

Abstract of the Thesis of

Richard R. Raines for the Master of Science Degree

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Title: COMPUTER SIMULATION

OF A GRASSLAND COMMUNITY

UNDERGOING SECONDARY SUCCESSION

Abstract Approved:

Carroll Prophet

Systems analysis techniques were utilized in identifying, defining, and quantifying the structure and controlling ecological processes and interactions of a grassland community undergoing secondary succession, and in the derivation and operation of a computer model in predicting community structure through time, during the period from January 1, 1973 through December 31, 1973, on the Ross Natural History Reservation, Lyon County, Kansas.

A seven-compartment model was designed to simulate the structure and controlling ecological processes and interactions of the study community. A series of mathematical functions related to biological or environmental phenomena were developed to mimic the quantified structure and controlling ecological processes and interactions of

the study community. A computer program was written, utilizing the mathematical functions, to simulate the redistribution of matter (biomass) through the system. The computer model was tested, utilizing data values derived from field measurements, separate studies, or abstracted from the literature, and results utilized to make predictions concerning community structure through time.

The computer simulation was successful in approximating the structure of the study community by manipulating the controlling ecological processes and interactions of the community through time as related to biological or environmental phenomena. Community structure was expressed as biomass per unit of measure per day ($\text{g/m}^2/\text{day}$) for live plant material, standing dead plant material, litter, birds, mammals, insects, and decomposers.

COMPUTER SIMULATION
OF A GRASSLAND COMMUNITY
UNDERGOING SECONDARY SUCCESSION

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Richard R. Raines

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Carl W Prophet

Approved for Major Department

Harold E Durst

Approved for Graduate Council

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INTRODUCTION

The concept of the ecosystem has long recognized that ecological systems are basically energy systems. Energy flows within and through the system leading to clearly defined trophic structures, biotic diversity, and material cycles. Early ecological studies described the specific components of the ecosystem (structure) and the sometimes special interaction between populations (Juday, 1940; Lindeman, 1942; Ivlev, 1945). While they recognized the entire unit, the tools and concepts of how to study the entire system were generally lacking. These descriptive studies could only "freeze" the system at long intervals, describe its state, and then hypothesize what happened or might happen. In recent years, there has been a change in emphasis of ecological research from a descriptive approach to a functional one in which the observer is primarily interested in the productivity of the system as well as in its composition.

The systems approach of looking at a problem stresses the interdependencies between elements of the system and focuses specifically on these relationships rather than on just the nature or behavior of individual elements. In productivity studies the ecologist is now interested not only in what species are present, but in the amounts of material (biomass, nutrients, or energy) that are present in the different trophic levels of the community.

Mathematical models are tools of the systems approach. In the process of constructing a model of a system, the mathematical form provides valuable guidance for research data collection and decision making. The model permits the ecologist to see how small but vitally important pieces of information and theory can fit together. The mathematical model provides the

link between the problem definition and electronic computers by means of operational mathematical techniques. The models allow for a more explicit description of the problem facilitating rapid examination of alternatives. This has contributed to an expansion and refinement of ecological concepts and offered more versatility in modeling. During the past few years many functional models have been designed and tested (Rosen, 1958, 1959; Rashevsky, 1960; Ashby, 1963; Olson, 1963; Patten, 1965, 1971, 1972; Holling, 1966; and Watt, 1966, 1968).

It was proposed that systems analysis techniques be used in the description and operation of a computer model of a grassland community undergoing secondary succession, and in the predictions of community structure through time. Specifically, the objectives of the study were: 1) to identify, define, and quantify the structure and controlling ecological processes and interactions of the study community; 2) to design and test a computer model of the study community and, 3) to use the computer model to simulate the operation of the study community under varying conditions and to make predictions concerning community structure through time.

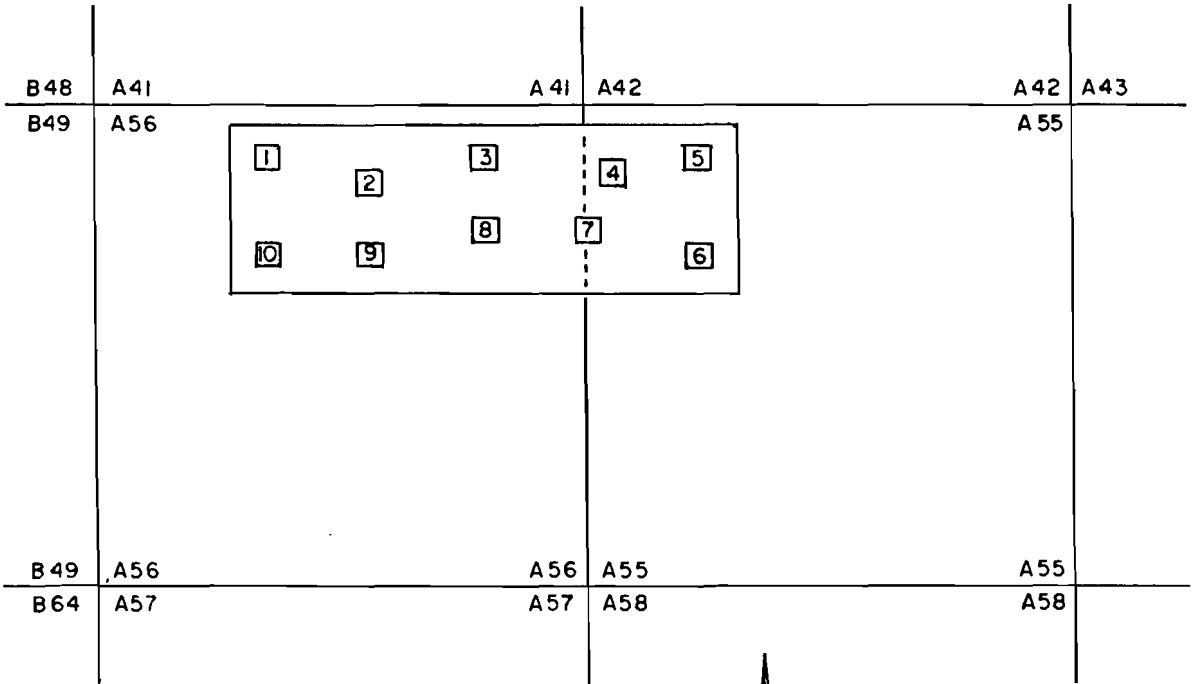
DESCRIPTION OF THE STUDY AREA

The Ross Natural History Reservation of the Division of Biology, Emporia State University, is located in west central Lyon County and northeast Chase County, approximately 23 km northwest of Emporia, Kansas. The reservation consists of a 421 ha area, of which 81 ha are state owned, and it is situated on the east face of the Flint Hills Upland and characterized by gently rolling hills with numerous limestone outcroppings (Hartman, 1960). The history, topography, and vegetation of the area have been described by Hartman (1960), and Wilson (1963).

