COMMUNITY AND SOIL ORGANIC MATTER STABLE CARBON ISOTOPE RATIOS: FOREST-GRASSLAND TRANSITIONS AT WIND CAVE NATIONAL PARK

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ABSTRACT

The analysis of past records and photographs shows the dynamic nature of the prairie to forest transition in the Black Hills of western South Dakota. In recent years the ponderosa pine forest has been advancing into prairie. Mature trees and the underlying ground cover are predominantly C_3 species. If these systems are climax and have reached a steady state, they should possess soil organic matter with a $\delta^{13}C$ value ranging from -25‰ to -28‰.

Systems which are strictly C_4 should produce a $\delta^{13}C$ signal around -12‰. Therefore, prairie systems, due to their mixture of C_3 and C_4 grasses, should produce an intermediate signal. We described the isotopic composition of the roots, mulch, and soil organic matter in the dominant communities at Wind Cave National Park in an attempt to define the successional status of the forest grassland boundary.

Soil $\delta^{13}C$ values in all communities except the mature forest were significantly different from root and mulch values. The soil values were 1 to 5‰ more enriched in ^{13}C. There is a tendency for soils under pine forests to be more negative than those under prairie at Wind Cave National Park; however, the soils did not display a $\delta^{13}C$ value that was as negative as those received from deep forest samples taken in the heart of the Black Hills. These isotopic results suggest that present forests in Wind Cave National Park are growing on soils that once supported a mixed prairie system.

INTRODUCTION

All plants can be placed in one of three categories -- C_3, C_4, or CAM, -- depending on the type of photosynthetic metabolism they possess. Each photosynthetic type has a characteristic natural $^{13}C/^{12}C$ ratio. The $\delta^{13}C$ values of C_3 plants range from -25‰ to -30‰ with the majority being -26‰ to -28‰; C_4 plants also range broadly but most possess a value around -12°/$_{oo}$ (Cerri et al., 1987, and Tieszen et al., 1988). CAM plants range from -12°/$_{oo}$ to -26°/$_{oo}$. These characteristic isotopic signals can be transmitted throughout the ecosystem in mainly two ways. Plants are consumed by herbivores and grainivores and consequently their characteristic signal is incorporated into the animals' body tissues as well as excreted in their wastes. Secondly, ungrazed plants die, decompose, and contribute their signal to the soil organic matter (SOM).

Balesdent et al. (1987, 1988) have shown that SOM consists of various fractions with varying turnover rates. Some fractions remain in the soil for long periods of time before they become completely broken down or are replaced. The results from these studies showed that after continuous cultivation of corn for 13 years on soil where a forest once stood 78% of the original organic matter still remained in the bulk soil sample (Balesdent et al., 1987). In a study in North America, soil which once supported a stable mixed prairie but had for the past 100 years been cultivated with C_3 crops showed evidence of containing no less than 50% of the original carbon (Balesdent et al., 1988).

The analysis of past records and photographs, particularly pages 98, 110, 132, 136, and 146 in Walter S. Phillips *Vegetational Changes in Northern Great Plains* (1963), clearly shows the dynamic nature of the prairie to forest transition in the Black Hills of western South Dakota. In Wind Cave National Park, where this study was conducted, the boundary between forest and prairie has fluctuated as a result of continual recent encroachment of the forest into the prairie. Current fire management practices are designed to restrict this advance of Ponderosa Pine. Since we are aware that the bulk soil organic matter and the characteristic $\delta^{13}C$ value which it possesses remains in the soil for a relatively long period, we should be able to analyze this organic matter and tell what type of vegetation has grown at that particular location in the past.

Soils from climax areas which appear to have reached a steady state, such as deep old standing forests and open prairies, should show delta values similar to the characteristic vegetation growing on them. Therefore, old forest soils are expected to have a delta value around -26°/$_{oo}$ because nearly all trees are C_3, while soil samples taken from an ecotone should have a more positive value if it indeed has periodically supported forest and prairie. Open prairie soils should have a value between -12°/$_{oo}$ and -26°/$_{oo}$ depending upon the specific mixture of both C_3 and C_4 vegetation. At the same time, we expect to find different steady state prairie community types to have different values due to the different ratio of C_3 to C_4 vegetation they support.

