VEGETATION UNITS AT WIND CAVE NATIONAL PARK FOR USE IN STABLE ISOTOPIC INTERPRETATIONS OF DIETS

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ABSTRACT

A map of eighteen vegetation/soil complexes at Wind Cave National Park was prepared from soils, topographic and vegetation data. These units varied in their dominance by C_3 and C_4 species and in early July possessed delta ^{13}C values ranging from pure C_3 signals to a predominantly C_4 ratio. Feces from the major herbivores showed some C_4 utilization by elk (*Cervus canadensis*) and bison (*Bison bison*) and more use by black-tailed prairie dogs (*Cynomys ludovicianus*). Prairie dogs also possessed greater individual variability likely reflecting greater vegetation variability in colonies of differing maturity. Collagen from elk and bison showed significant utilization of C_4 species. These data suggest that it will be possible to calculate park-wide delta ^{13}C values and to estimate selectivity by bison and elk. This holds the promise for paleoecological and paleoclimatic interpretations in North American grasslands.

INTRODUCTION

Temperate zone grasslands in most parts of the world contain varying proportions of C_3 and C_4 grasses. This variation is largely a function of temperature (Terri and Stowe, 1976; Stowe and Terri, 1978; Tieszen, et al., 1979a) with local distributions further affected by topography and nutrient availability (Barnes, Tieszen, and Ode, 1983). In the mixed-grass prairie of northern South Dakota C_3 plants occupy the wettest sites and C_4 species are more common on drier and warmer hillsides (Barnes, Tieszen, and Ode, 1983). Initial work at Wind Cave National Park (WCNP) also showed C_4 grasses with the highest importance values on well-drained sites where moisture was lowest and soils were coarsest. C_3 species, in contrast, predominated on the relatively moist uplands and bottomlands was also found in a similar grassland in Colorado (Archer, 1984).

In addition to spatial variation in the distributions of C_3 and C_4 grasses, Ode, Tieszen and Lerman (1980) have clearly established seasonal variation in the contribution of C_3 and C_4 species to net annual primary production. This variation ranges from 100% contribution by C_3 plants in spring and fall to a substantially lower level at mid-summer. Temperate zone grassland composition, therefore, is a complex mixture of C_3 and C_4 species governed largely by temperature and influenced by other abiotic factors.

It is also now well established that plants fractionate a variety of naturally occurring isotopes in a pattern which is predictable (Tieszen, et al., 1979a). Plants which photosynthesize by the C_3 pathway discriminate more against ^{13}C than do plants which photosynthesize by the C_4 mechanism. This fractionation results in two modal classes of delta ^{13}C values. C_4 plants possess values around -12°/oo and C_3 plants group around -26 to -28°/oo. These ratios are an integral part of the organic matter of these producers and serve as a permanent label for each photosynthetic type. The application of this label for ecosystem level and quantitative tracer studies has made available a powerful research tool (Tieszen, 1987) which is now making fundamental contributions to our study of ecology, especially in dietary reconstructions (Tieszen, et al., 1979b; Ambrose and DeNiro, 1986; DeNiro, 1987) and energy flow through trophic levels.

DeNiro (1987) has recently reviewed the use of these labels for archeological reconstructions. Our laboratory (Tieszen, et al., 1983) has confirmed our ability to quantitatively estimate diets, and we have established that it is possible to determine the proportions of C_3 and C_4 plants in the diet of an herbivore by measuring the delta ^{13}C value of one of its tissues. Essentially three orders of time resolution are available: collagen integrates the early or total lifetime assimilation by an individual, soft tissues reflect more recent periods as a function of their half lives, and rumen or fecal components are direct indicators of immediate dietary components. It is the ability of the delta ^{13}C of the collagen in an herbivore to reflect the vegetation and, therefore, climate that is of special interest to us. We should be able to examine the collagen and predict the vegetation assemblage used by the herbivore. Our study from a mixed grass prairie (36% C_4 grass composition) in South Dakota (Tieszen, et al., 1980) confirms the utility of this approach and identifies a potential difficulty. Bison (*Bison bison*) diets reflected the green biomass available, including 30 to 35% C_4 in July. However, very little C_4 biomass was consumed at other times of the year, including winter. Apparently frozen green C_3 species were preferred at that time. Therefore, the signal in bison feces and collagen was largely C_3 even though the floristic composition was 36% C_4.