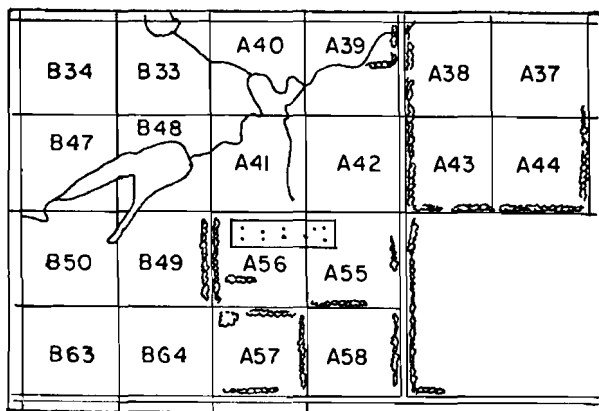
Description of the Study Plot

Within the state owned 81 ha, a 1.42 ha plot was selected for study. The study plot was located in T18, R10, Section 8--the southwest quarter of the southwest quarter; 38°30' latitude and 96°20' longitude, with an elevation of 376 m mean sea level. The study plot had a slope of three to five degrees in a northwesterly direction. As defined by Hartman (1960), the 1.42 ha study plot was located in grids A-56, and A-55 (Figure 1).

Prior to its inclusion as a portion of the Ross Natural History Reservation in 1959, the land had been in agricultural use, and the study plot had been a portion of a large cultivated field whose top soil had been extensively eroded. The land was reseeded to a mixture of cover grasses, predominantly Bromus inermis Leyss, in 1948. The land has not been disturbed since reseeded and has been designated as an old-field (grassland) community undergoing secondary succession.



SCALE: 3mm = 10m



Physical Environment

Tests made on soil samples collected at 15 cm depths within the study plot indicated the soil to be acidic (Table I). Most soils in this area tend to be neutral to slightly alkaline. The acidity, high potassium, low organic and phosphorous contents in the top soil probably indicates that little leaching of decaying organic matter was occurring.

Periodic measurements of available soil moisture within the study plot indicated that the community did not undergo a moisture stress during the duration of the study. It was doubtful that a moisture stress developed at any time during the study due to high precipitation received and drainage characteristics of the soils in the study plot.

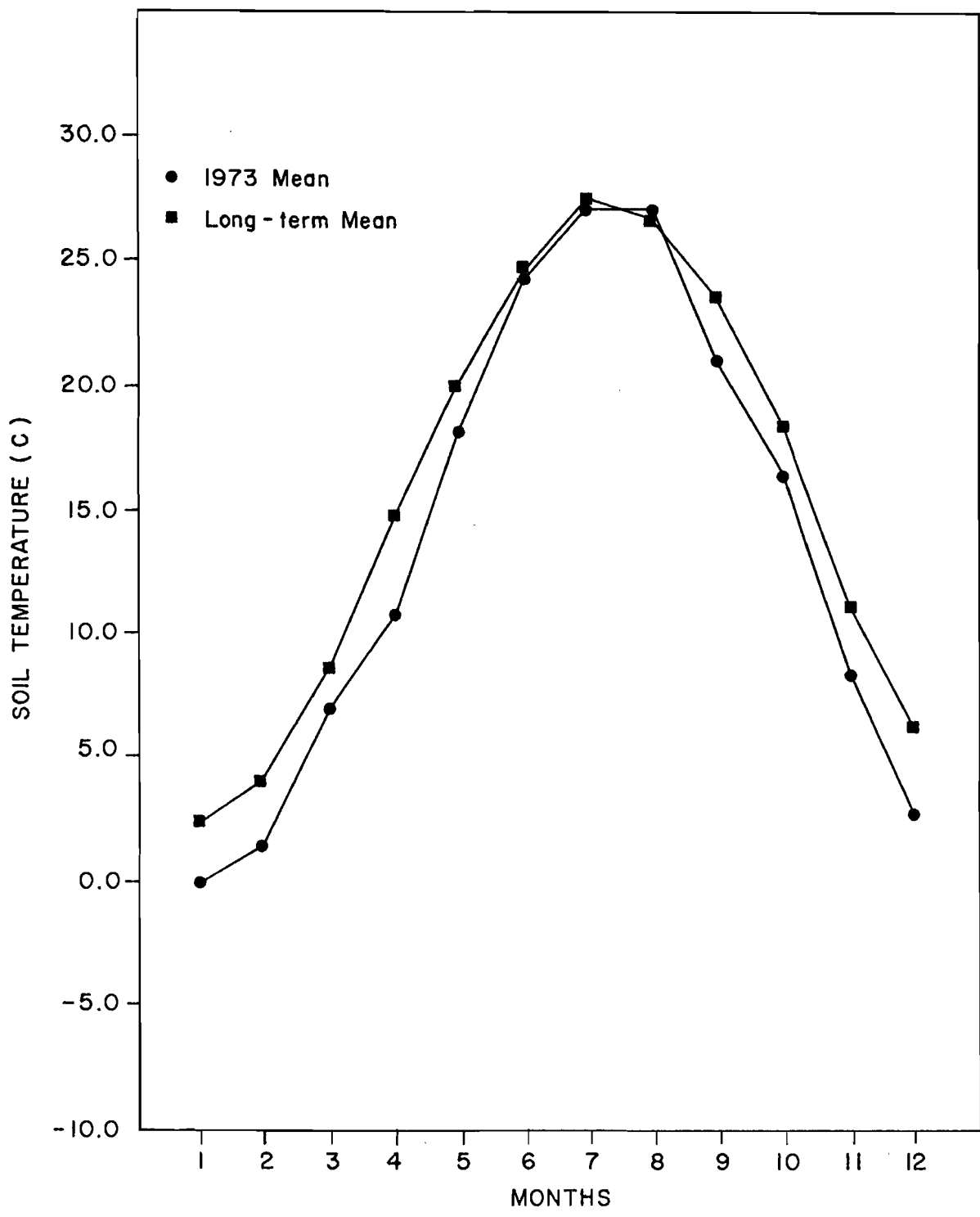
The mean seasonal soil temperatures at 10 cm depths in 1973 were: winter, 1.42 C; spring, 12.06 C; summer, 26.19 C; and fall, 15.36 C (U.S. Weather Bureau, 1973). As compared to calculated long-term seasonal averages of 4.3 C, 14.4 C, 26.3 C, and 17.9 C for the respective seasons, the 1973 values were lower but followed the long-term trend (Figure 2).

