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CHARACTERISTICS OF LITTER DECOMPOSITION IN THE GRASSLAND BIOME OF THE UNITED STATES

Janet Schnauss and C. L. Kucera

University of Missouri

Columbia, Missouri

GRASSLAND BIOME

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ABSTRACT

Carbon-14 labelled leaf litter (big bluestem, *Andropogon gerardi*, harvested green from the Tucker Prairie, Missouri) was placed in several sites in the U.S. Grassland Biome. Thirty-six bags were placed on the ground in January 1973, and triplicates retrieved at 3-month intervals through 1975. Bags were analyzed for dry weight loss and ^{14}C loss for the first 2 years of the experiment. From these data, half-life ($T_{1/2}$), and K, the decay constant, were calculated for each site (annual grassland, San Joaquin, California; shortgrass prairie, Pawnee Site, northeastern Colorado; tallgrass prairie, northcentral Missouri; high-mountain grassland, Bozeman, Montana; mixed-grass prairie, Cottonwood, South Dakota; desert grassland, near Las Cruces, New Mexico.

The following results were obtained. ^{14}C label disappeared faster than dry weight, presumably due to faster loss of soluble carbon compounds in the litter. Decomposition was highly variable, but could be explained largely as a function of temperature and precipitation. Temperature is an overriding variable controlling decomposition on mesic sites, whereas temperature and moisture, in combination, are more important on the more xenic sites.

Introduction

The Grassland Biome in the United States includes tallgrass, annual, shortgrass, mixed prairie, and mountain grasslands. This extensive region ranges from Indiana and portions of Ohio westward to the Rocky Mountains and beyond. Widespread areas such as these are subject to climatic variations. Similarly, this wide range of environmental conditions plays a major role in ecosystem dynamics. Rates of decomposition and nutrient recycling are especially influenced by temperature and moisture conditions. Warm, moist climates enhance decomposition rates, whereas, cooler and/or drier climates would have a retarding effect.

Climatic conditions determine the kinds and activities of organisms of a region and these organisms in turn contribute to soil development. The interaction of these biotic and abiotic components of the ecosystem involves two basic ecological processes, energy flow and nutrient movement. Energy flow is unidirectional and noncyclic, while nutrient movement is renewable and cyclic. Nutrient movement and mineral recycling is brought about by the process of decomposition. Essentially, this process is the mineralization of organic matters or the transferring of organically bound nutrients to their available inorganic status. In order to be available for recycling, decomposition of organic matter involves a three step process:

1) formation of particulate detritus by physical and biological action

2) production of humus and release of soluble organics by micro-organisms

3) slower mineralization of humus by micro-organisms

Organic turnover and development of soil organic matter thus are processes affected by the physico-chemical environment and the biotic assemblage. Temperature and moisture are key factors in the rate at which these processes occur at any point in the climatic gradient. The transition from east to west from tall to shortgrass is correlated with increasing aridity, a result of reduced rainfall coupled with increased evaporation. The regularity and amount of precipitation decreases from the tallgrass prairies westward to the plains. Rainfall in the tallgrass prairie, as well as the plains, is reduced toward the end of summer, but in the eastern portion of the Grassland Biome the pattern of temperature and rainfall is comparable to that of the deciduous forest. Since the annual P/E ratio averages less than 1.0 in the grasslands, compared to forests, mineral leaching is considerably less than on eastern soils on which forests occur. Grassland soils, thus, are among the most fertile in the world. This upper portion remains neutral to slightly alkaline because of the continued replenishment of cations like Ca and K through the upward movement associated with evaporation and uptake by roots. Westward, the conditions are not so much a limitation of nutrients, but rather increasing aridity.

The present study was initiated in 1970 in cooperation with the International Biological Program as part of an overall plan for ecosystem analysis of grasslands in the United States. In an effort to more fully understand the processes of decomposition and organic turnover, several questions were posed about this particular aspect of ecosystem dynamics. Since differences in decay occur across a climatic gradient, the question is asked how much variation in decay of plant residues occurs at designated sites within the Grassland Biome? Subsequently and intimately related is formation of soil organic matter. As a basic consideration here, is how much does plant residue from surface litter contribute to soil organic matter? The input of organic matter, of course, varies from place to place because of differences in temperature and rainfall. Lastly, what is the extent of accumulation of organic matter in the soil at the different sites and how does this accumulation relate to the decay factor? Specifically, the objectives were:

1) To determine dry weight losses of simulated litter samples at three month intervals over a three year period at selected sites in the Grassland Biome.

2) to determine losses in radioactive carbon in litter samples over the same time period which carried an initial label of known activity

3) to assess the effects of temperature and moisture on the decomposition processes at the several sites

4) to calculate the decay constant for organic decay from observations based on attrition in 1) dry weight and 2) total carbon-14 activity over comparable decay periods

5) to provide information on the relative importance of surface detritus to the development of soil organic matter in grassland systems.

REVIEW OF LITERATURE

Grasslands, as terrestrial ecosystems, are characterized by functional attributes of decomposition and turnover of organic matter. Depicting carbon turnover through trophic structure is a prerequisite to understanding both of these processes. Hence, these biotic and environmental factors pertinent to decomposition of organic matter and subsequent soil development assume great importance in rates of litter accumulation, organic breakdown, and recycling of nutrients. In recent years, the use of Carbon-14 as a tracer has been shown to play a significant role in measuring rates of transfer.

ENVIRONMENTAL FACTORS AFFECTING DECAY RATES

Waksman and Gerretsen (1928) early recognized the significance of temperature in the decomposition process. It markedly modifies the nature and rapidity of decomposition of plant remains in the soil, which exerts an important influence upon the nature and abundance of the organic matter. The lower the temperature the greater will be the accumulation of organic matter in the soil, within certain limits. The higher the temperature, the more rapid is the breakdown of the plant material.

At the same time Tenney and Waksman (1928) found the rapidity of decomposition of different organic substances also depended upon

1) chemical composition of the organic material, which in the case of plants and plant remains depends primarily upon the nature and age of the plant as well as upon the conditions of its nutrition

2) presence of sufficient nitrogen to enable the micro-organisms bringing about the decomposition to carry out this process in the shortest possible time

3) nature of the micro-organisms active in the decomposition process

4) environmental conditions at which decomposition is carried out, especially aeration, moisture supply, soil reaction, and the temperature

Waksman (1929) established 5 to 30° C as the temperature range for active decay of plant materials. He demonstrated a decrease in decomposition rate with decreasing temperature.

Kononova (1961) found activity of microbes increases with increasing temperature from 0 to 35° C being optimum. Optimum moisture level of soil micro-organisms of 60-80% of the maximum water holding capacity. The greatest intensity of decomposition of organic matter calculated from amounts of CO_2 in soil air is 30° C and with a moisture level of about 30% of soil weight corresponding to 60-80% of maximum moisture holding capacity.

ROLE OF MICROORGANISMS IN DECOMPOSITION

Micro-organisms occur freely in the soil. They prevent the buildup of large quantities of biomass. Oosting (pp. 216-217, 1956) stated that although the importance of soil micro-organisms to natural plant communities cannot be evaluated accurately, their significance is indicated by their general function of making nitrogen available through fixation or releasing it with other nutrients through their activities in decomposing organic matter. All nitrates appearing in the soil from sources other than fixation are products of organic decomposition, especially proteins. This breakdown involves a series of chemical changes in which the chemical composition of the new compound formed is different from that of the plant material from which it was obtained. These newly formed decomposition compounds are relatively high in nitrogen content and play a significant role in soil development.

Ivarson and Stevenson (1964) indicated that 70% of Carbon-14 acetate added to soil is assimilated into microbial tissue and deposited in the carbon compounds of humus within six to nine hours after incubation.

They concluded:

> "In the formation of humus or soil organic fractions micro-organisms play a major role: they effect the decomposition of the original plant and animal residues with a concomitant synthesis of the microbial tissue."

Numerous studies have been concerned with the processes of decomposition of many kinds of plant products. These include Waksman and Tenney (1927), Tenney and Waksman (1929), Waksman and Gerretsen (1931), Norman (1932), Russel (1961), Alexander (1961), and Tribe (1962).

Mineralization of organic matter is affected by a number of factors. Alexander (1961) stated:

> "The rapidity with which a given substrate is oxidized will depend upon its chemical composition and the physical and chemical conditions in the surrounding environment. Temperature, oxygen supply, moisture, pH, available minerals and the C:N ratio of the plant, its lignin content, and the degree of disintegration of the substrate presented to the microflora also govern decomposition."

DECOMPOSITION RATES AND RELATIONSHIPS UNDER VARYING ENVIRONMENTAL CONDITIONS

Decomposition of plant or animal residue is characterized by an initial rapid burst of breakdown followed by a marked decline in the decay process. Bocock and Gilbert (1957) found high rates of dry matter losses in the first few weeks were caused largely by the decrease in water soluble components. Similarly, Olson (1963) stated chemical composition of coniferous litters tends to retard biological activity in northern forests. Weigert and Evans (1964) showed initial rates of disappearance were greatest with a decrease as the growing season progressed. Minderman (1968) found, after a period of ten years, the accumulation of organic matter is mainly determined by those components of the leaves that are more or less unassailable even if originally added in only small quantities. He concluded,

> "it is evidently necessary to know the behavior of separate chemical constituents of the litter as to their speed of disappearing before the decomposition rate of the total litter mass can finally be calculated."