This study is an initial step toward the reconstruction of paleoecological interpretations of vegetation and climate based on collagen delta ^{13}C values. We intend to document the communities available at WCNP and the delta ^{13}C values from free-ranging bison and other herbivores. These comparisons will be necessary to validate the relationship among floristic composition, vegetation distribution, and collagen delta ^{13}C needed to reconstruct past climates.

MATERIALS AND METHODS

A map of vegetation units was generated from USDA/SCS advance soil survey on a 1:56,000 black and white 1962 aerial photograph (WCNP files). Eighteen map units were recognized based upon field surveys conducted in 1981/82 and SCS soils and range site descriptions (USDA 1969, 1982). Map units were digitized into a geographic information system. The contribution of each map unit and range site to Park area was then computed. When portions of the landscape were characterized by fine-scale mosaics of vegetation/soil assemblages, the proportion of each of the types contributing to the mosaic forming the map unit was estimated. More detailed descriptions of soils and range sites can be found in the WCNP Conservation Plan (USDA 1969). Prairie dog colonies, which constitute approximately 10% of the Park area, were not included in the analysis or summary. Details on colony size, location, and vegetation can be found in Coppock, et al. (1980).

Selected plots were identified in several community types and sampled in July 1984 for biomass and delta ^{13}C values in an attempt to determine initial estimates of C_3 and C_4 composition. Two plots ($0.25m^2$) were clipped to 1 cm of ground level. All material was dried at 70°C; separated into live grass, live sedge, live forbs, and dead material; weighed; ground to pass a 20 mesh sieve; and analyzed for delta ^{13}C values. Fresh fecal material was collected at the same time from individuals of elk, bison, mule deer, pronghorn and prairie dog.

Bones were secured from surface or near surface specimens of natural deaths from bison and elk. These bones are samples of a taphonomic study in which the date of death, age at death, sex, and exposure conditions have been carefully monitored. Soil was removed manually from bone fragments followed by sonication in distilled water for 15 minutes. Samples were oven-dried at 50°C and then ground in a Wiley mill to pass through a 20-mesh screen. Acid soluble carbonates were removed from the pulverized samples by placing 2g of sample in 200 ml of 1 N HCl at room temperature for 24 hours with stirring. The pulverized bone was washed to neutrality with distilled water. To remove soil humic substances, the sample was placed in 1 N NaOH at room temperature for 24 hours and agitated frequently. The bone sample was washed to neutrality with distilled water. Collagen was solubilized from the bone by incubation in acidified water at pH = 3 at 90°C for 24 hours and stirred occasionally. The mixture was centrifuged at 3000 x g for 15 min and the supernatant was removed and dried at 60°C to obtain the collagen.

Collagen and plant samples were combusted to CO_2 for mass spectrometric analysis of $^{13}C/^{12}C$ according to Buchanan and Corcoran (1959). Eight mg of dried sample was placed in a backed-out length (16 cm) of 6 mm O.D. Vycor tubing. Samples were mixed with 0.5 g of oxidant ($CuO:MnO_2:CuCl_3$ in a 5:1:1 ratio) and a 1 cm length of silver wire. Sample tubes were evacuated to $<10^{2}$ mbar, and sealed. Sealed tubes were combusted in a muffle furnace at 875°C for one hour.

Combustion gases were admitted to the evacuated inlet of the mass spectrometer and cryogenically purified. Water vapor was removed by passing the sample through a dry ice trap prior to the collection of CO_2 in a liquid nitrogen trap. Remaining gases were pumped to waste. All analyses were performed on a Micromass 602E isotope ratio mass spectrometer. Results are expressed as:

$$\text{delta } ^{13}C\ ^{\circ}/_{\circ\circ} = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000$$

where $R_{standard}$ is the mass 45 to mass 44 ratio of CO_2 of carbonate from the PDB standard. The standard error of the combustion procedure was determined to be 0.14°/oo, while the standard error due to instrument effects was 0.05°/oo, for an overall precision of 0.2°/oo on each determination.

