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A PRELIMINARY COMPARTMENT MODEL

OF A TALLGRASS PRAIRIE, OSAGE SITE, 1970

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ABSTRACT

A compartment model was constructed from the 1970 data collected on the Osage Site. The state variables were estimated from field data and the time of peak live plant production. Flow rates of carbon between compartments were estimated both from field data and literature values. The producer portion of this tallgrass ecosystem composed 73% of the biomass, and the decomposer biomass contributed 26%. The invertebrates, birds, and mammals together contributed less than 1% of the total biomass feature. Efforts with this model will include time varying considerations.

INTRODUCTION

The Osage Site represents the tallgrass prairie in the U.S. IBP Grassland Biome. During the 1970 growing season this grassland was studied intensively at several functional levels (Blocker and Reed, 1971; Harris, 1971; Hoffmann, Jones, and Genoways, 1971; Risser, 1970, 1971; Wiens, 1971). Systematic and coordinated data collection occurred in the abiotic, producer, invertebrate, bird, mammal, and decomposer components at this grassland ecosystem. Our objective was to evaluate the structure and function of this grassland ecosystem by simultaneous examination of these functional components. This now permits us to describe the system in a holistic manner and to examine some mechanistic detail between and within some components. The data synthesis contained in this report resulted from the cooperation of the principal investigators who worked on the Osage Site. They not only were responsible for data collection but also the data analysis in their area of specialty and within the whole Osage framework.

DESCRIPTION OF THE OSAGE SITE

The Osage Site is located on the Adams Ranch, 19 km north and 5 km east of Shidler, Oklahoma, in Osage County, which is in the northeast corner of Oklahoma. The ranch (approximately 14,000 ha) is owned by Mr. K.S. Adams and managed by Mr. Dick Whetsell.

The Osage Site is located at an elevation of 375 m on predominately rolling topography. Long-term climatic records are available from the U.S. Weather Bureau Station in Pawhuska, Oklahoma, which is 32 km southeast of the ranch. The average January temperature is 2.7°C, and the average July

temperature is 27.3°C. The average annual precipitation is 100 cm, with 60.0 cm occurring during the April-September warm season. The growing season is 205 days.

The soils of the Osage Site are Brunizems of the Labette-Summit-Sogan association. These are darkly-colored soils with mostly clay-like subsoils developed on shales, sandstones, and limestones under tallgrass. Specifically, the experimental area is on a Labette soil with a dark, silty, clay A horizon, 30 to 45 cm in depth. The B_1 is dark brown, 45 to 90 cm; the B_2 is reddish brown, 60 to 90 cm; the B_3 is a brown, silty clay, 90 to 120 cm; and most of the bedrock is limestone at 1 to 2 m.

The ungrazed treatment plot is 5 ha and has existed in an ungrazed condition for at least 20 years, although there has been some mowing for hay. The grazed area is located adjacent to the ungrazed treatment and is normally grazed during the fall and winter. The grazing intensity is light to moderate, and the grass is in good to excellent range condition.

METHODS

A small micrometeorology station was established on the ungrazed treatment. Accumulated precipitation was measured either biweekly or monthly in a standard Weather Bureau rain gage, 76 cm above the soil surface. Wind was measured with a totalizing anemometer mounted 153 cm above the soil surface, and solar radiation was recorded with a pyranometer located at a height of 76 cm. Air temperature and humidity were continuously measured with two recording hygrothermographs, 31 and 153 cm high, respectively. Continuous soil temperature was recorded at depths of 1.0 and 10.0

cm below the soil surface. Soil water was taken by the gravimetric technique from two quadrats per replicate on each sampling date.

Sampling Methods

The 5.0-ha ungrazed treatment was divided into two replicates of equal size, and a grid was established to coordinate sampling activities. Clipped quadrats, soil cores, insect traps, etc., were located within selected 18- and 30-m blocks on a given sample date. The location of each sample was recorded so that the same area would not be sampled repetitively. Each replicate was sampled once a month during April, May, September, October, and November and twice monthly during June, July, and August. Belowground biomass samples were collected in June, July, August, September, and November.