Clark and Paul (1970) stated individual plant constituents such as cellulose and lignin vary in their rates of decomposition:

> "Natural plant litter does not show a constant rate of decay even if given a constant environment. Initially, there is rapid breakdown of sugars and cellulose. In part these materials may be resynthesized into microbial tissues or products that are much more resistant to decay than the initial constituent. Because of this resynthesis, simple compounds such as dextrose do not uniformly lose all their carbon and CO_2. Nor can any uniform value be taken as the amount of the initial carbon that becomes resynthesized."

Paul op. cit. also emphasized that rather slow rates of decomposition were to be found after the initial flush of microbial activity. For example, when ^{14}C-labeled immature oak residues were added to a chernozemic soil, approximately one half of the carbon was lost during the degradation of an easily decomposable fraction having a half-life in the soil of 24 days. A second fraction of moderately resistant material showed a half-life of 325 days and a third fraction of the residue, a half-life of 802 days. Extrapolation to field conditions indicated that the two more resistent fractions combined would have a half-life of approximately ten years under semi-arid, cool conditions.

Bacon (1968) compared tropical and temperate conditions and found in tropical soils organic matter is decomposed very rapidly and may practically disappear under cultivation. In temperate regions it reaches a fairly stable equilibrium level, the reason for this not being immediately apparent. Repeated additions or organic manures do not produce any permanent increase; on the other hand if the rate of disposal continued unchecked all the organic matter would soon disappear. There are several reasons for this: perhaps, the first stage of degradation of plant residues may have ended and a more intractable "core" be left. This intractability could arise from complexity of structure: hemicelluloses would be more difficult to hydrolyze than starch or cellulose. Waxes and related lignins may resist decomposition because of their insolubility in water. A new microbial population has to be established and will confer new characteristics on the final stages of degradation.

Jenny, Gessel, and Bingham (1949) showed different climates affect the rate of decomposition of organic residues. Plant residues in tropical climates are small at high temperatures and high moistures. Abundant rainfall is especially effective in promoting decay and thereby reducing amounts of plant materials. On the other hand, plant residues in temperate climates are high while temperatures are lower and rainfall is reduced. Jenny et al. (1949) emphasized the importance of decomposition relationships through development of the equation:

$$k = A/(A + L)$$

where:

k = the decay constant
A = annual increment
L = total litter accumulation at the time of decomposition of A

This can further be elaborated in that (A + L) = P/B where P is production and B is biomass. Biomass is equal to production plus respiration or B = P + R. Hence,

$$k = A(A + L) = P/B$$

and

$$P = k \times B = D$$

where D is decomposition, and lastly, P (production) = D (decomposition). This relates annual increment and decay losses and is indicative of the decomposition potential of a given ecosystem. Where litter accumulation is slight compared to large amounts of productivity, k determinations are relatively large and thus indicative of rapid breakdown conditions as in the tropics. With increasing latitudes and lower temperatures, decreasing K values are obtained, as the amount of litter increases relative to periodic depositions of dry matter. Jenny et al. (1949) found the annual decomposition constant of litter in moist evergreen forests was 40-60% and the annual decomposition constant for litter under a temperate oak forest in California was found to be 6-12%. This shows a vastly accelerated rate of decomposition of litter in tropical forests.

Nye (1961) also considered decomposition under moist tropical conditions and found results similar to Jenny's work. He also noted though the rate of destruction of litter under tropical forests is much greater than under temperate forests, the humus in this tropical forest has been estimated to decompose at a rate of only 3% yearly. The time required for reaching a stable litter condition when growth and decay are in balance was also calculated:

$$Lt = Le(1-e^{-kt})$$

where Lt = amount of litter for any time prior to equilibrium
Le = amount of equilibrium
k = decomposition constant
t = time in years for a steady state to be achieved, or any % thereof
e = natural logarithum

Koelling and Kucera (1965) showed that geographic trends within the tallgrass prairie indicate temperature and moisture as significant factors in the development of litter compartment size through time. Specifically, they considered the processes of primary production and organic breakdown in three midwest prairies. A north-south trend was observed with the largest accumulation in an Iowa prairie and the least at the southerly station in Southwestern Missouri. Using Jenny's decomposition relationships for annual increment decay losses, and equilibrium time, the most southerly location in Missouri had the shortest estimated equilibrium time, while the northern Iowa site had the longest.

> "Lower litter values for Missouri prairies are indicative of more rapid breakdown of plant biomass. Although productivity was greater in Missouri due to climatic influences, turnover of the plant product was also more rapid. The effect thus is a shorter cycle of mineralization and also less average litter accumulation at any particular time."

Decomposition constants, k, were also calculated for the three prairie sites. The least decomposition and greatest accumulation relative to production was found in the northernmost prairie in Iowa, with the lowest k value of 0.427 (percent of total biomass/year). The most southern site in southwest Missouri, again, has the highest k value of 0.587, indicating the most rapid decay potential. Lutz and Chandler (1946) reported decay rates for different latitudes. The low latitudes had the highest rate of decomposition, the middle latitudes, an intermediate rate, and the cool high latitudes, the slowest rate.

Decomposition of organic matter in arctic soils is initially regulated by temperature. Douglas and Tedrow (1959) found although moisture levels are influential at low temperatures in decomposition, they are not as influential at low temperatures as at high temperatures. At the higher temperature, the rate of decomposition increases markedly with increasing moisture content until it reaches a high, after which increasing moisture has a depressing effect on decomposition.

Mikola's (1960) comparative experiments on decomposition rates of forest litter in southern and northern Finland showed parallel increases in temperature and decomposition rates. In this case, rainfall was even throughout the year and decay was not influenced by drought. Excessive moisture, which retards decomposition, probably did not occur either. Moreover, moisture can occur over wide ranges without any effect on the rate of decomposition. Finally, rate of litter decomposition increased proportionally to the higher mean summer temperature.

In comparing two forests of close proximity in the temperate climate, Shanks and Olson (1961) found there was a great range in accumulation of litter and humus. Differences were due to contrasting rates of breakdown, which are influenced by litter species and the environmental conditions in which litter is decomposing.

Whitkamp (1961) investigated several factors of decomposition rates and microflora populations. Specifically, he measured:

1) bacterial and fungal counts
2) mycelial growth
3) microbial evolution of CO_2
4) substrate moisture and temperature in bags with litter of either mulberry, redbud, white oak, loblolly pine or beech

Measurements were taken biweekly over a one year period in a temperate deciduous forest. He found the chief factor controlling microbial populations and rates of litter breakdown were temperature, moisture, and stage of decay. Later, Whitkamp and Olson (1963) found that of the weather effects, temperature dominates over moisture in humid climates, especially inside litter bags, where moisture rarely becomes limiting.

Whitkamp and Van Der Drift (1961) compared production and breakdown of litter on mull and mor forest floors. Litter production was almost equal in both mull and mor types. In an extremely dry year, less decayed plant material was produced in the mull, due to strong dessication and surface rooting species.

Olson (1963) found the wide range of decay rates estimated from data on forests of very contrasting climates helps to account for the great differences in total accumulation of organic carbon on top of mineral soil and in promptness in approaching maximum storage capacity for dead organic matter. Low storage of carbon in highly productive tropical forests contrasts with high levels of carbon and energy accumulation in relatively unproductive cool temperate forests. The major reason for this inverse relation was rate at which dead organic matter was broken down into mineral soil by organisms which were controlled by temperature and moisture condition.

^{14}C ASSAY METHODS AND ^{14}C TRACER STUDIES

Radioactive tracers provide a means of detecting flow rates of materials through the ecosystem while the best index of organic content, Carbon-14 is often difficult to measure because of weak beta emmission, especially with solid carbonaceous materials. O'brien and Wardlaw (1961) ground materials and directly assayed them for ^{14}C at infinite thickness.

Liquid scintillation provides an alternative and more useful means of assaying Carbon-14. Nathan (1958) found small amounts of compounds containing Carbon-14 of high specific activity may be either converted to barium carbonate, plated and counted in a gas flow counter or plated and counted directly. Large samples of low specific activity pose a more difficult problem. Nathan op. cit. demonstrated liquid scintillation counting is extremely useful for the measurement of weak beta emitters of low specific activity. Previously, only compounds which were soluble in a limited variety of hydrocarbon solvents were counted with liquid scintillation. Funt (1956) introduced scintillating gels and White and Helf (1956) refined the details of use of gels. Nathan (1958) concluded the liquid scintillation technique is simple, adaptable, and reproducible. The technique obviates the need for low efficiency "infinite thickness" counting and replaces the ionization chamber counting for most samples.