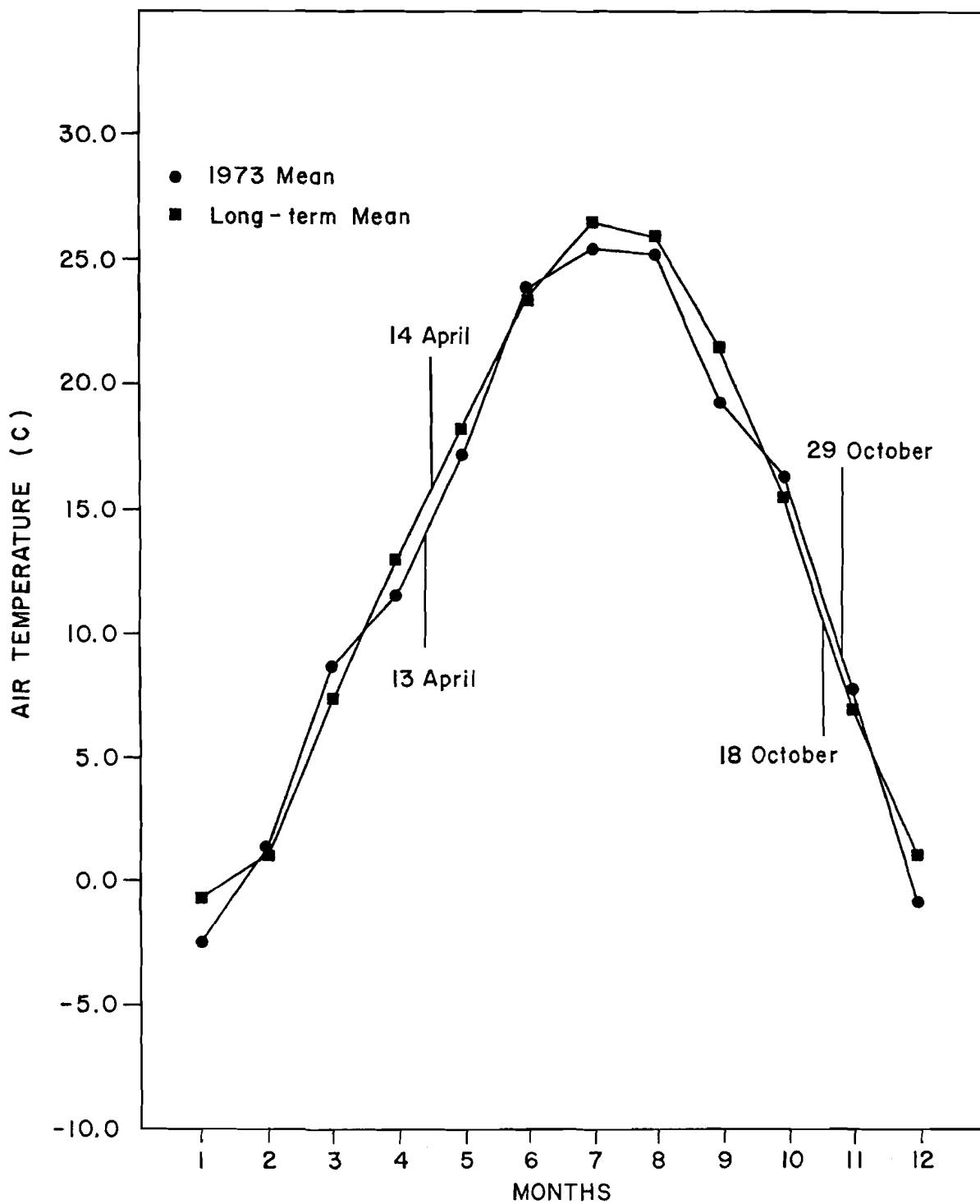
The mean seasonal air temperatures for 1973 were: winter, -0.60 C; spring, 12.42 C; summer, 25.03 C; and fall, 14.49 C. The long-term means for the same seasons as reported by Flora (1948) are 0.47 C, 12.90 C, 25.37 C, and 14.63 C respectively. Compared to the long-term seasonal means 1973 air temperature values were typical (Figure 3). The frost-free period of 1973 lasted from 13 April until 29 October, a total of 199 days. This is longer than the normal growing period of 187 days, 14 April to 18 October, for this area (Flora, 1948).

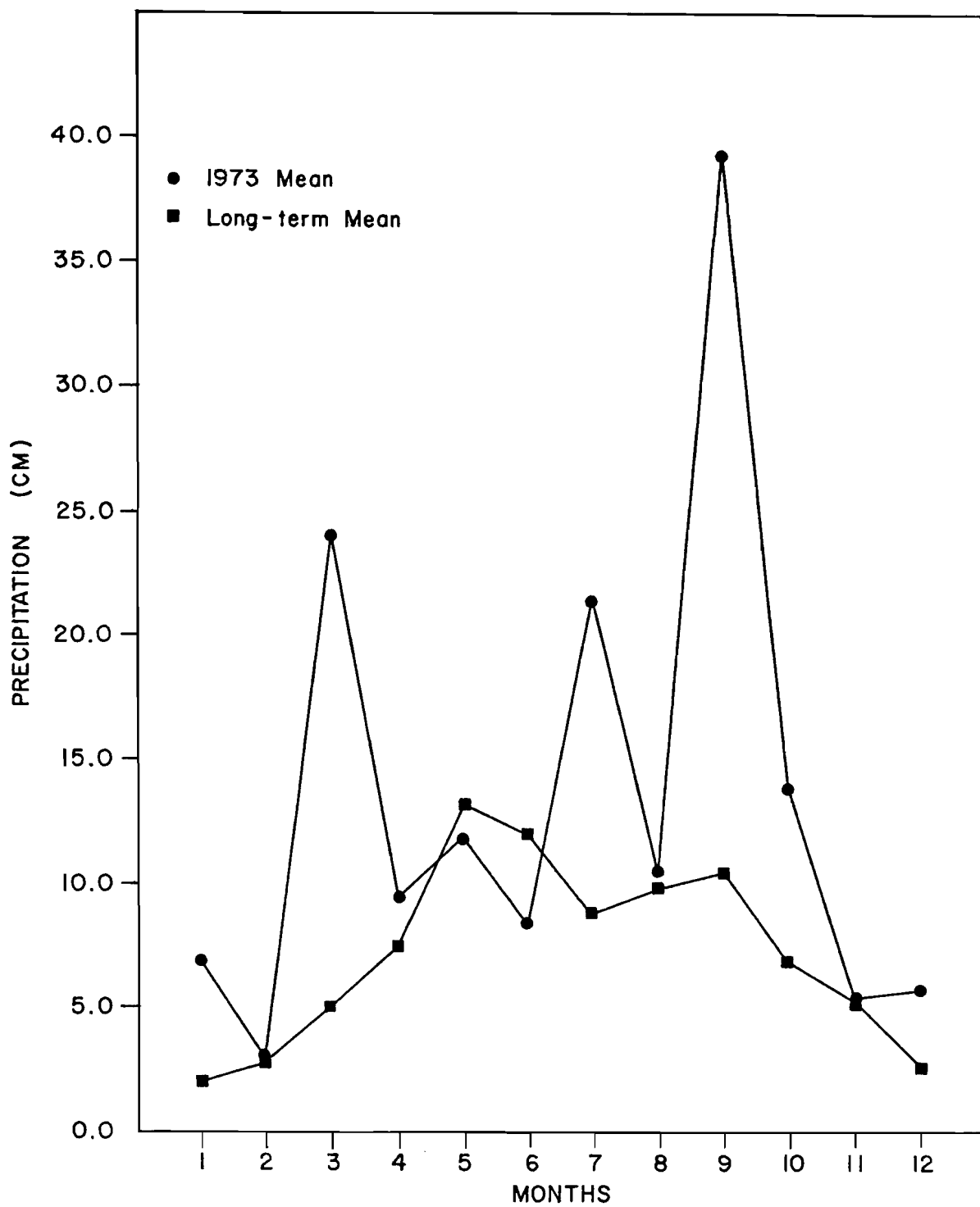
Precipitation seasonal means for 1973 in all cases exceeded the long-term seasonal means (Figure 4). The total annual precipitation for 1973 was 160.71 cm compared to the annual mean of 86.61 cm (Flora, 1948).