This study attempts to determine if variations in SOM carbon isotope values can be described among different communities located at Wind Cave National Park (WCNP). We apply this technique to determine historical or pre-historical distributions of forests and grasslands at WCNP by looking at several long term ecotones.

STUDY SITE

Community data were collected from five differing range types in the west central part of WCNP, on the southeastern edge of the Black Hills in southwestern South Dakota. Transects were taken along a prairie, ecotone, deeper forest continuum located on the east and west side of Rankin Ridge within the park. The park topography ranges from 1,111 m in the southeast to 1,528 m in the northwest. Mean annual precipitation for the park is 450 mm, of which 70% occurs between May and September, and air temperature during the year ranges from 21°C in July to -5°C in January. Nearly 25% of the 11,355 acre park contains pine forest dominated by *Pinus ponderosa* and the remainder is mixed-grass prairie. Graminoid constituents of the prairie include blue-grasses (*Poa* spp.), western wheatgrass (*Agropyron smithii*), needlegrasses (*Stipa* spp.), grama grasses (*Bouteloua* spp.), bluestems (*Andropogon* spp.), and sedges (*Carex* spp.). Major forbs include white sagewort (*Artemisia ludoviciana*), scurfpeas (*Psoralea* spp.), and goldenrod (*Solidago* spp.). Fringed sagewort (*Artemisia frigida*), western snowberry (*Symphoricarpos occidentalis*), lead plant (*Amorpha canescens*), and wild rose (*Rosa* spp.) are the principle prairie shrubs. Summaries of the climate and the vegetation for dominant range sites in WCNP are provided by USSCS (1969) and Lovaas and Bromley (1972) as seen in Coppock et al. (1983).

MATERIALS AND METHODS

C_3 and C_4 vegetation cover and relative C_4 cover were determined using a quarter square meter plot frame in each of eight replicated sample sites for the five community types (Table 1) identified by Tieszen et al. (1988) in WCNP. For all but two plots located in the pine community at WCNP, tree and sapling densities (number/hectare) were determined using the point quarter method, and the tree breast height circumferences were measured. Soil, mulch, and roots were also collected. For comparison we also selected and sampled two sites from a recently logged, deep forested area of the Black Hills National Forest near Custer. This mature pine forest is assumed to approach the steady state SOM and vegetation values for carbon isotopes.

In addition to the five communities, we sampled transects through old forested, ecotone and open prairie in selected areas east and west of Rankin Ridge. The tree and sapling densities for these areas were calculated using the point quarter method, and the breast height

Table 1. Descriptions of the major range sites and their areal percentage at Wind Cave National Park (Modified from Tieszen et al., 1988).

Topography and Soils

Shallow Sites - 37.31%
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.

Silty Sites - 28.29%
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.

Overflow Sites - 5.64%
Alluvial soils along intermittent streams. Deep, dark loams and silty clay loams on slopes of 0 to 2%.

Stoney Hills Sites - 10.48%
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.

Ponderosa Pine Sites - 18.28%
The *Pinus ponderosa* vegetation type at Wind Cave National Park can be broadly characterized into three groups. The pine-dominated sites occur primarily in the western half of the Park.

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 gerrardi*, *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.

Table 2. Calculated mean tree breast height circumferences and mean density in number/hectare for forested areas along transects on Rankin Ridge. Similiar lower case letters beside mean values indicate no significant difference at p<.05 based on the Fisher PLSD test, one factor ANOVA.

	Tree Mean B.H.C. (centimeters)		Density (numbers/hectare)			
	Forest	Ecotone	Forest		Ecotone	
			Trees	Saplings	Trees	Saplings
West side						
Transect 1	112.2	137.8	6543	3019	2260	2210
Transect 2	84.6	70.5	1720	2717	1647	2061
Transect 3	74.4	57.1	5109	2873	1194	3566
Transect 4	35.3	68.2	8138	2625	4318	1898
Mean	62.7	115.1	6577	2453 a	3135	2900 a
East side						
Transect 1	72.4	76.3	10424	5625	2400	3341
Transect 2	35.3	125.6	4393	1320	3432	2328
Transect 3	91.0	103.9	4209	3094	3683	2667
Transect 4	70.0	84.0	4574	2476	2873	2949
Mean	87.2 a	77.6 a	7011	2345 b	3269	3150 b

circumferences of the trees were measured (Table 2). Mulch was collected from each sample site before taking soil samples. Due to the rocky conditions, soil was sampled only to a depth of 15 to 25 centimeters. These samples were obtained by digging a hole and using a hand trowel to get nearly proportional amounts of soil down the entire profile. Roots were separated from the soil samples with a 2mm sieve.