Several studies have been conducted with labelled plant material in relation to decomposition rates and subsequent transfer of the tracer to the soil. Olson and Crossley (1961) investigated labelled leaf litter breakdown of several forest species. Later, Olson op. cit. used different tracers to measure breakdown rates of different litter species. Real differences were found to exist between rates of breakdown for the different leaf species, but losses were more pronounced in the rapid initial loss of weight than in the rate of subsequent breakdown. Radionuclide losses were similar to rates of weight loss on the average. However, some distortions of data resulted from the settling of the initially loose litter and consequently improved counting geometry, so that counts soon after the early readings were frequently higher than initial counts. This initial distortion would have obscured any rapid initial loss of radionuclide analogous with rapid change in weight immediately after exposures in the field. They concluded release and subsequent movement of nuclides may be similar to rate of litter breakdown in some cases and more rapid in other cases. For example, losses from Strontium-90 in dogwood leaves proceeded at a rate approximately similar to the overall rate of weight loss, where as loss of Rubidium-106 and Cobalt-60 from pine and oak leaves seemed slightly more rapid than loss of weight.

Jenkinson (1960) used Carbon-14 to study turnover of organic matter in the soil and emphasized the importance of uniformity of labelling. He sited several sources of nonuniform labelling:

1) diffusion and/or leakage of CO_2 through chambers and apparatus
2) dilution of chamber gas with atmospheric CO_2
3) presence of unlabelled carbon in plant seeds, which may or may not be distributed uniformly through plants as they grow.

4) isotopic fractionation during metabolism leading to preferential enrichment or depletion of some plant constituents in Carbon-14

To insure greater uniformity of Carbon-14, seed should be placed in the chamber immediately after germination.

Jenkinson (1965), later, labelled ryegrass roots and tops with Carbon-14 and allowed them to decompose for four years. Again, there was rapid initial loss of litter with a subsequent decline in decay. Similarly, during the first few months more labelled Carbon-14 was lost from ryegrass tops than from roots. This was probably due to differences in the composition of roots and tops. The percent of hot-water soluble Carbon is larger in the tops than in roots. He concluded the rate of loss slows greatly. Labelled Carbon was less resistant than unlabelled carbon.

IMPORTANCE OF ORGANIC MATTER IN SOIL FORMATION

Soil is the loose layer of earth which supports the various organisms dwelling within it and higher plants too. Soil is formed by the various physical, chemical, climatic, and biological factors. The inert solid particles are complexes of minerals and organic humus in which are dispersed organic molecules, inorganic salts, and ions, water and gases. Within the soil matrix are found micro- and macro-organisms in vast numbers together with dead roots and excrements of soil found in all stages of disintegration.

The organic fraction of soil and its role in soil development is of particular interest here. In considering the biochemistry of humus formation, Konova op. cit. considered the role of physical, chemical and biological factors. Humification of organic residues depends on chemical composition and upon conditions in the soil influencing the activity of the micro-organisms. These may be destructive changes due to physical action of natural factors and to the action of water. Changes occur in the chemical nature of organic residues under direct action of water, light, air, and reaction of the medium. Clark et al. (1970) considered the organic components of soil to be composed of at least three fractions when considered on a dynamic basis:

1) decomposing plant residues and the associated biomass which turn over at least once every few years

2) microbial metabolites and cell wall constituents that become stabilized in soil and possess half-lifes of 5 to 25 years

3) the resistent fractions, which in grassland soils are composed of humic components ranging in age from 50 to 2500 years

Grassland soils, as stated earlier, are typified by their high content of organic matter. Springer (1936) saw the natural fertility and humus accumulation of the grassland chernozems as being associated with the great stability of the clay-humus complex. Bremner (1954) proposed clay colloids of soil may plan an important role in stabilizing soil organic matter against biological attack.

> "...the interaction of clay and humus colloids may have an important bearing on the structure and fertility of soils and the maintenance of soil organic matter..."

Because soil humus is a dynamic system it is subject to continual changes during the processes of new formation and decomposition of its constituents. Kononova op. cit. pointed out that the nature of these extremely diverse processes depend on the conditions of soil formation, plant cover, activity of micro-organisms and animals, effect of climate, the chemical, physical and physico-chemical properties of soil and man's activity. The diverse combination and interaction of these factors determines the state of soil organic matter as indicated by the amount and composition of the humus, its distribution in the profile, nature of humus substances and their forms of combination with the mineral part of the soil.

In the earliest studies, Dukuchoev (1883) found humus accumulation in grassland chernozems is promoted by perennial grasses and in the second place, by the particular climatic conditions. Later, he proposed the best source of humus was produced by perennial grasses and legumes, which possess finely branched root systems capable of regeneration. Mishustin (1956) said chernozems are most favorable for humus activity because periods of summer drought suppress microbe activity in the soil. Kononova op. cit. established these conditions as being the most favorable for humus accumulation in soil: rhythmical combination of factors producing active microbiological activity (when new formation of humus substances takes place); subsequent depression, which inhibits decomposition of humus substances and finally, these conditions are found in chernozem soils of grasslands. Kononova emphasized the following points in considering the importance of organic matter in soil formation and soil fertility:

1) It is a bio-geo-chemical process in which micro-organisms are poineers in participation in the natural circulation of Fe, S, Ca, Si, and P.

2) The importance of organic matter in soil is implicit in the definition of soil which recognizes fertility as the unique and constant feature distinguishing soil from parent rock

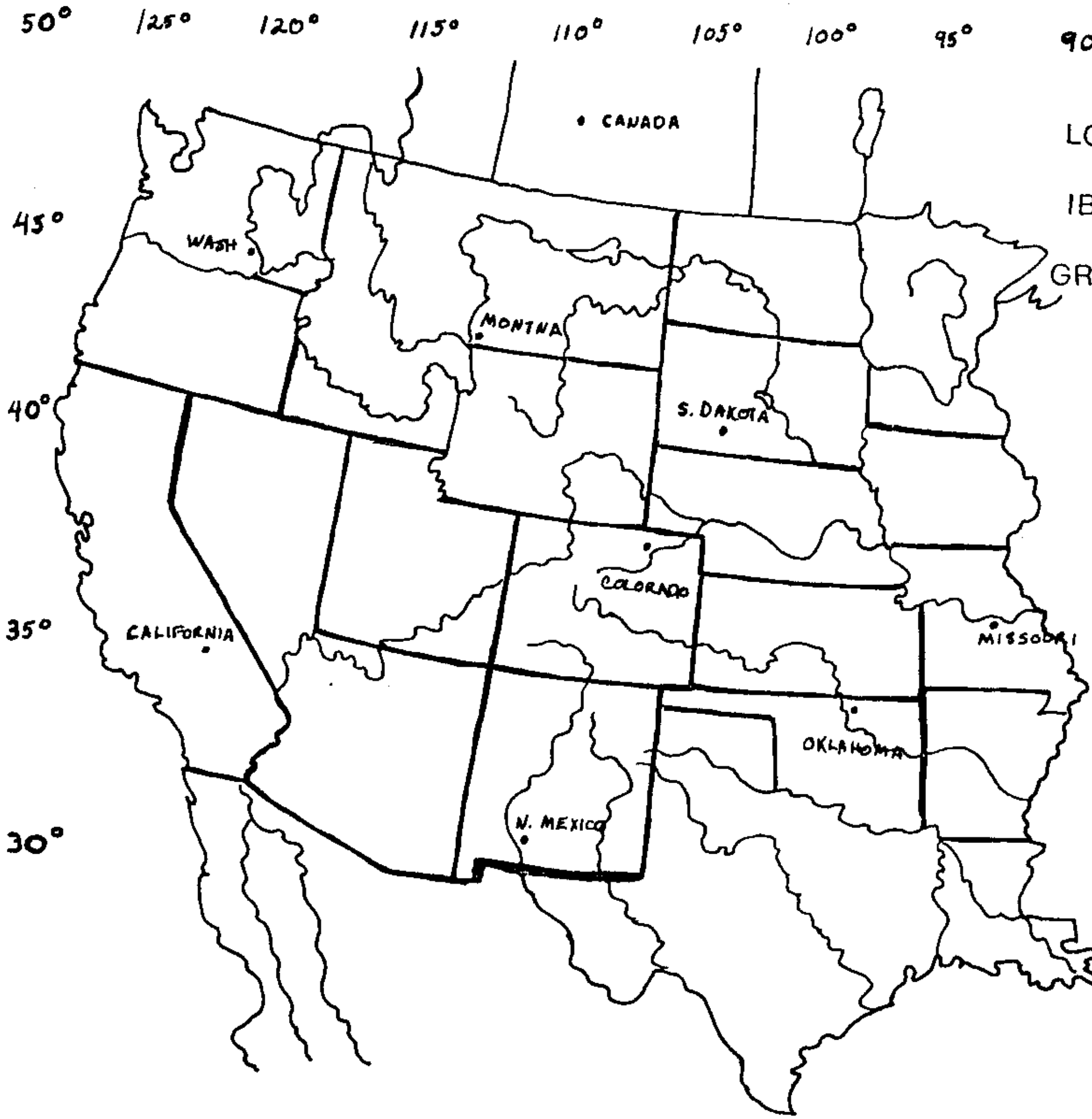
3) Besides being a source of nutrients for the plant, organic matter has also a fundamental effect on the physical properties of the soil; it determines such physico-chemical properties as the exchange capacity and buffering properties

4) Organic matter has a direct effect on the plant. Some substances in soil are toxic to the plant; while others have a definite positive effect on the growth and development of the plant.

