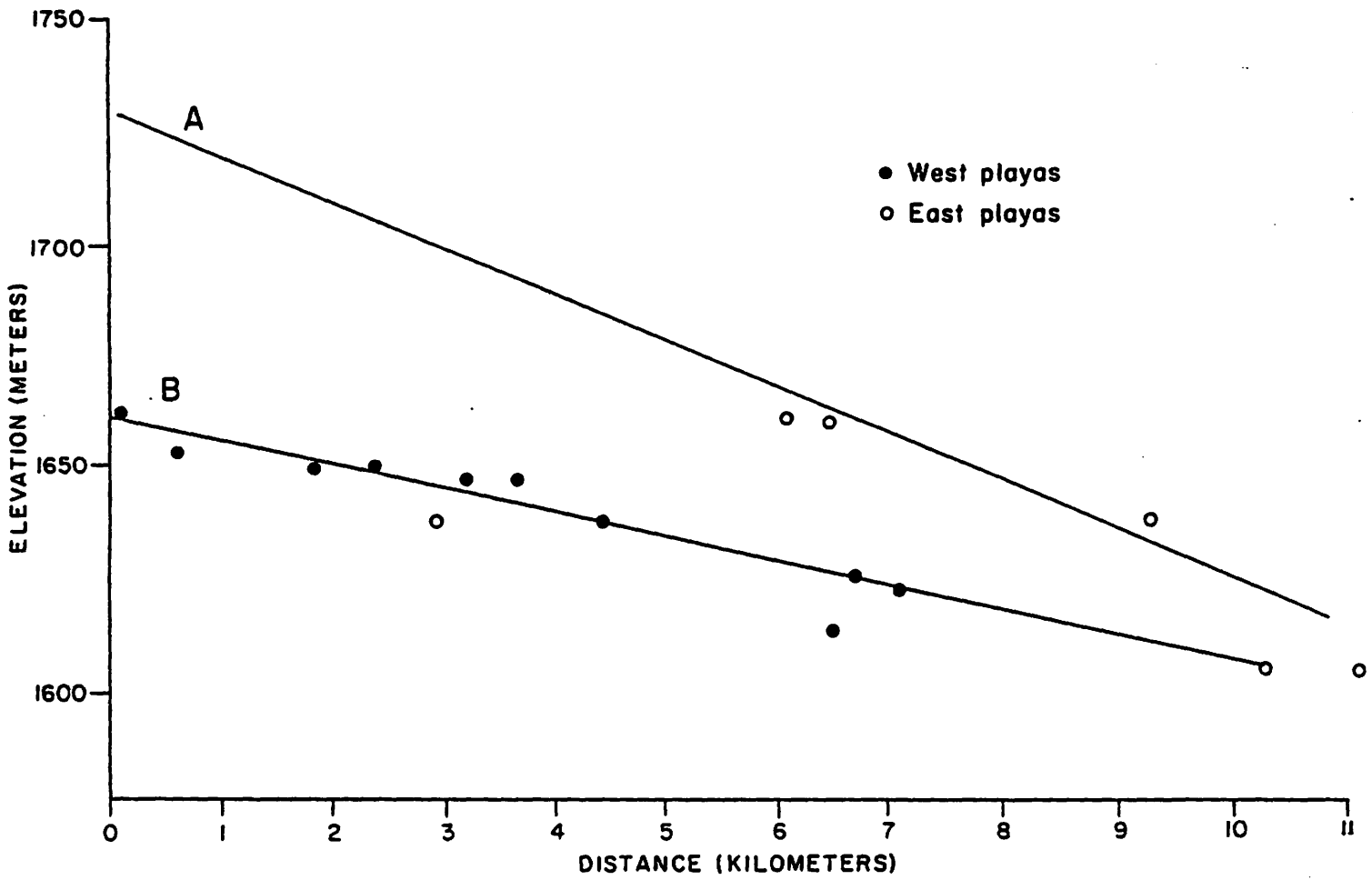
On the CPER site, remnants of three major regional surfaces are present. From west to east these are: 1) the area west of Owl and Cow Creeks, 2) the valley bounded on the west by Cow and Owl and on the east by Eastman Creek, and 3) the area east of Eastman Creek.

The two regional surfaces to the east and west are heavily dissected. Many younger surfaces within drainageways are cut into these regional surfaces. Summit divides are bedrock highs. Depressional areas, locally called playa lakes, occur on both surfaces. A systematic evaluation of their elevations (Figure 2) shows that the depressions on the regional surface to the west of Owl and Cow Creeks have a gradient of 6.2 m/km (33 ft/mile) to the southeast. Depressions to the east of Eastman Creek are on a surface with a gradient of 11.1 m/km (59 ft/mile). Aerial photography shows several of these depressions appear to be aligned along ephemeral drains that at one time emptied to the northwest. The modern gradient is in the opposite direction towards the southeast.

The lowest regional surface, the valley, is thought to be inset in, and below those on either side and therefore younger. By comparison, it is little dissected and is part of one of the large fans described earlier whose source is to the north. Longitudinal stream profiles on this surface have gradients of approximately 6.2 m/km. The field sites are in the upper Owl drainage just west of this regional surface.

Owl Creek Drainage

A geomorphic map of surfaces in this segment of Owl Creek illustrates several floodplain and terrace surfaces (Figure 3). For the purpose of this field trip, multiple surfaces were separated in elevational sequence from lowest to highest and may not imply relative age. The lowest surface is the channel composed of the active channel shelf and minor flood plain steps. Throughout its length, this surface contains a series of gravel and point bars with mixed-lithology cobbles as large as 30 cm. Two floodplain levels F1 and F2 are mapped. F1 is the lowest broad, continuously traceable surface. It is cobble-armoured

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Playa elevations on geomorphic surfaces west and east of Cow-Eastman Valley.

R. 66 W.

Road 122

Farmstead

35 | 36

2 | 1

N

T.
10
N.

FA
TI
F2
F1
T1
FA
F2
CS
T3
SD
F2
F2
F1
FA
CS
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F2
F1
SD
RE
F2
FA
SD
T3
F2
T4
F1
2 3
F2
F1
F2
F1
CS
F2
F1
1
RE
FA
T3
T4
F1
F2
TI
F1
F1
TI
T3
FA
FI
F2
RE
F1
F2
F1
F1

CS – Channel surface

F1 }
F2 } Flood plain surfaces

FA – Fans

T1
T2 } Terrace surfaces
T3
T4

RE – Rock exposures

SD – Summit divide

– ··· – Intermittent stream

– – – – Access roads

■ Soil pit

0   1 Mile

0   1 Kilometer
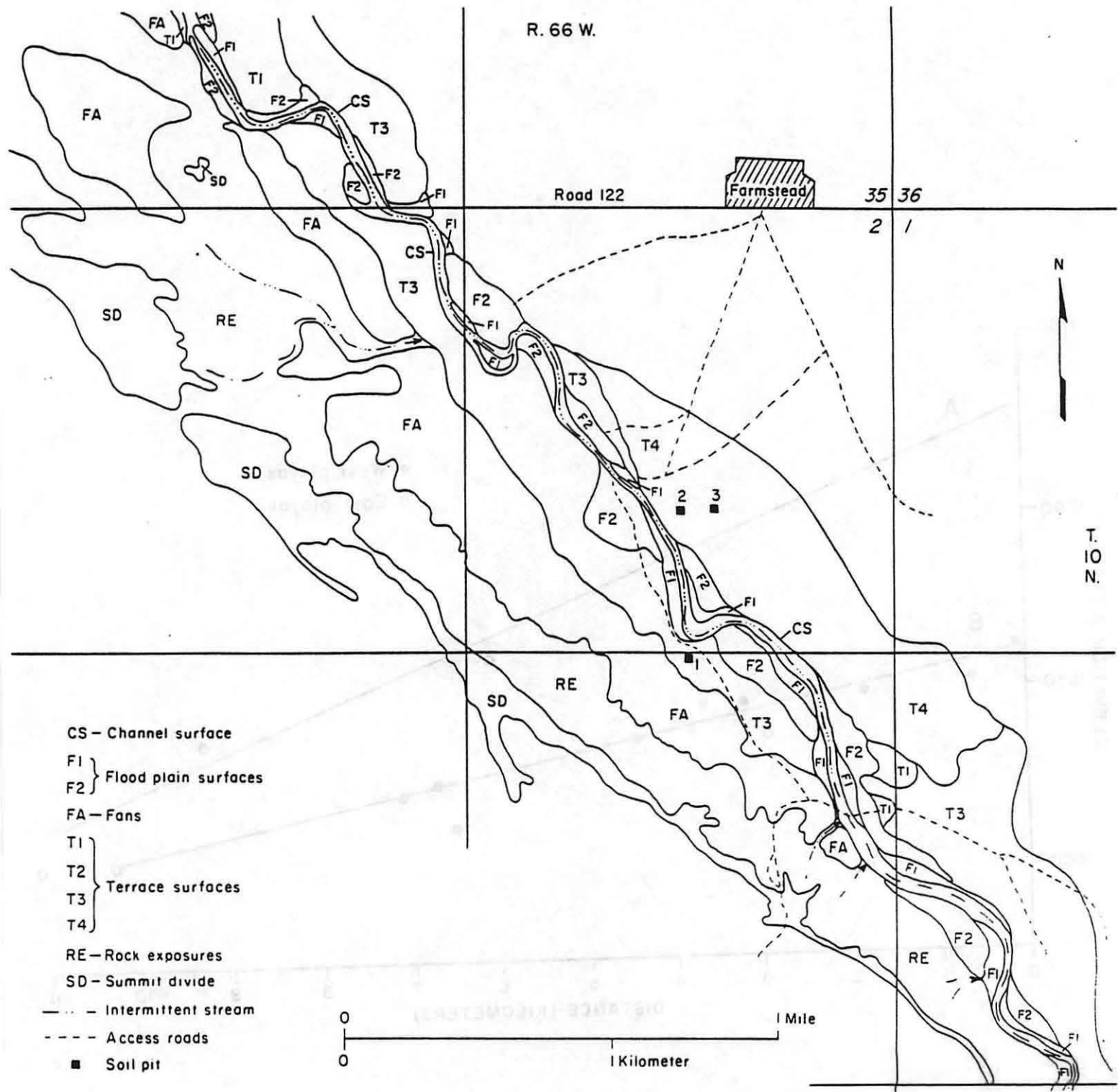
Geomorphic surfaces, upper Owl Creek drainage.

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and has discrete tufts of vegetation. F2 has noticeably more vegetation and a sandy surface with far fewer cobbles. Several terrace levels are present. All are heavily dissected, discontinuous remnants. T1 and T2 are lower fill terraces at some distance from study area. T3 is primarily a fill terrace. Soil pit 1 is located there. T4 is a strath terrace cut in bedrock of the Laramie Formation. Soil pits 2 and 3 are on T4. Fans extend downward from the ridges only on the southwest side of the drainage. These coalescent fan surfaces onlap T3 and therefore should be younger than the T3 suface. Coring for stratigraphic verification has not yet been completed. Radiocarbon dates from soil organic material and charcoal show the surficial materials on both T3 and T4 are of similar Holocene age. Above the fans, the Laramie Formation is exposed in gullies and steep escarpments. Summit divides are rock-cored. Some ridge tops are capped wtih alluvial gravels.

SOIL CHARACTERIZATION

Site 1.   The soil is classified as a coarse loamy, mixed, mesic, Aridic Haplustoll. It contains a number of lithologic discontinuities, at least one of which may be eolian in origin. An argillic horizon, absent from the modern soil, is present below the 3000 and 8000 yr old surfaces. Note the dramatic change in isotopic composition at 197 cm.

Table 1a.   Morphological characterization, site 1.

Site	Horizon	Depth	Texture	Sand	Silt	Clay	Dry Color (10 YR)	Moist Color (10 YR)	Structure
		cm			%				
001	A1	0-11	sl	78.2	9.0	12.8	5/2	3/2	2fcr
	A2	11-31	sl	70.6	13.2	16.2	5/3	3/2	1-2fsbk
	BA	31-42	sl	71.1	13.8	15.1	5/3	3/3	1-2fsbk
	Bw	42-57	sl	69.1	14.9	16.0	6/3	4/3	1-2msbk
	Bk1	57-80	sl	61.1	21.2	17.7	7/3	5/3	1msbk/ 1-2fsbk
	Bk2	80-90	scl	50.2	28.3	21.5	6/3	5/2	2fpr/2fsbk
	2Btkb1	90-100	sic	13.2	44.1	42.7	6/2	4/2	2-3fsbk
	2Btkb2	100-122	sicl	23.1	43.9	33.0	7/3	5/3	2fpr/2fsbk
	2Bkb1	122-150	sicl	27.4	41.9	30.7	8/3	6/3	2m6fpr/2fsbk
	3Bkb2	150-175	fsl	62.8	17.4	19.8	7/3	6/3	1f-mpr
	3BCkb	175-197	fscl	56.7	20.3	23.0	7/3	6/3	1mpr
	4ABb	197-219	sic	17.5	41.5	41.0	5/2	3/3	2fpr/2fsbk
	4BAb	219-248	sic	15.3	43.6	41.1	5/2	3/2	2fpr/2-3fsbk
	4Btkb3	248-280	cl	31.1	35.1	33.8	5/2	4/2	1fpr/1-2 fsbk

Table 1b.   Chemical characterization, Site 1.

Site	Horizon	Depth	Organic C	Total N	CEC	CaCO₃ⁿ	$\delta^{13}C$ OM	$\delta^{13}C$ CaCO₃	^{14}C date
		cm	%	%	Meq.100g⁻¹	%			
001	A1	0-11	.95	.084	11.3	-	-16.89		
	A2	11-31	.53	.056	14.9	TR	-		
	BA	31-42	.44	.046	13.2	1	-15.67	-4.66	
	Bw	42-57	.37	.042	13.5	2	-16.78	-4.65	
	Bk1	57-80	.30	.032	16.5	3	-17.57	-4.43	
	Bk2	80-90	.36		20.2	3	-17.70	-4.83	
	2Btkb1	90-100	.72	.047	38.9	5	-16.56	-4.64	3330±90 (o.m.)
	2Btkb2	100-122	.37	.036	33.9	5	-16.58	-4.95	
	2Bkb1	122-150	.30	.033	30.9	4	-17.18	-5.86	
	3Bkb2	150-175	.12		17.4	2	-17.48	-5.24	
	3BCkb	175-197	.15		21.1	2	-17.57	-5.53	
	4ABb	197-219	.75	.075	35.5	1	-17.23	-3.86	
	4BAb	219-248	1.29	.104	21.3	TR	-20.56	-4.12	8840±60 (o.m.)
	4Btkb3	248-280	.78	.063	29.2	4	-21.21	-6.33	

$\delta^{13}C$ (0/00) Value

% Organic Carbon

Figure 4A

Organic C vs Carbonate
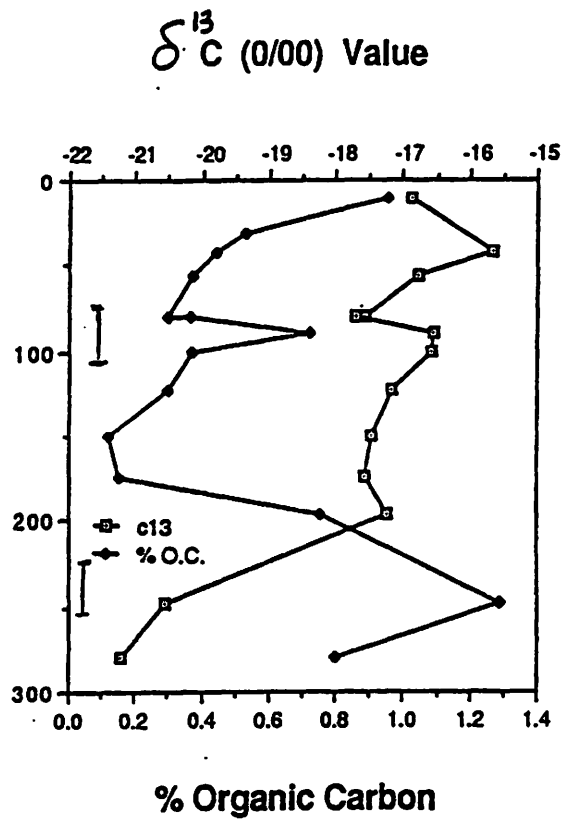

$\delta^{13}C$ (0/00) value
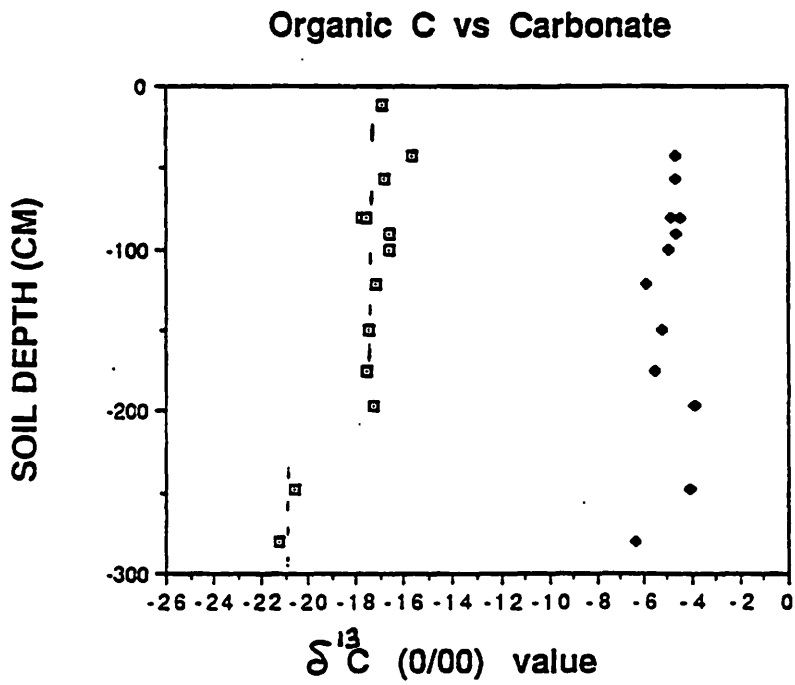
SOIL DEPTH (CM)

Figure 4B

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<u>Site 2.</u>   The soil is classified as a fine loamy, mixed, mesic Aridic Argiustoll. It is extensive along the upper terraces of the Owl Creek drainage, and consistently has a buried argillic subhorizon. The modern soil also has a strongly expressed argillic horizon. A charcoal fragment extracted from the second horizon of the paleosol yielded a radiocarbon date of approximately 4950 yr b.p.   Note the change in isotopic composition of the carbonates at 89 cm.

Table 2a.   Morphological characterization, site 2.

Site	Horizon	Depth	Texture	Sand	Silt	Clay	Dry Color (10 YR)	Moist Color (10 YR)	Structure
		cm			%				
002	A1	0-9	fsl	70.1	15.9	14.0	5/3	3/3	2fgr
	A2	9-30	fsl	66.5	14.7	18.8	5/3	3/2	1msbk/2fgr
	Bt	30-41	scl	50.9	22.5	26.6	5/3	3/3	1-2fsbk
	Btk	41-53	scl	50.5	22.2	27.3	6/3	4/3	1-2mpr/ 2f&msbk
	BAkb	53-62	scl	58.6	15.6	25.8	5/2	2/2	2m&fsbk
	Btkb	62-71	fscl	57.2	17.2	25.6	6/3	4/2	3f&msbk
	2Btkb1	71-89	cl	40.0	25.0	35.0	5/3	3/2	2-3fsbk
	2Btkb3	89-122	sl	75.2	6.5	18.3	6/4	5/4	3fpr/ 3f&msbk
	3BCk	122-200	exgrls	87.8	4.2	8.0	6/4	5/4	sg
	4C	200-360	s	91.0	3.1	5.9	7/3	6/3	m

Table 2b.   Chemical characterization, site 2.

Site	Horizon	Depth	Organic C	Total N	CEC	CaCO$_3$*	$\delta^{13}C$ OM	$\delta^{13}C$ CaCO$_3$	^{14}C date
		cm	%	%	Meq.100g^{-1}	%			
002	A1	0-9	1.27	.115	14.1	—	-14.94		
	A2	9-30	.88	.090	16.3	—	-17.60		
	Bt	30-41	.73	.081	21.3	—	-14.88	-1.94	
	Btk	41-53	.64	.069	22.3	—	-14.70	-1.94	
	BAkb	53-62	.64	.068	22.0	—	-14.85	-2.31	
	Btkb	62-71	.59	.066	21.7	—	-15.26		
	2Btkb1	71-89	.67	.075	27.1	TR	-16.60	-3.10	
	2Btkb2	89-122	.19	.024	16.2	TR	-16.62	-5.29	4950±90 (charcoal)
	3Btkb2	122-200	.05		7.3	—	-19.00	-5.71	
	4C	200-360	.01		11.0	TR			

δ^{13}C (o/oo) Value
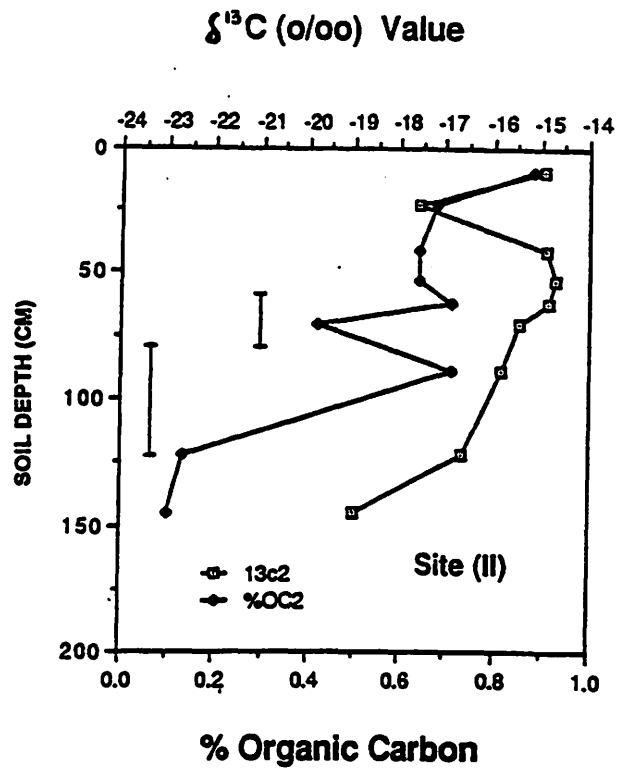

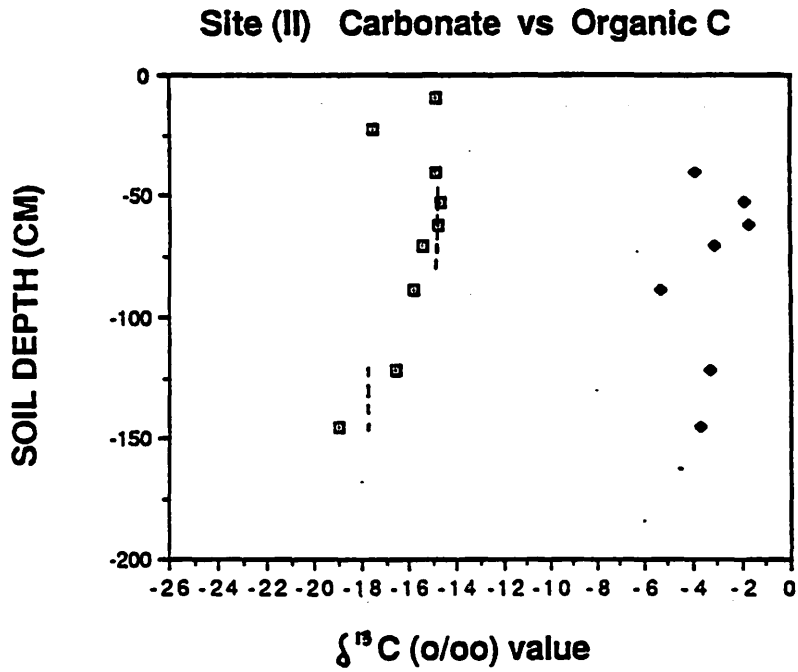Figure 5A

Site (II)   Carbonate vs Organic C

Figure 5B

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Site 3 The soil is classified as a coarse-loamy mixed, mesic Ustollic Cambortthid, and is extensive within the Owl-Eastman Creek Valley floor. It contains a number of lithologic discontinuities, but no paleosols. Note the uniform decrease with depth of the $\delta^{13}C$ value of both organic matter and carbonates, characteristic of constant environmental conditions.

Table 3a. Morphological characterization, site 3.