TABLE I. Soil analysis of the 1.42 ha study plot.

| Date | Where Sample Taken | Soil Type | Soil Depth (cm) | Sand (%) | Silt (%) | Clay (%) | 1st pH | 2nd pH | K (kg/ha) | P (kg/ha) | Organic Matter (%) |
|-----------|---------------------|-----------------|-----------------|----------|----------|----------|--------|--------|-----------|-----------|--------------------|
| June 1973 | Under Ground Litter | Silty Clay Loam | 15 | 29.2 | 25.6 | 45.2 | 5.9 | 6.8 | 470 | 24 | 1.9 |
| June 1973 | In Thick Vegetation | Silty Clay Loam | 15 | 29.2 | 25.6 | 45.2 | 5.8 | 6.9 | 492 | 21 | 1.9 |







Seasonal means for 1973 were: winter, 15.77 cm; spring, 45.57 cm; summer, 40.49 cm; and fall, 58.88 cm. The long-term seasonal means are: winter, 7.72 cm; spring, 25.73 cm; summer, 30.66 cm; and fall, 22.50 cm (Flora, 1948). September was the wettest month with 39.60 cm of precipitation. Most of the precipitation that fell during the summer came from heavy showers lasting several days at a time. February was the driest month with only 3.05 cm of precipitation. Precipitation in the form of ice and snow was normal for the year.

Recorded solar insolation values varied from season to season (Figure 5). As the angle of incidence decreased during July through December, solar radiation decreased. With the rotation of the earth causing the angle of incidence of the sun to increase during the spring months, measurements of solar radiation again increased.

Biotic Composition

Of the 55 species comprising the plant community, Bromus inermis Leyss was numerically the most common species (Table II). Bird species observed in the study plot are summarized in Table III. Of the 21 species observed in the study plot, Sturnella magna magna Linnaeus was the most common species frequenting the study plot throughout the year. Of the 13 species of mammals frequenting the study plot, Peromyscus maniculatus Wagner appeared to be the most common species numerically (Table IV). The majority of insects collected belonged to seven Orders (Table V). Numerically, the most common insect species were contained in two of these Orders: Homoptera and Orthoptera. They composed 62 and 26 percent respectively of the insect numbers. Of the seven classes of debris dwelling invertebrates collected, Class Insecta was numerically largest (Table VI). Of the Class Insecta, Order Collembola was the most