He goes on further to discuss the role of organic matter in weathering and decomposition of soil minerals. Phosphates and carbonates are dissolved by root exudates and micro-organisms decompose various types of minerals and rocks. Kononova concluded that organic matter is without doubt the most important factor in the formation of soil of good structure.

DESCRIPTION OF STUDY AREAS

Field data for this study were collected from six IBP sites in the Grassland Biome. Locations are shown in Figure I. The areas are Tucker Prairie (Missouri), Pawnee (Colorado), Cottonwood (South Dakota), Bridger (Montana), Jornada (New Mexico), and San Joaquin (California). The ALE and the Osage sites located in Washington and Oklahoma respectively, were burned accidentally and completion of the study was not possible. Table I gives the comparative meterological data for the six sites. Figure II presents the environmental gradients for the sites. Average annual precipitation in



LOCATION
OF
IBP SITES
IN
GRASSLAND
BIOME

figure I

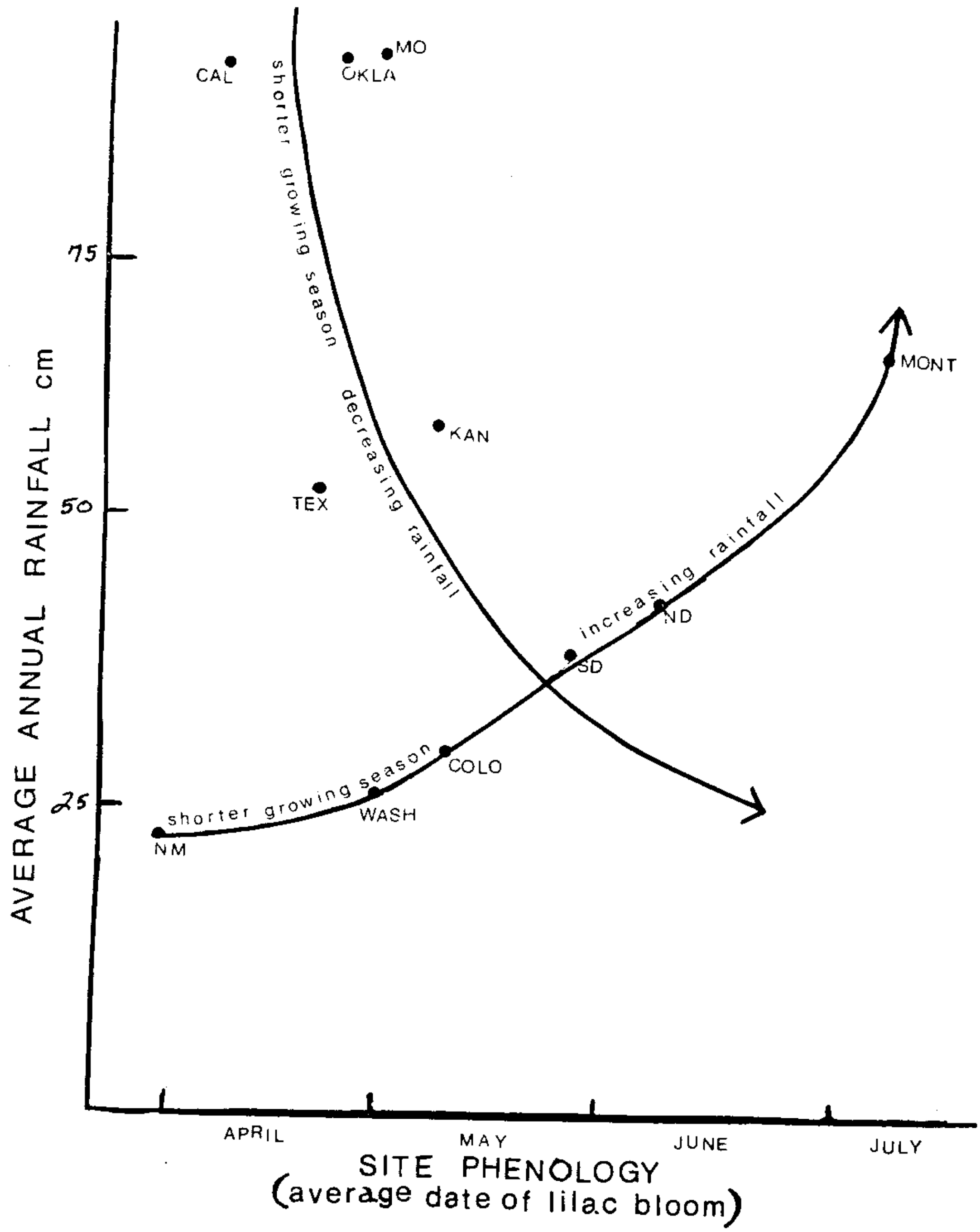
Table I Meterological Description of Participating Stations

Site	Precipitation		Ave Temp.	
Grassland Type	Annual mm	Growing Season mm	Annual -0°C	Growing Season No. days
California*				
shortgrass-desert	$\overline{X}$ = 468	--	17	--
Colorado				
shortgrass	300	240	16	170
Montana				
mountain	960	125	1	70
New Mexico				
shortgrass-desert	227	125	16	200
South Dakota				
mid grass-mixed	385	280	9	126
Tucker				
tallgrass	840	594	13	180

*not all data was available from California

Figure II

Environmental gradients in Grassland Biome



centimeters is plotted against site phenology. The individual sites will be discussed in the following order:

TUCKER PRAIRIE (MISSOURI)

The University of Missouri, Tucker Prairie Research Station is approximately 20 miles east of Columbia, Missouri. The area is an unbroken tallgrass prairie. The dominant grasses are big bluestem (*Andropogon gerardi*), little bluestem (*A. scoparius*), prairie dropseed (*Sporobolus heterolepis*), and Indian grass (*Sorghastrum nutans*). Switch grass (*Panicum virgatum*), and prairie cordgrass (*Spartina pectinata*) also occur. Forbs are dominated by the *Compositae* and include the genera, *Solidago*, *Eupatorium*, *Aster*, and *Helianthus*. Brown (1962), Kucera (1956), and Kucera and Koelling (1964) give detailed floristic descriptions. Physiographically, Tucker Prairie lies in the broad transition zone between the forested breaks toward the South and the flat prairie lands of Northern Missouri. The topography is flat to gently rolling and soils are deep and typically have a clay pan which makes the A horizon poorly drained and water logged in the spring. Scrivner (1966) placed the soils in the Mexico-Putnam group.

PAWNEE SITE (COLORADO)

The Central Plains Experimental Range portion of the Pawnee Site is about 12 miles northeast of Nunn, Colorado and 25 miles south of Cheyenne, Wyoming (Coleman, 1973). The area is characterized as a shortgrass prairie with the dominant grasses being blue grama (*Bouteloua gracilis*), and buffalograss (*Bucholoe dactyloides*). Several midgrasses are present including western wheat grass (*Apopyron smithii*), thread and needle (*Stipa* spp.) green needle grass (*Stipa* spp.) and side oats grama (*B. curtipendula*). Perennial forbs most abundant are scarlet globemallow (*Spaerolocea coccinea*), slim flower scurf pea (*Psoralea tenuiflora*), slenderbush erigonum (*Erigonium micrithecium*), and scarlet gaura (*Gaura coccinea*). Annual forbs include Russian thistle (*Salsola kalitenuifola*), *Cryptantha* spp., *Lappula* spp., pale evening primrose (*Oenothora pallida*) and *Chenopodium* spp.

The topography of this area is gently rolling with few predominant topographic features. The intensive portion of the Pawnee soil consists of shale and siltstone outcrops with a series of fluvial outwash materials. Interspersed among these upland soils are alluvial plains of more recent origin. These alluvial plains are high in clay content.

JORNADA EXPERIMENTAL RANGE (NEW MEXICO)

The Jornada site is located at 1350m elevation on the western side of the Range about 6 miles west of the Jornada Headquarters. The area is south and east of the West Well Range Gauge and northeast of Las Cruces, New Mexico. The Jornada site may be classified as a shortgrass/desert prairie with the principle grassland types black grama (*B. hirsuta*), tarbush (*Flourensia cernua*), and creosotebush (*Larrea divaricata*) are prevalent. The general aspect of the grassland areas is low growing herbaceous vegetation with scattered shrubs such as mesquite, soaptree yucca (Yucca elata), and 4-wing slatbush (Atriplex canscens).

Topography of the Jornada Experimental Range is characterized by level to gently rolling plains and a rough steep terrain in the mountain ranges. Jornada plain consists of unconsolidated pleistocene detritus.

COTTONWOOD (SOUTH DAKOTA)

Cottonwood Range Field Station is located in west central South Dakota, 75 miles east of Rapid City, 2 miles east of Cottonwood, and 11 miles west of Philip. The station lies in the central portion of the mixed prairie and the dominant midgrasses are wheatgrass (Agropyron smithii), and needlegrass (Stipa viridula). There is an understory of short grasses, mainly grama grass (Boutleoua gracilis) and buffalo grass (Buchloe dactyloides). Shrubs are of minor importance except in the wetter drainage ways where mulberry (Symphoricarps occidentalis) and Rosa spp. may be important. Patchiness of the vegetation is primarily related to soil heterogeneity and micro-relief.