Site	Horizon	Depth	Texture	Sand	Silt	Clay	Dry Color (10 YR)	Moist Color (10 YR)	Structure
		cm			%				
003	Al	0-9	sl	70.6	12.9	16.5	5/3	3/3	2fgr
	Bt1	9-19	sl	70.6	10.9	18.5	6/3	3/3	1msbk & 2fsbk
	Bt2	19-40	sl	73.4	9.5	17.1	6/3	5/4	3f&mpr/ 2f&msbk
	Bt3	40-55	sl	73.1	9.7	17.2	6/3, 7/3	5/4	1msbk
	Bk1	55-83	sl	74.1	10.4	15.5	6/3	5/4	1cpr/ 1msbk
	Bk2	83-120	sl	72.3	10.6	17.1	7/3	6/4	1mpr
	2Bk3	120-163	scl	48.9	25.7	25.4	8/3	6/4	m
	3Bk4	163-196	scl	48.8	27.0	24.2	7/4	6/4	m
	4BC	196-208	vgrls				6/4	5/4	sg

Table 3b. Chemical characterization, site 3

Horizon	Depth	Organic C	Total N	CEC	CaCO₃*	$\delta^{13}C$ OM	$\delta^{13}C$ CaCO₃	^{14}C date
	cm	%	%	Meq.100g⁻¹	%			
A1	0-9	1.40	.131	15.9	-	-17.15		
Bt1	9-19	.56	.070	16.9	-	-16.01		
Bt2	19-40	.45	.056	14.8	TR	-17.15		
Bt3	40-55	.30	.040	13.7	3	-17.15	-2.99	
Bk1	55-83	.15	.021	13.0	2	-	-2.84	
Bk2	83-120	.07	.014	13.6	2	-19.39	-5.81	
2Bk3	120-163	.13	.019	21.5	3	-19.73	-4.90	
3Bk4	163-196	.12	.018	22.0	2	-	-5.70	
4Bc	196-208							

* analysis of <2mm fraction

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$\delta^{13}C$ (o/oo) Value

Figure 6A

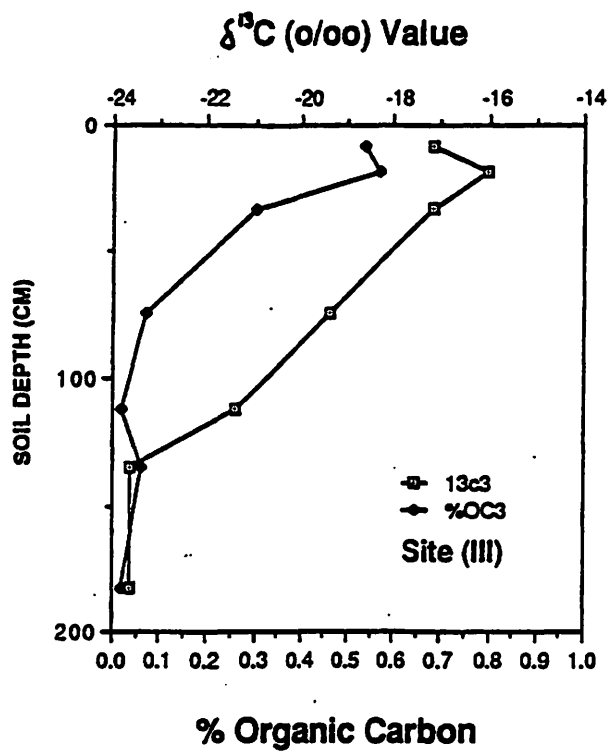Site (III)   Carbonate vs Organic C
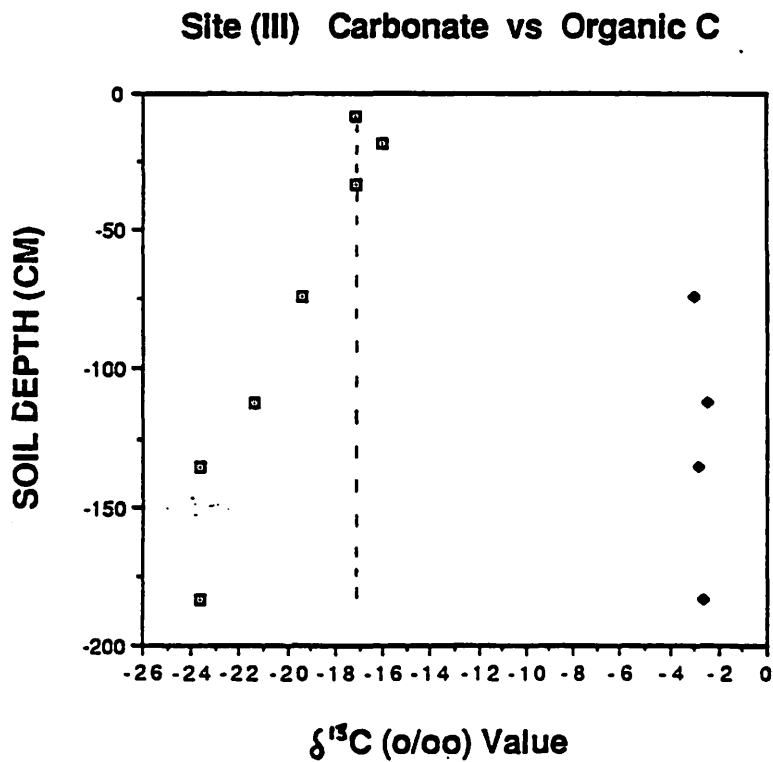

$\delta^{13}C$ (o/oo) Value

Figure 6B

3 0

ANALYTICAL METHODS

Soil Characterization and Sampling. Soil pits were excavated to a minimum depth of 2 meters. Soil profiles were described morphologically (Soil Survey Staff, 1990), sampled by genetic horizon, and taken to the NSSL, Lincoln, NE for standard chemical, physical and mineralogical characterization. Much of this intensive characterization is a product of the prototype research area soil survey recently completed by SCS, USDA-ARS and CSU.

Carbon 13. Phytoliths were extracted from the sand and silt size fractions (2 to 200 microns) using standard particle size sedimentation techniques (Jackson, 1969) and a zinc bromide heavy liquid separation procedure (Fredlund et al., 1985). Upon recovery, all phytolith samples were washed with hot 6N HCl, rinsed with water, and freeze-dried. Phytoliths were studied morphologically as described by Piperno (1989) and isotopically (Kelly et al., 1991). Soil samples used to determine the isotope composition of soil organic matter was passed through a 2 mm sieve, acidified with 0.1N HCl to assure carbonate removal, rinsed with H_2O, and were oven and then, freeze-dried.

Carbon concentrations and $\delta^{13}C$ values for these organic materials were determined by combusting the samples at 875°C, purifying the resulting CO_2 cryogenically, and determining its quantity and isotopic composition manometrically and mass spectrometrically.

Soil carbonate samples for isotopic study, such as nodules and powdery concretions, were physically separated from disseminated carbonates in the field and stored in vials. Soil carbonate samples were pretreated by baking the samples at 425°C for 4 hours under vacuum. The $\delta^{13}C$ values were determined by reacting each sample with 100% H_3PO_4 for 24 hours at 25°C. The liberated CO_2 was purified cryogenically and carbonate content was determined by measuring the quantity of CO_2 manometrically.

Carbon 14. Bulk soil organic carbon samples and charcoal fragments for radiometric dating were pretreated as follows: Soil samples were sieved to remove fine rootlets, dispersed in hot acid to eliminate carbonates, repeatedly rinsed to neutrality, brought to dryness and subjected to multiple combustions under vacuum. Soil samples were then subjected to benzene syntheses and subjected to extended counting procedures. Charcoal samples were subjected to microscopy to remove fine roots and also treated to acid, alkali, acid series of soaking to remove carbonates and humic acids. The CO_2 collected was purified and reacted with hydrogen on a cobalt catalyst to produce graphite. Samples were then subjected to Accelerator Mass Spectrometry.

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32

Central Plains Experimental Range
Soil Survey 1991

Soil Survey: USDA Soil Conservation Service
Digital Data: USDA-ARS Great Plains
Systems Research

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KM

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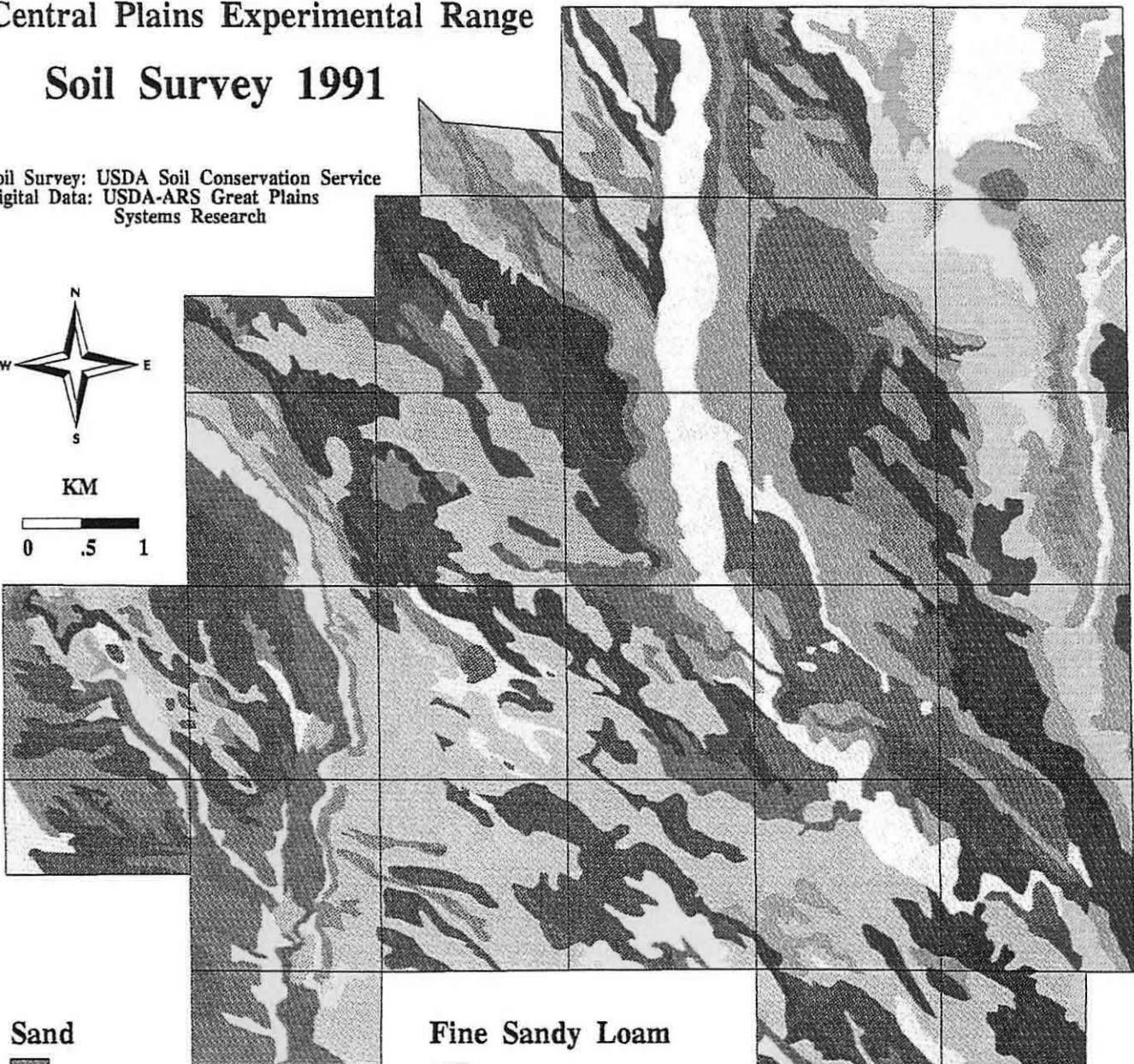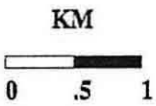
Sand
Bankard
Valent

Loamy Sand
Remmit
Vona

Sandy Loam
Otero-Altman
Remmit
Vona
Vona-Cushman-Otero

Fine Sandy Loam
Ascalon
Avar-Manzanola
Cushman
Kim-Cushman
Olney
Olney-Owlcreek
Owlcreek-Olney
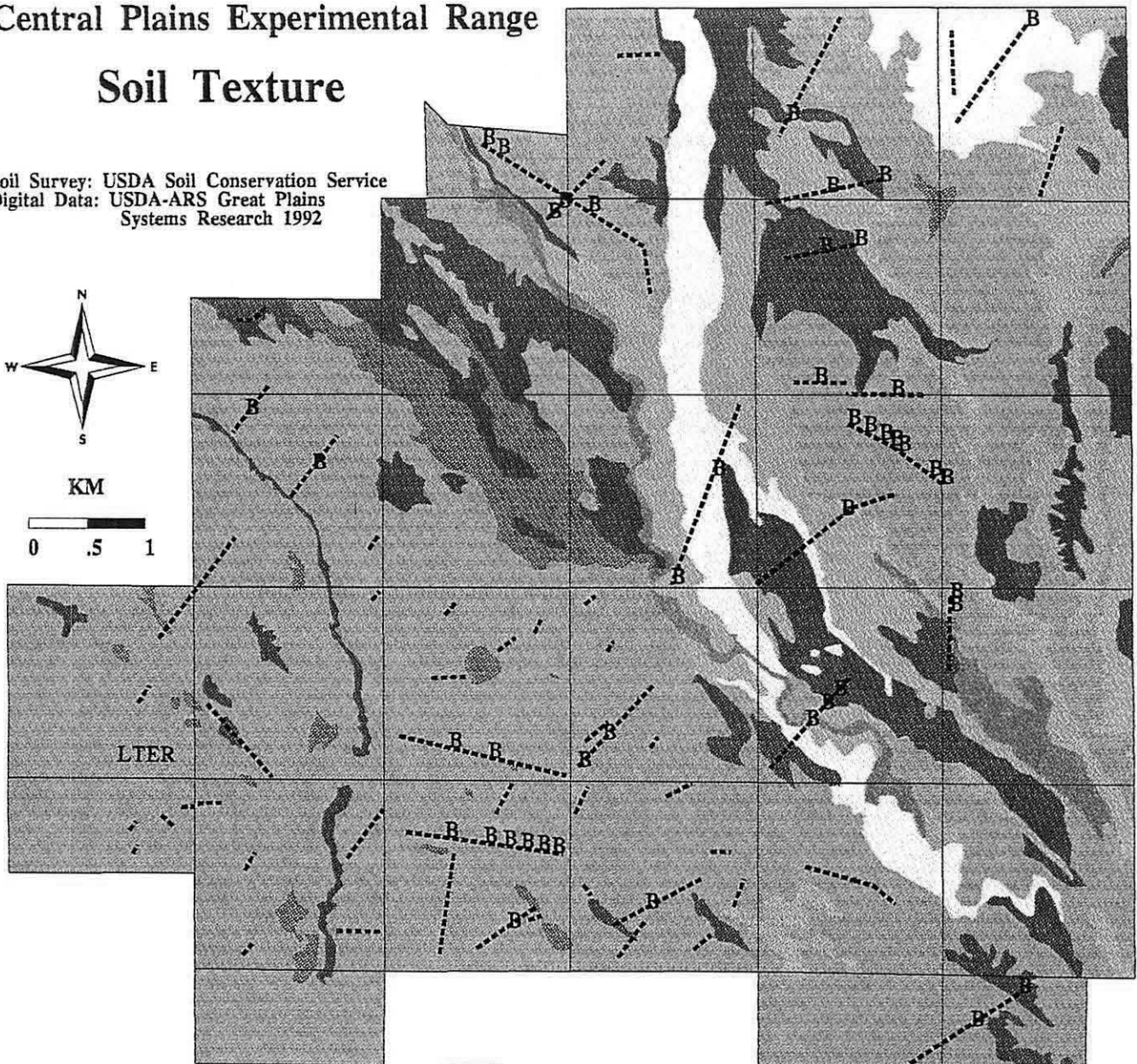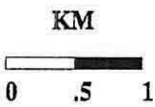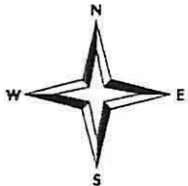Renohill-Cushman
Ulm
Ulm-Renohill
Zigweid

Loam
Edgar
Nucla

Sandy Clay Loam
Arvada-Manzanola
Pleasant-Typic Pellustert

33

Central Plains Experimental Range

Soil Texture

Soil Survey: USDA Soil Conservation Service
Digital Data: USDA-ARS Great Plains
Systems Research 1992

KM

0   .5   1

LTER

.............' Soil Inventory Transect

B   Buried Soil Horizons

LTER   LTER Headquarters

Sand

Loamy Sand

Sandy Loam

Fine Sandy Loam

Loam

Sandy Clay Loam

3 4

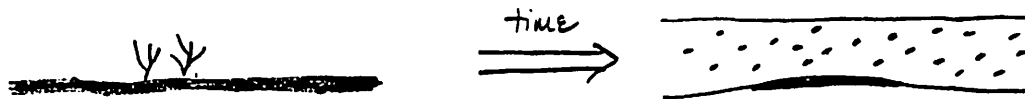CPER Paleosol Study - formation and persistence of paleosols

SCENARIO 1

depression in landscape; o.m. accumulation > than surrounding landscape; entire landscape buried

*CLIMATE: not cool & wet enough to produce substantive o.m. accumulation across entire landscape
*PALEOSOL: originally a depression

SCENARIO 2

entire landscape relatively level; o.m. accumulation relatively uniform; landscape differentially eroded; subsequent burial
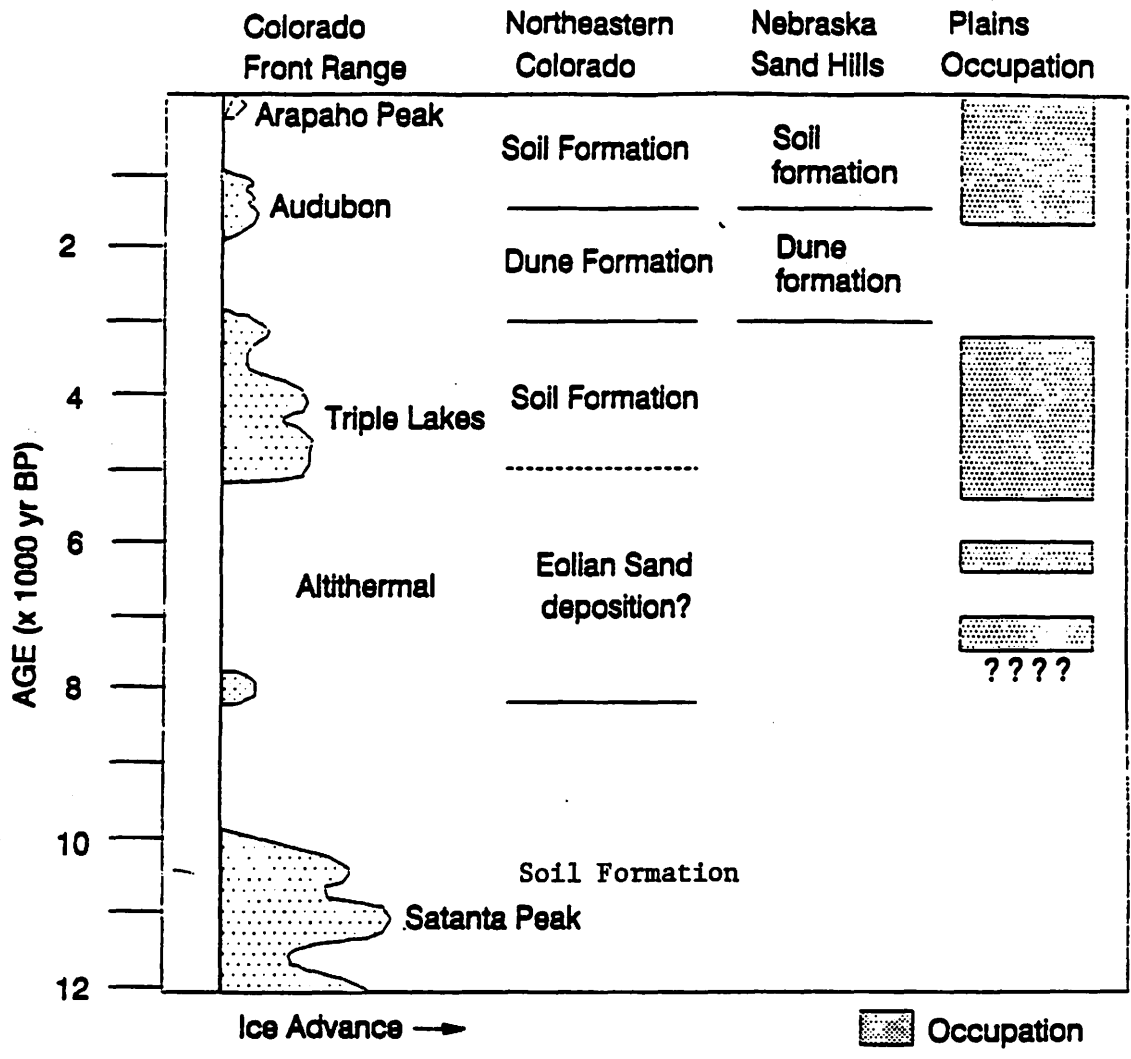
*CLIMATE: cool & wet enough to produce substantive o.m. accumulation across entire landscape
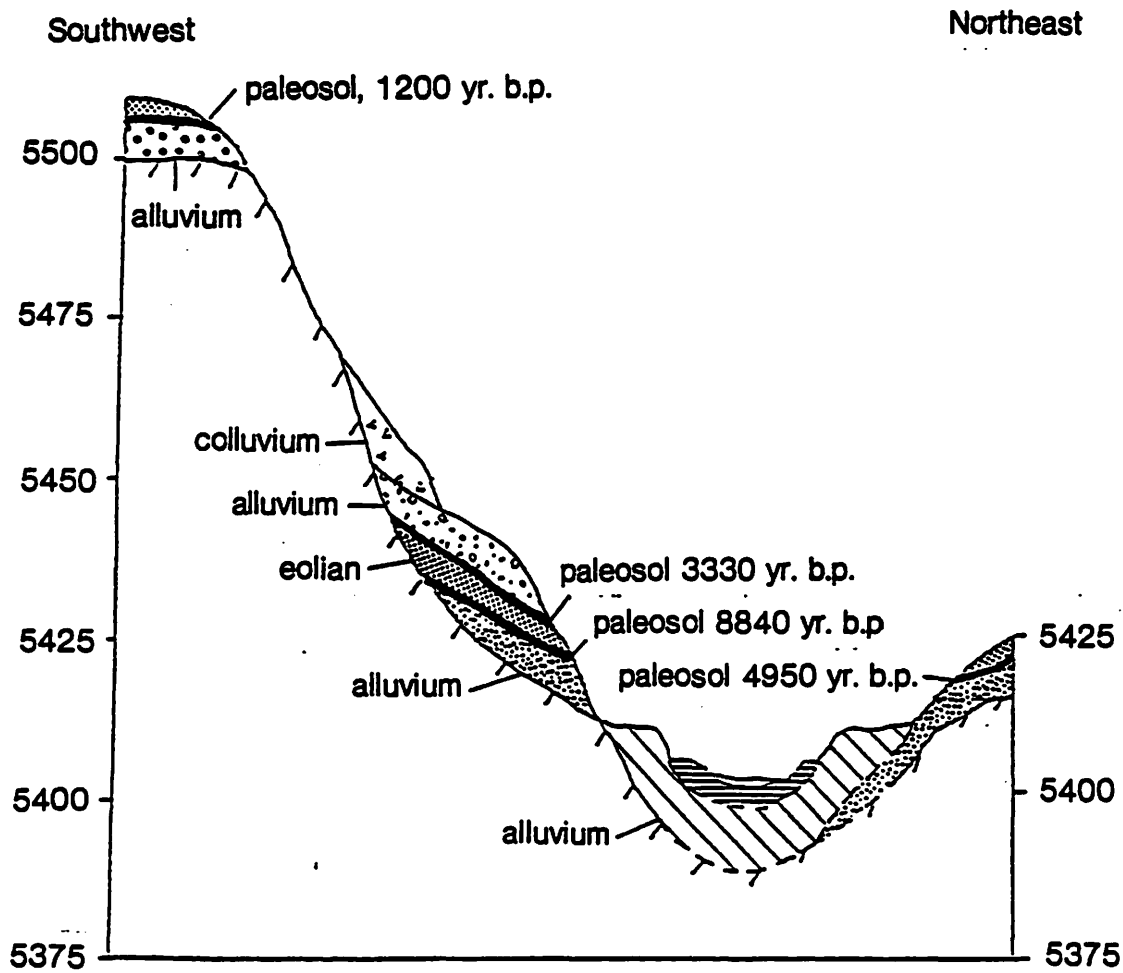*PALEOSOL: a "patch", stabilized by random patch of vegetation

SCENARIO 3
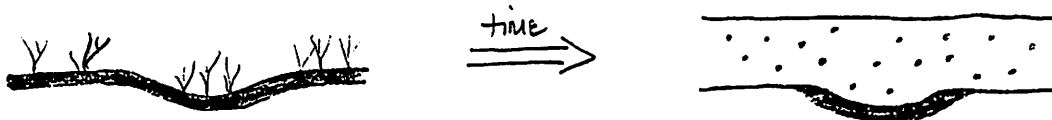
depression in landscape; o.m. accumulation substantive across landscape; landscape differentially eroded; subsequent burial

*CLIMATE: cool & wet enough to produce substantive o.m. accumulation across entire landscape
*PALEOSOL: originally a depression

Colorado Front Range | Northeastern Colorado | Nebraska Sand Hills | Plains Occupation

AGE (x 1000 yr BP)

Arapaho Peak

Audubon

Soil Formation

Soil formation

Dune Formation

Dune formation

Triple Lakes

Soil Formation

Altithermal

Eolian Sand deposition?