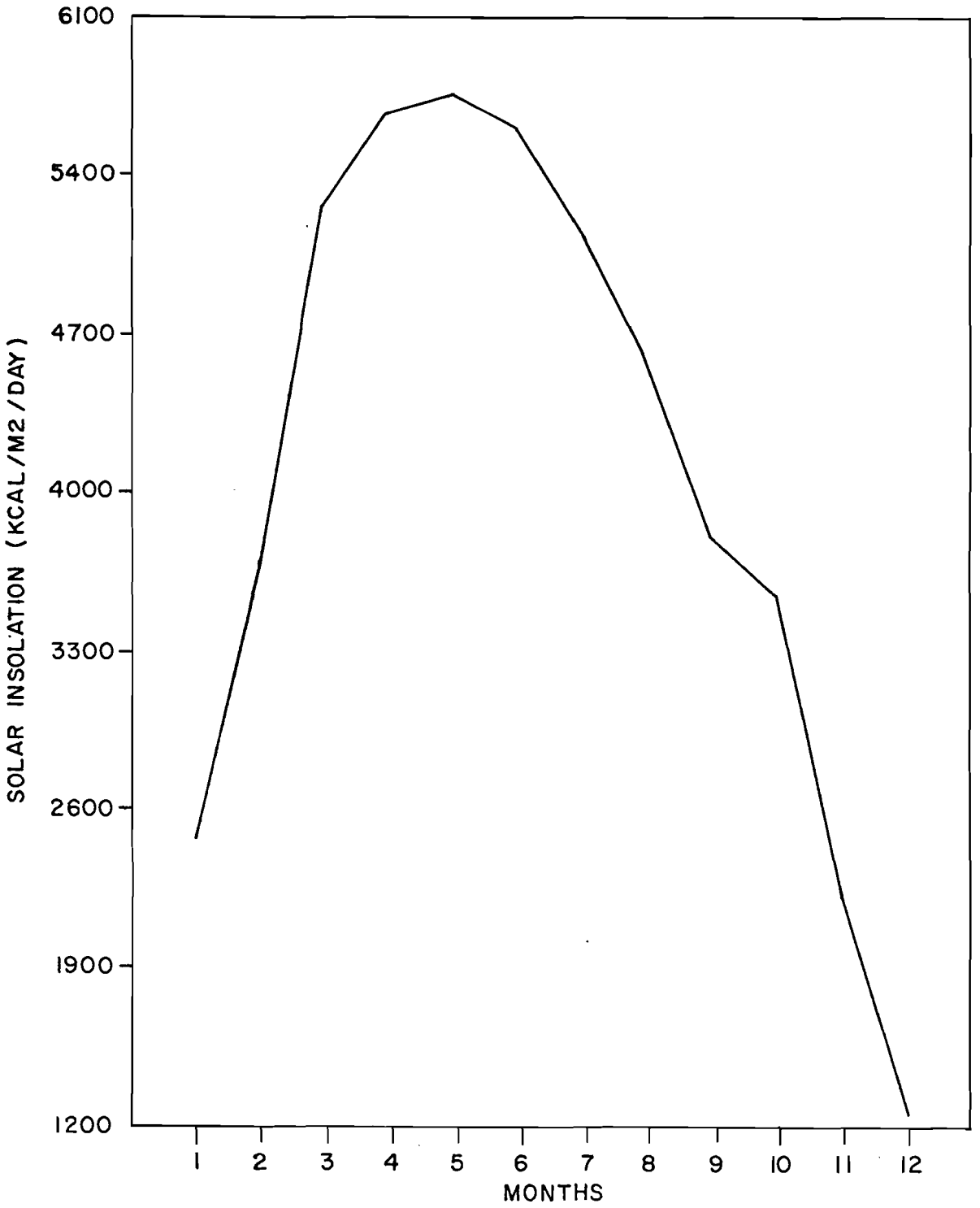


TABLE II. Plant species occurring in the study plot.

| TAXA | COMMON NAME |
|---|-----------------------|
| <u>Achillea millefolium</u> L. | yarrow |
| <u>Ambrosia artemisiifolia</u> L. | ragweed |
| <u>Amorpha canescens</u> Pursh. | leadplant |
| <u>Andropogon gerardi</u> Vitnam | big bluestem |
| <u>Andropogon scoparius</u> Michx. | little bluestem |
| <u>Artemisia ludoviciana</u> Nutt. | white sage |
| <u>Aristida oligantha</u> Michx. | needle-grass |
| <u>Asclepias verticillata</u> L. | whorled milkweed |
| <u>Aster ericoides</u> L. | white-heath aster |
| <u>Astragalus striatus</u> Nutt. | milk vetch |
| <u>Baptisia leucophaea</u> Nutt. | false indigo |
| <u>Baptisia minor</u> Lehm. | false indigo |
| <u>Bouteloua curtipendula</u> (Michx.) Torr. | side-oats grama |
| <u>Bromus inermis</u> Leyss | smooth brome |
| <u>Bromus japonicus</u> Thunb. | Japanese brome |
| <u>Bryophyta</u> sp. | mosses |
| <u>Buchloe dactyloides</u> (Nutt.) Engelm. | Buffalo grass |
| <u>Cacalia tuberosa</u> Nutt. | Indian plantain |
| <u>Carex</u> sp. | sedges |
| <u>Chloris verticillata</u> Nutt. | windmill-grass |
| <u>Convolvulus arvensis</u> L. | bindweed |
| <u>Cornus drummondii</u> Meyer | dogwood |
| <u>Croton monanthogynus</u> Michx. | rushfoil |
| <u>Desmanthus illinoense</u> Gray | Illinois bundleflower |
| <u>Elymus canadensis</u> L. | Canada wild-rye |
| <u>Eragrostis spectabilis</u> (Pursh) Steud. | lovegrass |
| <u>Erigeron canadensis</u> L. | horse-weed |
| <u>Euphorbia marginata</u> Pursh. | snow-on-the-mountain |
| <u>Gleditsia triacanthos</u> L. | honey locust |
| <u>Gutierrezia dracunculoides</u> (D.C.) Blake | broomweed |
| <u>Helianthus maximiliani</u> Schrad. | prairie sunflower |
| <u>Hibiscus trionum</u> L. | flower-of-the-hour |
| <u>Juniperus virginiana</u> L. | red cedar |
| <u>Kuhnia eupatorioides</u> L. | false boneset |
| <u>Liatris mucronata</u> D. C. | blazing star |
| <u>Maclura pomifera</u> (Raf.) Schneid. | osage orange |
| <u>Opuntia macrorhiza</u> Engelm. | prickly pear cactus |
| <u>Oxalis stricta</u> L. | wood sorrel or oxalis |
| <u>Panicum virgatum</u> L. | switchgrass |
| <u>Physalis pumila</u> Nutt. | ground cherry |
| <u>Plantago</u> sp. | plantain |
| <u>Rhus glabra</u> L. | smooth sumac |
| <u>Rudbeckia hirta</u> L. | blackeyed Susan |

TABLE II. (contd.)

| TAXA | COMMON NAME |
|---|-----------------|
| <u>Ruellia humilis</u> Nutt. | ruellia |
| <u>Schedonnardus paniculatus</u> (Nutt.) Trel. | tumble-grass |
| <u>Sisyrinchium campestre</u> Bickn. | blue-eyed grass |
| <u>Solidago altissima</u> L. | goldenrod |
| <u>Sorghastrum nutans</u> (L.) Nash. | Indian-grass |
| <u>Sporobolus asper</u> (Michx.) Kunth. | dropseed |
| <u>Symphoricarpos orbiculatus</u> Moench. | buckbrush |
| <u>Trifolium pratense</u> L. | red clover |
| <u>Trifolium repens</u> L. | white clover |
| <u>Triodia flava</u> (L.) Smyth. | purpletop |
| <u>Vernonia baldwini</u> Torr. | ironweed |
| <u>Xanthium pensylvanicum</u> Wallr. | cocklebur |

TABLE III. Birds recorded within the study plot.

| SCIENTIFIC NAME COMMON NAME | PERMANENT RESIDENT | SUMMER RESIDENT |
|---|-----------------------|--------------------|
| <u>Agelaius phoeniceus phoeniceus</u> (Linnaeus) Eastern red-wing blackbird | | X |
| <u>Ammodramus savannarum perpallidus</u> (Coues) grasshopper sparrow | X | |
| <u>Buteo borealis borealis</u> (Gmelin) Eastern red-tailed hawk | X | |
| <u>Chordeiles minor minor</u> (Forster) nighthawk | | X |
| <u>Corlinus virginianus virginianus</u> (Linnaeus) Eastern bobwhite quail | X | |
| <u>Corvus brachyrhynchos brachyrhynchos</u> (Brehm) Eastern crow | X | |
| <u>Cyanocitta cristata cristata</u> (Linnaeus) Northern blue jay | X | |
| <u>Falco sparverius sparverius</u> (Linnaeus) Eastern sparrow hawk | X | |
| <u>Hedumeles ludovicianus</u> (Linnaeus) Eastern cardinal | X | |
| <u>Molothrus ater ater</u> (Boddaert) Eastern cowbird | | X |
| <u>Oxyechus vociferus vociferus</u> (Linnaeus) Killdeer | | X |
| <u>Passer domesticus domesticus</u> (Linnaeus) English sparrow | X | |
| <u>Progne subis subis</u> (Linnaeus) Purple martin | | X |
| <u>Spiza americana</u> (Gmelin) Dickcissel | | X |
| <u>Spizella pusilla pusilla</u> (Wilson) Field sparrow | | X |
| <u>Sturnella magna magna</u> (Linnaeus) Eastern meadowlark | X | |
| <u>Sturnus vulgaris vulgaris</u> (Linnaeus) Starling | X | |
| <u>Turdus migratorius migratorius</u> (Linnaeus) Eastern robin | X | |