Soils were decarbonated with 1M HCl. After settling, the HCl and remaining suspended soil particles were centrifuged at 45500 x g for 10 minutes to recover the smallest particles of soil. The soil pellet was then returned to the bulk soil sample which was rinsed twice with 10 ml distilled water. After each rinsing, the suspended soil particles were recovered from the distilled water using the same recovery procedure. The bulk soil sample was then dried. Roots were washed to remove dirt particles, dried, and ground using a Wiley mill and a 20 mesh screen. Mulch samples were dried and ground using the same method.

Fifteen to eighteen mg soil samples and 1.5 to 2 mg root and mulch samples were loaded into tin capsules using a CAHN C-30 Micro Balance. The capsules were put into a Carlo Erba NA 1500 Nitrogen/Carbon Analyzer autosampler. Individual samples were fully combusted in a 1020°C combustion reactor. After passing through an oxidation catalyst and a reduction reactor the sample was admitted into a VG Sira 10 Isogas Isotopic Ratio Mass Spectrometer for analysis.

The sample gas molecules were ionized, formed into a beam, accelerated by an electric field, deflected in a magnetic field, and finally collected by the mass spectrometer.

The collected sample was then compared to a reference gas of known CO_2 isotopic ratio, and results were expressed as:

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

where R_{standard} is the mass 45 to mass 44 ratio of CO_2 of carbonate from the PDB standard.

RESULTS

Graphs in Figure 1 show the individual delta values for soil, roots, and mulch for each WCNP community and the mature pine forest. Arrows indicate our estimate of the annual contribution of biomass by C_3 and C_4 species weighted for abundance at biweekly intervals through one year (Tieszen, unpublished). This seasonally weighted value should approximate the carbon isotope signal going into SOM. Notice that soil $\delta^{13}C$ values are usually more positive than their associated root or mulch values. There were only two samples from all the communities in which soils did not have the most positive value. A one factor analysis of variance (Table 3) indicates that the mean values for soil are in fact always more positive, often by 3 to 4°/$_{oo}$, than the roots and more positive than the mulch in silty, shallow and pine communities. This is more clearly seen in the summarized data (Figure 2).

From the graphs in Figure 1 and 2, we see that even the soil $\delta^{13}C$ values from the pine community are more positive than the roots and mulch. Table 3 ANOVA shows that soil is actually between 5°/$_{oo}$ and 6°/$_{oo}$ more enriched in ^{13}C. All the pine communities where samples were taken fell in Group 3 of the ponderosa pine description in Table 1 with an average tree mean breast height circumference of 94.1, SE±19.9cm. The calculated mean tree density (number/hectare) was 2,359, SE±667, and the average sapling density was 3,196, SE±2,488. Only in the mature pine from outside WCNP did we find no difference among $\delta^{13}C$ values of soil, roots, and mulch. Simple regression