? ? ? ?

Soil Formation

Satanta Peak

2

4

6

8

10

12

Ice Advance →

Occupation

(After Muhs, 1985)

Southwest   Northeast

paleosol, 1200 yr. b.p.

5500

alluvium

5475

colluvium

5450
alluvium

eolian   paleosol 3330 yr. b.p.
                          paleosol 8840 yr. b.p   5425
5425   paleosol 4950 yr. b.p.

alluvium

5400   5400

alluvium

5375   5375

(After Davidson, 1988)

Soil water dynamics
Paul Hook & Bill Lauenroth

We have designated Water Dynamics as an additional core topic because we consider it to be fundamental for understanding the origin, structure and function, and sustainability of the shortgrass steppe. Questions about water dynamics focus on controls of temporal and spatial variation in soil water related to (1) variability of precipitation and (2) processes occurring at the scales of individual plants, patches representing typical shortgrass steppe, and hill slopes. Work includes studies of controls of soil water dynamics, analyses of long-term patterns of precipitation and soil water dynamics, and development of simulation models; this work has contributed to progress on other core topics and has been valuable for placing studies conducted at the CPER over relatively short periods in context.

Major long-term data sets:

>20 year record of soil water content and evapotranspiration estimated with neutron probe and weighing lysimeter

long-term (25 - >50 year) precipitation and temperature records

10 year record of soil water dynamics at sites representing variation in soil texture, parent material, and topographic positions on hill slopes.

Research has demonstrated:

ecological importance of small precipitation events (Sala and Lauenroth 1982 & 1985)

effects of soil texture on depth distribution of water and partitioning of water between grasses and shrubs (Liang et al. 1989)

effects of spatial variation in soil properties on runoff and run-on on hill slopes (DeCoursey, unpublished)

consistent importance of soil texture to soil water dynamics versus occasional importance of runoff and snow redistribution (10 year neutron probe record)

Key recent results

Individual plant scale patterns of soil water

Hook, P.B., and W.K. Lauenroth. Soil water dynamics in Bouteloua gracilis neighborhoods and gaps in shortgrass steppe. In preparation.

We used time domain reflectometry (TDR) to characterize small-scale spatial patterns of soil water. This allowed us to address questions about the spatial scale of water use by individual Bouteloua gracilis plants and the size of small-scale disturbance necessary to enhance water availability. Soil water content at 4 depths was monitored under plants, 5-30 cm from plants in interspaces and clearings around ant nests, and in root-free soil inside metal tubes.
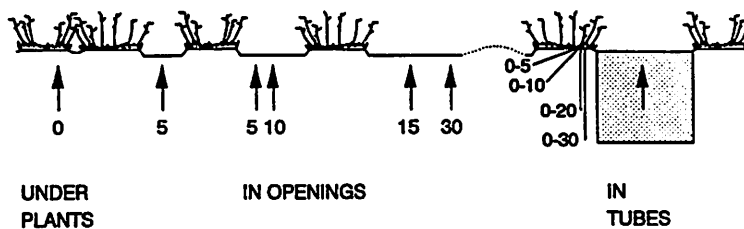
Time domain reflectometry TDR resolved fine-scale spatial and temporal patterns very effectively. Drying rates differed with depth and distance from plants. This study also demonstrated the feasibility of using TDR to resolve soil water dynamics in thin surface layers; near-surface water is critical to ecological dynamics but can not be estimated accurately with the neutron probe. We intend to use TDR in our long-term monitoring program.
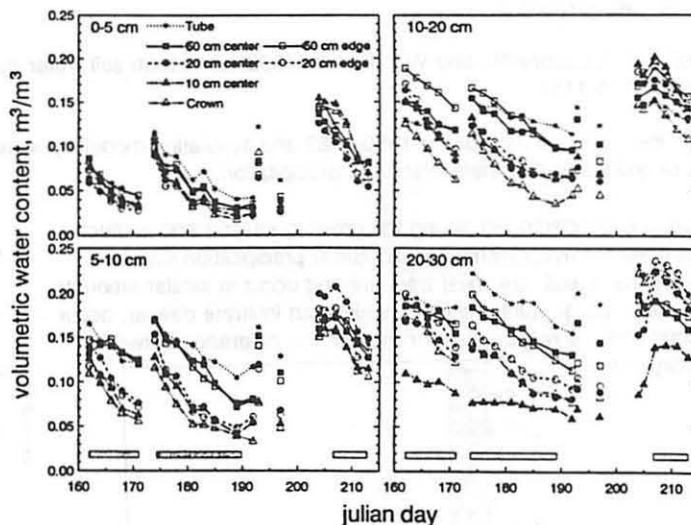

Water was used rapidly in the top 20 cm of soil and within about 10 cm horizontally from plants. The spatial scale of soil water heterogeneity is consistent with the scale of gap dynamics. This result supports one of the basic assumptions of the individual-plant-based models that we are using in analyses of vegetation and ecosystem dynamics.

Soil water use in *Bouteloua gracilis* neighborhoods
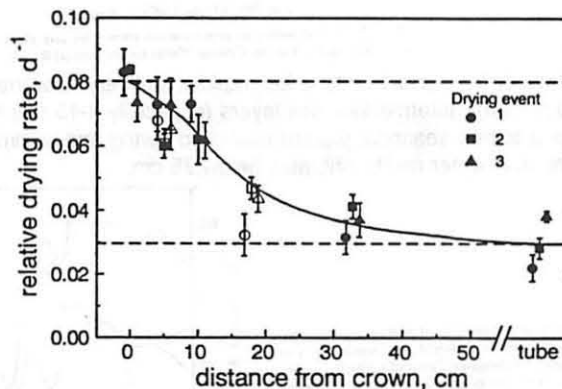
The zone of rapid water use by a *Bouteloua gracilis* plant is a small fraction of the total volume of the root system. Resource gaps are not root gaps.

spatial pattern of drying by transpiration
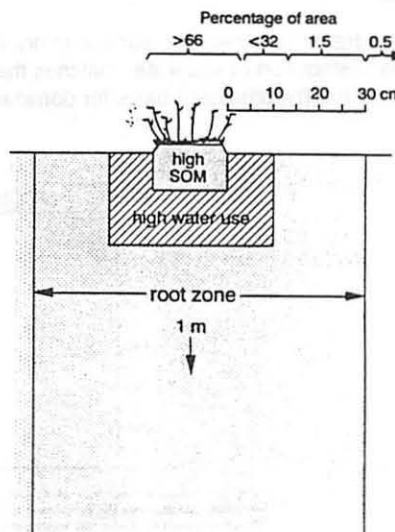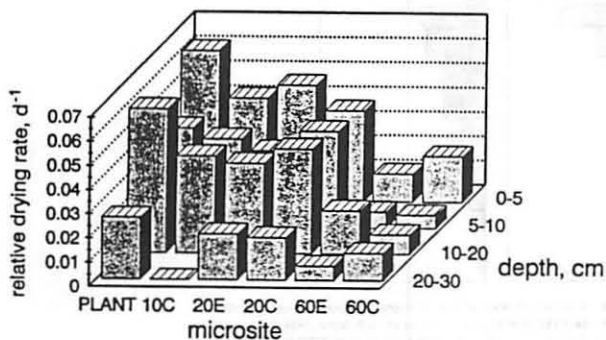
<u>Long-term water dynamics</u>

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

Meteorological records for 1950-1983 and simulation modelling were used to estimate long-term
patterns of soil water and their relation to precipitation.

Precipitation is concentrated during the growing season and is much
less than potential evapotranspiration. Small precipitation events,
which wet surface soil, are most frequent and occur in similar amounts
in most years. Large rainfall events, which can infiltrate deeper, occur
infrequently and are responsible for most of the difference between
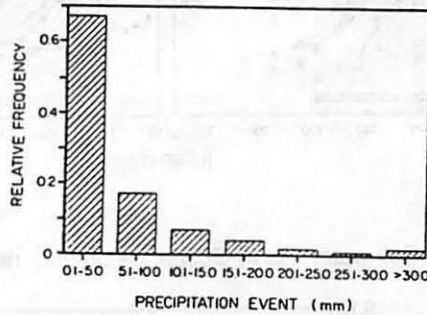wet and dry years.

Fig. 2. Distribution of precipitation events by size class
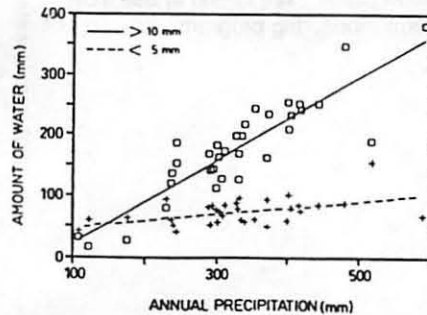from 1950 to 1983 at the Central Plains Experimental Range.

Fig. 3. Amount of water per year received in rainfall events
≥10 mm (□) and ≤5 mm (+) calculated for 33 yr from 1950
to 1983. Least squares regression shows that the amount of
water received in large rainfall events (≥10 mm, ——, L)
sharply increased as annual precipitation (PPT) increased (L
$= -4.7 + 0.69 \cdot$ PPT, $r = 0.88$, $P \leq .05$). In contrast, the
amount of water received in small rainfall events (S, ---)
increased very slowly ($S = 3.7 + 0.11 \cdot$ PPT, $r = 0.51$, $P \leq$
.05).

Because water from small rains is lost rapidly, soil very near the surface (0-2.5 cm) is usually dry and shows no
seasonal pattern. Intermediate soil layers (especially 4-15 cm) have highest soil water availability over the year
and show a strong seasonal pattern related to spring and summer precipitation. Recharge below 15 cm is
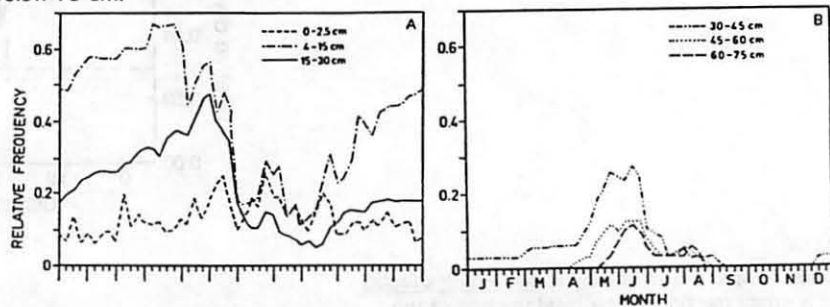infrequent, and water rarely infiltrates below 75 cm.

Fig. 5. Frequency of occurrence of soil water potential
> -1.0 MPa through time for different soil depth layers in
the shortgrass steppe of northcentral Colorado. The frequency
was calculated as the number of days in each calendar week
that had soil water potential > -1.0 MPa, out of 231 d (33
yr·7 d/wk). Soil water potential between 0 and -1.0 MPa
indicates that water is available for plants. (A) for upper soil
layers and (B) for lower soil layers.

Soil water is concentrated very near the surface in dry years and percolates up to 1.3 m deep in wet years.
The shallow modal distribution of soil water matches the distributions of roots of the dominant grass, <u>B. gracilis</u>,
providing support for the hypothesized basis for dominance of <u>B. gracilis</u> and its coexistence with other species.
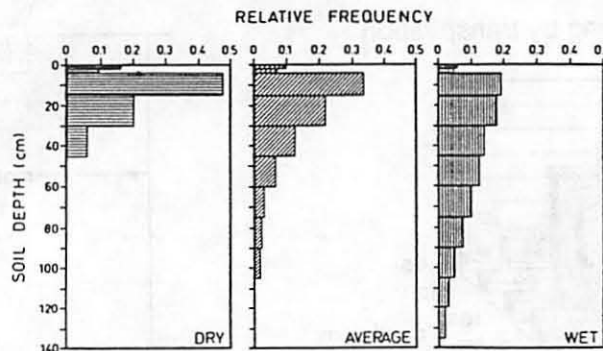

Fig. 8. Relative frequency of available water, as a function of depth in soils of the shortgrass steppe of northcentral
Colorado, calculated as the proportion of the total number of wet days (all layers) that occurred in each layer. Wet days were
defined as those that had a soil water potential > -1.0 MPa. Results from the eight driest and eight wettest years are graphed
separately from the remaining 17 yr.

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Analysis of lysimeter and micrometeorological data.

Micloclimatic data commonly used to estimate water and energy balance were compared with weighing lysimeter data, which provided a direct estimate of water balance. This work contributes to development of simple methods for estimating energy balance, evapotranspiration, and soil water balance in dry region ecosystems with high proportions of bare soil. Observations suggest that dew formation may be common during the growing season, potentially sustaining biological activity in surface soil between rains.

The proportion of energy from net radiation (Rn) that is conducted into the soil (G) varied seasonally with changes leaf area.
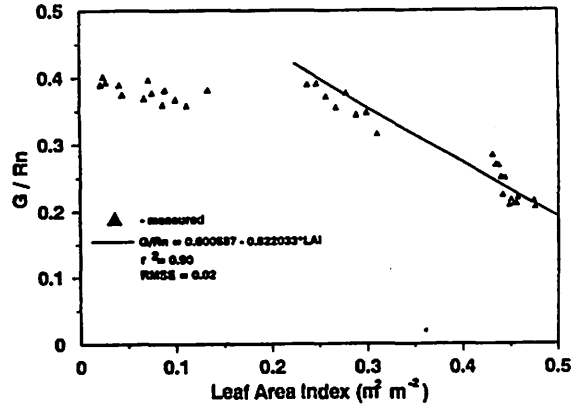

The partitioning of energy (Rn, net radiation) between sensible heat flux (H) and evapotranspiration was directly related to the mid-day difference between soil surface and air temperatures.

Table 5. Correlation* between sensible heat flux (H), Bowen ratio (β) and surface thermal gradients

Variables**	β	$T_{can} - T_{air}$	$T_{sol} - T_{air}$
H	0.96	0.69	0.94
β		0.66	0.58

* correlations are significant at P ≤ 0.01.
** T_{can} - canopy temperature; T_{sol} - surface soil temperature; T_{air} - air temperature
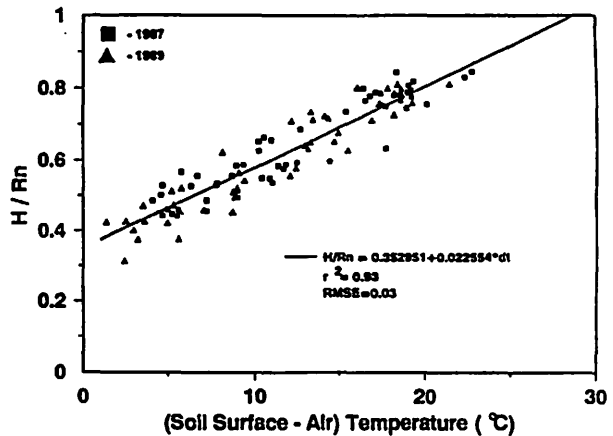

Evapotranspiration estimated using this relationship compared favorably with lysimeter data. This approach may provide a basis for estimating regional patterns of evapotranspiration from remotely sensed data and standard meteorological station data or for estimating water balance in site specific research where weighing lysimeters are not present.
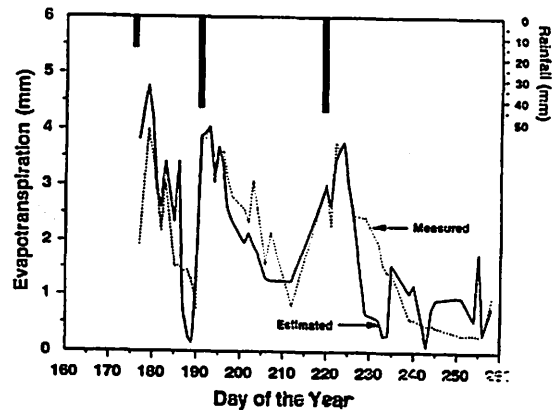
DISTURBANCES AND PLANT POPULATIONS

Presenter: Debra Coffin
September 8, 1993

Most successional studies in the shortgrass steppe have focused on recovery following large-scale disturbances, and in particular on abandoned agricultural fields. An important conclusion from these studies is that the dominant plant species, Bouteloua gracilis, either fails to recover or recovers very slowly after disturbance. This inability to recover has primarily been attributed to constraints on the population dynamics of B. gracilis (ie., climatic constraints on seed germination and seedling establishment, and low tillering rates). Since 1984, we have been studying disturbances at the CPER in order to evaluate the apparent contradiction between the results from previous large-scale disturbance studies and the continued dominance of B. gracilis through time and space in the presence of a number of types of disturbances that affect shortgrass communities (Fig. 1). Our disturbance work and plant population studies are tightly connected in that we are focusing on both the recovery process for a number of types of disturbances as well as on the plant population processes that are important in recovery. Because of the overwhelming dominance by B. gracilis in shortgrass communities (80-90% of aboveground biomass is this species), our studies focus on the population dynamics and recovery dynamics after disturbance of B. gracilis.
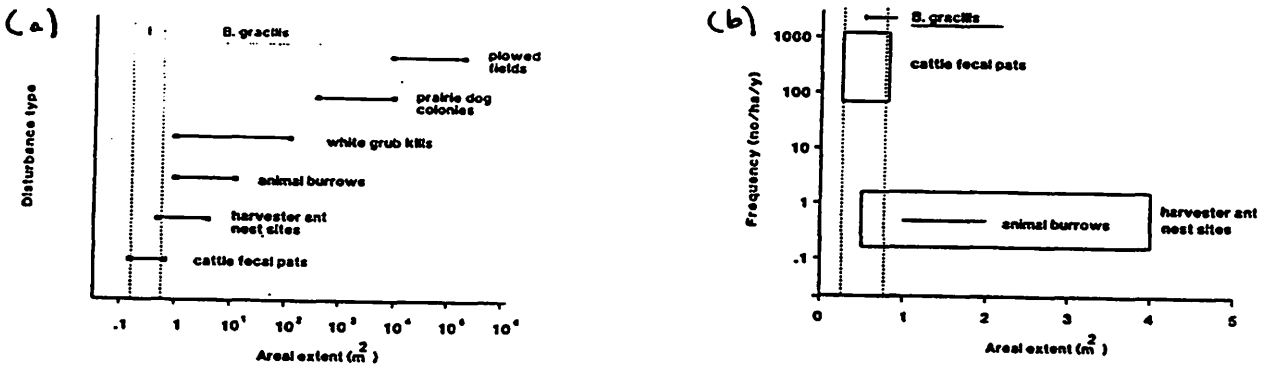
. Disturbance regime of shortgrass communities indicating 6 major types of disturbances, ranging in size from 50 cm² to 100 ha (shown on ln scale). Size of B. gracilis plants also shown.

Range in size and frequency of occurrence for the three smallest, most frequently-occurring disturbances in shortgrass communities at the CPER (from Coffin and Lauenroth 1988).

Fig. 1. Disturbance regime of shortgrass steppe ecosystems (from Coffin and Lauenroth 1988).

Our approach is to use a gap dynamics conceptualization of shortgrass communities that focuses on interactions among individual plants and their environment, including resource availability and effects of disturbance. This view of plant communities has been used extensively in forests where the death or removal of individual trees results in a gap in the canopy and an increase in the availability of light resources for successional dynamics by other plants. Because of the importance of belowground processes in semiarid grasslands, our application of a gap dynamics conceptualization to shortgrass communities focuses on gaps in the belowground resource space, or "root" gaps. We hypothesized that the important gaps for plant community structure are those associated with death of individual B. gracilis plants. For example, small, patchy disturbances may kill one to tens of plants whereas large disturbances may kill hundreds or thousands of plants. In both examples, the important processes during succession are occurring at the scale of individual B. gracilis plants, and the landscape is viewed as a shifting mosaic of patches, each undergoing its own successional dynamics through time.

We are using a combination of field studies, simulation analyses, and geographic information system (GIS) analyses to evaluate the importance of disturbances to shortgrass communities in order to resolve the apparent contradiction between previous successional studies and current observations of B. gracilis dominance. The simulation analyses and GIS will be discussed during the presentations on Thursday, September 9.

I. Plant population studies

<u>Recruitment Studies</u>

Because tillering rates of <u>B. gracilis</u> are very slow, the inability of this species to recover after disturbance has primarily been attributed to constraints associated with the recruitment of seedlings. We have conducted a number of studies to evaluate these constraints on the recruitment process by <u>B. gracilis</u>.

1. Our initial attempts focused on the availability of seeds stored in the soil seed bank. Seeds were germinated from soil samples collected at a coarse- and a fine-textured site for eight dates over a two-year period in 1984 and 1985. Most seeds in the seed bank were annuals; for other species, including <u>B. gracilis</u>, storage of seeds was found to be low and variable in time and space (Coffin and Lauenroth 1989b). These results led us to conduct studies on processes associated with inputs (ie., seed production) and losses (ie., seed germination, seedling establishment and growth) of seeds in an attempt to better understand the recruitment process.

2. We initiated a study in 1989 to evaluate variability in space and time in the production of <u>B. gracilis</u> seeds. Ten locations were selected to represent soil texture and grazing intensity at the CPER. Data on a number of measures of reproductive effort have been collected annually for 96 <u>B. gracilis</u> plants at each location. Results from the first year of the study indicate that seed production and other indicators of reproductive effort by <u>B. gracilis</u> varied spatially both with soil texture and grazing by cattle (Fig. 2; Coffin and Lauenroth 1993). Grazing was important in mediating the effects of soil texture. Locations protected from grazing had significant effects of soil texture with the largest number of viable seeds produced on the locations with the coarsest-textured soil, and the smallest number of seeds produced on the locations with the finest-textured soil. This relationship is consistent with the inverse-texture hypothesis where higher aboveground production is expected for semiarid sites on coarse- compared to fine-textured soils. The uniformity in reproductive effort among locations grazed by cattle has been observed for other plant community characteristics in semiarid grasslands. Variability in time in seed production has also been observed from 1989 to 1992. <u>B. gracilis</u> plants at these sites will continue to be sampled annually for reproductive effort.
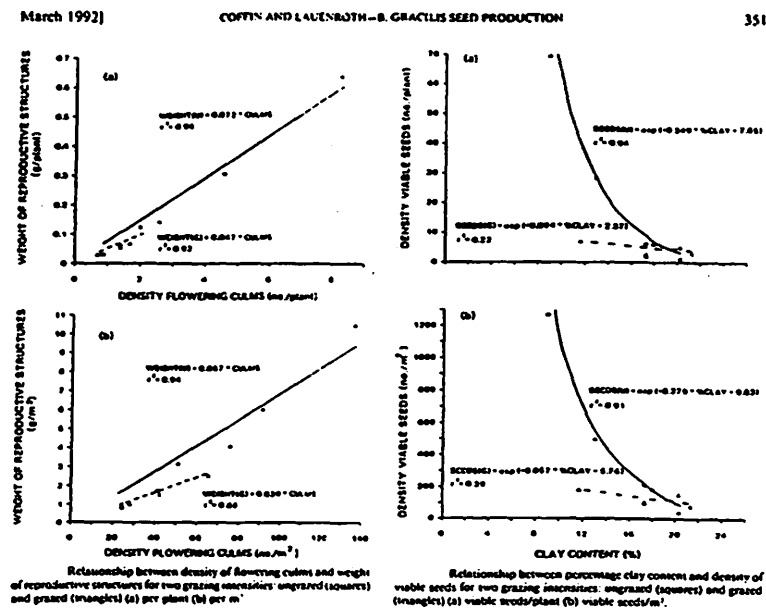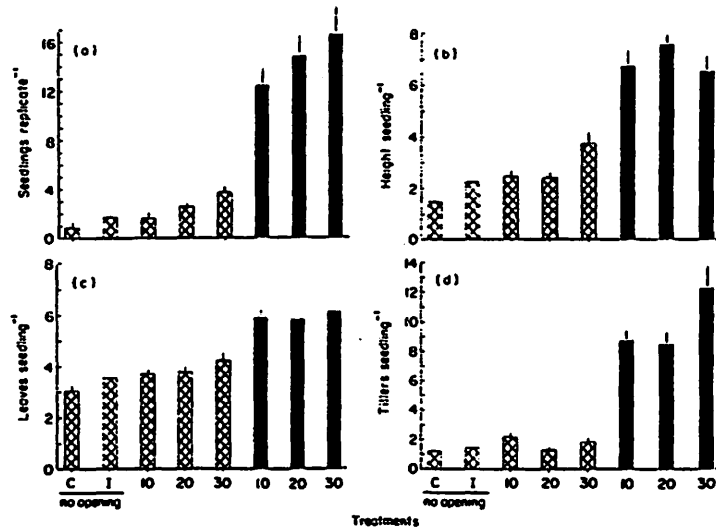

Fig. 2. Reproductive effort of <u>B. gracilis</u> for 10 sites differing in soil texture and grazing intensity.