Primary producers. Herbage biomass was sampled with 0.25 m^2 quadrats. The number of quadrats was adjusted so that the standard error of the total biomass was estimated within 10% of the sample mean at the 80% confidence level. This represented between 3 and 10 quadrats per replicate per sample date. In each quadrat the major species were separated: *Andropogon scoparius, A. gerardi, Panicum virgatum, Sorghastrum nutans, Sporobolus asper, Bromus japonicus, Poa pratensis,* and *Ambrosia psilostachya.* The remainder of the plants were classified as miscellaneous grasses, forbs, or sedges. In each of these categories the material was harvested and divided into live standing crop, previous year's standing dead, and current year's standing dead. Each sample was dried at 60°C for 48 hr and weighed. Litter was collected from each of the quadrats, dried, weighed, ashed, reweighed, and was expressed as ash-free weight. Belowground biomass was

collected with a hydraulic corer to a depth of 90 cm. Two cores were taken from each quadrat, and each core was divided into depth segments of 0 to 5, 5 to 10, 10 to 20, 20 to 30, 30 to 50, 50 to 70, and 70 to 90 cm. Root cores were analyzed separately from crowns and washed through a 30-mesh screen, dried, weighed, ashed, reweighed, and were expressed as ash-free weight.

The rate of litter accumulation was measured by installing 36, 15 x 15 cm, 2-mm mesh screen wire quadrats on the soil surface. These screen quadrats were nailed to the soil surface, and the material which fell on the screen was collected at five different sampling dates throughout the season.

The rate of litter decomposition was measured with 15 x 15 cm, 2-mm mesh screen wire litter bags which were established on May 26. The material placed in the bags was freshly fallen litter, and the amount coincided with that normally present on the soil surface at that time. Sub-samples of these bags were collected twice during the growing season, September 30 and November 14.

Invertebrates. Invertebrate sampling was conducted to obtain quantitative estimates of numbers and biomass of major groups. A 0.5-m^2 modified "quick trap" patterned after Turnbull and Nicholls (1966) was used. After the trap was dropped the enclosed vegetation was clipped and removed to a paper sack. The interior of the trap was then vacuumed with a "D-vac" collector and the material returned to the laboratory in ice chests for separation. A total of 20 samples, five samples from each of two replicates and for two treatments each, were taken adjacent to the herbage biomass

samples at each collecting period. Samples were collected on July 3, July 16, August 3, August 17, September 27, October 25, and November 23. These dates correspond closely with the dates of vegetation sampling with the exception of the November collection, which was taken late and during sub-freezing temperature.

Laboratory separations were done in four stages:

(1)   Extraction of the D-vac collections into 70% isoprophyl alcohol from Berlese funnels (48 hr).

(2)   Hand-sorting of the D-vac collections after removal from the funnels.

(3)   Extraction of vegetation clippings into 70% isoprophyl alcohol from Berlese funnels (48 hr).

(4)   Hand-sorting of vegetation clippings after removal from funnels (when necessary).

Insects were then separated into families (when possible) and into life stages. Representatives of each taxon were removed and oven-dried at $60^{\circ}C$ for 24 hr and weighed for biomass determinations.

Birds. Breeding bird populations were censused between June 12 and June 15 on one 8.4-ha plot located in the grazed treatment. Populations were censused using the territory flush technique (Wiens, 1969): singing individuals were approached and flushed from their display sites, and their movements were recorded on a scaled field map of the plot. Individuals tended to remain within clearly delimited areas during these flushings, and these areas corresponded closely with breeding territories. To estimate population densities, territories of all individuals present on the plot were mapped; and, for each species, the number of territories (by area) present in the 8.4-ha plot was determined. This number was then multiplied by a mating system conversion factor (generally 2.0, except for polygynous

species) to account for the presence of females, and the estimate of plot

population density was converted to individuals/ha. Changes in population

density throughout the season were not directly measured, but were estimated

from phenological data presented by Sutton (1967) and Johnston (1964) using

the mid-June census value as an estimate of the stable breeding population

density. Recruitment rates were also estimated using information on clutch

sizes and hatching success from the works of Sutton and Johnston, from the

studies of Ryder (personal communication) and his students at Pawnee, and

from Maher and Felske (personal communication) in the Canadian IBP Grassland

studies at the Matador Site, Saskatchewan. Bird weights were recorded

from specimens collected in other portions of the Adams Ranch and were

converted to dry weight by assuming a water content of 70%. Dietary composi-

tion was estimated from a preliminary analysis of the stomach contents of

specimens collected at Osage; and for the four species recorded in the

census plot, these values were:

Upland Plover (*Bartramia longicauda*)   100% insect

Eastern Meadowlark (*Sturnella magna*)   100% insect

Dickcissel (*Spiza americana*)   40% seed; 60% insect

Grasshopper Sparrow (*Ammodramus savannarum*)   30% seed; 70% insect

Small mammals. Populations were sampled by means of adjacent live-trap

and snap-trap grids. Both grids were a square of 12 x 12 stations (144

total). The interval between each station in the rows and columns was 15 m,

giving the grid a minimum area of 2.76 ha. The live-trap grid was located

on the east end of the ungrazed treatment, except for rows 11 and 12,

which were in an area that was cultivated 12 years ago. The snap-trap

grid was located just west of the ungrazed treatment in an area which was lightly grazed during parts of the winter season.

Two Museum Special snap traps were placed at each station on the snap-trap grid, and two aluminum Sherman live traps were placed at each station on the live-trap grid. All traps were prebaited for 5 days before they were set to catch animals. Traps were baited with a mixture of oatmeal and peanut butter. After the prebaiting period all traps were set for 10 con-secutive days unless rainy weather interfered.

Decomposers. Bacterial biomass was calculated by the plate-count method on samples taken from a soil depth of 0 to 50 cm. Plate counts were done using plate-count agar with incubation at $28^{o}C$ for 5 days. Colonies counted included actinomycetes for biomass calculations. The average cell was assumed to be a sphere with an average volume of 1 μ^3 and 80% water.

Fungal hypae measurements were made on diluted water-soil (not homoge-nized) spread over an area of 1 cm^2 and stained with dilute methylene blue. With a calibrated ocular and camera lucida a map measurer was used to trace the total length of hypae in 100 microscopic fields per dilution. Knowing the area counted, the total length per g of soil was calculated. The average fungal strand diameter was assumed to be 5 μ, had a specific gravity of 1.2 and a water content of 90%.

To estimate carbon dioxide evolution in the field, 10 ml of NaKOH were exposed in a 100-ml beaker in a closed system of 10 cm in diameter for 24 hr. The absorption chamber was a metal cylinder enclosed in a tightly fitting plastic bag, and it was driven into the soil. These systems were shaded where necessary. Measurements were taken from both bare soil and

chambers containing two to four crowns of *Andropogon scoparius*. The CO_2 absorbed was determined after barium chloride precipitation of the carbonates and titration of the residual alkali with standard HCl using phenolphthalein indicator.

ASSUMPTIONS AND CONDITIONS FOR THE OSAGE COMPARTMENT MODEL

In the preliminary calculations of this model (Fig. 1), when possible, all principal system variables were expressed as g/m^2 and rates are expressed as $g/m^2/day$. The calculations could have been converted to energy (calories) to more easily express the respiration rates.

Eventually the model will be converted to a dynamic model with time-varying coefficients; in fact, the primary producer part of the model is already at this stage. However, during the 1970 season, small mammals were measured only twice and birds only once. Insect measurements were made throughout the year, but measurements were initiated fairly late in the growing season. Since time-series measurements were not available for all compartments, this model will employ the producer biomass values and rates which occurred nearest the date of peak live standing crop. For the other compartments data from the sample interval nearest this date (1 July 1970) have been utilized. Data for the microorganisms, primary producers, invertebrates, small mammals, and abiotic factors were obtained on the ungrazed treatment. The bird studies were performed on the grazed treatment adjacent to the ungrazed treatment.