Table 1. Descriptions of the major range sites at Wind Cave National Park used as a basis for the vegetation/soil complexes in Figure 1.

Topography and Soils	Vegetation	
Thin Upland Sites		
Characterizes mid- and lower slopes of steep uplands in the northeastern portion of the Park. Soils deep but immature, with a thin dark colored surface layer over calcerous loam.	Bouteloua gracilis	25%
	Carex filifolia	25%
	Agropyron smithii	15%
	Stipa comata	15%
Shallow Sites		
Occurs on steep slopes and ridgetops with textures ranging from loams to clays. Soils often less than 50 cm deep over sandstone, quartzitic schists and granites. Rock outcrops common.	Andropogon scoparius	60%
	Bouteloua curtipendula	15%
	B. hirsuta	10%
	Carex filifolia	10%
Silty Sites		
Open parklands and level to gently undulating prairie uplands with 2 to 9% slopes. Soils dark and moderately deep to deep loams, silts and silty loams that may have loamy or clayey subsoils. Some occur over grey limestone.	Agropyron smithii	45%
	Stipa virdula	15%
	S. comata	15%
	Bouteloua gracilis	15%
Clayey Sites		
Found on gently sloping and steep uplands primarily in the northeastern portion. Soils are deep, dark colored clays on 2 to 9% slopes, deep stoney clays and clays on 6 to 25% slopes.	Agropyron smithii	55%
	Stipa viridula	20%
	Bouteloua gracilis	15%

Overflow Sites		
Alluvial soils along intermittent streams. Deep, dark loams and silty clay loams on slopes of 0 to 2%	Agropyron smithii Stipa viridula Bouteloua gracilis	50% 20% 10%
Stoney Hills Sites		
Soils are deep cobbly loams and deep stoney clays with cobbles and stones on the surface. Characterized topographically by rolling hills with 6 to 40% slopes.	Andropogon scoparius A. gerardi Stipa comata Bouteloua curtipendula	35% 20% 10% 10%

Ponderosa Pine Sites

The *Pinus ponderosa* vegetation type at Wind Cave National Park, comprising about 18% of the Park's land surface, can be broadly characterized into three groups. The pine-dominated sites occur primarily in the western half of the Park and their areal extent is shown in Table 3.

Group 1 (Ponderosa pine site index > 60). Continuous and closed canopy sites with poorly developed understories. Such stands are found on moderately steep slopes in the western half of the Park on deep stoney loams developed over schist and granite. Grasses, when present, are *Poa* spp. and *Stipa viridula.*

Group 2 (Ponderosa pine site index = 45 to 60). Clearly dominated by Ponderosa pine but grasses are much more abundant here than in Group 1. These sites, often found on northfacing slopes, have understories of *Andropogon gerardi, A. scoparius, Poa* spp.,*Stipa spartea, S. viridula,* and *Agropyron* spp. Soils are deep, stoney loams and silt loams developed under woodland conditions.

Group 3 (Ponderosa pine site index < 45). Thinly wooded sites with fairly complete graminoid understories of *Andropogon scoparius, Bouteloua curtipendula, Stipa comata*, and *Carex filifolia.* Soils are generally moderately deep loams showing some woodland influence and represent a transition between deep woodland soils and shallow grassland soil types.