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3. Intraspecific effects of adult plants on the germination and establishment of B. gracilis seedlings was studied in 1990 (Fig. 3; Aguilera and Lauenroth 1993b). B. gracilis seeds were added to openings of different sizes (0, 10, 20, and 30-cm-diameter) in adult neighborhoods dominated by B. gracilis plants. Competition from adults was excluded by using tubes for half of the 10 to 30-cm-diameter openings. Emergence of seedlings 20 days after seeding, height and number of leaves per seedling 70 days after seeding, and the number of tillers per seedling were higher for seedlings growing without competition from neighboring adults than for seedlings growing in unprotected openings. We also studied effects of neighborhood interactions among individual B. gracilis plants through an analysis of space partitioning (Aguilera and Lauenroth 1993a).

Effect of opening size and neighbour exclusion on (a) number of seedlings per replicate at emergence (20 days from seeding), (b) height of seedlings at end of watering (70 days from seeding), (c) number of leaves at end of watering (70 days from seeding) and (d) number of tillers at end of growing season (114 days from seeding) of seedlings of *Bouteloua gracilis*. Seeding was on 8 June 1990. Bars represent treatment means ± 1 SE: (□) neighbours present; (■) neighbours excluded. For neighbours present: 'no opening' included centre (C) and interspace (I); and openings 10cm (10), 20cm (20) and 30cm (30) in diameter. For neighbours excluded by tubes: opening diameters were 10cm (10), 20cm (20) and 30cm (30).

Fig. 3. Effect of opening size and neighbor exclusion on the germination and establishment of B. gracilis seedlings.

Mortality Studies

4. Cattle fecal pats are the most frequently-occurring disturbance with the potential to kill B. gracilis plants (Fig. 1b). The size distribution of fecal pats overlaps the size distribution of B. gracilis plants (Fig. 1a); therefore, a pat may or may not cover and kill an entire plant each time it is deposited. Similarly, western harvester ants and digging by small animals are sufficiently large to kill B. gracilis plants by removing entire plants in most cases, and removing parts of some plants in other cases. Because little is known about the physiological integration of B. gracilis tillers within a plant, we conducted a study in 1991 and 1992 to determine how much of a plant needed to be covered or removed before mortality of the entire plant resulted (Fair in prep). Our results indicate that even if 90% of the tillers of a B. gracilis plant are covered or removed, the remaining tillers survive (Fig. 4). The removal of tillers was a more severe disturbance than covering or shading tillers since tiller number did not change one year after removal compared to significant increases in tillers one year after covering or shading. The trends through time were the same for all three proportion classes of the plant removed or covered. Although the study was conducted at three sites differing in soil texture (silt loam, sandy loam, and clay loam) and under two grazing regimes (moderately grazed and protected from grazing), these two factors did not have significant effects on the results.
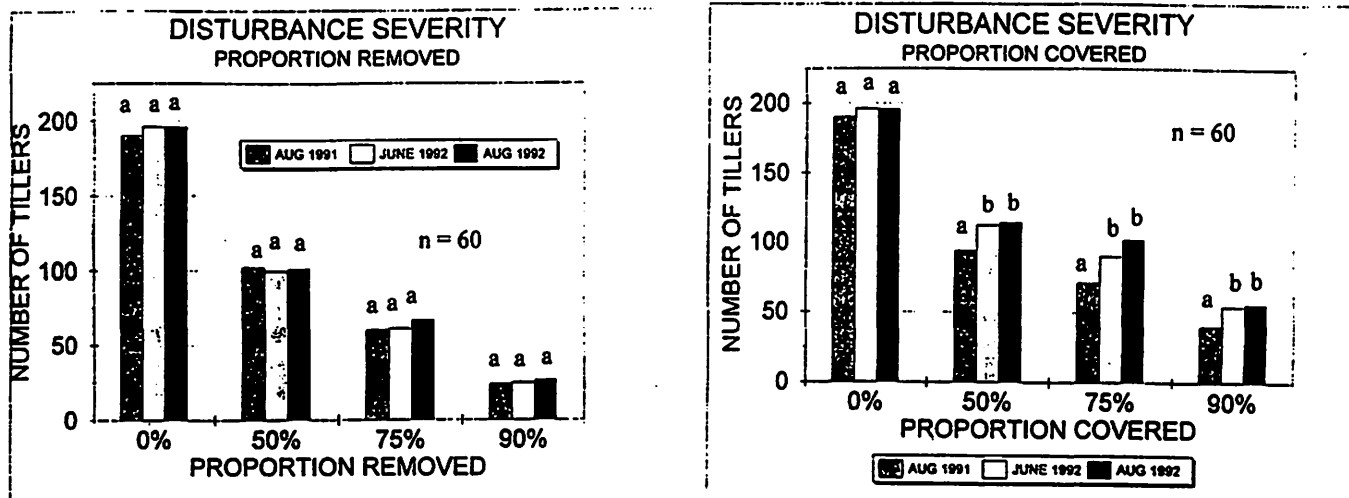
Fig. 4. Number of tillers of B. gracilis on areas where proportions of plants were killed either by removing or covering tillers.

II. Plant recovery and disturbance studies

1. Our initial studies of recovery considered small, patch-producing disturbances. We are evaluating plant recovery on two types of naturally-occurring disturbances (nest sites of western harvester ants and burrows from small mammals) and on artificially-produced plots (plant material was removed to 10-cm-depth) of three sizes (50, 100, 150 cm-diameter), produced at four different times (September, 1984; March, May, and July, 1985) at two locations differing in soil texture (sandy loam, clay to clay loam). Annual data collection for each plot includes density and cover by species. Statistical analyses for data collected one year after recolonization began indicate that functional group composition on the two naturally-occurring disturbances were similar, and were different from composition on artificially-produced plots (Coffin and Lauenroth 1989a; 1990). High density and cover of perennial grasses on nest sites and burrows compared to high density and cover of annuals on the artificially-produced plots suggest a faster recovery by shortgrasses on the naturally-occurring disturbances compared to the other plots. Because B. gracilis seedlings have been observed on plots produced artificially, we can confirm that seedling establishment events do occur naturally and may be an important source of propagules in the recovery of B. gracilis. Long-term monitoring of plots is necessary to evaluate the time required for B. gracilis to dominate each disturbed area.

2. We are also evaluating the importance of cattle fecal pats, the most frequently-occurring disturbance in shortgrass communities. In semiarid regions, observations indicate that pats typically dry out and become very hard shortly after deposition. There are a number of consequences of this drying-out process: (1) there is a delay before plant recovery can begin with little or no additional nitrogen available to plants at that time, and (2) the cumulative effect of pats on shortgrass communities is related to the length of time required for pat decomposition. We are evaluating the time required for decomposition of pats by following marked pats through time for sites differing in topographic position and grazing intensity. Most pats (90%) decompose within 2 years after deposition; slow decomposition occurs after that time (Fig. 5a). Pat decomposition rate is not related to topography or grazing intensity. We also have preliminary data on the recovery of B. gracilis and a codominant on some sites, the perennial C_4 grass Buchloe dactyloides, on areas killed by pats. For communities dominated by these two species, B. gracilis and total cover increased through time whereas B. dactyloides cover decreased (Fig. 5b). These pats and areas killed by pats are permanently marked, and are being monitored annually.

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(a)

(b)
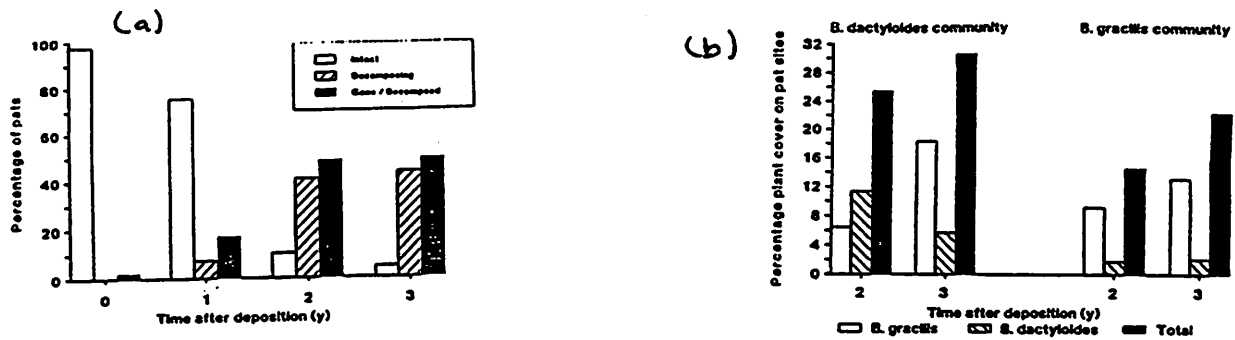
Preliminary data of fecal pat decomposition through time for three types of pats (intact, decomposing, gone or decomposed). Results are average of 112 pats from five sites at the CPER (two B. dactyloides and three B. gracilis-dominated communities). Study began in 1987 (year 0). Most (90%) pats decomposed within 2 years after deposition; slow decomposition occurred after that time.

Preliminary data for recovery of B. gracilis, B. dactyloides, and total cover on sites disturbed by fecal pats in two community types (B. dactyloides- and B. gracilis-dominated) at the CPER. Pats of variable sizes (5 to 40 cm diameter) were deposited in Year 0 (1987). Plant recovery is shown for Year 2 (1989) and 3 (1990). Note increase in B. gracilis and total cover through time, and decrease in B. dactyloides cover.

Fig. 5. Decomposition of fecal pats and recovery of B. gracilis and B. dactyloides on areas killed by pats.

3. We recently collaborated with the USDA-ARS on a study of successional dynamics on areas killed by white grubs. Larvae of June beetles (ie., white grubs) feed on roots of perennial grasses in a patchy manner that results in incomplete mortality of tillers and plants. This study was initiated by Dr. Bill Laycock, currently of the Department of Range Management at the University of Wyoming; the CPER-LTER took over responsibility for data collection and analysis in 1990. At the start of the study in 1977, 32 areas that had recently been killed by white grubs were selected for long-term monitoring. The objective of the study was to evaluate the successional dynamics on areas killed by grubs and to determine the effects of grazing intensity on plant recovery. Therefore, 16 of the areas consisted of 4 sites at the CPER where 2 patches were located within long-term grazing exclosures and two patches were located in the adjacent grazed pasture. A series of permanent transects and permanent 30 x 30 cm plots was designed to allow repeated sampling of each patch through time. The transects and plots were located both within each patch of disturbed vegetation as well as in the surrounding undisturbed area. Cover of perennials and density of annuals have been sampled five times since 1977 (1978, 1979, 1980, 1982, and 1990). In addition, cover of dead B. gracilis crowns and litter, and density of B. gracilis tillers in a 10x10cm subplot have also been estimated for each plot.

Disturbed areas (patches) had small cover of B. gracilis that increased through time from 1977 to 1982 (Coffin et al. in prep). Other perennial grasses and perennial forbs were important components of the vegetation on patches (Fig. 6). Undisturbed areas were typical of shortgrass communities in being dominated by B. gracilis. The decrease in total cover from 1982 to 1990 for both the undisturbed and disturbed patches is likely the result of a series of years with average and below-average precipitation.

Cover of B. gracilis through time was not affected by grazing; however the patchiness in survival of B. gracilis tillers was important to recovery dynamics (Fig. 7a). Another measure of recovery, the cover on patches as a proportion of the undisturbed cover, indicates the recovery of B. gracilis through time was affected by grazing for only two of the six sample years (Fig. 7b). B. gracilis had recovered to 40 to 60% of the undisturbed cover 13 years after recovery began.
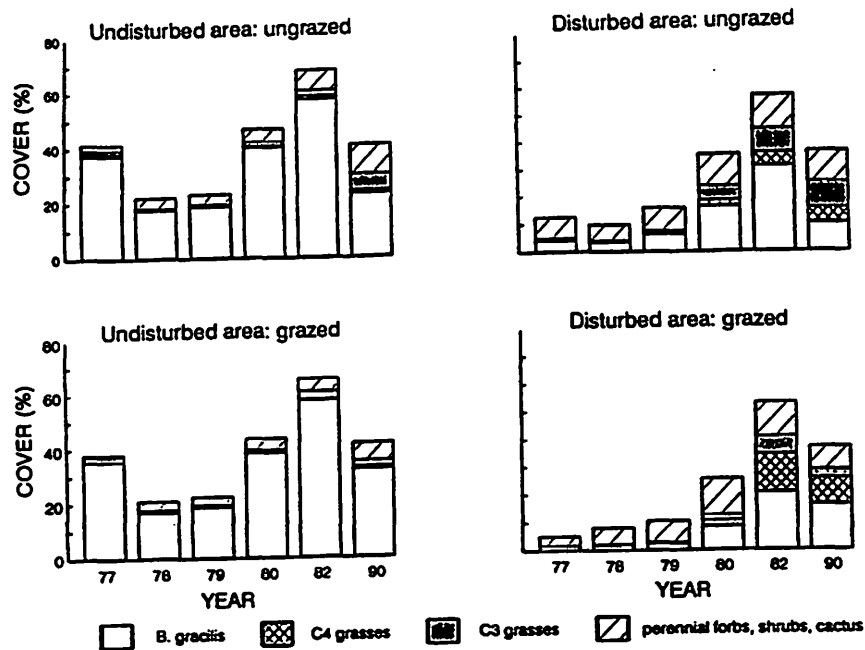
Fig. 6. Basal cover of <u>B. gracilis</u> and three functional groups on patches killed by white grubs and the surrounding undisturbed vegetation for two grazing treatments.
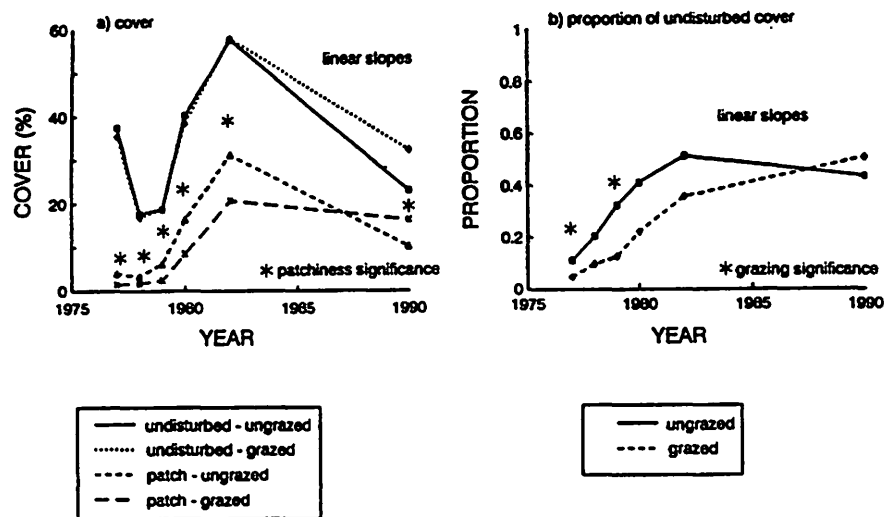

Fig. 7. Basal cover of <u>B. gracilis</u> through time on patches killed by white grubs and undisturbed vegetation for two grazing treatments.

4. We are also conducting field studies of the largest type of disturbance to affect shortgrass communities, the cultivation and subsequent abandonment of agricultural fields. We are monitoring the recovery of shortgrass steppe ecosystems on old fields abandoned for 53 years at the CPER and in the adjacent Pawnee National Grasslands (PNG). We used aerial photos from 1937 to locate thirteen fields with similar abandonment dates that represented the soils and climatic gradients of precipitation and temperature in the CPER and PNG. Spatially-explicit sampling of plant cover and density by species, and of soils for

carbon, nitrogen, microbial biomass, and texture were conducted in 1990 to account for patterns within each field. This represented a large field sampling program that was aided by volunteers from the Earthwatch Foundation. These fields were permanently marked and will be resampled in the future.

Cover or density and distance from the edge of a field were described by either a negative exponential or a linear relationship (Coffin et al. in prep). B. gracilis was found on all fields sampled, and dominated the cover on two fields. Four types of fields were distinguishable based on the relationship between B. gracilis cover and distance: (1) fields with uniformly high cover (Fig. 8c), (2) fields with a decrease in cover with distance and cover dominated by B. gracilis (Fig. 8a), (3) fields with a decrease in cover of B. gracilis and cover dominated by B. dactyloides (Fig. 8b), and (4) fields with uniformly low cover of B. gracilis (Fig. 8c).
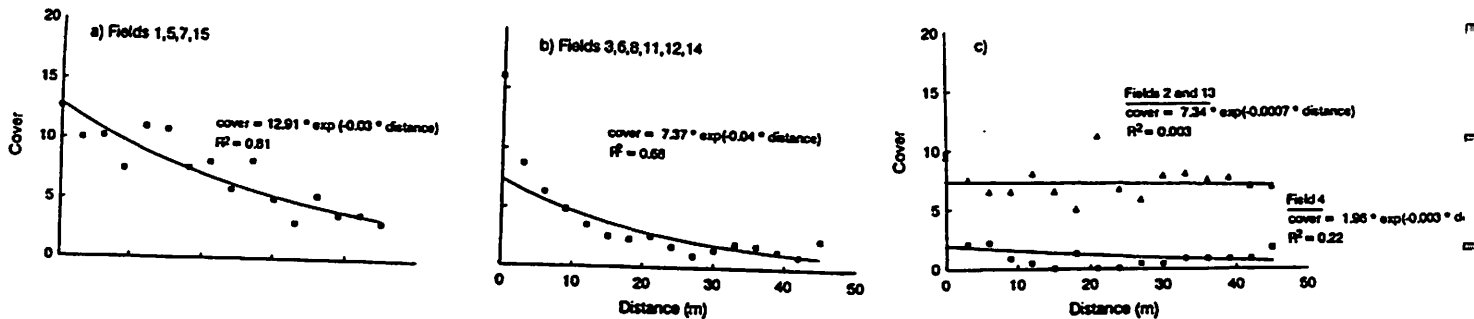

Fig. 8. Basal cover of B. gracilis by distance from the edge of a field, the major source of propagules at the time of abandonment. Four types of fields are distinguishable based upon the relationship between cover and distance.

We compared our results with predictions from two successional models for shortgrass communities. For most fields (9 of 13), relative shortgrass cover did not fit the predictions of the traditional Clementsian model of succession communities (Fig. 9a). In addition, most fields did not fit a Clementsian model modified for northeastern Colorado where long-term dominance by the perennial bunchgrass, Aristida longiseta, is suggested to result in a disclimax (Fig. 9). The contrast between our results and the traditional and modified models of shortgrass community response to disturbance suggests an alternative role of disturbance in these systems with a focus on the relationship between disturbance characteristics, recovery rate, and patterns in recovery.
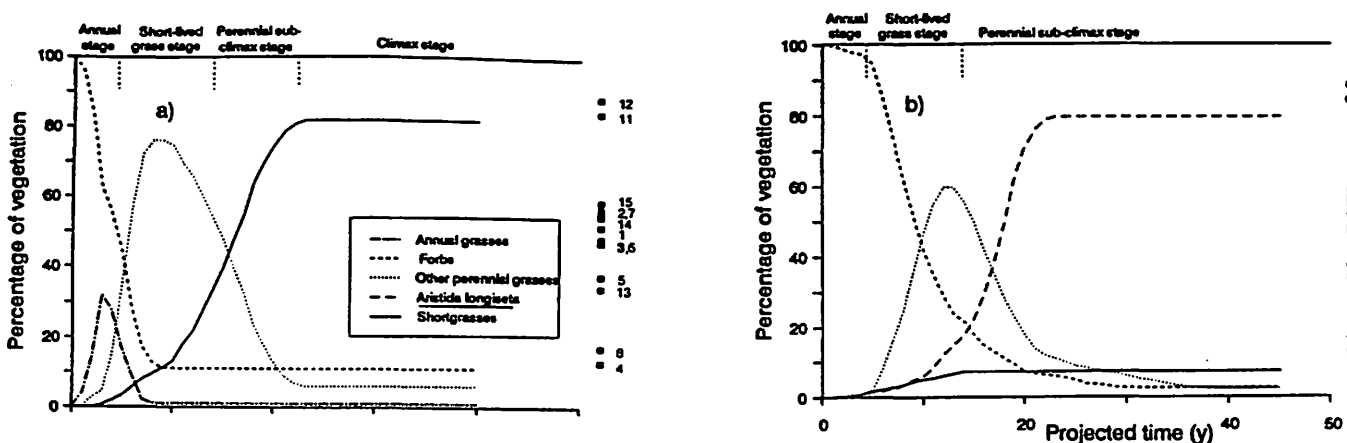

Fig. 9. Comparison of shortgrass cover from 13 fields sampled at CPER and PNG with predictions from (a) traditional Clementsian model and (b) Clementsian model modified for eastern Colorado.

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Our results from the soil samples indicate that soil organic matter, silt content, microbial biomass, potentially mineralizable N, and potentially respirable C were significantly lower on cultivated fields than native, unplowed fields (Burke et al. in prep). Although abandoned fields had significantly lower soil organic matter and silt content than unplowed fields, they were not significantly different with respect to microbial biomass or potentially mineralizable N or potentially respirable C. In addition, we found the characteristic small-scale heterogeneity of the shortgrass steppe associated with individual B. gracilis plant had recovered on abandoned fields (Fig. 10). Under-plant locations had an average of 200 g m^{-1} more C than between-plant locations.
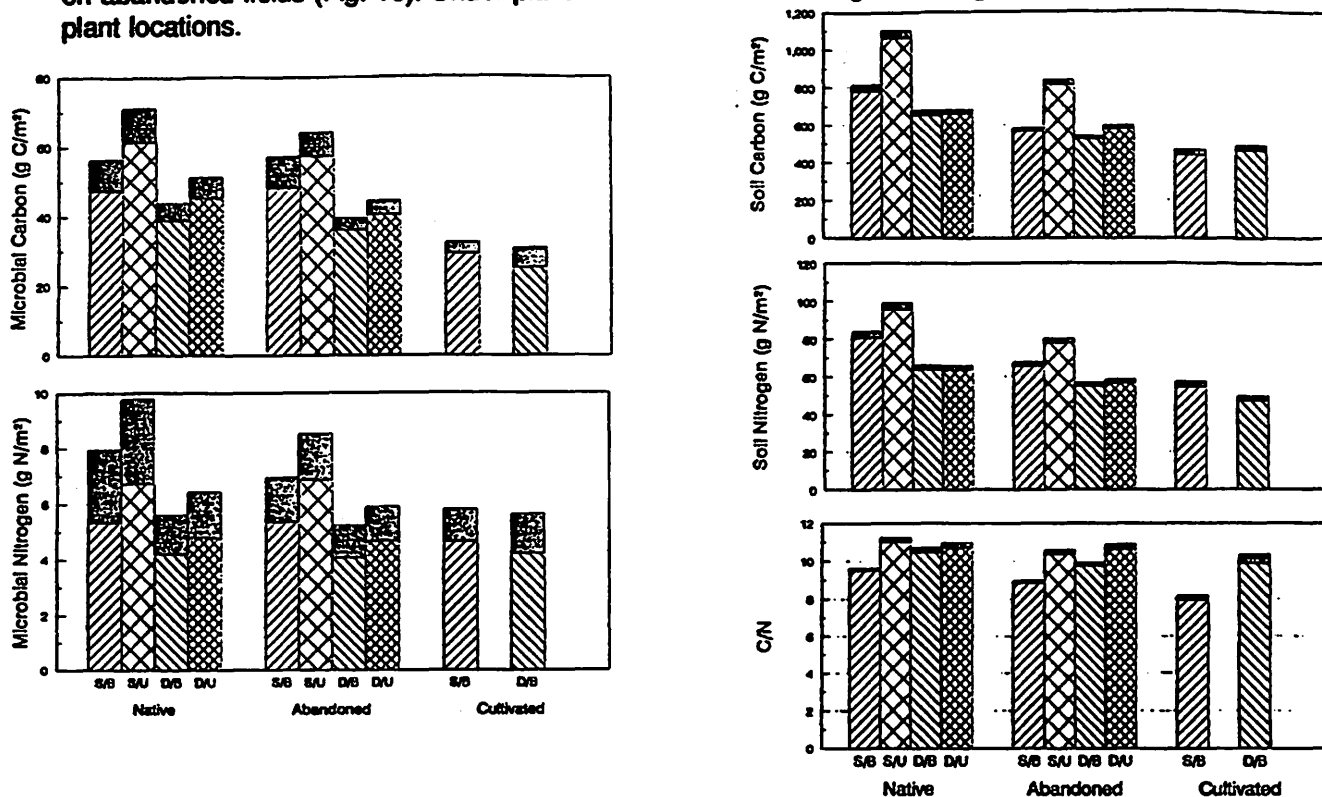

Fig. 10. (a) Microbial biomass C and N and (b) carbon, nitrogen,and carbon:nitrogen ratios from under and between individual B. gracilis plants in soils from 12 native and abandoned fields and 5 cultivated fields for two depths (S=shallow, 0-10cm; D=deep, 10-20cm) and two microsites (U= under and B=between plants).