TABLE III. (contd.)

| SCIENTIFIC NAME COMMON NAME | PERMANENT RESIDENT | SUMMER RESIDENT |
|---|-----------------------|--------------------|
| <u>Tyrannus tyrannus</u> (Linnaeus) Eastern kingbird | | X |
| <u>Tyrannus verticalis</u> (Say) Western kingbird | | X |
| <u>Zenaidura macroura carolinensis</u> (Linnaeus) Eastern mourning dove | | X |

TABLE IV. Mammals recorded within the study plot.

| SCIENTIFIC NAME COMMON NAME | TRAP LINE CAPTURE | OBSERVED IN AREA |
|--|----------------------|---------------------|
| <u>Blarina brevicauda</u> Say short-tailed shrew | X | |
| <u>Canis latrans</u> Say coyote | | X |
| <u>Mephitis mephitis</u> Schreber striped skunk | | X |
| <u>Microtus ochrogaster</u> Wagner prairie vole | X | |
| <u>Neotoma floridana</u> Ord Eastern wood rat | X | |
| <u>Odocoileus virginianus</u> Boddaert white-tailed deer | | X |
| <u>Peromyscus leucopus</u> Rafinesque woods mouse | X | |
| <u>Peromyscus maniculatus</u> Wagner deer mouse | X | |
| <u>Procyon lotor</u> Linnaeus raccoon | | X |
| <u>Reithrodontomys montanus</u> Baird plains harvest mouse | X | |
| <u>Sciurus niger</u> Linnaeus fox squirrel | | X |
| <u>Sigmodon hispidus</u> Say and Ord hispid cotton rat | X | |
| <u>Sylvilagus floridanus</u> J.A. Allen Eastern cottontail rabbit | | X |

TABLE V. List of families comprising the insect population recorded within the study plot.

| Order | Family (or Group) | Trophic Level |
|-------------|-------------------|---------------------|
| Orthoptera | Acrididae | Herbivore |
| | Mantidae | Predator |
| | Phasmidae | Herbivore |
| | Tettigoniidae | Herbivore |
| Hemiptera | Coreidae | Herbivore |
| | Lygaeidae | Herbivore |
| | Miridae | Herbivore |
| | Neididae | Herbivore |
| | Pentatomidae | Herbivore |
| | Phymatidae | Predator |
| | Scutelleridae | Herbivore |
| | Tingidae | Herbivore |
| Homoptera | Aphididae | Herbivore |
| | Cercopidae | Herbivore |
| | Cicadellidae | Herbivore |
| | Coccidae | Herbivore |
| | Fulgoridae | Herbivore |
| Lepidoptera | Amatidae | Herbivore |
| | Lasiocampidae | Herbivore |
| | Noctuidae | Herbivore |
| | Nymphalidae | Herbivore |
| | Pieridae | Herbivore |
| Coleoptera | Chrysomelidae | Herbivore |
| | Coccinellidae | Predator |
| | Meloidae | Herbivore, Predator |
| | Phalacridae | Herbivore |
| Diptera | Asilidae | Predator |
| | Calliphoridae | Omnivore |
| | Chloropidae | Predator |
| | Culicidae | Predator |
| | Muscidae | Herbivore, Predator |
| | Sarcophagidae | Scavenger |
| | Tabinidae | Herbivore, Predator |
| | Tachinidae | Parasitic |
| Hymenoptera | Apidae | Herbivore |
| | Halictidae | Herbivore |
| | Ichneumonoidae | Parasitic |
| | Tenthredinidae | Herbivore |

TABLE VI. Listing of microorganism and debris dwelling invertebrate groups identified within the study plot.

| Group | Trophic Level |
|-------------------------|---------------------|
| Microorganisms: | |
| Actinomycetes | Primary Decomposer |
| Bacteria | Primary Decomposer |
| Fungi | Primary Decomposer |
| Class Arachnida: | |
| Order Acarina | Parasitic |
| Order Araneae | Predator |
| Order Opiliones | Omnivore |
| Order Pseudoscorpiones | Predator |
| Class Crustacea: | |
| Order Isopoda | Scavenger |
| Class Diplopoda | |
| | Herbivore |
| Class Chilopoda | |
| | Predator |
| Class Insecta | |
| Order Collembola | |
| Families: Entomobryidae | Herbivore, Omnivore |
| Poduridae | Herbivore, Omnivore |
| Smithuridae | Herbivore |
| Order Orthoptera | |
| Families: Blattidae | Omnivore |
| Gryllidae | Herbivore, Omnivore |
| Order Hemiptera | |
| Family: Reduviidae | Predator |
| Order Coleoptera | |
| Families: Carabidae | Predator |
| Cerambycidae | Herbivore |
| Curculionidae | Herbivore |
| Elateridae | Herbivore |
| Ptinidae | Herbivore |
| Scarabaeidae | Scavenger |
| Silphidae | Scavenger |
| Staphylinidae | Predator |
| Order Hymenoptera | |
| Families: Formicidae | Omnivore |
| Tiphidae | Parasitic |