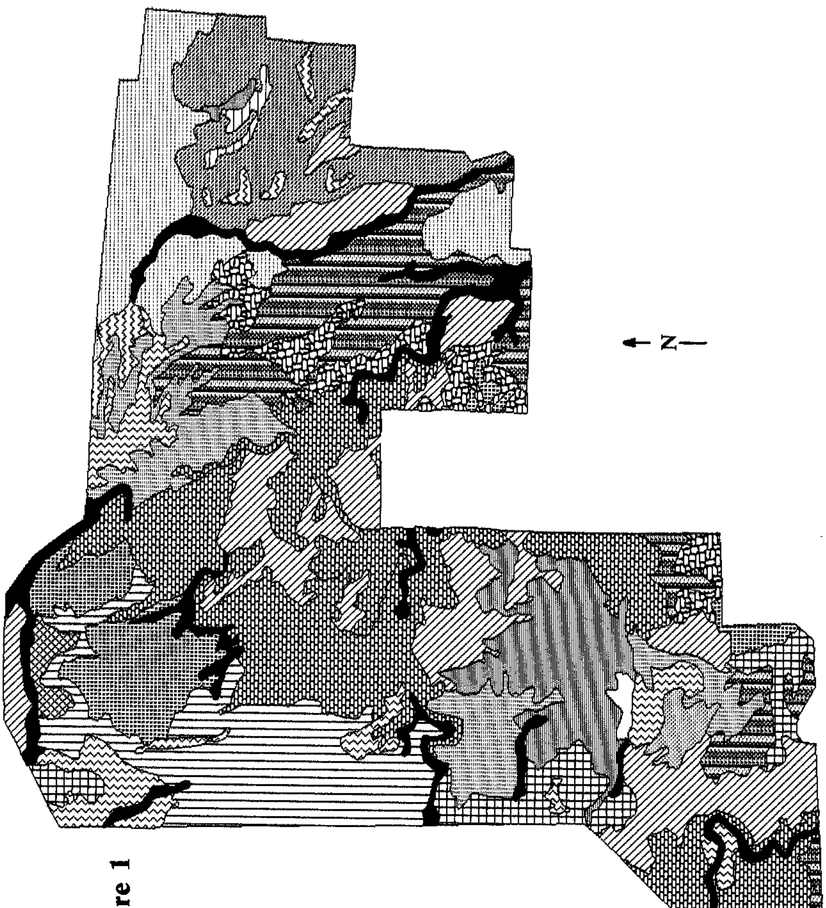
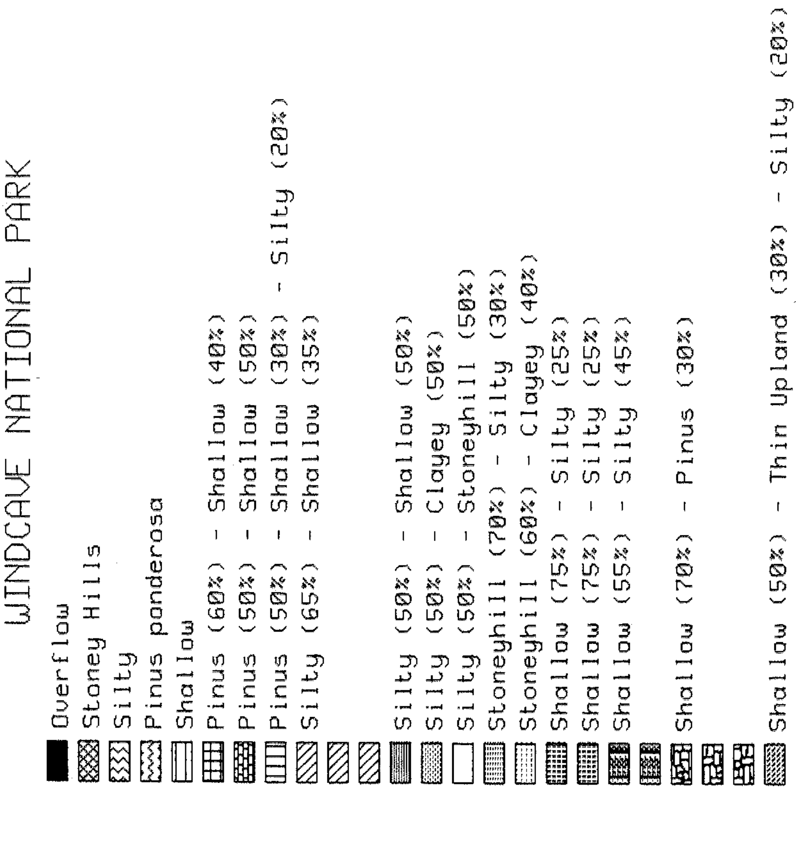