5. We are also conducting an intensive study of recovery of vegetation and soils on old fields at the CPER. Approximately 25-30% of the CPER was plowed and abandoned prior to government acquisition of the land in 1937. Although these old fields have similar climatic characteristics, they vary in other factors such as soil texture and whether or not they have been grazed by cattle. In 1991, we started this study by sampling vegetation and soils on old fields of similar soil texture and contained a long-term cattle exclosure on part of the old field. Therefore, we were able to examine the effects of grazing or protection from grazing on the recovery of vegetation and soils for two old fields that met these criteria. Preliminary results indicate that significant differences in vegetative cover do not occur as a result of grazing of old fields after 50+ years of recovery. These results suggest that recovery of vegetation can occur within 50 years, in contrast to predictions of successional models described above. We expect to develop a sampling program to evaluate the recovery of vegetation and soils on most, if not all, old fields at the CPER sometime during the next five years.

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# SOIL-ATMOSPHERE EXCHANGE OF METHANE AND NITROUS OXIDE IN THE COLORADO SHORT GRASS STEPPE

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| Site		Research Question	Measurement Period	Mean Annual Gas Flux Rate	
				CH$_4$-C Uptake	N$_2$O-N Efflux
				μg m^{-2} hr^{-1}	
Pasture					
	Native	Site variability	5/90-Present	34	1.1
	+New N	New N effect	5/90-Present	21	3.3
	New plow	New plow effect	7/92-Present	19	17
Sand catena					
	Midslope	Site variability	3/90-Present	33	1.1
	+ N	Old N effect	3/90-Present	23	3.3
	Swale	Site variability	3/90-Present	19	1.1
	+ N	Old N effect	3/90-Present	21	2.3
Clay catena					
	Top	Site variability and soil texture	9/91-Present	33	1.1
	Midslope		9/91-Present	32	1.1
	Swale		9/91-Present	19	1.1
Old field					
	Native	Site variability	4/92-7/93	34	2.3
	Abandoned 1939	Old plow effect	4/92-7/93	30	4.6
Land Use 1					
	CRP	Recovery from tillage	3/92-Present	24	7.8
	Wheat-fallow A	Cultivation + sludge	3/92-Present	21	3.0
	Wheat-fallow B	Cultivation + sludge	8/92-Present	17	15
Land Use 2					
	Abandoned 1939	Old plow effect	6/90-2/92	11	1.1
	Wheat-fallow A	Cultivation	6/90-2/92	3.4	2.3
	Wheat-fallow B	Cultivation	6/90-2/92	5.7	2.3
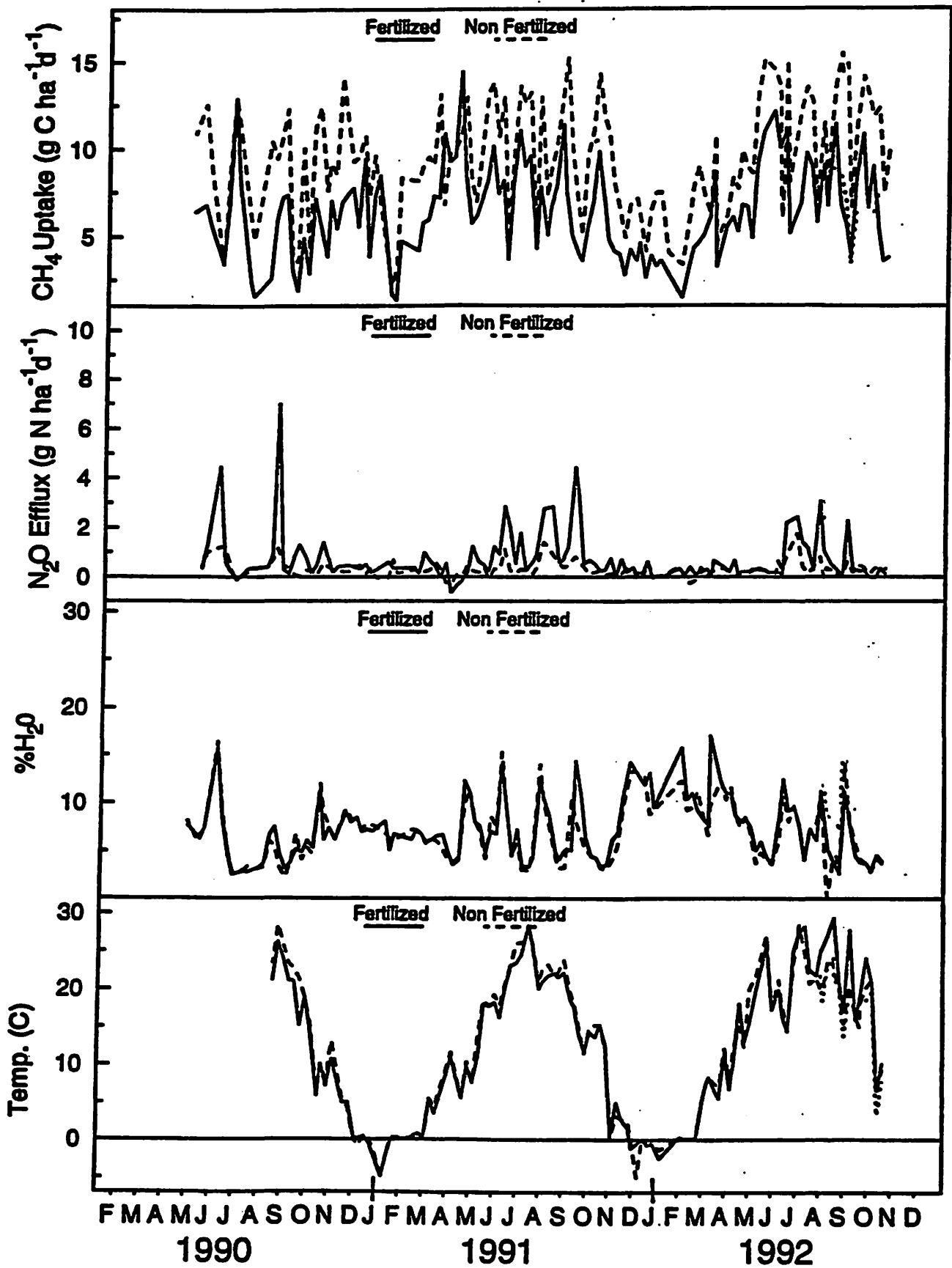
Soil Gas Methane Concentrations
Earth Watch NoPlow 3/19/93
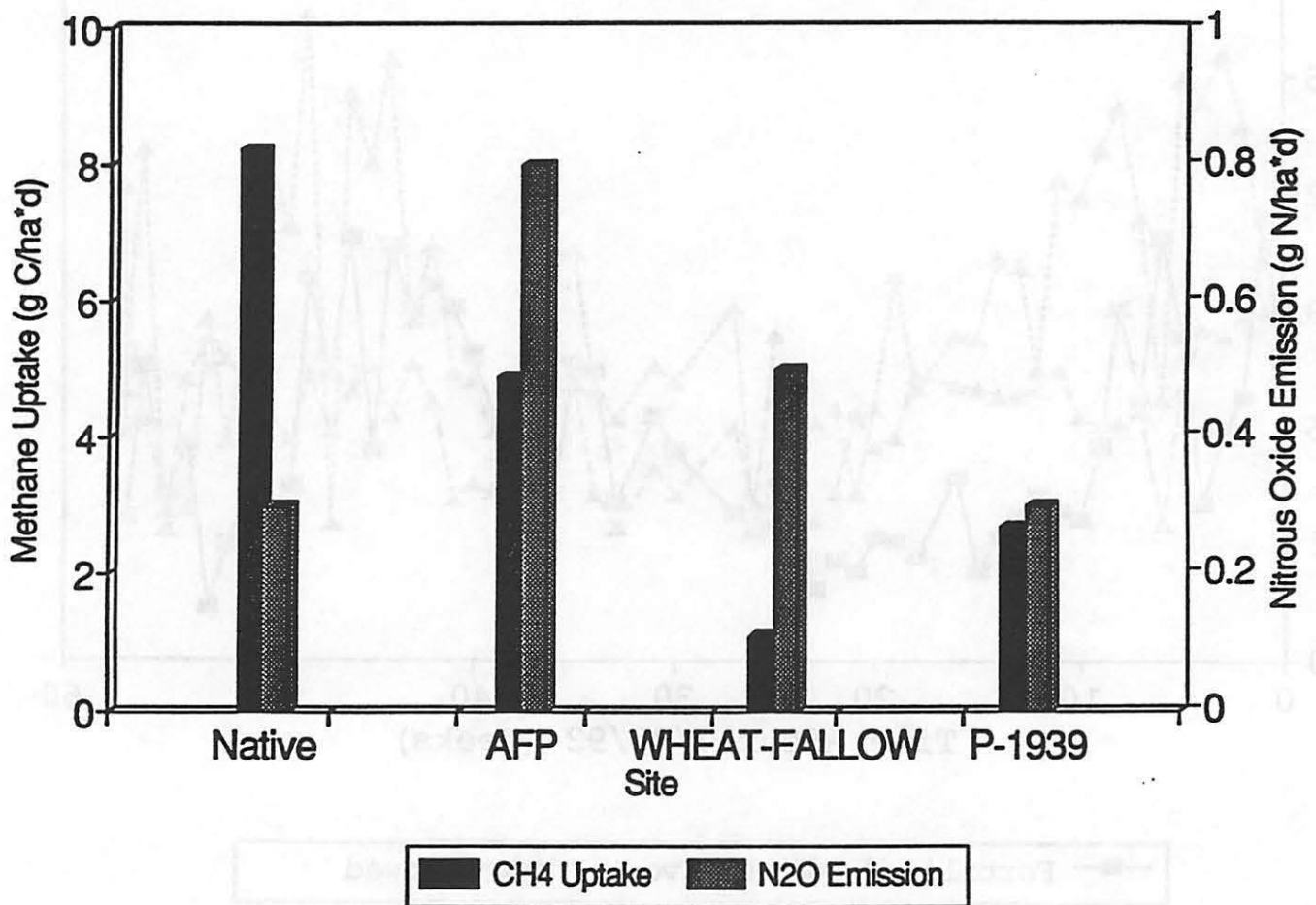

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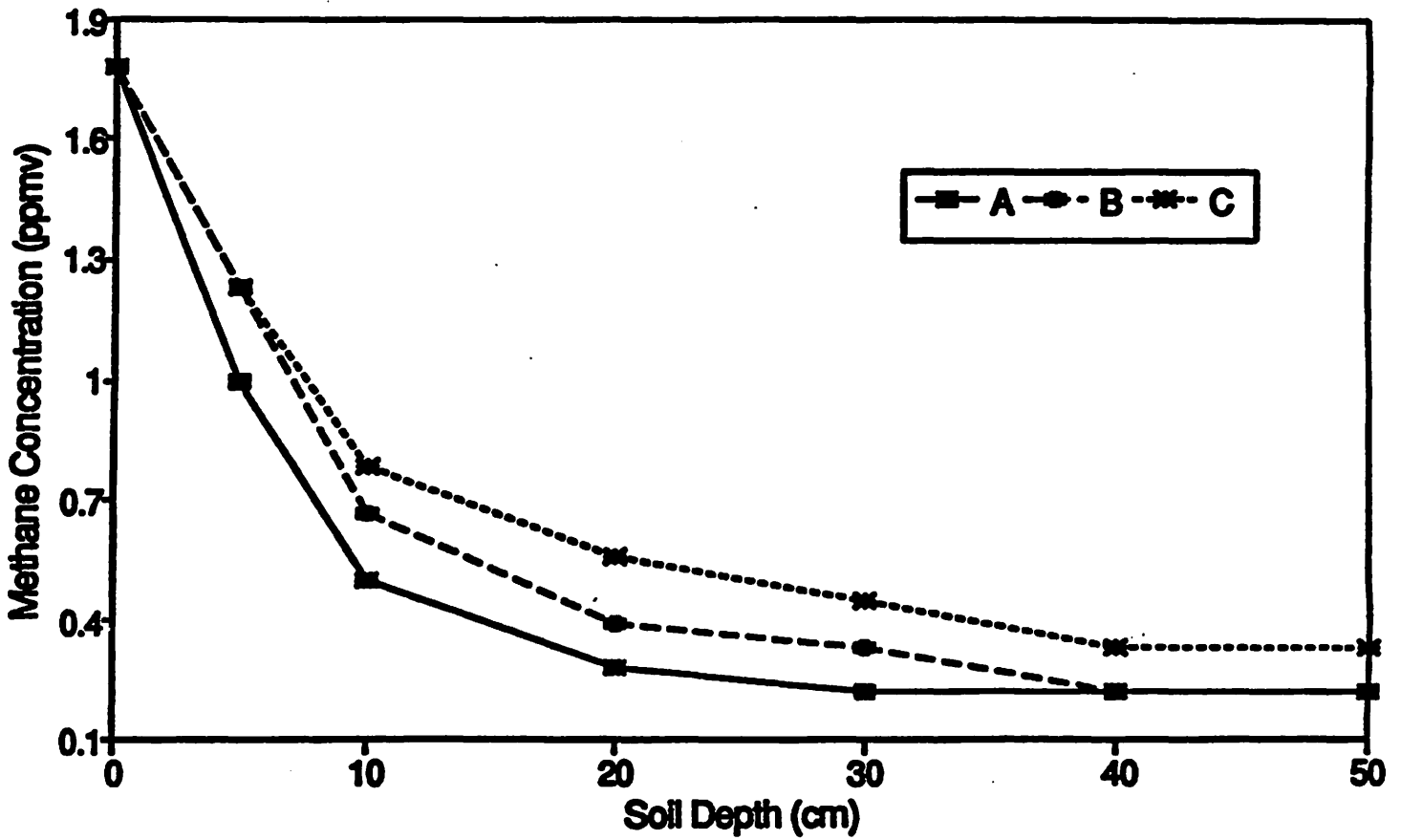
Model performance
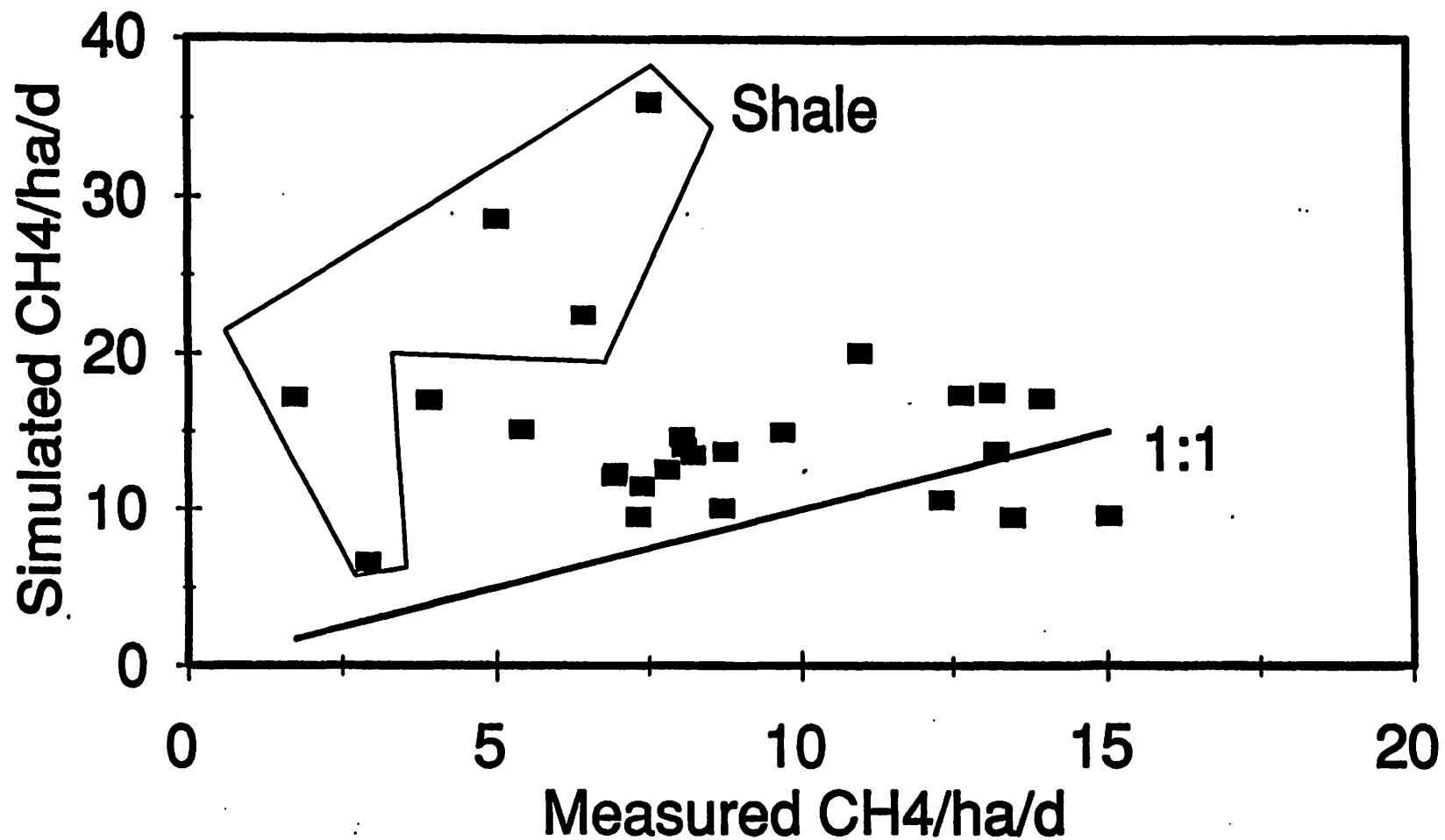
PASTURE-N ADDITION-PLOW
Nitrous Oxide Flux
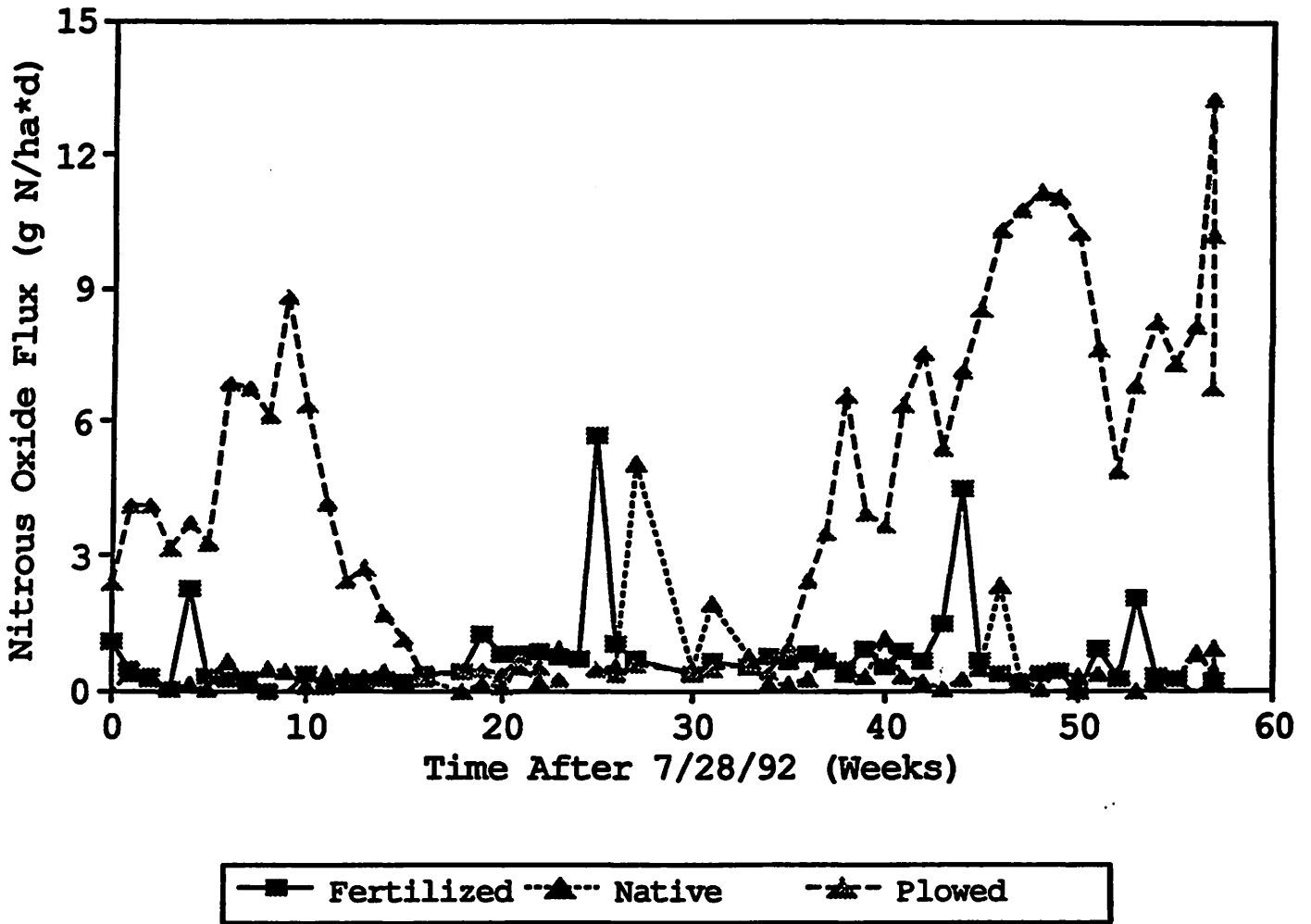
PASTURE-N ADDITION-PLOW
Methane Uptake
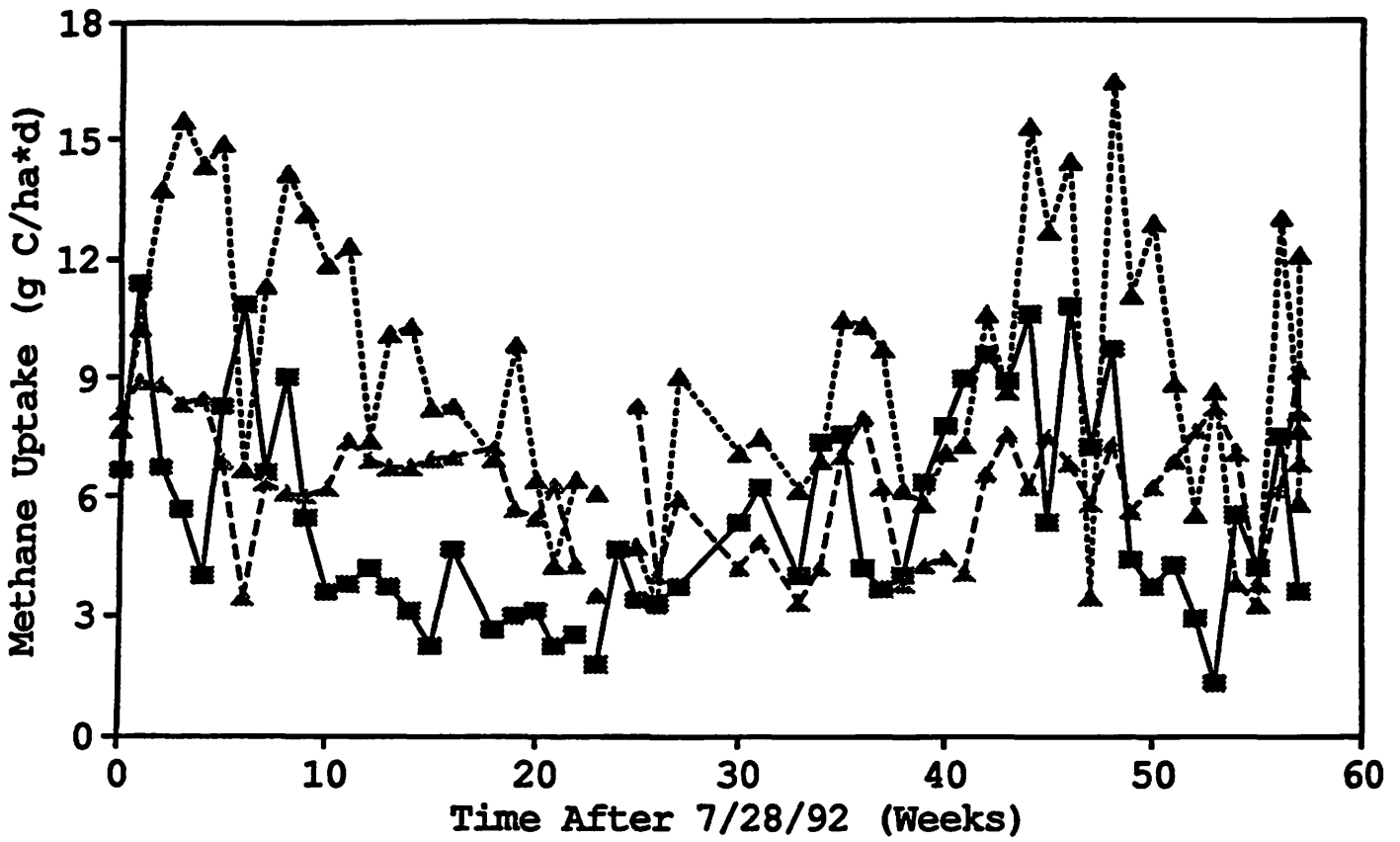
FIGURE   CH4 UPTAKE & N2O EMISSION
Effect of Use & Management

Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands

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METHANE and nitrous oxide are long-lived, radiatively active trace gases that account for ~20% of the total anticipated atmospheric warming[1]. The atmospheric concentrations of both gases have increased dramatically over the past few decades, and continue to increase at a rate of ~1.1 and 0.25% yr^{-1} for CH_4 (ref. 2) and N_2O (ref. 3) respectively. Increased biospheric production is generally suggested as the reason for the increases, but decreases in global sinks may also be important. It has been suggested, for example, that nitrogen fertilization may decrease the rate at which tropical[4,5] and temperate forest soils[6] take up methane from the atmosphere. Furthermore, the recent extensive changes in land management and cultivation could be contributing to the observed increases in both atmospheric CH_4 and N_2O, as has been suggested for tropical soils[7]. Little information exists on CH_4 uptake in temperate grasslands (which currently occupy ~8% of the Earth's surface), its relation to N_2O production, or the effect of land management or cultivation[8,9]. Here we report measurements of CH_4 uptake and N_2O emissions in native, nitrogen-fertilized and wheat-growing prairie soils from spring to late autumn, 1990. We found that nitrogen fertilization and cultivation can both decrease CH_4 uptake and increase N_2O production, thereby contributing to the increasing atmospheric concentrations of these gases.