Erosion has shaped the landscape into rather gentle, long sloping hills with a total relief of about 200 ft. Higher hills appear to flat-topped and have probably been protected from erosion by capping or more resistant strata of sandier limestone and sandstone. Soil textures are predominantly silty clay, but range from heavy clays to fine aeolian sands.

BRIDGER (MONTANA)

The Bridger site is located in southwestern Montana, 14 air miles northeast of Bozeman, Montana. Bridger Mt. Range has an elevation of 7600 ft. This is a roughly north-south oriented mountain chain with precipitous slopes on both east and west, and a crest altitude generally exceeding 8500 ft. The landscape is gently rolling with a major defile provided by the cutting action of the Yellowstone River. The actual research area is approximately 35 acres, and has been enclosed by fence and used as an occasional horse pasture by US Forest Service since the 1930s.

Mountain bunchgrass-forb is the major vegetational type on the Bridger site. The dominant producers are fescue (*Festuca idahoensis*), wheatgrass (*Agropyron cainum*), and *Lupinus argentus*. Wild oats grass (*Panthonia intermedia*), and *Carex* spp. are the next most important graminoids. Important forbs are sandwort (*Arenaria congesta*), sneezeweed (*Achillea millefolium*), *Agoseris* spp., daisy (*Erigeron speciosus*), chickweed (*Cerastium arvense*), and bedstraw (*Galium boreale*).

Soils of the Bridger site are described by Buchanan (1972). Meadow sites are generally rolling. Bedrock appears at the surface in windswept ridges. In the A horizon sand and clay make up 49 and 18 per cent of the soil weight respectively.

SAN JOAQUIN (CALIFORNIA)

The San Joaquin Experimental Range is an area of about

4600 acres near the center of the state of California in Madera County near Fresno, California. This is the so-called "granite" area of the Sierra Nevada foothills. The land is rolling, exposures in general southwesterly and the elevation ranges from 700 to 1700 ft. above sea level, with most of the area between 1000 and 1500 ft. The area is typical of large areas of the poorer soil types in the foothills throughout the state; it is characterized by frequent granitic outcrops, and the soils are mostly residual and formed from the decomposition of the underlying granitic bedrock.

Vegetation is of the woodland-grass type. The tree and brush cover consists of scattered trees and digger pine (Pinus sabiniana), blue oak (Quercus douglasii), interior live oak (Quercus wislizeni), and California buckeye (Aesculus californica). There is a variable shrub cover consisting mostly of wedgeleaf ceanothus (Ceanothus cuneatus), and whitehorn ceanothus (Ceanothus leucodermis) with considerable hollyleaf buckhorn (Rhamnus crocea var. cupsidata), Mariposa manzanita (Arctosphylos mariposa), elderberry (Sambucus glauca), and poison oak (Rhus diversiloba). The herbaceous plant cover consists mainly of annual plants, many of which have been introduced from the Old World. The bulk of the forage is composed of broadleaf filaree (Erodium botrip sp.), and E. obtusiplicatum, soft chess (Bromus midlis), and foxtail fescue (Festuca megalura).

METHODS AND MATERIALS

During July, 1972, a plot of mixed bluestem vegetation at the Tucker Prairie Research Station was labelled with Carbon-14 via photosynthesis. The method employed had been successfully used by Moss et. al. (1961), and Baker and Musgrave (1964). A full description of the application at the Tucker site can be found in Dahlman (1967).

Vegetation was harvested, chopped and air dried. A total of 333 aluminum mesh bags were prepared from the air dried material. Each bag was approximately 10 x 10 cm and the dried material ranged in weight from 7 to 8 grams per bag. The total activity for each bag was 8μCi. Thirty-six bags were randomly selected for distribution to each of the six IBP grassland sites. Total activity for each shipment was about 300μCi.

Litter bags were distributed in the field in a checkerboard fashion of 6 rows of 6 bags each 2 meters apart. To prevent dislocation by wind or rodents, bags were anchored by wire pins to the soil.

The litter bags were deposited in November, 1962. Beginning April 1, 1973, and at 3 month intervals thereafter, 3 bags were randomly removed from each site and sent to the University of Missouri laboratory for processing. A soil core, 5 cm in diameter, and 10 cm in depth was also taken from under each of the litter bags. The 10 cm depth was divided into 3 samples with depths of 0-1 cm, 1-5 cm, and 5-10 cm.

Determination of Dry Weight Remaining

To determine residual weight of litter, foreign debris, such as soil particles, insects, seeds, twigs were extracted by hand and tweezers, seiving, and alcohol flotation. Hand, tweezers and seiving was used for larger particles. For smaller debris, litter was placed in 25% ethyl alcohol solution. Ethyl alcohol would kill any bacterial action and allow litter to float to the surface. The solution was then poured over a cheesecloth covered jar and the litter sample retained in this manner. Litter samples were dried at 70°C for 24 hours. The following day, litter samples were removed from the drying oven and weighed to determine the amount remaining expressed in grams. Percent dry weight remaining was determined as follows:

$$1 - \frac{\text{retrieval weight}}{\text{original weight}} \times 100$$

An average value was determined for the three samples and was plotted against elapsed time on 2 cycle semi-log paper.

Determination of Carbon-14 Activity in Litter Samples

Homogeneity of samples is necessary in the assaying of Carbon-14 activity. Litter samples were ground thoroughly after dry weight determination. Ten milligrams of each ground sample was weighed and placed in counting vials of liquid scintillation cocktail (Awuasol and Cab-o-sil), and 2 mls of distilled water. A liquid scintillation counter (Packard Tri-Carb) was used to determine the amount of radioactive carbon. Each sample was counted for five minutes.

The original activity of litter samples averaged $\frac{747,020}{2.22 \times 10}$ cpms 6 µCi/g and was the basis for calculating percent loss of Carbon-14 under field conditions when retrieved samples were again counted. A correction factor of .225 counter efficiency for 10 mg litter was used to determine total activity. The percent total Carbon-14 remaining after each decay period was determined as follows:

$$1 - \frac{\text{retrieval wght. in grams x specific activity } (\mu Ci/g)}{\text{original wght. in grams x specific activity } (\mu Ci/g)} \times 100$$

The mean percent remaining for the three litter samples was calculated and plotted on the 2-cycle semi-log paper for comparison with dry weight losses.

RESULTS

SITE COMPARISON OF THE ATTRITION RATES FOR LITTER AND CARBON-14 ACTIVITY BETWEEN APRIL, 1973 THROUGH APRIL, 1975

The results of this study provide information important in relating decomposition rates to varying environmental conditions. These data emphasize the significance of temperature, precipitation, latitudinal and/or altitudinal effects on decaying plant material. While annual precipitation generally establishes patterns for productivity and structure, seasonality of distribution in conjunction with given temperature values are significant interactants in the decomposition process. In general, one would expect moist, humid, hot climates to hasten the decay process, whereas slower rates would occur in cooler and/or drier regimes. Implicit in the overall picture is the existence of a complex relationship between the physical environment and the decomposer community.

However, one should recognize that although general trends for decay rates in conjunction with environmental gradients were found to hold true in this study, there were variables in particular cases, such as the New Mexico site that caused significant deviations in the decay rate. Such deviations will be considered in the discussion.

A pilot study, which led to the present project was initiated in December, 1970. At that time, the sites chosen for deposition of simulated litter samples were Oak Ridge, Tennessee, Tucker Prairie near Columbia, Missouri, and the Matador Project, Saskatchewan, Canada. The results for decomposition for these three sites are presented in Table II. These particular sites were chosen for the wide variations in environmental conditions they provided. The Tennessee data are complete, but only limited data are available from Missouri and Canada. Although Tennessee and the Canada sites were not included in the present study, the results are important in further extending trends of decomposition rates under varying environmental conditions. Although retrieval dates vary from the suggested three month interval certain comparisons and suggestions can be noted. In considering the Tennessee and Missouri sites, litter samples were allowed to decay from December, 1970 to early March, 1971 before the first retrieval date. During this time, approximately 4 months, the Tennessee samples lost 24.4% of actual litter weight while the Missouri site lost 12.7% actual litter weight.

TABLE II

Dry Matter Losses and Percent Remaining in Simulated Litter Samples at Oak Ridge, Tennessee

Date of Retrieval	Decomposition month	Litter Remaining - % $\bar{X}$
March, 1971	4	75.6
June, 1971	7	67.6
September, 1971	10	53.7
December, 1971	13	31.3
March, 1972	17	35.9
June, 1972	20	26.0
October, 1972	24	18.2
December, 1972	26	12.4
March, 1973	30	15.8
June, 1973	33	8.8
October, 1973	39	8.4
December, 1973	41	7.9
	Missouri	
March, 1971	4	87.3
September, 1972	10	50.7
January, 1973	13	44.0
April, 1973	16	50.1
	Canada	
July, 1971	7	90.2
October, 1971	10	82.9
November, 1971	11	82.9
June, 1972	18	77.2

Although lack of correlation of collection dates exists, the general trend is a loss in actual weight from one collection date to the next. It should be noted that at the Tennessee site, by June, 1973, although decay continued, losses from the last collection dates were not nearly so great and marked as at the initiation of the study. Specifically, in June, 1973, only 8.8% of the sample remained, and similarly, in October and December of that year, only 8.4% and 7.9% remained respectively. Perhaps, what is seen here in the litter remaining comprises the more insoluble, resistant residues of decomposition. Whereas, at the initiation of the study the larger losses of decay can be attributed to losses of more soluble compounds. It should be noted, also, that in humid regions of the grasslands, where soil moisture is not as critical, temperature may play a relatively more decisive role in decay processes. The Tennessee site may well be a case in point. This idea is also borne out in that in comparison with IBP sites subsequently included in the study that Tennessee litter samples had the most rapid turnover rate.