Figure 1


WINDCAVE NATIONAL PARK
Overflow
Stoney Hills
Silty
Pinus ponderosa
Shallow
Pinus (60%) - Shallow (40%)
Pinus (50%) - Shallow (50%)
Pinus (50%) - Shallow (30%) - Silty (20%)
Silty (65%) - Shallow (35%)
Silty (50%) - Shallow (50%)
Silty (50%) - Clayey (50%)
Silty (50%) - Stoneyhill (50%)
Stoneyhill (70%) - Silty (30%)
Stoneyhill (60%) - Clayey (40%)
Shallow (75%) - Silty (25%)
Shallow (75%) - Silty (25%)
Shallow (55%) - Silty (45%)
Shallow (70%) - Pinus (30%)
Shallow (50%) - Thin Upland (30%) - Silty (20%)

RESULTS

The distribution of eighteen vegetation map units identified from nine range sites are illustrated in Figure 1. Grasses clearly dominate these communities regardless of topography, except in the Group 1 ponderosa pine sites (Table 1). Tables 2 and 3 describe the areal extent and patchiness of the units. Units consisting of silty, shallow and ponderosa pine range sites make up around 80% of the vegetation-soil areas in WCNP. Thus, the major types are quite different and are dominated by C_3 grasses, C_4 grasses, or pines.

Table 2. Proportion and number of occurrences of vegetation/soil complexes (Figure 1 map units) within the boundary of Wind Cave National Park. "Pinus" refers to stands of *Pinus ponderosa*. See Table 1 for description of vegetation and soils associated with primary range sites.

Map Unit	% Cover	Number of Occurences
Overflow	5.3	11
Stoney Hills	0.6	1
Silty	4.7	10
Pinus ponderosa	1.1	6
Shallow	0.4	1
Clayey	0.0	0
Thin Upland	0.0	0
Pinus (60%)-Shallow (40%)	3.6	4
Pinus (50%)-Shallow (50%)	18.3	10
Pinus (50%)-Shallow (30%)-Silty (20%)	8.6	1
Silty (65%)-Shallow (35%)	13.1	12
Silty (50%)-Shallow (50%)	5.6	2
Silty (50%)-Clayey (50%)	0.7	2
Silty (50%)-Stoney Hill (50%)	0.2	1
Stoney Hill (70%)-Silty (30%)	6.9	4
Stoney Hill (60%)-Clayey (40%)	7.2	4
Shallow (75%)-Silty (25%)	5.1	6
Shallow (55%)-Silty (45%)	8.1	1
Shallow (70%)-Pinus (30%)	3.7	5
Shallow (50%)-Thin Upland (30%) -Silty (20%)	6.8	1

Table 3. Areal extent and proportion of the principal range sites, Wind Cave National Park. See Table 1 for descriptions.

Map Unit	Area (ha)	Proportion %
Herbaceous		
Overflow	595	5.3
Stoney Hills	1105	9.9
Silty	2983	26.8
Shallow	3934	35.3
Clayey	360	3.3
Thin Upland	228	2.1
Total	9205	82.7
Ponderosa pine Type		
2 only	43	0.4
3 only	482	4.3
2+3 mixed	889	8.0
1+3 mixed	514	4.6
Total	1928	17.2
Rock Outcrop	10	0.1
TOTAL	11143	100.0

The vegetation types differed markedly in the biomass available in each compartment during the July 10 period (Table 4). Grass dominated all sites except the mature prairie dog colonies and beneath closed ponderosa pine canopies (Group 1). Sedges were abundant on shallow, stoney hills, thin upland and open ponderosa pine sites but were uncommon on clayey and overflow sites. The dead compartment varied widely from 535 $g \cdot m^{-2}$ in productive overflow areas to low values in prairie dog colonies and in stoney hills and shallow communities.

Table 4. Biomass present during the July sample period ($g \cdot m^{-2}$). These estimates are derived from two samples each.