We established three sets of sites in the Colorado shortgrass steppe during late winter and spring, 1990. One set was established along a toposequence (catena) to determine whether the landscape position—sandy loam upland (midslope) versus sandy clay loam lowland (swale)—in the native prairie (catena site[10]) affected CH_4 uptake. Previous investigations[10,11] had found that ammonia and N_2O fluxes differed markedly with landscape position. A second set of sites was established in unamended and annually nitrogen-fertilized native grass pastures. The third set was established in a pair of wheat fields, cropped in alternating years (wheat-fallow system), and in an adjacent native grassland for comparison. All sites were in or

near the United States Department of Agriculture-Agricultural Research Service Central Plains Experimental Range located north of Nunn, Colorado (latitude 40° 48′ 23″ N, longitude 104° 45′ 15″ W). Table 1 summarizes the soil characteristics.

On the catena, the fertilized midslope site was treated with $45\,g\,m^{-2}$ of urea-N in July 1981, and the fertilized swale site was similarly treated in May 1982 (ref. 11). Four replicate, permanent plots for gas flux measurement were established in the fertilized and unfertilized midslope and swale sites by driving 20.3-cm diameter PVC pipes into the soil to a depth of 8 cm. Cattle have been excluded from the catena site since 1980. Weather and soil temperature data were continuously collected ~200 m from the site.

The annual fertilization experiment was ~1 km north of the catena site. We established six replicate plots in both nitrogen-fertilized and control grazed pastures, hereafter called AFS (annual fertilized) and CAFS (control annual fertilized) sites. The terrain in these two pastures is essentially flat, and the soil is similar to the catena midslope (Table 1). The AFS received $2.2\,g\,N\,m^{-2}$ of ammonium nitrate annually from 1976 to 1989.

Finally, we established six plots in each of three adjacent sites—wheat, fallow, and native grassland—6 km east of the Central Plains Experimental Range. The wheat and fallow sites had been in continuous cultivation without irrigation or application of nitrogen fertilizer, pesticides or herbicides since the native prairie was ploughed in 1981. Winter wheat was planted in September 1989, and the fallow site was kept weed-free by cultivation following harvest in July 1989. The crop was harvested in July 1990, and the fallow site was planted with wheat in September 1990. The native grassland is 200 m east of the wheat-fallow field.

We measured methane and nitrous oxide fluxes by placing a closed chamber[12] over the established plots and taking gas samples from inside the chambers with 50-ml polypropylene syringes fitted with nylon stopcocks, usually 0, 15 and 30 minutes after the chambers were installed. We analysed the samples within six hours by gas chromatography using a Porapak N column and flame ionization detector for CH_4, and Porapak Q and electron capture detector[13] for N_2O from the same syringe. Flux measurements were made mid-morning on each sampling day, generally weekly at each site. We tested sampling time periods ranging from 10 to 60 minutes and taken at 2 or 3 time intervals, and in all cases CH_4 uptake was greater during the first sampling period than in subsequent periods. We therefore calculated CH_4 uptake rates assuming first-order kinetics rather than linear decay as had been suggested[6]. Measurements of CH_4 and N_2O fluxes were made at 6:00, 12:00 and 18:00 on several days. Over a 24-hour period, changes in CH_4 uptake averaged

TABLE 1 Physical and chemical properties of soils and flux rates of CH_4 and N_2O from each site

		Soil analysis*				Gas flux rates§				
				NO_3^-	NH_4^+	CH_4 uptake $\bar{X}$			N_2O emission $\bar{X}$	
		Total N	Total C	mg N	mg N		s.d.			s.d.
Site	pH	(%)		per kg	per kg	n	$(g\,C\,ha^{-1}\,d^{-1})$	n	$(g\,N\,ha^{-1}\,d^{-1})$	
Swale†										
Fertilized	5.6	0.223	2.215	5.1	0.7	128	3.6	1.6	108	6.2	15.5
Unfertilized	6.0	0.189	1.841	1.6	0.9	136	3.6	1.3	116	3.0	3.7
Midslope‡										
Fertilized	5.6	0.138	1.216	1.3	0.9	124	4.1	1.4	112	3.1	4.0
Unfertilized	6.5	0.141	1.245	1.1	0.9	132	6.3	2.1	120	1.8	1.7
Pasture‡										
Fertilized	5.6	0.138	1.177	6.4	20.3	180	3.8	1.8	162	6.1	10.7
Unfertilized	6.2	0.120	1.066	1.0	1.5	180	5.8	1.9	162	2.5	2.4
Wheat‡	5.8	0.116	0.955	1.1	1.4	162	1.3	0.6	162	2.8	2.7
Fallow‡	6.0	0.111	0.850	10.1	1.9	162	1.8	0.8	162	4.5	6.7
Grass‡	6.4	0.104	0.841	0.6	1.3	162	2.6	1.1	162	3.5	5.6

*Data are means for soil samples (0–15 cm) collected on each gas sampling day.
†The swale is a sandy clay loam soil classified as a Pachic argiustoll.
‡These are sandy loam soils classified as Ustollic haplargids.
§n, number of samples; $\bar{X}$, mean; s.d., standard deviation.

wetter conditions in 1990. The inverse relationship between N_2O flux and CH_4 uptake was apparent with or without nitrogen fertilization. The influence of nitrogen fertilization on N_2O flux was most evident in moist soils, whereas its influence on CH_4 uptake was most evident as soils began to dry after rain (Fig. 1).

To determine whether cultivation affects CH_4 uptake in grassland soils, as observed in tropical soils[7], we began monitoring CH_4 uptake in the wheat-fallow system. During 6 months of weekly measurements, CH_4 uptake averaged 2.6, 1.8 and 1.3 g C ha^{-1} d^{-1} in native grassland, fallow and wheat sites, respectively (Fig. 2). These data indicate that disturbing the natural grassland decreased CH_4 uptake ($P < 0.01$). Soil moisture contents averaged 8.6, 11.1 and 12.9% in grassland, fallow and wheat, respectively. Soil ammonium content did not differ among the three sites but soil nitrate was on average ~10 times higher in the fallow soil than in the other two sites. Long-term experimentation and frequent flux measurements are needed to understand the reasons for differing CH_4 uptake rates in different soils and crop pastures.

Our data indicate that the semi-arid grasslands represent a significant global sink for CH_4 (ref. 8). Methane uptake in the grassland ranged from 6 to 61 μg CH_4 m^{-2} h^{-1}, compared with uptake rates of 6-24, 52, 0-112, and 10-160 μg CH_4 m^{-2} h^{-1} in tropical forest[17], subtropical broad-leafed savannah[18], tundra[19] and temperate forest soils[6,8], respectively. If our measurements are representative of CH_4 uptake by these grasslands globally, then 0.5 to 5.6 Tg of CH_4 are removed from the atmosphere in these grasslands each year.

Out data suggest that nitrogen fertilization in natural ecosystems increases N_2O emissions and decreases CH_4 uptake[6]. These data also indicate that recent changes in use or management of grasslands, such as cultivation, have decreased CH_4 uptake from and increased N_2O efflux to the atmosphere. In addition to increased production from rice paddies, ruminants and other sources[20], decreased consumption by soils may contribute to increasing atmospheric methane. □

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Influence of Agricultural Nitrogen on Atmospheric Methane and Nitrous Oxide

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Have land use and management changes during the past two centuries contributed to increasing atmospheric concentrations of 'greenhouse gases'?

Carbon dioxide, water vapour, chlorofluorocarbons, methane, nitrous oxide and ozone in the atmosphere are the gases mainly responsible for atmospheric warming, or the 'greenhouse effect'. Although these gases are nearly transparent to the visible and near-infrared wavelengths in sunlight, warming occurs because they absorb and re-emit downward a large fraction of the longer infrared wavelengths emitted by earth. As a result of this heat-trapping, the atmosphere radiates large amounts of long-wavelength energy downward to the earth's surface. Consequently, long-wavelength radiant energy received on Earth is nearly double that received directly from the sun.[1] Although it is uncertain how much climate change can be expected from increasing greenhouse gas concentrations, when it began or will begin to occur, or where its effect will be most evident, it is certain that atmospheric concentrations of radiatively active trace gases are increasing.

Methane (CH_4) and nitrous oxide (N_2O) production occur primarily (about 70 and 90 per cent, respectively) in the soil. These two gases are increasing rapidly, about 1.1 and 0.3 per cent annually, respectively, and are responsible collectively for about 20 per cent of anticipated global warming annually (Table 1).[2] Both are produced where soil management practices can exert control over emissions. Understanding production and consumption mechanisms of the gases is therefore critical so that mitigating procedures can be developed.

Despite considerable research efforts over the past two decades, large uncertainties exist in the global budgets of both CH_4 and N_2O. For example, CH_4 source budgets are 'balanced' against estimates of CH_4 destruction. Recent estimates of CH_4 destruction suggest that the total magnitude of sources may be about 25 per cent less than the commonly accepted value.[3] The observation of high rates of CH_4 consumption in soils suggests a new term for consideration in the global CH_4 budget.[4-6] In 1988, the global budget of N_2O was thrown into disarray when a large source of that gas from combustion was shown to be an artifact.[7,8] Despite much research, scientists find themselves going back through topics once considered closed, seeking answers to still unbalanced budgets.

While the controls over atmospheric concentrations of CH_4 and N_2O are still a subject of debate, the role of land use and management is becoming clearer. Changes of land use and other human activity during the past 100 to 200 years are probably contributing to decreased CH_4 oxidation and increased N_2O production in soils. This may play a role in observed increases in atmospheric concentration of both gases. Extensive use of nitrogen fertilisers in agriculture during the past half century probably contributed to this increase as well. Increased use of agricultural N-fertilisation is a primary factor in the tremendous global increase in agricultural productivity. A consequence of increased agricultural productivity is the apparent increased N_2O production and decreased soil CH_4 uptake in agroecosystems.

Methane

Earth's atmosphere currently contains about 4800Tg (4800 x 10^{12}g) of CH_4.[9] The average lifetime of each molecule of CH_4 that reaches the atmosphere is about 10 years and the total

Flooded rice fields, like this one in Canton, make a substantial contribution to methane emissions

Nirman Myers/Bruce Coleman Ltd

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Our ongoing research[4] in the shortgrass prairie in north-eastern Colorado demonstrates a strong interaction between agricultural practice and CH_4 uptake by the soil. Our measurements of methane uptake and N_2O emissions in native, nitrogen-fertilised and wheat-growing prairie soils show that both N-fertilisation and cultivation decrease soil CH_4 uptake (Table 4).[4] A pasture fertilised with about 20kg ammonium nitrate N/ha/a for 15 years oxidises about 35 per cent less CH_4 than an adjoining unfertilised pasture. Conversion of a native grassland to non-irrigated, unfertilised wheat reduced methane consumption by about 40 per cent. Methane uptake in an irrigated wheat field averaged about 20 per cent of the native grassland. Interestingly, N-fertilisation in the irrigated wheat field did not further decrease methane uptake (Table 4). These studies suggest that CH_4 uptake is related to soil N turnover and not simply to soil mineral N content. Field studies relating type of N-fertiliser, mineral N or organic N, and different agricultural management practices to methane flux have not been conducted.

Nitrous oxide

Nitrous oxide is present in the earth's atmosphere at very low concentration, about 310ppb (v/v). This low concentration is important to atmospheric warming because each molecule of N_2O emitted into the atmosphere has an average life time of about 150 years and a net greenhouse effect about 300 times greater than CO_2.[2] So despite its low and slowly increasing concentration (0.3 per cent/a), it is becoming increasingly important in the overall global warming picture.[17]

Soil is the principal source of N_2O (Table 3). Nitrous oxide is produced during two soil microbial processes, nitrification,

Table 3 Global budget of tropospheric N_2O[10]

	Tg N/a
Sources	
Fossil fuel burning	2 ± 1
Biomass burning	1.5 ± 0.5
Oceans, estuaries	2 ± 1
Fertilised soils	1.5 ± 1
Natural soils	6 ± 3
Plants	< 0.1
Gain of cultivated land	0.4 ± 0.2
Total production	14 ± 7
Sinks	
Stratosphere	9 ± 2

the oxidation of ammonium to nitrate,[18] and denitrification, the reduction of nitrate to dinitrogen.[19] Both of these microbial processes are influenced by soil mineral N content, and therefore are influenced by N-fertilisation.

A large body of information concerning N_2O emissions from agricultural systems and the influence of N-fertilisation was accumulated during the late 1970s and early 1980s and is summarised by Bouwman[10] and Eichner.[20] In her review Eichner[20] concluded that if 100Tg of N fertiliser is consumed annually, worldwide, then the global release of fertiliser-derived emissions into the atmosphere will be 2-3Tg N_2O-N. Some studies indicate that N_2O emission rates are higher for ammonium-based fertilisers than for nitrate.[18,21,22] Bouwman's[10] review suggested no particular trend in N_2O emissions related to fertiliser type. Mineral N applications along with organic matter amendments generally increase total denitrification and N_2O production.

N-fertilisation has little effect on N_2O emissions from temperate hardwoods

Interrelationship of CH_4 and N_2O

In a temperate hardwood forest[5] N-fertilisation decreased methane uptake but had little effect on N_2O emissions.[23] In the shortgrass prairie, however, it decreased methane uptake by a third and increased N_2O emissions by a factor of two to three at all sites. In soils that have been cultivated, irrigated and fertilised for decades, methane uptake is greatly reduced from the native prairie (Table 3), but addition of fertiliser N has no effect on the level of CH_4 uptake. Application of 200kg of urea-N/ha in these fields resulted in the emission of about 1.65mg N_2O-N $m^{-2}d^{-1}$ compared with 0.11mg N_2O-N $m^{-2}d^{-1}$ from maize field plots that were not fertilised during that cropping season.[24]

In the grassland studies, an interesting relationship between soil water content and methane and nitrous oxide fluxes has appeared. At prolonged low moisture levels, N_2O production and CH_4 uptake rates were low. Following precipitation, N_2O production rapidly peaked while CH_4 uptake dropped to near zero and, in rare cases, CH_4 production occurred. As soils began to dry, N_2O production rates plummeted while CH_4 uptake rates climbed and remained high until soils dried and stayed dry for several weeks. Generally, soils with high ammonium and nitrate concentrations had much higher N_2O production rates and lower CH_4 uptake rates than soils containing little mineral N.

Mitigating fertiliser side effects

To increase agricultural production to meet growing demands for food required by our rapidly growing world population, nitrogen fertiliser use will necessarily increase. While fertilisation is not the largest source of N_2O, it is susceptible to management for reduced impact. Fertiliser's undesirable effects of increased N_2O production and methane uptake can be mitigated by agricultural management without decreasing production. Using nitrification inhibitors in conjunction with fertiliser N

LONG-TERM GRAZING

Daniel G. Milchunas et al.

I) Background Information from Previous On-Site Grazing Research.

A) Species Composition (Milchunas et al. 1989):
   1) Grazing was three times more intense in lowlands compared with uplands.
   2) Relatively small differences in species composition of heavily grazed vs ungrazed communities.
   3) Greater differences between communities due to landscape topography than grazing treatments, but grazing smoothed species distributions across the environmental gradient.
   4) Total vegetation and grass basal cover and density increased with grazing.
   5) Opportunistic-colonizer species ('weeds') more abundant in ungrazed than in heavily grazed communities.

B) Comparison with Other Disturbances (Milchunas et al. 1990):
   1) Ungrazed communities more similar to disturbed communities than were heavily grazed communities.
   2) Removal of grazers from this system promoted attributes of early seral stages.

C) Root Biomass and Spatial Distributions (Milchunas and Lauenroth 1989):
   1) Grazing had only small effects on root biomass and no effect on crowns.
   2) Greatest influence of grazing was on horizontal, rather than vertical, spatial distributions of root biomass.
   3) Belowground "grazing lawns" suggest that the soil volume is more extensively exploited in grazed compared with ungrazed shortgrass steppe.
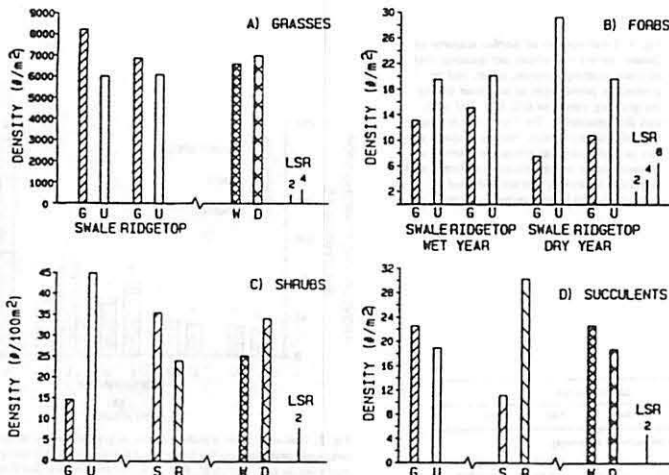

Fig. 3. Functional group densities (# of individuals m² or /100 m² for shrubs) of shortgrass steppe plant communities in grazed (G) and ungrazed (U), swales (S) and ridgetops (R), wet year (W) and dry year (D). See Fig. 1 for statistical explanations.

Table 2. Densities of six opportunist-generalist species in seven plant communities of the shortgrass steppe. Values are means of all replicates and dates for each treatment. Kp = Kochia scoparia; Cu = Cirsium undulatum; Si = Salsola iberica; Sa = Sisymbrium altissimum; Cl = Chenopodium leptophyllum; Sh = Sitanion hystrix.

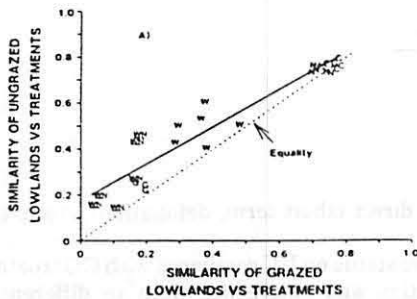| Comm. / Treatment	Opportunistic species density (per 10 m²)					
	Ks	Cu	Si	Sa	Cl	Sh
Control	0.0	0.3	0.8	1.3	2.0	16.5
Grazed	0.0	0.0	0.3	0.0	1.3	5.9
Ungrazed	0.2	0.7	1.4	0.2	3.0	18.5
Nitrogen	92.3	1.0	13.0	1.3	17.0	32.8
Water	75.5	8.5	9.0	0.8	4.3	4.0
White Grub	1.0	0.0	3.5	2.0	0.5	164.0
Water + Nitrogen	632.0	18.8	8.5	6.8	2.5	50.3

Fig. 1. Plant community similarity of ungrazed versus other treatments compared with the similarity of grazed versus other treatments. (a) lowlands: $Y = 0.80x + 0.16$; $r^2 = 0.88$
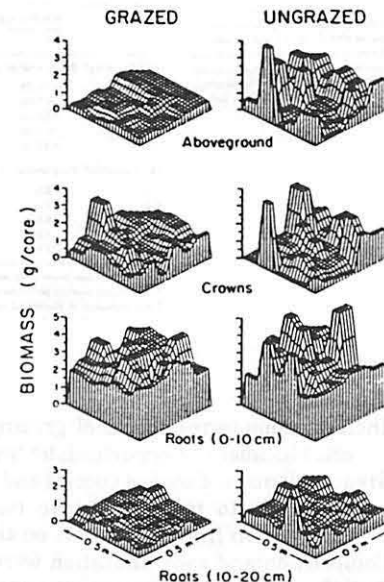

Fig 1. Horizontal and vertical distributions of plant biomass for one representative replicate of the 0.25-m² plots from grazed and ungrazed swales.

II) New On-Site Research

A) Plant Competition - Exotic Invasibility (Milchunas et al. 1992):

Introduction: Based upon structural differences between grazing treatments observed in previous work, we designed an experiment to test hypotheses concerning levels of competition on the long-term grazing treatments, the relative importance of direct vs indirect (short- vs long-term) effects of grazing, and grazing vs abiotic controls on the invasion of exotics.

Experimental Design:

3 locations X 3 plots X 2 topographic positions X 5 treatments X 5 species X 500 seeds sown

Germination, survival, and phenology were followed using x,y coordinate frames.

Treatments:

GG = long-term grazed -- grazed during experiment.

GU = long-term grazed -- ungrazed during experiment.

UU = long-term ungrazed -- ungrazed during experiment.

UK = ungrazed during experiment -- vegetation previously killed (herbicide) - left undisturbed.

UD = ungrazed during experiment -- soil disturbed (bladed, hoed) vegetation removed.
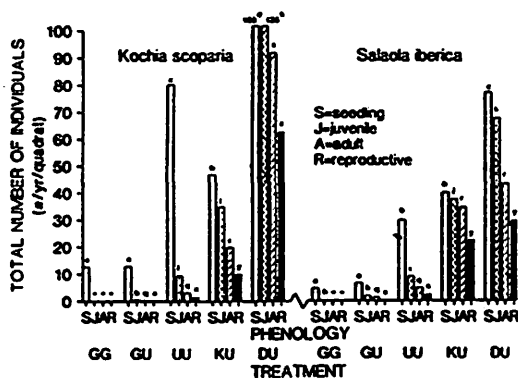
Results:

Fig. 4. Total number of *Kochia scoparia* or *Salsola iberica* individuals per quadrat that attained seedling, juvenile, adult, and reproductive phenologies at any time during the growing season in GG, GU, UU, KU, and DU treatments. See Fig. 1 for description of treatment codes. Means within a species and phenological group not sharing a common letter are significantly different with respect to treatment. * = not included in analyses due to large number of zeros
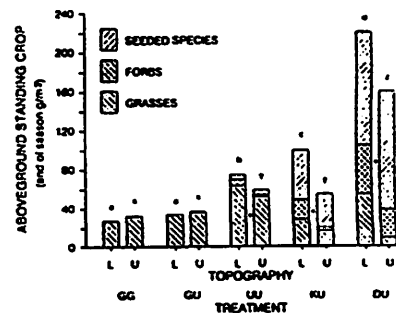

Fig. 5. End-of-season standing crops of grasses, forbs, seeded species, and total biomass for lowland (L) and upland (U) topographic positions in GG, GU, UU, KU, and DU treatments. See Fig. 1 for description of treatment codes. Treatments not sharing a common letter within topographic position are significantly different. A * between bars indicates a significant difference between topographic positions within a treatment

Table 2. Monthly death rate and monthly proportion of deaths for June cohort of *K. scoparia* and *S. iberica* individuals. Means within a species and date not sharing a common subscript are significantly different. See text or Table 1 for description of treatment codes. ANOVA conducted for each date

Treatment	Kochia scoparia			Salsola iberica		
	Jul	Aug	Sep	Jul	Aug	Sep
(A) Monthly* death rate of June Cohort (slope of survival numbers)						
GG	-11.2b	-1.5*	-	-3.7a	-0.6*	-0.1*
GU	-9.0b	-1.7a	-1.3*	-2.1a	-1.4a	-2.9ab
UU	-34.2d	-11.8b	-13.4b	-7.0b	-4.6b	-4.9b
KU	-4.1a	-2.0a	-2.4a	-1.7a	-0.5a	-0.3a
DU	-18.3c	-16.1b	-56.1c¹	-8.1b	-4.0b	-29.0c¹
(B) Monthly* Proportion of Deaths of June Cohort (% of previous month's population)						
GG	88a	100*	-	84a	91a	100*
GU	71a	46a	69a	28b	23b	67a
UU	43b	27b	40b	26b	23b	3c
KU	12c	7c	8d	6c	2c	1d
DU	13c	13d	51b¹	12c	2c	52b¹

* from previous month, to month indicated
¹ high value due to senescence after flowering rather than premature death
* not included in statistical analysis due to large number of zero's

Conclusions:

1) Indirect (long-term) effects of grazing were more important than direct (short-term, defoliation) effects in the establishment of opportunistic 'weeds'.

2) Greater biomass of seeded species and numbers reaching reproductive status on UU compared with GU treatments were due to more favorable microenvironment for germination and emergence than to differences in competition from perennials on the two treatments.

3) Competition and seed limitation were both large factors limiting invasion.

4) End-of-season standing crops were lower on long-term grazed than on ungrazed treatment, but equal compensation to current-year defoliation occurred.