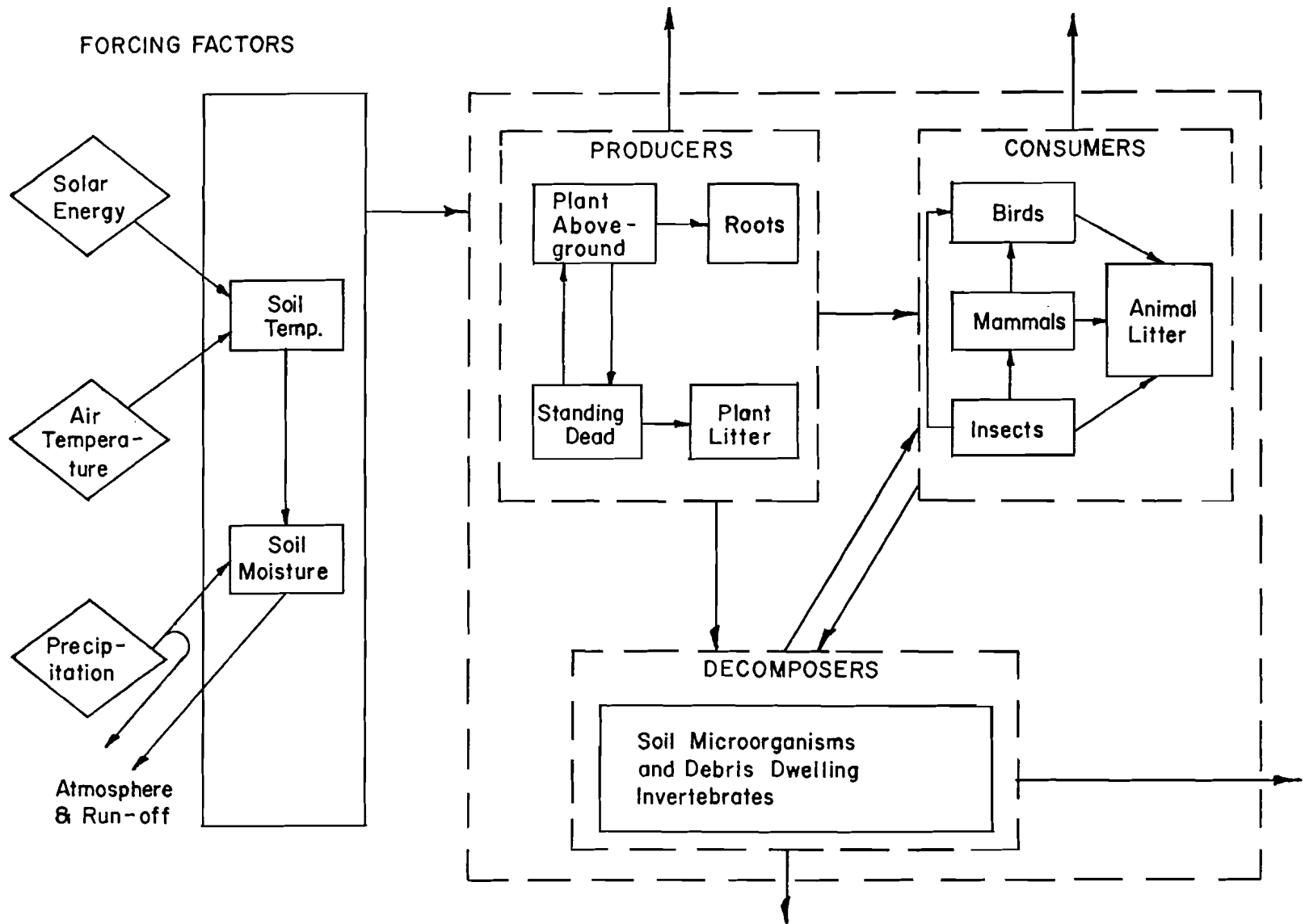
common numerically while Order Coleoptera yielded greater dry biomass. Of the Class Arachnida, the Orders Acarina and Araneae were common in activity and numbers.

SYSTEMS ANALYSIS AND MODEL BUILDING

A system is an assemblage of objects united by some form of interaction or interdependence in such a manner as to function as a whole (Patten, 1971). Systems analysis is the process of translation of the physical, chemical, and biological processes that occur in a system into mathematical expressions that can be manipulated for predictive purposes. Fundamental to systems analysis is the assumption that natural processes are organized in a hierarchy of complexity. Each process or system in the hierarchy is assumed to be the combined result of the actions and interactions of a set of simpler processes. Every system interacts with others on its own level of organization, as well as within itself. This interaction constitutes the flow into or from the system of matter, energy, or information (Hubbell, 1971). Inputs and outputs associated with the system can be depicted in an energy flow diagram. The energy flow diagram represents a model, i.e., the physical or abstract representation of the structure and function of the real system (Walters, 1971).

Schematic Model

The energy flow model presented in this section represents a pictorial model of the grassland community. The major environmental factors influencing the behavior of the biotic community and the general composition of each of the trophic units comprising the biotic community are identified in Figure 6. Interactions between units comprising this system are represented by arrows, i.e., respiration, grazing, and mortality. A brief explanation of the pictorial model is presented below to facilitate understanding the functional model which will be described in another section.



Forcing functions are environmental factors affecting but not affected by the trophic or biotic components of the system. The major forcing factors identified as affecting the functioning of the study community were solar energy, air temperature, precipitation, soil temperature, and soil moisture. Organisms constituting the biotic community were grouped into three major compartments identified as Producers, Consumers, and Decomposers.

The Producer Compartment was composed of the plants of the community. No attempt was made to subdivide producers into taxonomic units; rather the living, green plants were divided into an above ground unit and a root unit. Field observations indicated a considerable mass of organic matter existed periodically in the form of standing dead plant material and ground litter. Hence, Standing Dead and Plant Litter units were added to the Producer Compartment. The Consumer Compartment was comprised of four units: Birds, Mammals, Insects, and Animal Litter. Soil microorganisms and debris dwelling invertebrates constituted the Decomposer Compartment.

Energy values (mass of organic matter) of each compartment for a given interval of time were affected by quantities of energy entering and leaving each compartment. Basic processes affecting the storage and flow of energy within compartments were respiration, mortality, excretion, reproduction, immigration, emigration, grazing or predation, and certain environmental forces. These processes are represented by arrows in the schematic model and are described in more detail in the next section.

This schematic model provided the logical framework from which the operational model was built.

Operational Model

The operational model was designed to be simple and flexible yet allow duplication of the observed behavior of the study community. The schematic model was modified into a seven compartment system (Figure 7) in which abiotic processes were applied as forcing functions on the various components of the system. Figure 7 describes the direction of energy transfers occurring within the community and between the community and its abiotic environment. A description of each of the symbols in Figure 7 is presented in Table VII. For each of the symbols represented in Figure 7 a FORTRAN mnemonic name also appears in Table VII. FORTRAN mnemonic names were used to represent the components or processes in the mathematical model and computer program, which are discussed in another section. The model's construction was premised on quantitative data assimilated for standing crops, energy inputs, and energy losses of organisms in the community and on the energy transfer pathways among the organisms themselves and between the organisms and their abiotic environment. Quantitative values were obtained from the pertinent literature and direct field measurements. The source and unit of measurement for each symbol are given in Table VII.

After defining the system and assigning values to each component and process of the system, the next step was the development of differential equations to calculate the change in compartment biomass from one time interval to the next.