Since only four sets of collection data are available from Missouri and Canada, only general trends can be considered. The Canada data cover approximately a one year period. In that time the accumulated losses for dry weight averaged 22.8% of the original weight. Losses for similar decay periods were 49.9 and 54.1% for the Missouri and the Tennessee sites, respectively. Comparative data for selected decay periods are shown in Table III. Although a complete

Table III

Mean Percent Litter Remaining for Initial IBP Sites
Based on a Total of 18 Months Decay Period

MONTHS OF DECAY	TENNESSEE	MISSOURI	CANADA
4-6	75.6	87.3	82.9
12	35.9	--	77.2
18	18.2	50.7	--

table was impossible due to lack of data, there is a definite trend of decreasing decay rates as one moves from Tennessee, the most southerly location, through Missouri to Canada, the northernmost site.

Table IV shows the results of two years decomposition of simulated litter samples from the six IBP sites eventually selected for study. Each site is representative of different environmental conditions and latitudinal and/or altitudinal variation. Likewise, each is representative of a different grassland type ranging from tallgrass communities in the eastern portions of the biome to desert and mountain habitats at site locations further west. Collection dates for all samples began in April, 1973, and were sent to Missouri for processing at three month intervals thereafter. Original open air dried litter weights, varying between 7.0 and 8.0 grams were the basis for calculating dry matter losses over a 2-year period.

A composite of these data is presented in Table V. Here the mean percent litter remaining is taken at 6 month intervals from each site and is compared with all sites in the study. Not all data are available from the Montana station because the site location is snowbound during parts of the year, hence, collection of samples was impossible. One collection from the South Dakota site is also lacking.

In considering six sites at widely dispersed regions, a much broader comprehensive view is presented of decomposition trends of plant materials. Although trends with respect

Table IV

Dry Matter Losses and Percent Remaining in Simulated Litter Samples for IBP Sites

CALIFORNIA

Date of Retrieval	Deposition month	Litter Remaining %
April, 1973	6	88.1
July, 1973	9	77.3
October, 1973	12	74.3
January, 1974	15	69.2
May, 1974	19	55.9
August, 1974	22	53.2
October, 1974	24	54.5
January, 1975	27	29.3
April, 1975	30	36.9

COLORADO

Date of Retrieval	Deposition month	Litter Remaining %
April, 1973	6	94.9
July, 1973	9	92.3
October, 1973	12	92.1
January, 1974	15	84.0
April, 1974	18	87.7
July, 1974	21	82.2
October, 1974	24	90.0
January, 1975	27	73.4
April, 1975	30	87.5

Table IV Continued -

Date of Retrieval	Deposition month	Litter Remaining %
	MISSOURI	
April, 1973	6	74.9
July, 1973	9	62.5
October, 1973	12	49.8
March, 1974	17	31.4
May, 1974	19	40.7
August, 1974	22	26.7
October, 1974	24	10.5
January, 1975	27	15.9
April, 1975	30	29.1
	MONTANA	
July, 1973	9	77.9
September, 1973	11	72.9
July, 1974	21	61.6
October, 1974	24	69.5

Table IV Continued -

Date of Retrieval	Deposition month	Litter Remaining %
	NEW MEXICO	
April, 1973	6	93.0
July, 1973	9	88.2
November, 1973	13	57.3
January, 1974	15	36.0
April, 1974	18	8.8
July, 1974	21	4.3
January, 1975	27	22.6
April, 1975	30	4.0
	SOUTH DAKOTA	
April, 1973	6	87.9
July, 1973	9	82.3
October, 1973	12	73.4
January, 1974	15	68.8
June, 1974	20	62.0
August, 1974	22	65.1

TABLE V

Mean Percent Litter Remaining for Six IBP Sites Based on Two Years Attrition of Simulated Litter Samples
Mean Percent Litter Remaining

Months of Decay	CAL.	COLO.	MO.	MONT.	N.M.	S.D.
6	88.1	94.9	74.9	--	93.0	87.9
12	69.2	84.0	49.8	72.9	36.0	68.8
18	53.2	82.2	26.7	61.6	4.3	65.1
24	29.3	73.4	15.9	--	22.6	--

to temperature, precipitation, and site location generally held true in the findings of this study, exceptions did occur and will be noted.

The Missouri site is in the tallgrass prairie and the most easterly location. Warm temperatures coupled with abundant precipitation are indicative of high attrition rates for plant materials. In considering Table V, the Missouri site has the highest attrition rate in the first 6 months after decomposition of litter samples. During that time nearly 25% of the samples were lost, while the next highest attrition rates were found in California and South Dakota at only about 12%. Colorado and New Mexico lost approximately 6% plant material during the same time span. Montana samples were not available. This trend is followed throughout the following time intervals in Table V, with one exception. At the 18 month collection date, New Mexico had only 4.3% litter remaining compared to 26.7% for the Missouri site. However, at the end of 24 months, the trend is resumed with the Missouri site having the smallest amount of the litter samples remaining.

The South Dakota site is a midgrass prairie. Located further north and more westerly than the Missouri site, annual precipitation is reduced to only 385 mm annually and the mean annual temperature is, likewise, much lower, at 9°C. Decay rates were calculated to be much lower than those of the Missouri site.

The slowest decay of plant material was found to occur at the Colorado site. This shortgrass/desert area receives only 300mm annual precipitation, while averaging 10°C yearly.

Perhaps, here it is appropriate to note the distribution of precipitation throughout the year is important in the decay process. Drought during the growing season months results in decreased decay of plant materials. This, likewise, reemphasizes the point, that the more northerly and westerly the site, the more important precipitation becomes in the decomposition process. The New Mexico site exhibits the same semi-arid shortgrass/desert characteristics, but at a much more southerly location. Precipitation is further reduced to only 277mm yearly, while the annual mean temperature is increased to 16°C. The results of the calculations show an important deviation from other sites in the study. While percent losses at the initiation of the study, shown in Table IV, follow a gradual decrease in plant material, there is a sudden drop in the April and July, 1974, collections. Termites were determined to be the cause of the drop in litter remaining.

Montana is a midgrass or mountain grassland. Location of the study area in a mountainous region made only four collections of litter samples possible during the entire study. Snow was deterrent to scheduled intervals. Likewise, although this site averages 960mm precipitation throughout the year, a major part of this occurs as snow during the winter months when microbial activity is at a low. Hence, although we see a gradual decrease in plant material, collections were only available in summer and early autumn when one would expect most decay to occur. It would be interesting to speculate what winter and spring values would be if collections could have been made then.

The California results followed a trend similar to South Dakota in gradual decreases of litter samples. Although temperatures are generally consistent throughout the year, fluctuations in precipitation are common during the seasons throughout the year. Again this would emphasize the importance of distribution of precipitation in the decay of plant material.

In considering the overall results of the six sites in Table III, a consistent pattern emerged in decomposing rates. Although, on the average, in the first 4 or 5 collection months there is a gradual decline in litter samples, all six sites showed an increase in litter remaining most often in the January or April collections in 1974 and 1975. A possible explanation will be discussed in a later section.

Table VI presents the percent Carbon-14 remaining in simulated litter samples for the six IBP sites in this study. All calculations were based upon a known number of counts of Carbon-14 per gram of initial plant material prior to the decay period. Table VII shows the mean Carbon-14 remaining in samples for each six month decay period.