B) Grazing History, Defoliation, and Precipitation
   Production and Rain Use Efficiency (Varnamkhasti et al. 1993).

Introduction: Although there are many studies which examine the effects of either long-term grazing or short-term defoliation, few have addressed interactions between the two. Potentials for compensatory regrowth after defoliation and the ability of long-term grazed communities to sustain production are both often centered around resource utilization efficiency mechanisms.

Methods: Plots in long-term ungrazed, lightly, and heavily grazed communities were clipped to simulate the natural patterns and intensities of defoliation by cattle or not clipped, and supplemented with additional water to simulate a wet year or not supplemented in a year of average precipitation.

Results:
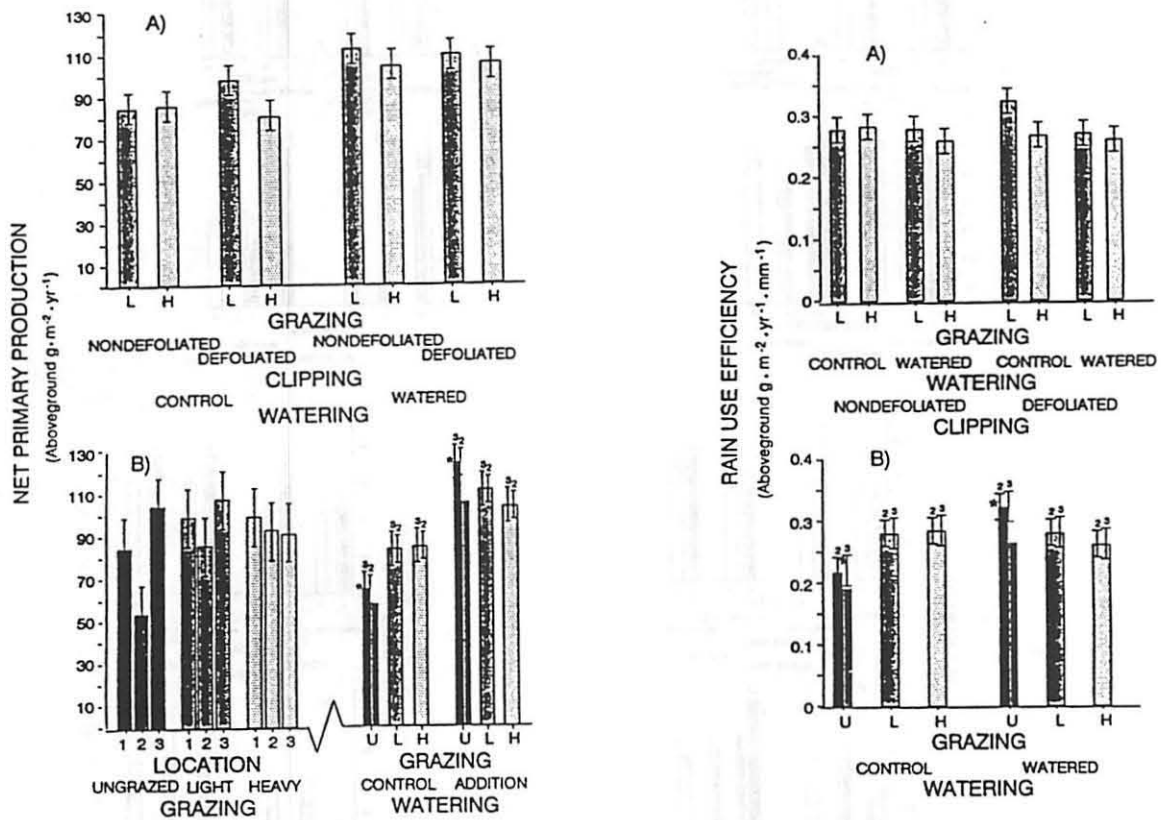
Conclusions:
  1) A positive-negative difference in ANPP of ungrazed vs grazed treatments depended upon level of precipitation, and the response to defoliation was complexly related to both grazing history and resource avaiability.
  2) Inconsistencies between this and two other studies appear in terms of the way long-term grazing intensities interact with current defoliation, but limited data suggest that potential for increased ANPP with defoliation is greatest when periods of water stress are relatively greater. Inconsistencies may be due to interactions between the effect of litter cover on soil water (interception, soil temperatures, evaporation), rainfall event size distribution, and direct effect of defoliation on transpiration:growth efficiencies.
  3) Long-term grazing decreased the potential response in ANPP to high precipitation, but the opposite was also true - grazing increased the potential for production under conditions of relatively low precipitation.

B) Grazing History, Defoliation, and Precipitation
   Plant Nitrogen and Digestibility (Milchunas et al. 1993).

Introduction: The ability of a range to sustain consumer populations depends upon forage quality as well as quantity. Defoliation can, in some instances, increase plant nitrogen and digestibility even when production is not affected. Studies of the long-term effects of grazing on forage quality generally fall into two scenarios which would offset or compliment the physiological responses to current-year defoliation; increases in unpalatable species=decreased quality, or increased leaf:stem ratios, etc.=increased forage quality.

Results:
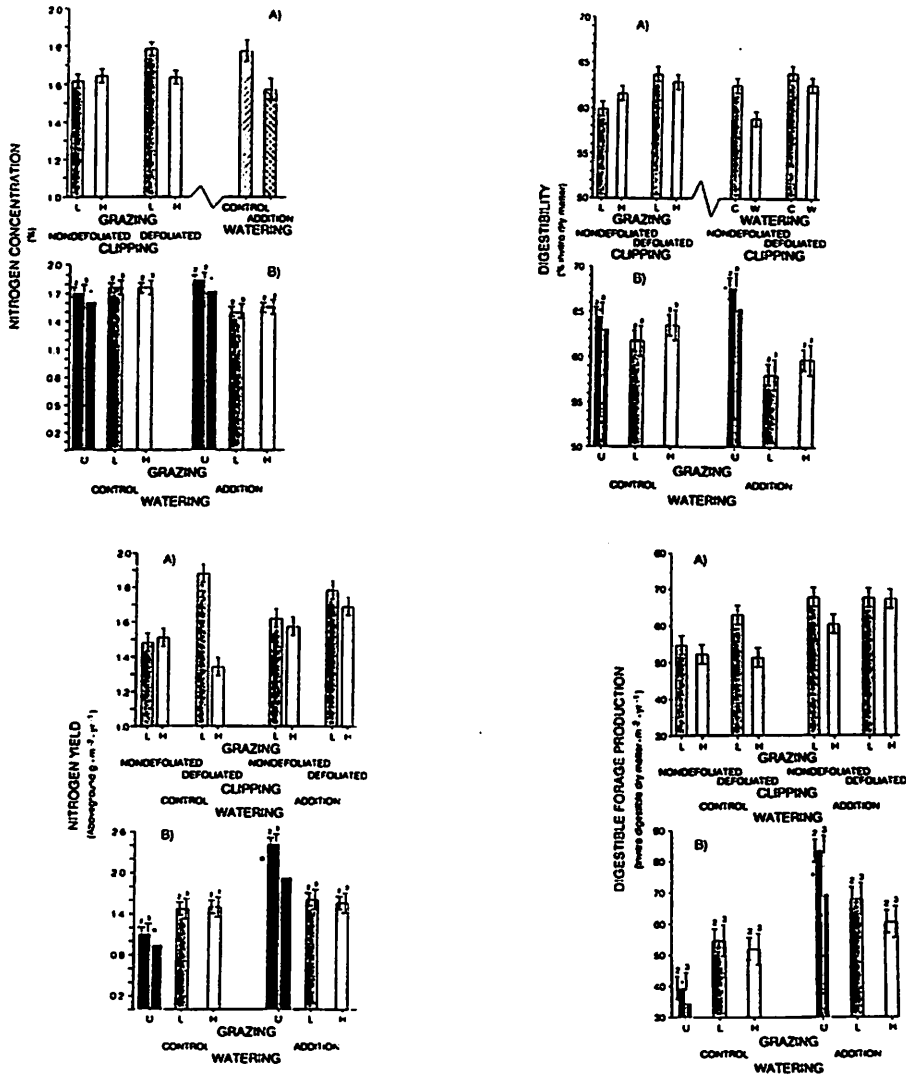
Conclusions:
1) Increases in concentrations and yields of N and digestible forage in response to defoliation were greater than the response in terms of ANPP in lightly grazed grassland.
2) The positive feed-back loop of increased forage quality with defoliation was diminished with long-term heavy grazing.
3) Currently defoliated long-term lightly grazed shortgrass steppe often provided better nutritional conditions than did nondefoliated ungrazed grassland.
4) Quantity, quality yields, and nutrient concentrations do not necessarily respond similarly in interactions between current-year defoliation, long-term grazing history, and level of water resource; implications can be different for non-selective vs selective consumers co-inhabiting the range.

C) Productivity of Grazing Treatments in Response to Seasonal Precipitation (Milchunas et al. 1993)

Introduction: Forage production data from 1939-62 (USDA-ARS) was combined with IBP and LTER data to assess the relative importance of climatic, edaphic, and biotic controls.

Methods: Step-wise regression analysis of production against 1) grazing intensity (20, 40, 60% removal), 2) years of grazing treatment, 3) warm-season precipitation, 4) cool-season precipitation, 5) previous year's precipitation, 6) precipitation two-years-previous, 7) pasture inherent productivity, and interaction and quadratic terms.

Results:

Average productivities from 1939-91 were 75, 71, 68, and 57 $g/m^2/yr$ for ungrazed, lightly, moderately, and heavily grazed treatments, respectively.
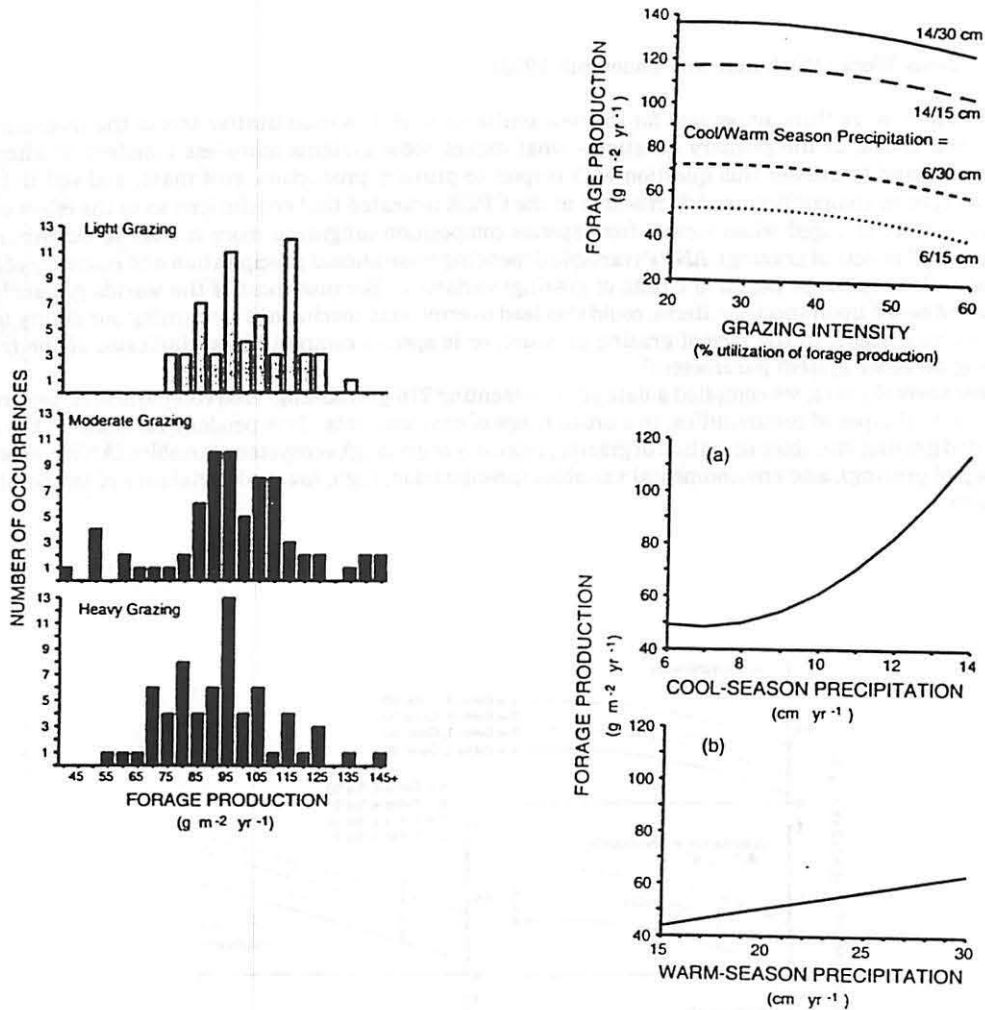
Conclusions:

1) Compared with light grazing intensity, rain-use efficiency declined with heavy grazing, but not with moderate grazing.

2) Variability in production was explained mostly by cool-season precipitation, and magnitude of production was more sensitive to annual fluctuations in precipitation than to long-term grazing treatments.

3) Production per unit increase of precipitation was greater for cool-season than warm season precipitation, but only when cool-season precipitation was above average. This was attributed to differences in evaporative demand of the atmosphere resulting in different utilization efficiencies of small and large rainfall events in the two seasons.

4) Sensitivity analyses suggest a ranking of importance of climatic > edaphic > biotic as controls on production.

III) Background Information from Previous Synthesis Work (Milchunas et al. 1988).

Summary: Our previous synthesis work was a qualitative, theoretical model that dealt primarily with species composition. The driving question was - On a global basis, why are some grasslands more resistant to grazing than others? Comparisons of results from the shortgrass steppe, the Serengeti, and the flooding pampa in Argentina indicated that current disturbance models, such as the Intermediate Disturbance Hypothesis and the Houston hypothesis, did not adequately explain the varied plant community responses to grazing. A model was developed based upon competition, convergent/divergent selection forces of environmental moisture and evolutionary history of grazing, and the interactions of the two on plant morphology and avoidance/tolerance mechanisms.

IV) New Synthesis Work (Milchunas and Lauenroth 1993).

Introduction: There were three impetuses for the new synthesis work 1) a quantitative test of the theoretical model described above, 2) the primary question - what makes some systems more/less resistent to alteration by grazing? - and to answer this question with respect to primary production, root mass, and soil nutrients as well as species composition, and 3) research at the CPER indicated that conclusions as to the effect of grazing on the system changed when viewed from species composition (ungrazed more similar to disturbance), root mass (small effects of grazing), ANPP (variable depending upon annual precipitation and intensity of grazing), to soil nutrients (large negative effects of grazing) variables. Because most of the worlds grazinglands are managed based upon species criteria, could this lead to erroneous conclusions concerning our ability to sustain productive systems in the face of grazing pressure, or is species composition an indicator of the impacts of grazing on other system parameters?

Methods: Over several years, we compiled a data set representing 276 grazed-ungrazed comparisons from around the world, for all types of communities, in a broad range of environments. Independent variables in the analyses included grazing variables (duration of grazing, intensity of grazing), ecosystem variables (ANPP, evolutionary history of grazing), and environmental variables (precipitation, high, low and variability of temperature, and latitude.
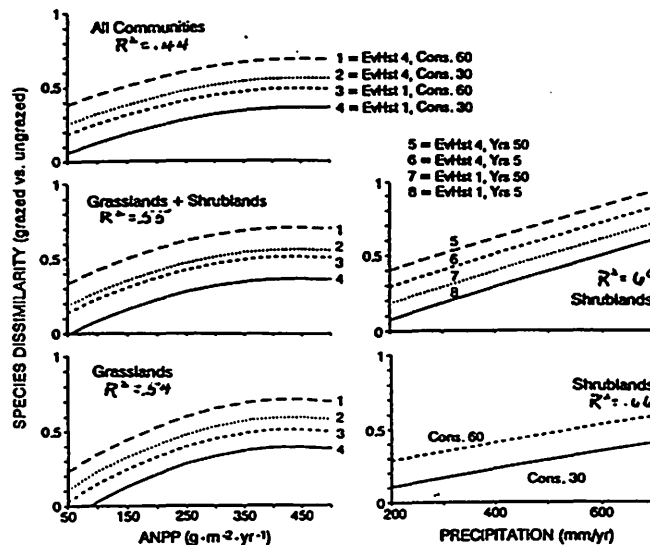
Results:

FIG. 3. Sensitivity analyses of species dissimilarity of grazed vs. ungrazed sites around the world (1 — Whittaker's [1952] index of association) based on regression models for all community types combined, grasslands-plus-shrublands, grasslands, or shrublands. Ranges were chosen to provide examples of reasonable low–high values; this approach was taken to make it possible to represent the response of models with ≥4 independent variables. See Table 2 for statistical description of the models. A dissimilarity value of 0 indicates no difference between grazed and ungrazed communities, and a value of 1 indicates completely distinct communities. Evttst = evolutionary history of grazing, ranked 1 to 4 for lower to higher values of past grazing. Cons. = consumption—recent grazing intensity (in percentage of aboveground net primary productivity [ANPP]). Time period = length of protection from grazing.
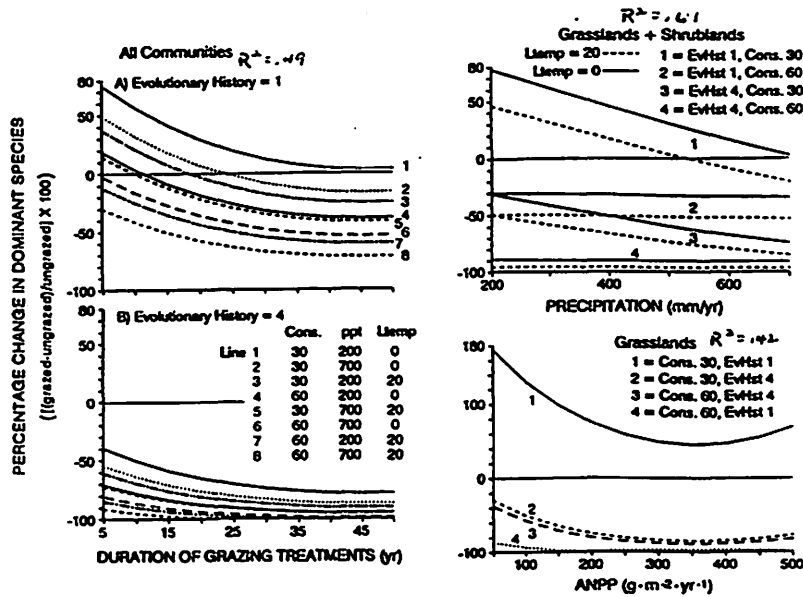
FIG. 4. Sensitivity analyses of percentage of change in the absolute abundance of the dominant species between grazed and ungrazed treatments for sites around the world, based upon regression models for all community types combined, grasslands-plus-shrublands, or grasslands. Ranges were chosen to provide examples of reasonable low–high values; this approach was taken to make it possible to represent the responses of models with ≥4 independent variables. See Table 3 for statistical description of the models. See Fig. 3 legend for abbreviation definitions.
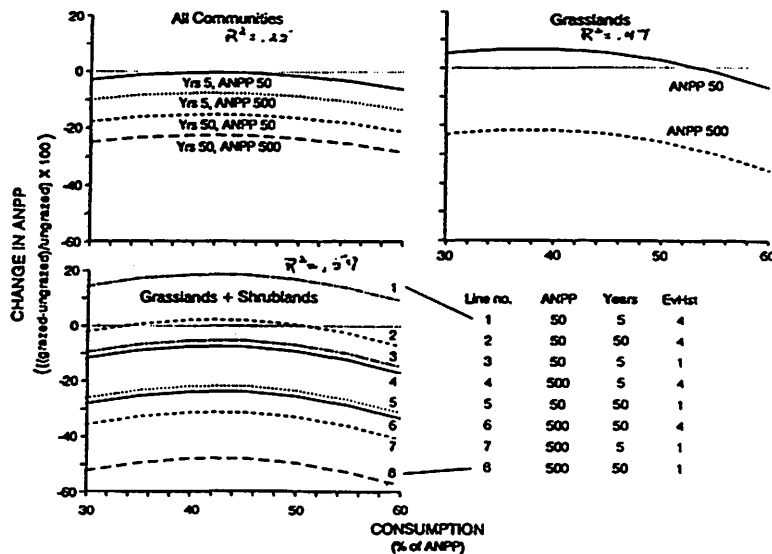
FIG. 5. Sensitivity analyses of percentage of difference in aboveground net primary production (ANPP) between grazed and ungrazed treatments for sites around the world. Ranges were chosen to provide examples of reasonable low–high values; this approach was taken to make it possible to represent the responses of models with ≥4 independent variables. See Table 4 for statistical description of the models. See Fig. 3 legend for Evttst definition.
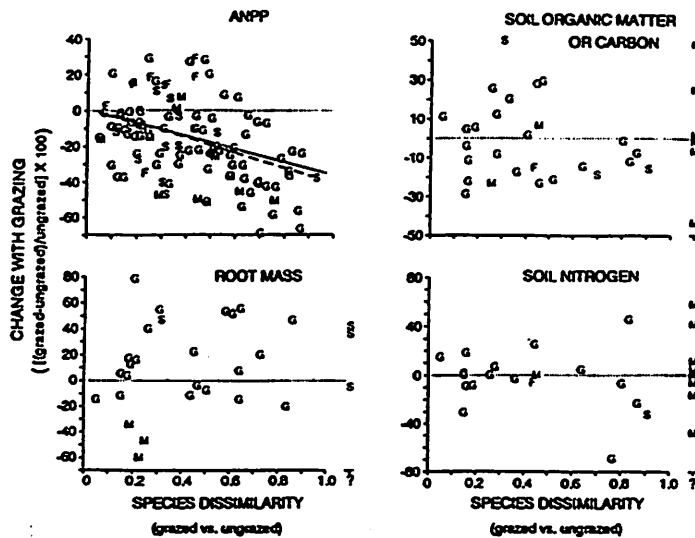
69

FIG. 7. Change in aboveground net primary production (ANPP), root mass, soil organic matter or carbon, and soil nitrogen in relation to species dissimilarity of grazed vs. ungrazed sites (1 − Whittaker's [1952] index of association). G = Grasslands, S = Shrublands, F = Forests, M = Mountain sites (meadow or alpine). In ANPP graph ⎯⎯ = regression for grasslands (r^2 = 0.19, N = 74) and − − − = all communities combined (r^2 = 0.18, N = 113). In the other three graphs "?" represents sites with no data for the independent variable, but included for positive-negative comparisons of the dependent variable.
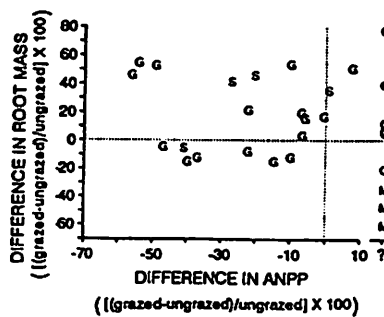
FIG. 8. Difference in root mass in relation to difference in aboveground net primary production (ANPP). G = Grasslands, S = Shrublands, M = Mountain sites (meadow or alpine). See Fig. 7 legend for explanation of "?".

Conclusions:
1) Changes in species composition increased with increasing productivity and with longer, more intense evolutionary histories of grazing, and increasing intensities of grazing.
2) As with species composition, sensitivities of change in dominant species to varying ecosystem-environmental variables was greater than to varying grazing variables from low to high values. Increases of the dominant species were predicted under some conditions, and decreases were more likely among bunch-grasses than other life-forms and among perennials than annuals.
3) The response of shrublands was different from that of grasslands, both in terms of species composition and the dominant species. Our analyses support the perception of grazing as a factor in the conversion of grasslands to less desirable shrublands, but also suggest that we may be inadvertently grazing shrublands more intensively than grasslands.
4) Although most effects of grazing on ANPP were negative some were not, and the statistical models predicted increases in ANPP with grazing under conditions of long evolutionary history, low consumption, few years of treatment and low ANPP for grasslands-plus-shrublands.
5) The data and the models support the controversial hypothesis that grazing can increase ANPP in some situations.
6) Similar to species-variables, percentage differences in ANPP between grazed and ungrazed treatments were more sensitive to varying ecosystem-environmental variables than to varying grazing variables. Within levels not considered abusive 'overgrazing', where grazing occurs may be more important than how many animals are grazed or how intensively an area is grazed.
7) Counter to the commonly held view that grazing negatively impacts root systems, there was no relationship between difference in ANPP with grazing or difference in root mass; as many positive as negative differences occurred even though most ANPP differences were negative.
8) Further, there was a weak relationship between change in species composition and change in ANPP, and no relationship with root mass, soil organic matter, or soil nitrogen. All three belowground variables displayed both positive and negative values in response to grazing.
9) Current management of much of the worlds grazinglands based on species composition criteria may lead to erroneous conclusions concerning the long-term ability of a system to sustain productivity.

V) Literature Cited

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Long Term 15-N Experiment:
Interactions of Grazing and Landscape Position on N Retention and N Cycling.

<u>General Question:</u> How does long-term grazing influence soil organic matter pools and processes?

<u>Specific questions:</u>

How much N is removed from the shortgrass steppe as a result of grazing, and how does this effect interact with landscape position?