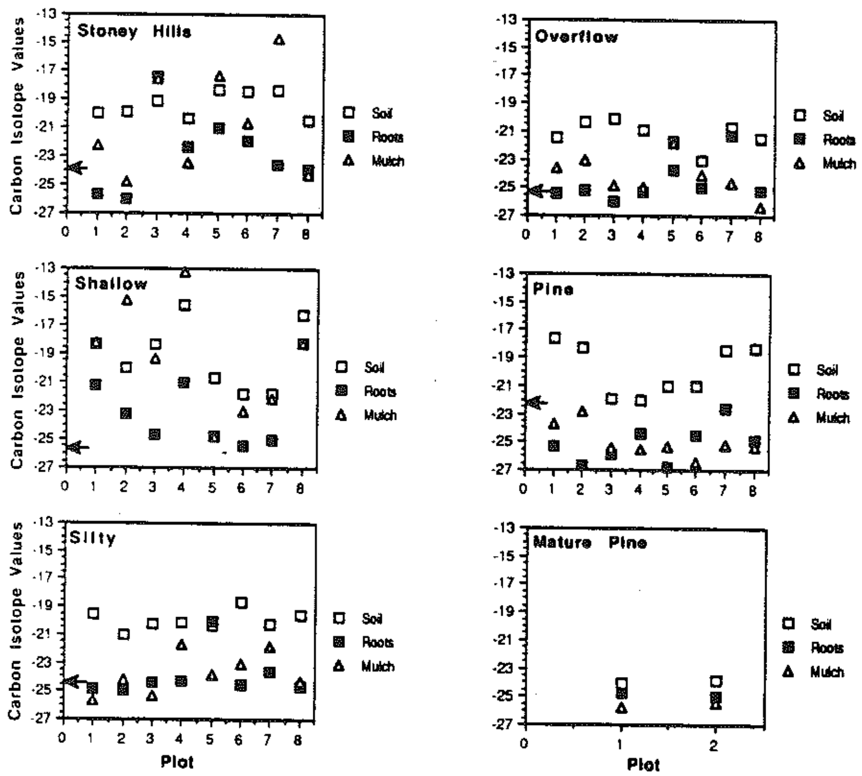

Figure 1. Carbon isotope values, °/$_{oo}$, for soil organic matter, roots, and mulch from each of eight plots within each community. Arrows indicate the calculated seasonal weighted biomass for that community. Mature Pine was taken from an old forest near Custer, S.D.

Table 3. Mean carbon isotope values for soil, roots, and mulch components of each community. Same letters indicate no significant difference at $p<0.05$ based on the Fisher PLSD test, one factor ANOVA.

Component	Stoney Hills	Shallow	Silty	Overflow	Pine	Mature Pine
Soil	-19.4 a	-19.1 a	-20.0	-21.2	-19.8	-23.9
Roots	-22.7 b	-22.9	-23.9 a	-24.6 a	-25.1 a	-24.8
Mulch	-20.6 a b	-19.2 a	-23.7 a	-24.2 a	-25.0 a	-25.6
F=	16.4	4.1	22.2	7.6	34.0	1.6 (n.s.)

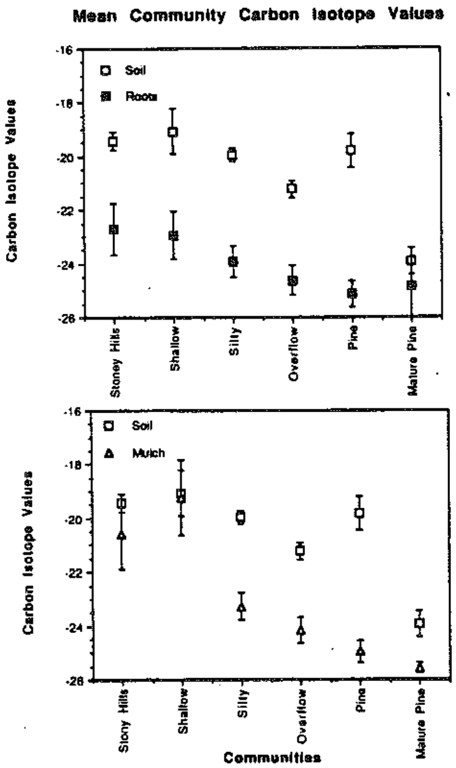

Figure 2. Mean community carbon isotope values and standard errors for SOM, roots, mulch for each community.

Table 4. Mean % cover for C_4, C_3, and relative %C_4 cover for the five WCNP communities. %C_4 and C_3 equal the sum percentages for each individual species. Probability tests whether the slope differs from zero for relative %C_4 against soil organic matter $\delta^{13}C$ for each community.

Community	C_4	C_3	Relative %C_4	Probability
Stoney Hills	23%	39%	37%	.63
Shallow	22%	38%	37%	.10
Silty	17%	63%	21%	.38
Overflow	06%	49%	11%	.25
Pine	02%	72%	02%	.23