Loss of Carbon-14 followed dry weight trends, but occurred at a much more rapid rate. Similarly, where an increase in dry weight occurred, Carbon-14 activity was also found to increase. Temperature and precipitation apparently had the same effect on Carbon-14 as on dry weight losses. At

TABLE VI

Mean Percent Carbon-14 Remaining in Simulated Litter Samples for IBP Sites

Date of Retrieval	Deposition month	Carbon-14 Remaining - %
	CALIFORNIA	
April, 1973	6	28.3
July, 1973	9	9.9
October, 1972	12	13.8
January, 1974	15	17.9
May, 1974	19	12.5
August, 1974	22	3.0
October, 1974	24	6.7
January, 1975	27	5.6
	COLORADO	
April, 1973	6	75.8
July, 1973	9	24.8
October, 1973	12	14.3
January, 1974	15	30.6
April, 1974	18	34.5
July, 1974	21	31.3
October 1974	24	33.1
January, 1975	27	23.1

Table VI Continued -

Date of Retrieval	Deposition month	Carbon-14 Remaining - %
	MISSOURI	
April, 1973	6	18.0
July, 1973	9	15.5
October, 1973	12	8.3
March, 1974	17	10.1
May, 1974	19	6.4
August, 1974	22	0.8
October, 1974	24	0.8
January, 1975	27	2.2
April, 1975	30	6.3
	MONTANA	
July, 1973	9	22.8
September, 1973	11	19.6
July, 1974	21	18.0
October, 1974	24	19.2
	NEW MEXICO	
April, 1973	6	36.0
July, 1973	9	41.7
November, 1973	13	9.3
January, 1974	15	15.0
April, 1974	18	12.8
July, 1974	21	4.8
January, 1975	27	10.1
April, 1975	30	3.8

Table VI Continued -

SOUTH DAKOTA		
April, 1973	6	33.8
July, 1973	9	26.9
October, 1973	12	27.8
January, 1974	15	10.0
June, 1974	20	16.1
August, 1974	22	15.5

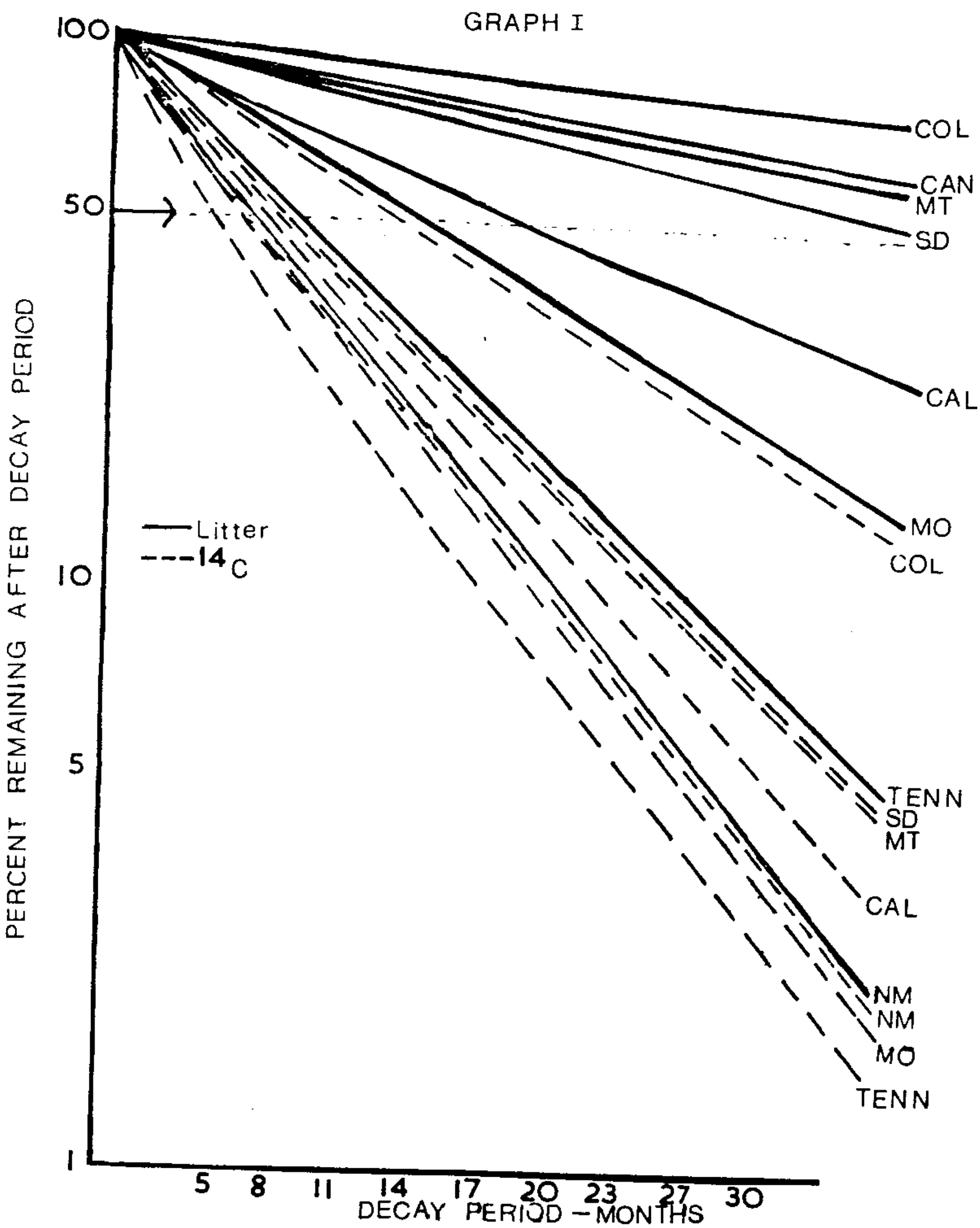
Table VII

Mean Percent Carbon-14 Remaining for 6 IBP Sites Based on Two Years Attrition of Simulated Litter Samples
Mean Percent Litter Remaining

Months of Decay	CAL.	COLO.	MO.	MONT.	N.M.	S.D.
6	28.3	75.8	18.0	--	36.0	33.8
12	13.8	14.3	8.3	22.8	9.3	27.8
18	12.5	34.5	6.4	18.0	12.8	16.1
24	6.7	33.1	0.8	--	--	--

the Missouri site, attrition rates for carbon activity were greatest for any site with Colorado showing the least, thus exhibiting cognate losses with dry matter decay. All other sites were found to follow this trend generally, with some exceptions. At the California sites, for example, four collection dates show an increase in Carbon-14, while litter weight continued to decrease. This occurred at the October and January collections during the course of the study. The occurrence of such anomalies is thought to be an inherent problem throughout the course of the study. The importance of homogenity in labelling litter samples is a possible explanation for such discrepancies. Reabsorption of Carbon-14 due to moisture or presence of soil animals within the sample may also be possible explanations for such variations in Carbon-14 activity.

The results for dry matter and radioactive losses are illustrated in graph I. Both sets of data for percent dry weight remaining and percent Carbon-14 remaining are plotted on each graph for the six IBP sites and the three sites in the pilot study. The graph was the basis for determining a half-life, $T\frac{1}{2}$ for both litter and Carbon-14. The medial point between the second last and last collection date for both litter and ^{14}C was calculated. This point was extended back to 100 percent or deposition date of the samples. The x-axis intercept of this curve at the 50% level of original activity and dry weight was determined. This value is an estimate of the half-life, $T\frac{1}{2}$, or the number of months required


GRAPH I
100
50
10
5
1
PERCENT REMAINING AFTER DECAY PERIOD
Litter
^{14}C
COL
CAN
MT
SD
CAL
MO
COL
TENN
SD
MT
CAL
NM
NM
MO
TENN
5 8 11 14 17 20 23 27 30
DECAY PERIOD – MONTHS

during which one half of dry sample weight and Carbon-14 activity were lost. In considering the results visually, trends at the individual sites become more readily apparent. Generally speaking, dry weight shows a more gradual decrease over extended periods of time, whereas the Carbon-14 losses are more rapid. Also greater of Carbon-14 fluctuations occurred during the same time span. While Tennessee and Missouri show steeper curves, the Canada and Colorado lines show more gradual slow decay rates.

The decay constant, of k, was determined using

$$k\ (\%\ \text{decay yr}^{-1}) = \frac{0.693}{T\tfrac{1}{2}\ (\text{yr})}$$

for each site. The half-life, T½, and decay constant, k, for dry litter weights and Carbon-14 are shown in Table VIII. T½ and k inversely related, that is, the lower the half-life, T½, the greater will be the decay constant, k. In terms of environmental gradients, decreasing k values and longer T½'s occur from south to north and from moist to drier regions. In examining Table VIII it is evident that the most southerly sites, Tennessee, Missouri, and New Mexico exhibit the shortest half-life, T½, and the largest k values. Such findings are indicative of rapid plant decomposition. It should be noted that the New Mexico values are a special case, where dramatic weight losses at 7.5 months and a k of 1.04 yearly occurred. Reasons for this anomaly will be considered in discussion. The more northerly sites, Montana, South Dakota, and Canada exhibited longer half-lives and lower k values. Likewise,

Table VIII

Comparison of Half-lifes, $T_{1/2}$, and Decay Constants (k) for Simulated Litter Based on Actual Weight Losses and Actual Carbon-14 Losses for all Stations

State	Litter (months) $T_{1/2}$	K	14C (months) $T_{1/2}$	K
Canada	49	0.17	--	--
Colorado	42	0.20	12	0.69
Montana	37	0.22	9.5	0.84
S. Dakota	34	0.25	7.5	1.04
California	19.5	0.44	7.5	1.04
Missouri	12.5	0.69	5.5	1.65
Tennessee	10.0	0.83	6.0	1.38
New Mexico	7.5	1.04	6.0	1.38

California, the most westerly site showed an increased half-life, $T_{1/2}$, and a decreased k rate. Slower k rates and longer half-lifes, $T_{1/2}$, indicate slower plant decomposition rates, which in turn, are influenced by decreased precipitation and/or decreased temperature gradients. For example, the Canada site has a half-life of 49 months and a k value of 17 percent yearly with respect to dry weight. Carbon-14 half-lifes and k values are also shown in Table VIII and give similar trends. However, there was less variation in these values when compared to dry weight calculations.