Compartment Values and Transfer Rates

Primary producers. The value for the total incoming solar radiation is the amount of energy available on a clear day at the approximate date
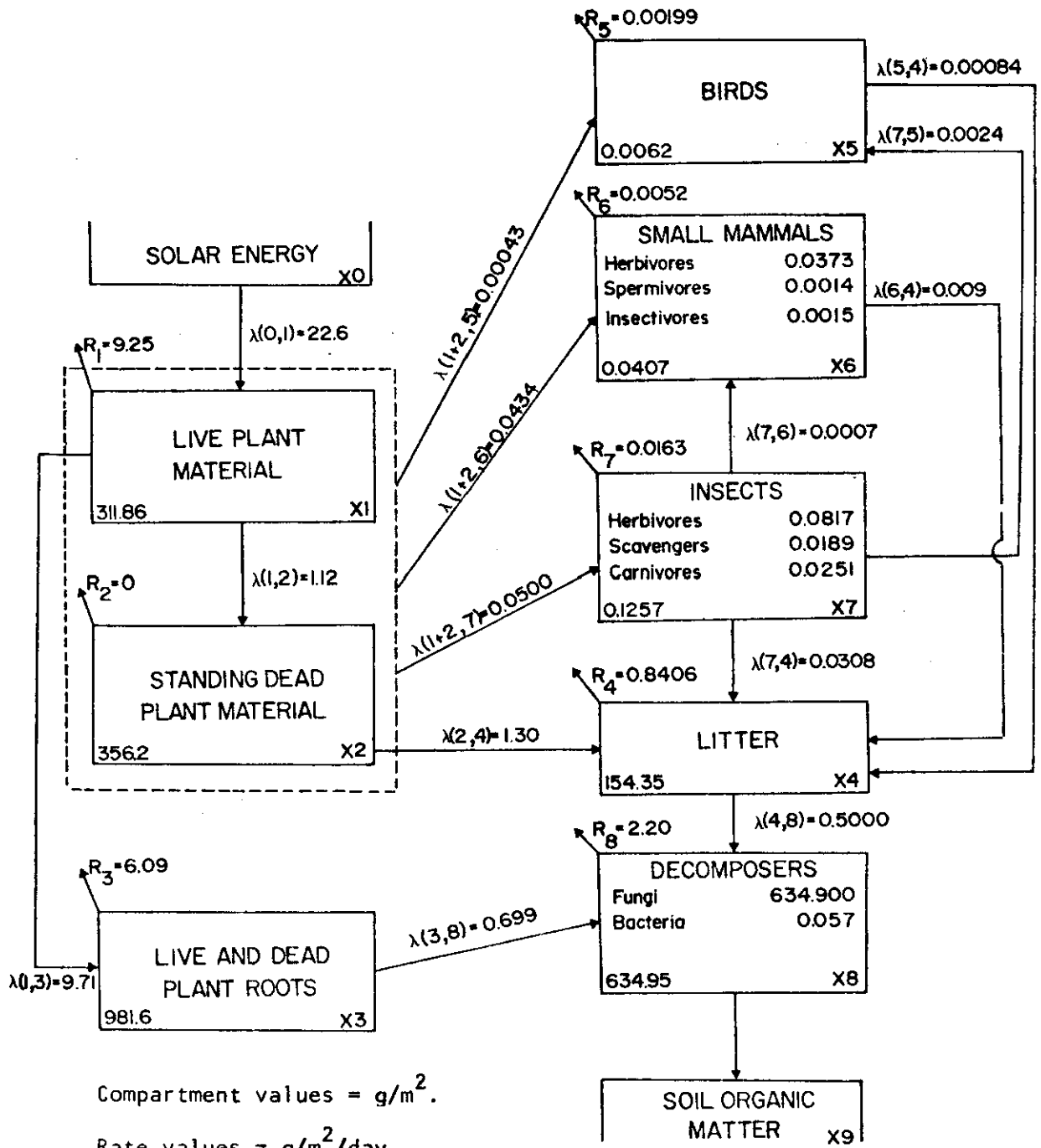
Compartment values = g/m^2.

Rate values = $g/m^2/day$.

Fig. 1. Osage compartment model.

of the peak live standing crop. The highest radiation value was 1.3 $cal/cm^2/$ min, and the daily value was calculated from the solar radiation recorded on the strip chart of the pyranometer.