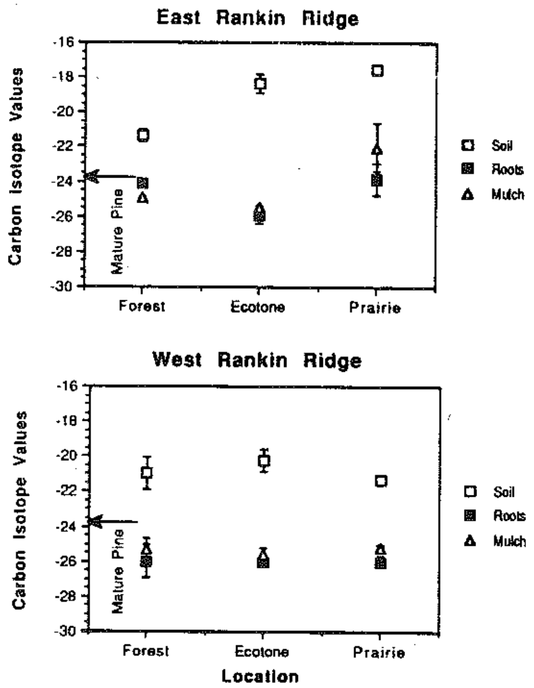

Figure 3. Mean carbon isotope values for four transects on both east and west sides of Rankin Ridge from the most closed forest to open prairie.

Table 5. Analysis of variance comparing the $\delta^{13}C$ values of soil, root, and mulch components among the different communities for each of the four transects. Similiar lower case letters indicate no significant difference between the same components within each area at $p<.05$ based on the Fisher PLSD test, one factor ANOVA.

	West side of Rankin Ridge			East side of Rankin Ridge		
Component	Soil	Roots	Mulch	Soil	Roots	Mulch
Prairie	-21.3	-26.0	-25.3	-17.6 a	-23.9	-22.0
Ecotone	-20.3	-26.0	-25.6	-18.4 a	-25.9	-25.5 a
Forest	-20.9	-26.0	-25.3	-21.3	-24.1	-25.0 a
F=	.7 (n.s)	<.1 (n.s.)	.2 (n.s.)	24.8	3.6 (n.s)	5.1

Table 6. Analysis of variance comparing the δ^{13}C values of pooled soil, root, and mulch components from the same community from the four transects for both east and west Rankin Ridge areas. Same lower case letters indicate no significant difference at $p<.05$ based on the Fisher PLSD test, one factor ANOVA.

	West side of Rankin Ridge			East side of Rankin Ridge		
Component	Soil	Roots	Mulch	Soil	Roots	Mulch
Soil	-21.3	-20.3	-20.9	-17.6	-18.4	-21.3 a
Roots	-26.0 a	-26.0 a	-26.0 a	-23.9 a	-25.9 a	-24.1 a
Mulch	-25.3 a	-25.6 a	-25.3 a	-22.0 a	-25.5 a	-25.0
F=	95.5	54.1	10.8	11.2	108.6	51.4

comparisons of the δ^{13}C values of soil, root, and mulch components for each of the WCNP communities showed no correlation among them with the exception of soil and mulch samples from the Stoney Hills community, and between soil and roots as well as soil and mulch components of the Shallow community. A one factor ANOVA test comparing soil (F=2.37, p=.07) and roots (F=2.10, p=.11) from the different WCNP communities showed that we could not distinguish between the communities on the basis of soil or root δ^{13}C values. However, a comparison of the mulch δ^{13}C values from different communities (F=7.01, p<.01) showed that they were statistically different from one another in agreement with different estimates of annual inputs (Figure 1).

Table 4 summarizes mean %C_3, %C_4, and relative %C_4 cover for each of the WCNP community types. A simple regression comparing the relative percent cover by C_4 species in each individual plot to the δ^{13}C values generally shows no significant relationship. Only in the Silty community is there a significant correlation between the δ^{13}C value and the relative %C_4 cover.

Figure 3 compares the mean soil, mulch, and root δ^{13}C values from four deep forest, ecotone, open prairie transects taken in two areas. The mean δ^{13}C soil value of the mature pine is shown to identify the representative δ^{13}C signal we would expect to receive from forest soils approaching a steady state. The δ^{13}C values from the east Rankin Ridge soils become more negative (Figure 3) from the prairie to forest. An ANOVA (Table 5) comparing the same components from different communities along the transects shows that the prairie and ecotone soils were significantly more positive than the forest soil. Roots did not differ among communities. Prairie mulch was significantly more positive than either the ecotone or forest mulches. The ANOVA

results from west Rankin Ridge showed no statistical differences among any of the communities. Roots, soil and mulch values were similar. We then compared the δ^{13}C values of soil, root, and mulch components within each community along the four transects in each area. In east Rankin Ridge area the prairie and ecotone soils were significantly more positive than the root and mulch components; and in the forest community the soil is statistically more positive than mulch. Results comparing the west Rankin Ridge area components show that in each community soils are more positive than roots and mulch.