How does grazing alter organic matter inputs into the system, as evidenced by the amount of N that is in "active" soil organic matter, and the quality of inputs as evidenced by C/N ratios?

Is the stabilization of soil organic matter reduced by grazing?

Past work has shown that soil C and N are significantly lower on the long-term, heavily grazed pasture than the long-term ungrazed pasture. This effect is most evident in toeslope positions.

<u>Design:</u>
2 treatments, heavily grazed and ungrazed
2 landscape positions
3 blocks

15-N added at a rate of 2 $g/m2$ in summer of 1989 as ammonium sulfate.

That summer, we tested for initial levels of 15-N in the following pools:

mineralizable N - 30-day incubations
mineralizable N, monthly for one year
microbial N
total soil organic N
plant biomass N, above and belowground
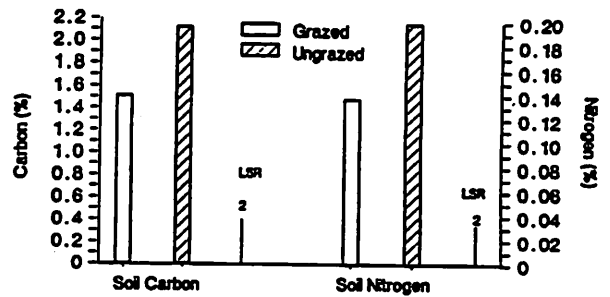C in all the above pools and CO_2 from incubations.

Figure 2.7 Soil organic C and N in soils in long-term grazed and ungrazed locations at the CPER
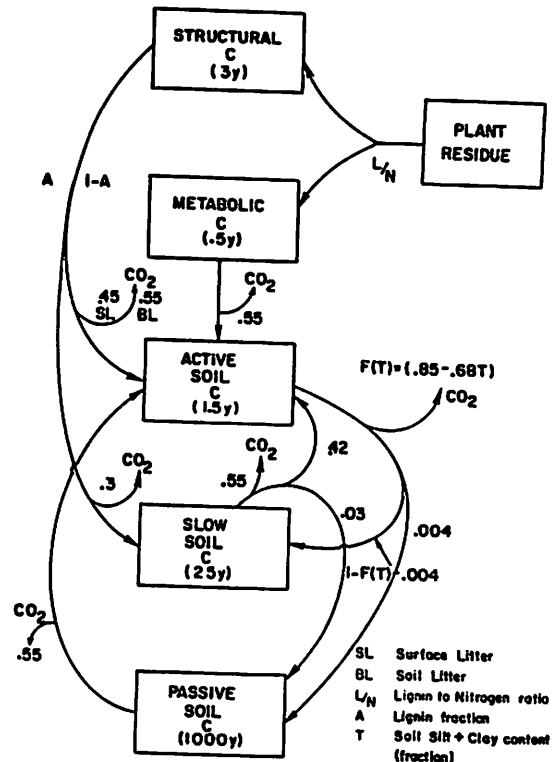

Fig. 1. Flow diagram for the C flows in the Century model.

Defoliation effects on western wheatgrass (<u>Pascopyrum</u> <u>smithii</u> Rybd. A. Love) plants in long-term protected and long-term grazed pastures.

Menwyelet Atsedu, James K. Detling

Introduction:

Grazing effects become better understood as the level of observation is carried out at individual species level. Two grazing units that include long-term protected and still protected (LPP) and long-term grazed and recently (since 1992) protected (LGP) were established in four CPER pastures to investigate differences in aboveground biomass production, nitrogen yield, and morphology of individual Western wheatgrass tillers (hereafter referred to as <u>Pasm</u>) following defoliation. The main objectives are to (a) examine the effect of defoliation on herbage production and morphology of LPP and LGP <u>Pasm</u> plants and, (b) determine the effect of defoliation on nitrogen accumulation in individual tillers.

Materials and methods:

Four plots containing 30 <u>Pasm</u> tillers were used at LPP and LGP sites. Ten were defoliated at a height of 6 cm, ten were defoliated at 4 cm, and ten were left intact (controls). Clipping was done three times at 4 weeks intervals. Accumulated biomass was analyzed for herbage and nitrogen yield. Morphological measurements (pre- and post-clipping) were also carried out.

Results:

Pre-defoliation morphological differences in 1992 indicated that <u>Pasm</u> plants were shorter in grazed sites (Fig. 1). Biomass accumulation was lower following defoliation in both LGP and LPP and the two populations responded similarly (Fig. 2). However, nitrogen yield increased in LPP following defoliation and a similar trend occurred in the

LGP sites (Fig. 3). There were more new tillers in 6 cm defoliated LGP plants than controls (Fig. 4). LPP plants defoliated at both levels also produced more tillers compared to controls. Average height of new tillers was greater at the 3 cm defoliation intensity in LGP plants than in non-defoliated controls (Fig. 5).
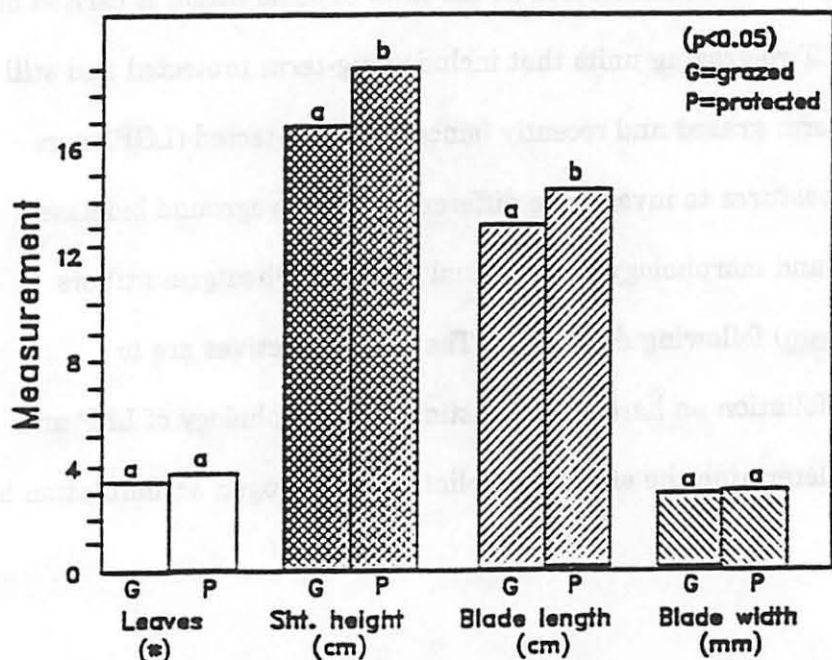

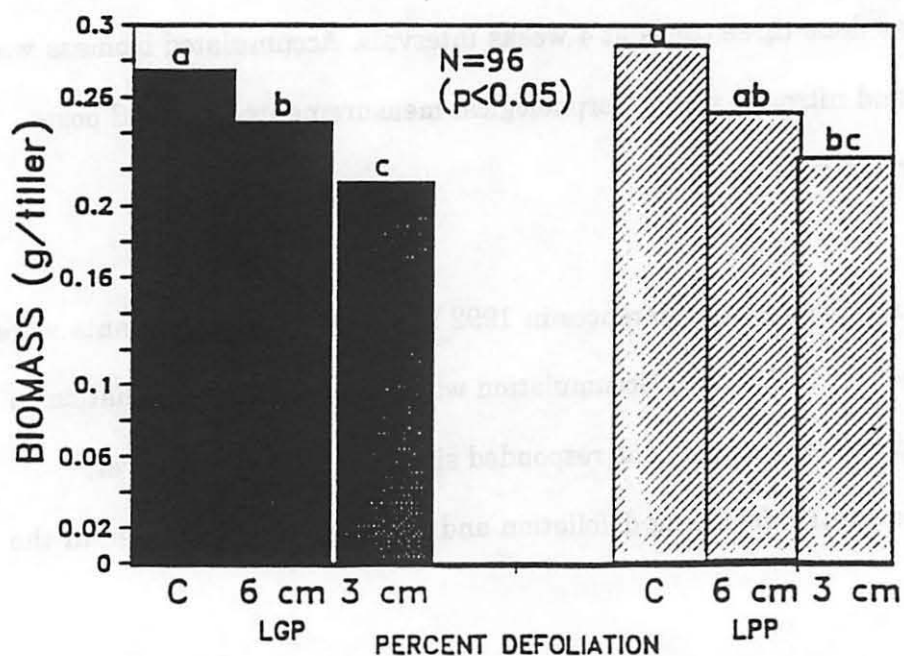Fig. 1. Morphological differences between LGP and LPP sites prior to defoliation.

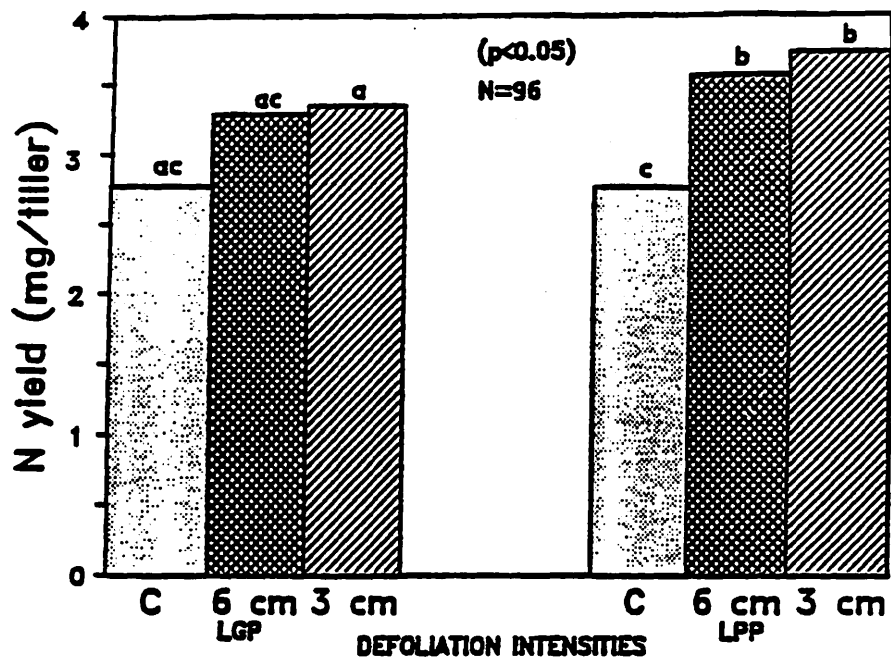Fig. 2. Biomass of defoliated and non-defoliated Pasm plants in LPP and LGP sites.

Fig. 3. Nitrogen yield of defoliated and
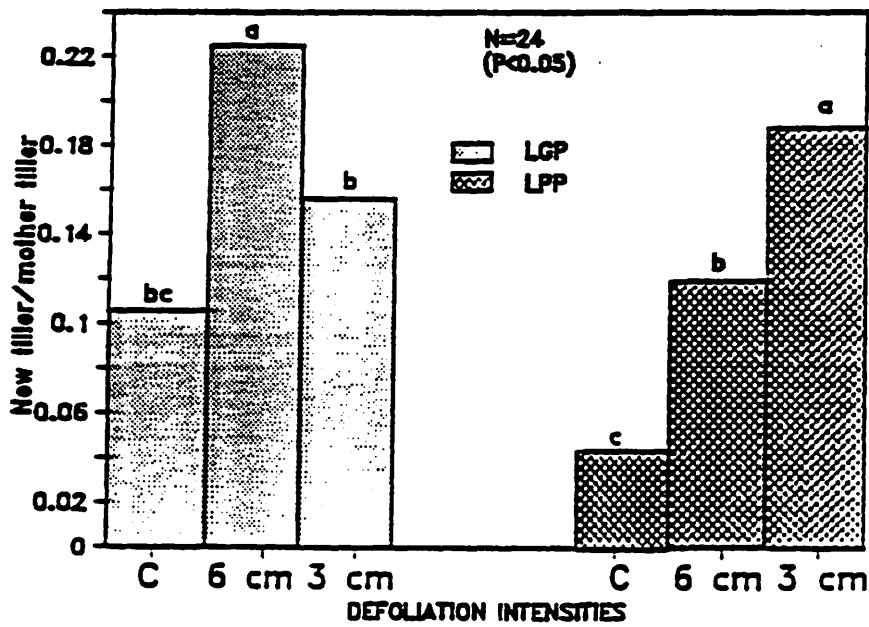non-defoliated Pasm plants in
LPP and LGP sites.

Fig. 4. Average number of tillers/mother tiller
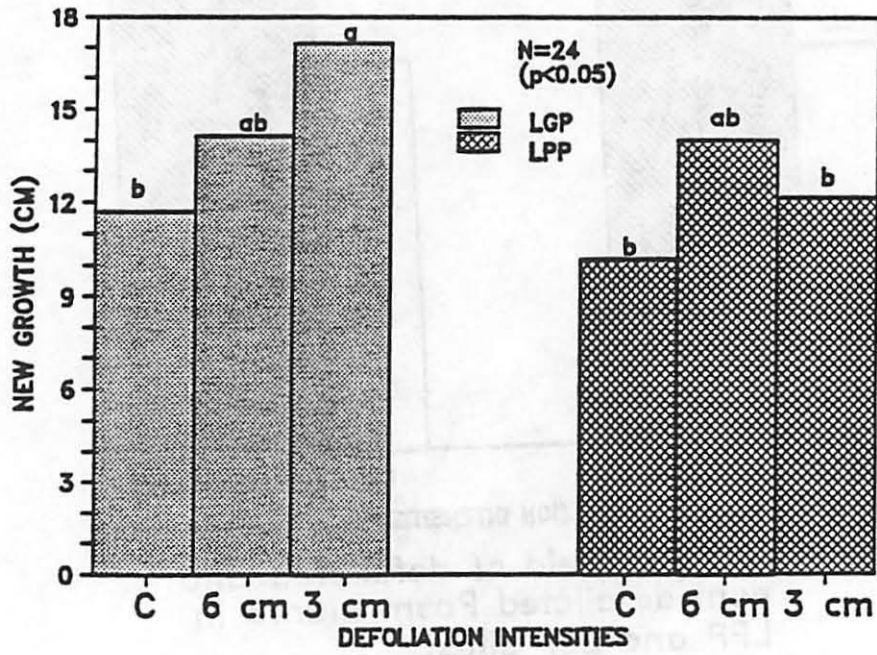for defoliated and non-defoliated plants.

Fig. 5. Average height of new tillers for defoliated
and non-defoliated plants.

COMPETITION BETWEEN DOMINANT SPECIES OF A GUILD OF WARM SEASON SHORT GRASESS

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Ecology is moving towards the use of guilds as a way to study and understand community and ecosystem functioning. *Bouteloua gracilis* and *Buchloë dactyloides* are the dominant grasses throughout the semiarid Shortgrass steppe and integer a guild of warm season short grasses. Both are perennial species with similar: morphology, amount of above- and below-ground biomass, and photosynthetic pathways. We performed an experiment to study the competitive relationship between dominant species in a guild in the Shortgrass steppe. These are the results from the first year (1992).

OBJECTIVES

Our experiment was designed to allow us to answer the following questions:
1. What is the importance and the intensity of competition between the two dominant species in a guild in a water limited environment?.
2. To what extend is interspecific competition equal to intraspecific competition between species in a guild of warm season grasses?.
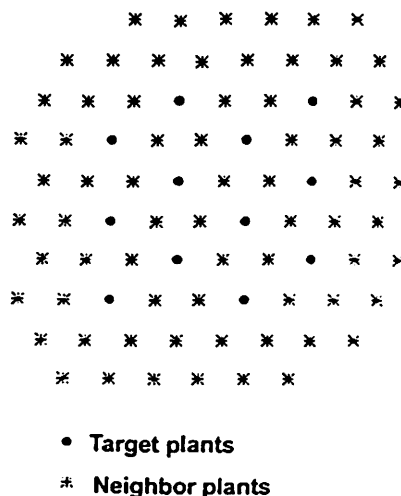
EXPERIMENTAL DESIGN

We prepared an area for our experiment by plowing the existing shortgrass vegetation. We planted cores (7 cm in diameter and 15 cm depth) of the two species. Target plants of both species were surrounded by neighbor plants of the same or different species (2 target sp. x 2 neighbor sp. = 4 combination). In order to put in evidence the effect of competition (intra- or inter-specific) we surrounded half of target plants in each combination with a metal pipe 30 cm in depth (4 x 2 = 8 treatment) (Fig 1). We also planted isolated plants to study conditions of no competition. Response variables were measured in target plants in each of the six replication of the treatments.

Fig 1.

a)

EXPERIMENTAL LAYOUT

• Target plants
✳ Neighbor plants

b)

RULES IN THE EXPERIMENTAL DESIGN

1) Only one species as neighbor in each plot.

2) Both species as target plants in each plot.

3) All plants were surrounded by six plants.

4) Distance between plants was always 15 cm.

5) Plants were the same size at the start.

6) Some target plants growth inside metal pipes.

7) Response variables were measured in target plants.

PRINCIPAL RESULTS

1. Competition played an important role in a community from a water limited ecosystem. It reduced biomass accumulation and seed production in the dominant species of the dominant guild (Fig 2).

2. Competition was a more important and intense influence for the growth of *Bouteloua gracilis* than for *Buchloë dactyloides* (Fig 3a). This could be interpreted as a more significant impact of environmental conditions (i.e. water limitation) on *Buchloë dactyloides* than *Bouteloua gracilis*. The intensity of intra- and interspecific competition was not different for these members of a warm season grasses guild (Fig 3b).

3. Isolated plants of *Bouteloua gracilis* responded to the increased availability of soil volume, but *Buchloë dactyloides* plants did not respond (Fig 2). Preliminary observations support that the difference could be the result of a water limitation.

4. Species in a guild defined on base of important morphological and ecophysiological characters, could differ in important ecological characters (i.e. importance and/or intensity of competition).

5. Greater biomass accumulation of *Bouteloua gracilis* than *Buchloë dactyloides* explain the relative dominance of these two species.
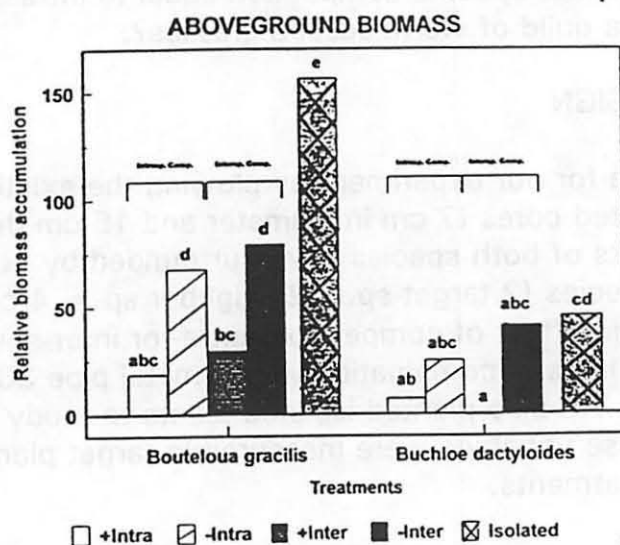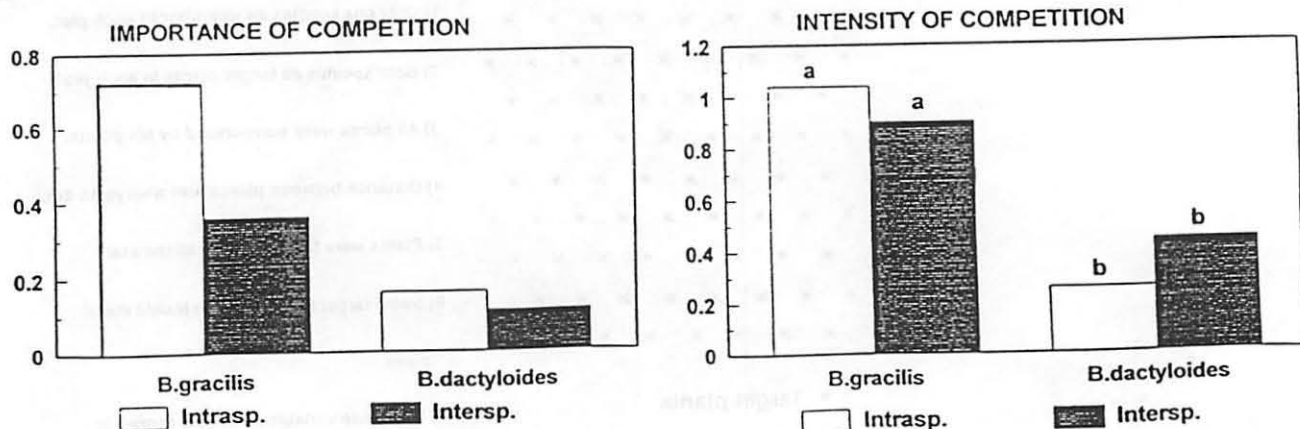
Fig 2.

ABOVEGROUND BIOMASS

☐ +Intra   ▨ -Intra   ▩ +Inter   ■ -Inter   ⊠ Isolated

Fig 3.

IMPORTANCE OF COMPETITION

B.gracilis   B.dactyloides
☐ Intrasp.   ▨ Intersp.

INTENSITY OF COMPETITION

B.gracilis   B.dactyloides
☐ Intrasp.   ▨ Intersp.

Short- and Long-Term Effects of Grazing on Shortgrass Steppe Ecosystem Structure and Function

Past research at the CPER has indicated that long-term grazing has minimal effects on plant community structure. We interpret this as an indication that the shortgrass steppe evolved under grazing, and plants are thus adapted for grazing.

Other results indicate that soil organic matter is significantly lower on long-term grazed than long-term ungrazed locations.

At least two intepretations are possible. First, it is possible that grazing by cattle has resulted in losses of soil organic matter, and that the long-term ungrazed areas are at steady-state relative to prehistorical conditions. Such losses would be the result of decreased litter inputs relative to prior conditions.

The second interpretation is that long-term protection from grazing has resulted in increases in soil organic matter, as a result of reduced litter removal by large herbivores. Such an interpretation is consistent with our results regarding plant community responses to grazing and protection.

We have designed an experiment to address the question: "What are the short- and long-term responses of ecosystem structure and function to grazing or protection from grazing?"

There are a number of 50-year-old exclosures on the CPER. Using our site-level GIS, which includes data on grazing treatment, soils, and
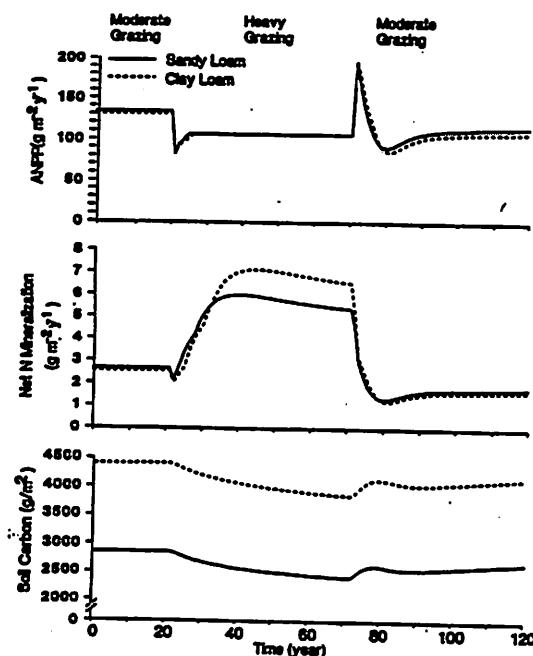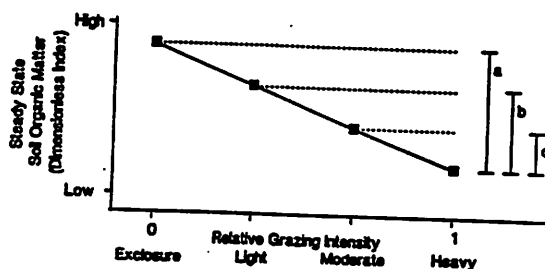
Figure 2.10 Simulated ANPP, net N mineralization, and soil organic carbon under long-term moderate grazing, 50 years of heavy grazing, and release to light grazing.

exclosure locations, we chose 7 of these
exclosures to modify. During the summer of
1991, we sampled each of these exclosures
intensively to characterize initial conditions.
We disgarded one exclosure on teh basis of
nonuniform soil conditions inside and out of
the exclosure.

During 1992, we manipulated the exclosure
boundaries to provide 2 new treatments, long-
term grazed areas that are newly protected,
and long-term protected areas that are newly
grazed. Areas that are long-term grazed and
long-term protected from grazing are
maintained.

We are collecting data related to numerous
aspects of ecosystem structure and function.
All were sampled in the original treatment
plots (grazed and ungrazed) during the first
year, before new treatments were started.
Depending upon the time constant of the
process, we will sample at 1, 3, or 5-year
intervals:

Belowground food-web structure
Plant community structure
Small-scale disturbances
Plant tissue chemistry
Aboveground net primary production
Belowground net primary production (planned)
Soil organic matter - total C, N, and P
Particulate soil organic matter
Mineralizable C and N
Microbial biomass C and N

grazed - grazed

protected - grazed

protected - protected

grazed - protected