The photosynthesis rate [$\lambda(0,1)$] was calculated from gas exchange rates determined under laboratory conditions for 40-day-old seedlings of *Andropogon scoparius*, *A. gerardi*, *Sorghastrum nutans*, and *Panicum virgatum*. The measured values were 8.8, 6.3, 18.8, and 19.0 mg $CO_2/g/hr$, respectively. These rates were prorated among these four species, and the proportions were used to calculate daily photosynthesis for the total aboveground biomass. The final gas exchange values for each of the four species were summed to provide a value of 19.59 g $CO_2/m^2/day$ as the fixation rate at peak live standing crop.

Respiration was calculated in a similar manner using laboratory data for *Andropogon scoparius*, *A. gerardi*, *Sorghastrum nutans*, and *Panicum virgatum*. The respective respiration rates were 1.9, 1.6, 1.5, and 3.4 mg $CO_2/g/hr$. At peak standing crop the respiration component is 13.61 g $CO_2/m^2/day$, and gross photosynthesis (respiration plus net photosynthesis) is then assumed to be 33.20 g $CO_2/m^2/day$.

This estimate of net photosynthesis [$\lambda(0,1)$] is probably an overestimate since the rate studies were conducted on 40-day-old seedlings which presumably have a higher proportion of photosynthetic tissue than older plants which constitute a majority at the stage of peak standing crop. Both photosynthesis and respiration rates were calculated at $27^{\circ}C$, and previous experimental work in our laboratory has shown that photosynthesis rates increase up to about $35^{\circ}C$. During July the average daily temperature is considerably above $27^{\circ}C$, so that respiration is probably higher than

the laboratory conditions which may lead to an underestimate. Since net photosynthesis is probably an overestimate and respiration an underestimate, there may be a compensation in the final photosynthesis value.

The transfer rate from the live biomass compartment to the standing dead compartment was estimated from root turnover and root respiration. Root-turnover rate is calculated as 26% per year, root respiration was estimated at 0.5 g CO_2/g/hr, and it was assumed that 75% of the root biomass was respiring.

The above calculations suggest a net gain in biomass of 2.50 g/m^2/day at the time of peak standing crop which conforms with the field data. If one assumes a caloric value of 4.1 cal/g, then the photosynthetic fixation of energy on a clear day (1 July 1970) is approximately 1.2% of the incoming solar radiation.

Birds. The calculations of the bird compartment were based upon procedures of bioenergetic estimation developed more fully elsewhere (Wiens and Innis, in prep.). Briefly, existence-energy demands per individual were calculated for each species using weight-dependent, temperature-dependent metabolic functions modified from Kendeigh (1963, 1970) and the temperature records for the Osage Site. This estimate was adjusted for activity by a factor of 1.4 (Schartz and Zimmerman, 1971) and was multiplied by population density to obtain the population energy demands for the species. The additional energy demands placed on the system by the production of young were considered by projecting changes in population density resulting from reproduction and adding the estimated existence and growth-energy requirements of young to those of the adults.

Bird populations were not censused at the time of peak standing crop of the vegetation components. The bioenergetic estimates used to obtain the values reported here were obtained by projection from the mid-June census estimate of adult population densities to values for July 1. Estimated avian immigration and emigration rates for the Osage populations are as follows:

Immigration Rates

April 1-30	0.00017 g/m^2/day
May 1-15	0.00500 g/m^2/day
May 16-20	0.00026 g/m^2/day

Emigration Rates

| August 1-15 | 0.00029 g/m^2/day |
| August 16-31 | 0.00010 g/m^2/day |

Estimates were not projected beyond August 31. These values are not included in the overall compartment model.