DISCUSSION

The five main communities at WCNP have similar soil δ^{13}C values even though the vegetation composition differs markedly. This difference in present aboveground biomass is also suggested by the mulch values which do differ among the communities. The similar soil organic matter values suggest that in the past the communities possessed similar vegetation or that various vegetation assemblages (C_3 and C_4 mixtures) moved across the landscape. Climatic, nutrient, or herbivore (Cid, et al. 1981) induced changes in grass mixtures from one community to another through time could explain the similar δ^{13}C SOM values we see today under different communities. The more positive soil δ^{13}C values than the root and mulch values in the same WCNP communities suggests that there was a higher contribution by C_4 grasses to the SOM in the past, even in the landscape positions occupied today by ponderosa pine.

Results of the simple regression comparison (Table 4) between the communities' relative %C_4 and their respective δ^{13}C values lends support to our hypothesis. If present day communities, with their characteristic mixture of C_3 and C_4 grasses, were to remain in the same location for several hundred years, we would expect the SOM underneath these communities to have a more negative δ^{13}C value, one which is comparable to the seasonal weighted biomass value we calculated using vegetation productivity data from Tieszen et al. (unpublished). Similarly, we would expect to see a correlation between the SOM δ^{13}C value and the relative amount of C_4 in each community. Results from the transects along Rankin Ridge lead us to the same conclusion. The similar SOM δ^{13}C values suggest that at one time each supported vegetation containing more C_4 components. The forest data from the west Rankin Ridge area (Table 2) did show, as we would expect, that there was a significant difference in the density of the trees in the location where we took our deep forest samples compared to the selected ecotone area. These findings fit our assumptions that the trees occupying the sites where we took our deep forest samples were older than the trees in the ecotone. However, the breast height circumference results showed the ecotone trees were larger in circumference than the deep forest trees. We attribute this to possibly less competition for resources in the ecotone which may be due to thinning by fire, thus resulting in the younger trees being able to exceed the breast height circumference of the trees in the deep forest. Even though we think that the deep forest trees were older than the trees in the ecotone, the positive nature of the forest soils' $\delta^{13}C$ value in this area suggests that the forest has not been there long enough to dominate the bulk SOM. Confirmation of this, however, awaits tree core dating and dating of SOM. In east Rankin Ridge the soil $\delta^{13}C$ from the forest is significantly more negative than the soil from the prairie, but it still is not as negative as the soil from the heart of the Black Hills National Forest. This suggests that the soil under this forest also once supported a community which had more C_4 vegetation.

The SOM values from the best developed forests in WCNP are more positive than those from the heart of the Black Hills suggesting a more recent establishment of forest at WCNP, similar to that proposed for the Niobrara in Nebraska (Steuter, et al. 1990), and a more recent displacement of a C_3-C_4 prairie mixture. If this interpretation is correct, a detailed soil particle size fractionation (Martin, et al. 1990) and carbon isotope analysis would show a predictable pattern. Pools (Parton, et al. 1987) which turn over quickly (1-15 years) should bear the recent signal, that of C_3 trees, around $-26^{\circ}/_{oo}$. Pools which are recalcitrant and may have half lives of several hundred to a 1000 years should reflect the older signal, a more positive one from the C_3 and C_4 grass mixture. Carbon-14 dating of these same fractions would provide a rough estimate of the dates for these conversions.

One other explanation is possible. There is evidence (Stout, et al. 1975; Nadelhoffer and Fry, 1988) that $\delta^{13}C$ enrichment occurs with depth during decomposition and SOM formation. When enrichment occurs, however, it is minor (1 to $2^{\circ}/_{oo}$) and less than the departures we have found. This 1 to $2^{\circ}/_{oo}$ enrichment is consistent with the enriched value we see in the most mature pine forests in the Black Hills, thus, we do not believe enrichment during decomposition can account for our results.

Since the soil $\delta^{13}C$ values in both the community study as well as the transect study tended to be significantly more positive than SOM from the mature forest and their respective root and mulch values, we believe that the park has been grassland containing a large C_4 constituent or grassland-pine mosaic for much of the Holocene. Confirmation of this awaits size fractionation isotope analysis of the SOM. Our interpretations are contrary to White et. al (1969) who suggests that the soil structures in WCNP appear to have developed under forest. Presently, there is no isotopic evidence to suggest present grassland on former forest systems.

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