DISCUSSION

Temperature, rainfall, and growing season characteristics are key variables in establishing decay patterns and rates of energy transfer through the ecosystem. The six IBP sites in this project plus preliminary findings from Tennessee, Missouri, and Canada provided several combinations of rainfall and temperature regimes. These variations in climatic conditions, ranging from humid to semi-arid, not only yield information about decay patterns in a particular region, but also the basis for comparison of differing decay potentials for the Grassland Biome as a whole. Since annual precipitation and seasonality of distribution in conjunction with given temperature values are recognized as significant interactants in the decomposition process, this would imply there is a complex relationship between the physical environment and the decomposer community.

The initial hypothesis of this project was that within the

Grassland Biome there are wide variations in decay potential. Bearing in mind the importance of the particular climatic conditions of a region, the IBP sites will be discussed and elaborated upon concerning the uniqueness of their individual decay potentials and reasons for this individuality will be noted.

In the humid regions of the grasslands, where soil moisture is not as critical, temperature may play a relatively more decisive role in decay processes. The high rates of decomposition for Tennessee and Missouri, the latter in the tallgrass prairie region, reflect warmer temperatures over longer periods and more soil moisture than other sections of the biome. Jenny et al. (1949), Nye op. cit. (1961), and Koelling and Kucera (1965) all give pertinent information about the importance of high humidity and warm temperatures in the decay process. The results for the Tennessee and Missouri sites indicate losses of nearly 70% and 50% respectively for simulated litter samples after 12 months of the initial decay process. These relatively high values are indicative of rapid attrition of plant materials at both sites. It would appear that winter temperature is the more limiting factor in decomposition since precipitation is available in one form or another throughout the year.

The Pawnee site in Colorado is an arid shortgrass prairie in the Grassland Biome. Here, precipitation appears to be the limiting factor in the decomposition process. Coleman (1973) emphasized the intra-seasonal importance of moisture availability of microbial activity in characteristically dry regimes. The relatively long half-life, 42 months, for the Pawnee site is probably due to moisture deficiencies. During the course of this study precipitation was less than normal. With more adequate moisture, decay rates probably would be greater.

The South Dakota station is representative of the northern grasslands and is noted for higher accumulations of litter and soil organic matter compared to the southern counterparts in the Grassland Biome. This cool-climate station had a half-life, $T\frac{1}{2}$, of 34 months for litter samples.

At the end of 12 months decay 68 percent of the litter sampled remained. Similar findings are available from the Canada site. Being the northernmost of all sites this region would also be characterized by high litter accumulations, decreasing temperatures and moisture. Only four collections of litter samples were made, but rudimentary data are available. Here, a litter half-life, $T\frac{1}{2}$, of 49 months and k value of 17 percent per year were calculated. This low decay potential coincides with characteristic climatic conditions of the region.

Storage values or low litter accumulations are characterized of warm desert grasslands such as the New Mexico site. However, despite rapid attrition rates, there is limited rainfall. This would lead one to conclude that the comparatively high temperatures on an extended basis through the year are responsible for rapid breakdown of litter. With prevailing conditions such as this, rainfall would be the limiting factor. A half-life, $T^{1/2}$, of 7.5 months and a k value of 104 percent yearly were calculated. The high loss rate is attributed to termites instead of microbial decomposition. Termites can rapidly convert litter so that it can be readily attacked by smaller organisms. Nye op. cit. (1961) found this to be true of litter samples located in tropical forests. Observers at the Jornada site reported that termites had, indeed, caused the great irregularities in samples from New Mexico.

Although the Bridger site in Montana receives as much moisture as the tallgrass prairie station in Missouri, decreased decomposition of plant material occurred. There are two major reasons for this. Difference in the kind and seasonal distribution of moisture is important here. At the high elevations in Bridger, most of the precipitation occurs as snow during the period of low temperatures, when growth and decay processes are minimal. Summer rainfall would be a more suitable index to decomposition. As mentioned above, low temperature would be the second impediment to decomposition. Because the Montana site was snowbound much of the year litter sample collections could only be made during late summer and early autumn. A calculated half-life, $T^{1/2}$, of 37 months and a k value of 22 percent total biomass per year was determined from litter collections. It would be interesting to speculate the outcome if more samples were accessible the remainder of the year.

California is a shortgrass/arid site. As such, there is considerable variation in total annual precipitation from year to year, although temperatures remain fairly consistent (Duncan, personal communication, 1975). Decomposition rates are largely dependent upon amount and seasonality of precipitation. Because of these irregularities slower decomposition values were found. A half-life, T½, of 19.5 months and a k value of 44 percent total biomass per year indicate decreased decay potential for plant materials.

The preceeding discussion of the six IBP sites and data from Tennessee and Canada have been discussed as well as the individual and/or unique climatic conditions and limiting factors which would affect decomposition rates in a particular region. Now, it is appropriate to mention the similarities found among all the sites with respect to decomposition of plant material. In all sites there was found a rapid initial loss of dry weight with a gradual slowing, thereafter, of weight losses. This can be attributed to losses of the soluble components of decomposition occurring rapidly after deposition dates. Bocock et al. (1957), Olson op. cit. (1963), Weigert et al. (1964), Minderman op. cit. (1968), and Clark et al. (1970 all reported that in the decomposition of plant materials decay occurs rapidly at first followed by a gradual decline in magnitude of loss. Clark et al. (1970) and Bacon op. cit. (1968) attributed these losses to the soluble components of decomposition being lost first.

With exception of the Montana site when a January collection was unattainable, all sites in the present project showed an increase in dry weight remaining in either the January or

April collections. Generally, the cold season is the dry season. So not only would there be a lower moisture value, but also lower temperatures. Consequently, decomposition would be decreased until warmer, wetter seasons arrived. However, it is important to note that these conditions in themselves would not be a reason for an increase in litter weight. Probably the main reason for an increase is that there is an accumulation and adherence of foreign debris, such as dust or mud to litter samples. This could result in, perhaps, the inability to separate all the debris from the litter samples. Since no one has reported any findings similar to this pehnomenon the proceeding possibility at this time could only be speculation.

LOSSES OF CARBON 14 IN LITTER SAMPLES

Incorporation of a Carbon-14 label into litter samples provided a means of assessing carbon turnover through measurment of losses of Carbon-14 in simulated samples. Decay rates were determined from half-life curves plotted for each station. A half-life, $T\frac{1}{2}$, and a k value were calculated and were presented in the results section. In general, the losses in Carbon-14 occurred more rapidly than for total dry matter. This suggests a lack of uniform labeling in all plant parts and the incorporation of Carbon-14 only in the more oxidizable fraction. Chahal and Wagner (1965) showed that 75 percent of Carbon-14 labeled glucose added to soils was lost in three months. During the same period only about 5 percent of the native organic material such as humus was oxidized. In a comprehensive discussion of Carbon-14 labeled compounds added to soils, Wagner (1974) cited several investigators who showed rapid breakdown of readily metabolized substances in the initial phases of decay. In one study, about 20 percent of the labeled carbon still remained after three years.

Paul, Biederbeck, and Rosha (1970) recognized the importance of several carbon fractions and the role played in the turnover of organic matter. The youngest and the most readily metabolized fraction of soil organic matter, humic acid hydrolysate, yielded 64 percent of the total carbon released per year. Yet, this fraction comprised only seven percent of the total soil carbon.

To effect a more uniform distribution of radiocarbon in grass foliage under field conditions, a longer period of fixation is required. In the present study, labeling was performed in the morning for a six hour period, on each of three consecutive days. This method was followed to avoid excessive heating, and to minimize respiration losses caused by high temperatures when photosynthesis would be minimal. In future work, where uniform labelling is required, provision should be made for effective temperature control on an extended basis.

SUMMARY AND CONCLUSIONS

A study of decomposition of simulated litter samples made from bluestem foliage at Tucker Prairie was initiated as a cooperative project in 1970 with the International Biological Program. Initially, three stations were selected, but later increased to six to give a more comprehensive view of decay processes within an expanded climatic gradient. The purpose of the study was to measure and evaluate differences in decay of plant litter at selected stations in the Grassland Biome. Labelling for the expanded study took place in July 1972 and beginning in April 1973, and continuing at three month intervals through 1975, triplicate litter samples labeled with Carbon-14 were returned to the Missouri site for analysis. Losses in dry weight and Carbon-14 activity were determined from which the half-life, T½, and k, decay constant, were calculated. The principal findings are as follows:

1) Widely divergent decomposition potentials for surface residues occur within the Grassland Biome.

2) Temperature and precipitation are the main functional variables explaining differences in litter losses with colder and/or drier sites showing slowest decay. For example, the disappearance rate for litter deposited at the Canadian site was 0.17 per year, while the decay rate at the Missouri site was 0.43 per year (expressed as per cent per year).

3) Losses in both dry weight of samples and total radioactivity showed similar trends among stations, but rates of decline in these measurements differed.

4) Losses in radioactivity occurred universally at a faster rate than the respective weight decreases, and is attributed to the more soluble nature of the photosynthate carrying the tracer following the labelling process. Losses in dry matter, however would reflect also degradation of more resistant products including cellulose and lignin in differential and aging tissues.

5) The study suggests that temperature differences are more distinctive as a decay determination in the humid grassland, but temperature as well as the moisture are more difficultly separated in western portions of the biome.

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