Compartment values for biomass flux through the bird populations were calculated from the bioenergetic estimates for July 1. The energy intake by each species was divided into seed and insect sources according to the dietary composition values given in the methods section of this report; these were then converted to grams dry weight by assuming that seeds had a mean caloric value of 5.2 cal/g dry weight and insects had a value of 5.6/cal/g dry weight. A digestive efficiency of 70% was assumed so that the contribution to the litter compartment via egestion of undigested food and excretion was 30% of the food-intake rate. Respiratory rate was calculated by the difference (Respiration = Gross Intake - Egestion). The estimated inputs for bird biomass were from plants (seeds--0.00043 g/m^2/day)

and invertebrates (0.0024 g/m^2/day). The outputs were respiration
.(0.00199 g/m^2/day) and transfer to litter (0.00084 g/m^2/day). Avian
standing crop on July was estimated as 0.00620 g/m^2.

Small mammals. Small mammals were sampled on May 28 and August 27,
so biomass measurements in the compartment model represent the mean of
these two dates. Field measurements were in terms of liveweight and
were converted to dry weights by assuming a water content of 70%
(Golley, 1960). Nearly 90% of the biomass was contributed by *Microtus
ochrogaster.* Consumption rates for the various species were derived from
Golley (1960) for *Microtus,* McNab (1963) for *Reithrodontomys,* Pearson
(1947) and Rood (1958) for *Blarina,* and Douglas (1969) for *Spermophilus.*
The rate of food consumption for *Sigmodon* was assumed to be similar to
that of *Microtus. Cryptotis* made negligible contributions to the total
biomass and was simply estimated. Most of the material flow into the small
mammal compartment was via the foliage-eating *M. ochrogaster.* The
material transfer from the aboveground vegetation to the small mammal
biomass was calculated as 0.107 m^2/day from the literature. The vegetation
at this date was approximately 60% water, so the consumption rate was
converted to dry weight. Similarly, the material transfer from the
invertebrate compartment was converted to dry weight by assuming a 30%
dry weight of invertebrate material. The contribution of the small
mammal compartment to the litter compartment was calculated on the basis
of estimates made by Golley (1960) concerning caloric losses in feces
and urine and are thought to be on the order of 20% of the total energy
intake into the small mammal compartment or 0.009 g/m^2/day dry weight.

Respiratory losses were estimated by employing values from McNab (1963), Pearson (1947, 1948, 1960), and Wiegert (1961). Overall, small mammal respiration was estimated to be about 5,000 cc oxygen/ha/hr or 11.8 cc O_2/m^2/day. This may be converted to .057 cal/m^2/day. For the compartment model, respiration (R_6) may also be estimated by the differences between inputs and outputs and is approximately 131 cal/m^2/day; or may be converted and is $(44 \times 10^{-6}) \times$ cc O_2/m^2/day = g/m^2/day. These two estimates of respiration are of the same order of magnitude, and the discrepancies are probably due to the underestimation of rates of active metabolism by small mammals, failure to include any energy contribution to small mammal production rates, and/or overestimation of energy intake in food. Considering the many assumptions involved and their relative lack of quantitative precision, a two-fold discrepancy represents reasonably good agreement.

Invertebrates. The invertebrate biomass was partitioned among herbivores, scavengers, and carnivores. Of the total biomass in the invertebrate compartment (0.1257 g/m^2) the herbivores contributed approximately 65%, the scavengers 15%, and the carnivores 20%. It was estimated that the invertebrates consumed approximately 10 g of primary productivity throughout the season, and assuming a 200-day growing season, the daily rate is approximately 0.05 g/m^2/day. The literature suggested that 50% or more of the material (0.0250 g/m^2/day) was transferred directly to the litter compartment. The remainder of the litter transfer (fig. 1) includes transfer through insect and other secondary consumers as well as carcass values of dead insects. The respiration was assumed

to be approximately 65% of the assimilated biomass or 0.0163 $g/m^2/day$.
The amount of transfer from invertebrates to birds was estimated to be
0.0024 g/m^2 by Wiens and Innis (see Compartment Values and Transfer Rates;
Birds).

Litter. The litter biomass at peak standing crop was 154.35 g/m^2.
The litter screen experiments provided an approximate rate of 1.3 $g/m^2/$
day for material moved from the aboveground compartment to the litter
compartment. At the time of peak standing crop of the aboveground
components the litter biomass was essentially constant. Data from litter-
bag experiments indicated that the rate of transfer from litter, through
decomposers, to soil organic material was 0.5 $g/m^2/day$. Inputs from the
birds, mammals, and invertebrates are included as suggested from these
compartments. No data were available for litter respiration, so the
value of 0.8406 $g/m^2/day$ was calculated as the difference between the other
output and the inputs.