Range Site	Grass	Sedge	Forbs	Dead
Clayey	236.4	0	10	282.0
Overflow	203.6	0	0	535.2
Shallow	36.8	39.2	3.6	15.6
Silty	183.6	0	1.6	140.0
Stoney Hills (group 1)	90.0	14.8	20.8	61.2
Stoney Hills (group 2)	48.8	5.2	11.6	34.0
Thin Upland	78.0	40.8	29.6	81.6
Prairie Dog Colony	0	0	84.8	0
Ponderosa Pine (group 1)	8.0	0	33.2	211.2
Ponderosa Pine (group 2)	263.2	7.2	18.0	178.0

Table 5. Delta ^{13}C values for biomass compartments from Wind Cave National Park.

Range Site	Live Grass	Live Sedge	Live Forbs	Dead	Roots 0-15 cm	Roots 30-45 cm
Clayey		-25.4	na	-26.4	-24.0	-24.2
Overflow	-28.0	na	-27.0	-27.0	-26.0	-26.0
Shallow	-23.4	-27.0	-26.0	-21.3	-16.0	
Silty	-26.0	na	-27.0	-24.4	-22.3	-21.2
Stoney Hills (group 1)	-13.4	-26.0	-27.0	-14.0	-20.0	
Stoney Hills (group 2)	-14.0	-27.0	-28.0	-16.0	-16.0	
Thin Upland	-16.0	-26.0	-27.0	-19.3	-21.0	-22.0
Prairie Dog Colony	na	na	-27.0	na	-26.0	-26.0
Ponderosa Pine (group 1)	-27.0	na	-28.0	-25.0	-27.2	
Ponderosa Pine (group 2)	-14.0	-26.4	-17.1	-21.0	-20.0	

Table 5 summarizes delta ^{13}C values for each compartment in each plot. Forbs possess values around -27°/oo and are clearly C_3 with the exception of the open ponderosa pine site. The value of -17.1°/oo indicates the contribution of one or more C_4 species. Sedges are clearly C_3, averaging -26.5. The bulk live grass shows some variability and ranges from -13.4°/oo to -28.0°/oo. Both stoney hills sites are quite positive as are thin upland and open ponderosa pine sites. Other communities have grass compartments indicating strong dominance by C_3 species. These general differences are basically reflected in root samples as well. In addition, the pattern in the dead compartment is very similar to that of the live grasses, providing assurance that green biomass estimates are representative of annual contributions.

One-way analyses variance of fecal delta ^{13}C from the July 10 sampling indicated significantly ($P<0.001$) different food habits among herbivores (Table 6). Pronghorn (*Antilocapra americana*) show little variation with negative values around -27.4. Elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionius*) are similarly negative. Bison, however, had greater variability and were more positive, with a mean of -24.9°/oo. Black-tailed prairie dogs (*Cynomys ludovicianus*) showed substantial variation with a range of -17.1 to -27.1.

Table 6. Delta ^{13}C(°/oo) of fresh fecal material collected on July 10, 1984 from Wind Cave National Park. Means followed by same letter were not significantly different at $P<0.05$ based on Turkey's HSD test. SE = standard error; CV = coefficient of variation.

Herbivore	Mean	SE	CV	MAX	MIN	N
Pronghorn	-27.4 a	0.3	0.04	-24.4	-29.0	14
Deer	-26.9 a	0.3	0.03	-26.0	-28.3	10
Elk	-26.8 a	0.2	0.03	-25.0	-28.0	17
Bison	-24.9 b	0.6	0.08	-22.0	-28.0	14
Prairie Dog	-22.9 c	0.9	0.14	-17.1	-27.1	12

The bone material collected from bison and elk yielded ample collagen in most cases for spectrometric analysis. Delta ^{13}C values for bison collagen averaged -18.7°/oo (N=20) and showed little variation. Values for elk were slightly more negative (-19.0°/oo; N=20) than those of bison. There was no relationship between delta ^{13}C values and sex, exposure or age in either elk or bison.

DISCUSSION

The vegetation/soil complexes at WCNP consist of a diversity of types ranging from systems dominated by pines which grade into grasslands to a diversity of mixed grass units. Hardwood associations typical of riparian zones and ephemeral drainages in the region are poorly represented in the Park. Grassland complexes may be strongly dominated by C_3 species, typically *Agropyron smithii* and *Stipa* spp., as exemplified by the lowland clayey and overflow sites. Alternatively, well-drained topographic units with lesser developed soils are typically dominated by C_4 species, such as *Andropogon* and *Bouteloua*. The map units (Fig. 1) thus indicate substantial community diversity and heterogeneity which was reflected in our sample harvests for delta ^{13}C analyses (Table 5).