Decomposers. The decomposer biomass was determined on June 19 and
September 30, so the biomass estimates represent averages between these
two dates. The amount of CO_2 released, recalculated as g $C/m^2/day$, was
obtained from cores in the laboratory and also represents a mean of the
two sampling dates. The fungal biomass and bacterial counts represent
values to a depth of 50 cm in the field. The inputs to this compartment
are represented by the transfer of material from the litter (0.50 $g/m^2/day$)
and from the roots (0.699 $g/m^2/day$), and are less than the measured
output of respiration (2.20 $g/m^2/day$). This would indicate that at the
time of peak standing crop for the live material, the decomposers are
working on stored organic material in the soil.

SUMMARY

Since all this information has been collected on one grassland at roughly the same time a number of intriguing comparisons are possible. Table 1 shows the amount of biomass in each compartment. It is obvious that the greatest percentage of biomass (66%) is in the producer component of the ecosystem; and that birds, mammals, and invertebrates contribute a very small amount of biomass. If one considers mammals, insects, and birds to represent aboveground biomass as well as the live, dead, and litter-plant categories, then approximately 34% of the biomass is aboveground and 66% is belowground. If we categorize producers as including live plants, dead plants, roots, and litter, then 74% of the biomass is in the producer-trophic level, 0.007% is in the consumer level, and 26% is in the decomposer level.

At the time of peak live herbage standing crop, only the decomposer compartment shows a net loss in carbon. It should be recalled that litter "respiration" was calculated by differences since the net amount of litter showed very little change at this time of year. Clearly, then, the net change in the compartment model will be zero (Table 2).

Throughout this data manipulation, estimates of respiration have proved to be difficult. Actual measurements were made in the laboratory for aboveground live material and in the field for the decomposer compartment. All other compartments have been estimated from literature values. The invertebrate section of this report has shown that because of substrate differences, laboratory techniques, etc., respiration should probably be included as caloric values. In fact, the estimates for small mammal respiration in this model are based on caloric estimates.

There are many literature values for calorific equivalents (Cummins, 1967; Kendeigh and West, 1965), and we have accumulated a large amount of calorific data in the U.S. IBP Grassland Biome. Because of the difficulties of preparing a meaningful representation of respiration as $g/m^2/day$, future modeling on the Osage Site will probably utilize $cal/m^2/day$.

The above analysis is quite noteworthy in that all the trophic levels have been simultaneously analyzed. Since the data were taken in a comparable fashion, these intertrophic-level relationships can be examined. However, it is readily apparent that all the included data are time-varying and need to be dealt with mathematically in the same sense. The artificiality of comparing all trophic levels at one date is readily apparent when one observes the data and thinks intuitively about the mechanics of a tallgrass ecosystem. It is clear that our next Osage endeavor should be to build a time-varying model which begins to account for the dynamics of these compartments. This is well within our capability; and, in fact, the primary producer compartments are already at this point. By this time next year, we should have produced such a model.

ACKNOWLEDGMENTS

Table 1. Total biomass in each of eight compartments of the preliminary
Osage Site model. These biomass estimates are at the time of
peak live herbage.

Compartment	Biomass (g/m^2)	Percentage
Roots	981.6000	40.24360 (40)
Decomposers	634.9600	36.03207 (36)
Dead plant parts	356.2000	14.60347 (15)
Live plant parts	311.8600	12.78562 (13)
Litter	154.3500	6.32804 (6)
Invertebrates	0.1257	0.00515 (<1)
Mammals	0.0438	0.00180 (<1)
Birds	0.0062	0.00025 (<1)
Total	2439.1457	100.00000

Table 2. Summary of inputs and outputs of each compartment at the time
of peak live herbage standing crop. All tabular values are
in terms of $g/m^2/day$.

Component	Inputs	Outputs	Net Change
Aboveground biomass	22.6000	19.0038	+3.5962
Belowground biomass	2.9200	6.7890	+2.9210
Birds	0.0028	0.0028	0.0000
Mammals	0.0441	0.0142	+0.0299
Insects	0.0500	0.0500	0.0000
Litter	1.3406	1.3406	0.0000
Decomposers	1.0990	2.2000	-1.0010

LITERATURE CITED

Blocker, H.D., and R. Reed. 1971. 1970 insect studies at Osage Comprehensive Site. U.S. IBP Grassland Biome Tech. Rep. No. 93. Colorado State Univ., Fort Collins. 38 p.

Cummins, K.W. 1967. Calorific equivalents for studies in ecological energetics. Pymatuning Lab. Ecol., Univ. Pittsburgh. 52 p. (Mimeo).

Douglas, C.L. 1969. Comparative ecology of pinyon mice and deer mice in Mesa Verde National Park, Colorado. Mus. Natur. Hist., Univ., Kansas Pub. 18:421-504.

Golley, F.B. 1960. Energy dynamics of a food chain in an old-field community. Ecol. Monogr. 30:187-206.

Harris, J.O. 1971. Microbiological studies at the Osage Site, 1970. U.S. IBP Grassland Biome Tech. Rep. No. 102. Colorado State Univ., Fort Collins. 39 p.

Hoffmann, R.S., J.K. Jones, Jr., and H.H. Genoways. 1971. Small mammal survey on the Bison, Bridger, Cottonwood, Dickinson, and Osage Sites, 1970. U.S. IBP Grassland Biome Tech. Rep. No. 109. Colorado State Univ., Fort Collins. 69 p.

Johnston, R.F. 1964. The breeding birds of Kansas. Mus. Natur. Hist., Univ. Kansas Pub. 12:575-655.

Kendeigh, S.C. 1963. Relation of existence energy requirements to size of bird. Amer. Zool. 3:497.

Kendeigh, S.C., and G.C. West. 1965. Caloric values of plant seeds eaten by birds. Ecology 46:553-555.

Kendeigh, S.C. 1970. Energy requirements for existence in relation to size of bird. Condor 72:60-65.

McNab, B.K. 1963. A model of the energy budget of a wild mouse. Ecology 44:521-532.

Pearson, O.P. 1947. The rate of metabolism of some small mammals. Ecology 28:127-145.

Pearson, O.P. 1948. Metabolism and bioenergetic. Sci. Monthly 66:131-134.

Pearson, O.P. 1960. The oxygen consumption and bioenergetics of harvest mice. Physiol. Zool. 33:152-160.

Risser, P.G. 1970. Comprehensive network site description, Osage. U.S. IBP Grassland Biome Tech. Rep. No. 44. Colorado State Univ., Fort Collins. 5 p.

Risser, P.G. 1971. Osage site, 1970 report, primary production. U.S. IBP Grassland Biome Tech. Rep. No. 80. Colorado State Univ., Fort Collins. 41 p.

Rood, J.P. 1958. Habits of the short-tailed shrew in captivity. J. Mammal. 39:499-507.

Schartz, R.L., and J.L. Zimmerman. 1971. The time and energy budget of the male Dickcissel (*Spiza americana*). Condor 73:65-76.

Sutton, G.M. 1967. Oklahoma birds. Univ. Oklahoma Press, Norman. 674 p.

Turnbull, A., and C.F. Nicholls. 1966. A "quick trap" for area sampling of arthropods in grassland communities. J. Econ. Entomol. 59:1100-1104.

Wiegert, R.G. 1961. Respiratory energy loss and activity patterns in the meadow vole, *Microtus pennsylvanicus pennsylvanicus*. Ecology 42:245-253.

Wiens, J.A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithol. Monogr. 8:1-93.

Wiens, J.A. 1971. Avian ecology and distribution in the Comprehensive Network, 1970. U.S. IBP Grassland Biome Tech. Rep. No. 77. Colorado State Univ., Fort Collins. 49 p.

Wiens, J.A., and G.S. Innis. 1972. Estimation of energy flow in bird communities: a bio-energetic model. (In preparation).