Delta ^{13}C values for sedges and forbs were low, verifying the dominance of the C_3 photosynthetic pathway in these taxonomic groups in the Great Plains area. The live grass compartment, in contrast, varies from low delta ^{13}C values to values indicative of strong dominance by C_4 species in stoney hills, thin upland and some ponderosa pine sites. These higher values likely represent the extreme positive C_4 signal to be derived from WCNP, since the sampling date (July 10) should be near the peak of C_4 biomass accumulation (Tieszen, et al., 1980). It is clear that some vegetation/soil complexes at WCNP should provide a strong, C_4-dominated signal to herbivores, especially grazers. Browsers, on the other hand, should reflect C_3 biomass regardless of the units in which they feed.

The fecal analyses from this single collection verify this assumption (Table 6). Pronghorn show no C_4 signal at this time and are clearly feeding only on forbs or C_3 grasses. In contrast, elk and mule deer both show some dependence on C_4 species at this time but only a minor one. Bison are 2.5°/oo more enriched in ^{13}C than pronghorn, indicating a significant, though not extensive, dependence on C_4 species at this time. This is in agreement with diet studies of Peden (1976) on shortgrass prairie. Bison also showed substantially more variation than other ungulates, suggesting a more generalized foraging strategy. Prairie dogs had highest mean delta ^{13}C values but variation was great. The individual with 17.1°/oo for example, had consumed approximately two times more C_4 food than C_3 food. The wide range observed in prairie dogs likely reflects vegetation differences associated with colony location and maturity (Coppock et al. 1980).

Interestingly, the mean collagen values for elk and bison are very similar suggesting a comparable annual dependence on C_4 plants. This surprising similarity is not indicated in the fecal determinations from the July sample period (Table 6). Apparently, bison and elk converge more on C_4 food resources during other times of the year. In addition, collagen values are biased +5°/oo relative to diet (Tieszen, 1987; van der Merwe, 1982). Therefore, our numbers suggest the annual dependence of bison and elk on C_4 grasses exceeded that of the July sample period. At this time we have no way of knowing when this greater utilization might occur. Late July and August may be one such period. At this time of year, C_4 species dominate many sites and the C_3 species on others exhibit low productivity.

The data presented suggest it will be possible to relate collagen and fecal delta ^{13}C values to available vegetation. We could calculate a crude Park estimate of vegetation delta ^{13}C for each plant compartment for July 10. However, such a calculation based on so few data points would be quite meaningless. Weighted values for major vegetation/soil complexes at frequent time intervals will eventually allow us to derive a mean annual delta ^{13}C for WCNP. This value will serve as a base to which annual dietary estimates can be compared. Selectivity of C_3 or C_4 species will then be apparent; however, we will not know whether these resulted from species or habitat preferences.

Bone collagen should integrate and reflect the vegetation present during an individual's lifetime. Thus, once the relationship between the delta ^{13}C of collagen and available vegetation is determined, it may then be possible to reconstruct prehistoric patterns of vegetation and climate from fossil collagen. For example, Chisholm et al. (1986) have attempted to establish migratory behavior by the C_4 signal present in bison collagen from C_3-dominated areas. We would expect past, cooler climates to have favored C_3 plants and warmer climates C_4 plants. The corresponding changes in the isotopic labels should be apparent in collagen of "obligate" grazers. As such, the technique holds the possibility of quantifying paleotemperature changes. Vegetation changes associated with changing rainfall patterns are less clear, but would likely approach tallgrass systems with more moisture and shortgrass systems with greater aridity. Corresponding changes in the isotopic signals in this case would be less certain.

In summary, the mosaics of vegetation complexes in WCNP are likely responsive to climatic change. Shift in vegetation resulting from climatic change should result in different isotopic signatures in the collagen of dominant grazers. Analyses of collagen from historical and fossil bone may therefore allow us to reconstruct past vegetation assemblages and to make inferences about paleoclimates.

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