Mathematical Model

The mathematical model of the study community consisted of a set of differential equations. The system's behavior was studied by simultaneous solution of these equations with the aid of a digital computer. The mathematical model had four basic elements: 1) system variables, i.e.

Figure 7. Operational model.

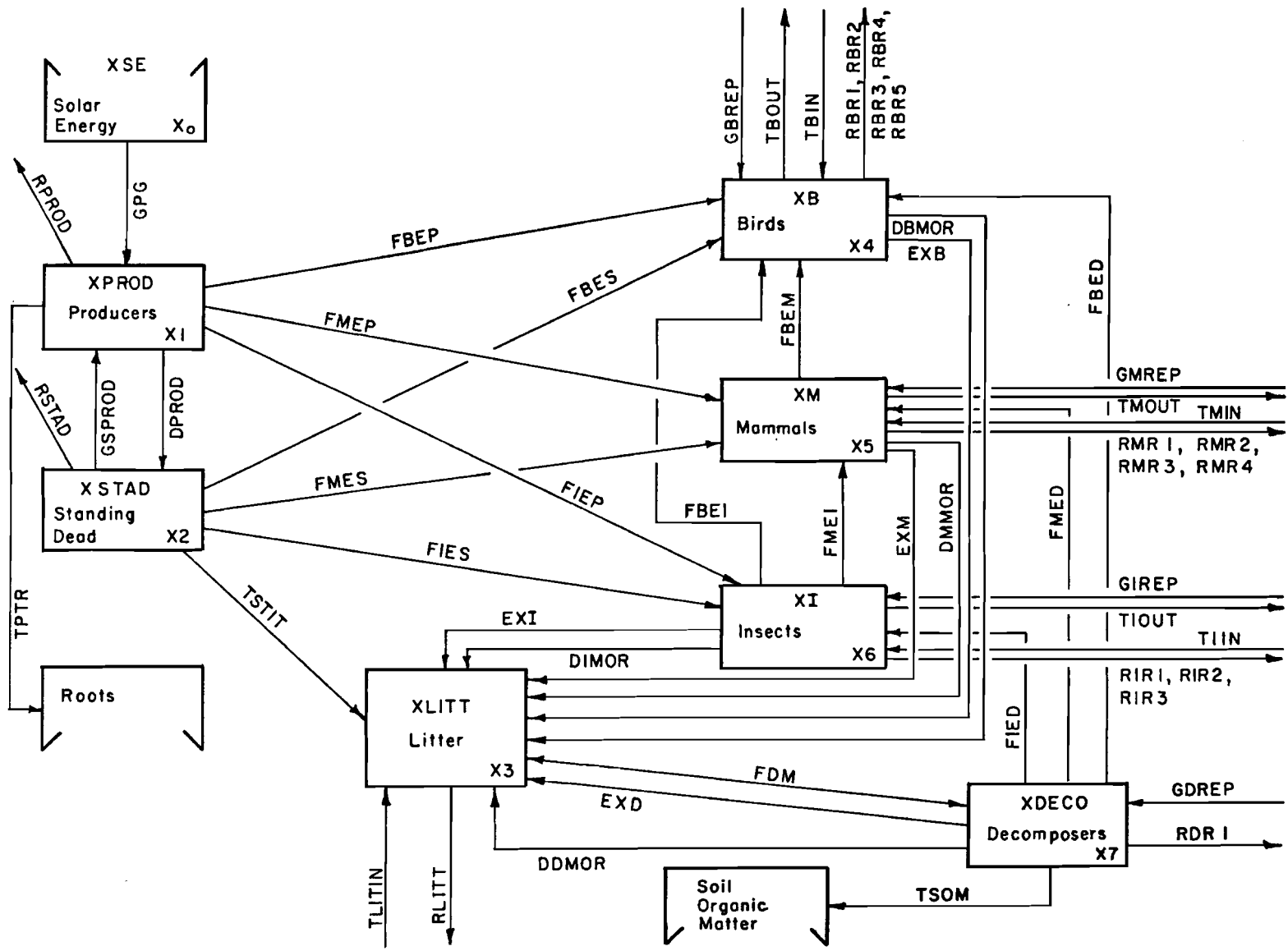


TABLE VII. Definition of symbols used in the operational model and source of data utilized.

| SYMBOLS (FORTRAN) | SYMBOL MEANING | UNITS OF MEASUREMENT | DATA SOURCE |
|----------------------|--|-------------------------|---|
| XSE | Solar radiation entering the system | kcal/m ² /hr | Osborne (1968) |
| XPROD | Live plant material (grasses and forbs) | g/m ² | Field measurement |
| XSTAD | Standing dead plant material (grasses and forbs) | g/m ² | Field measurement |
| XLITT | Litter (plant and animal matter) | g/m ² | Field measurement |
| XB | Bird population | g/m ² | Calculation |
| XM | Mammal population | g/m ² | Johnson (1968) |
| XI | Insect population | g/m ² | Field measurement |
| XDECO | Decomposer population (on soil surface and above ground) | g/m ² | Field measurement |
| GPG | Gross production of the plant community | g/m ² /day | Golley (1960); Macfadyen (1964); Odum (1971) |
| RPROD | Live plant material respiration | g/m ² /day | Lundegardh (1931); Macfadyen (1964); Golley (1965); Williams and Murdock (1968); Risser (1972) |
| DPROD | Transfer of live plant material to standing dead plant material | g/m ² /day | Field measurement |
| TPTR | Transfer from solar energy (through photosynthesis) of live plant material to root system (translocation) | g/m ² /day | Risser (1972) |
| FBEP | Grazing by bird population on live plant material | g/m ² /day | Risser (1972); Wiens and Innis (1972) |
| FMEP | Grazing by small mammal population on live plant material | g/m ² /day | Pearson (1947); Rood (1958); Golley (1960); Odum, Connell, Davenport (1962); McNab (1963); Douglas (1969); Risser (1972) |
| FIEP | Grazing by insect popula- tion on live plant material | g/m ² /day | Smalley (1960); Teal (1962); Blocker and Reed (1971); Risser (1972) |

TABLE VII. (contd.)

| SYMBOLS (FORTRAN) | SYMBOL MEANING | UNITS OF MEASUREMENT | DATA SOURCE |
|----------------------|--|---------------------------|--|
| RSTAD | Standing dead plant material respiration | $\text{g/m}^2/\text{day}$ | None |
| GSPROD | Transfer from standing dead plant material to live plant material (regrowth) | $\text{g/m}^2/\text{day}$ | Calculation |
| TSTIT | Transfer from standing dead plant material to litter | $\text{g/m}^2/\text{day}$ | Field measurement |
| FBES | Grazing by bird population on standing dead plant material | $\text{g/m}^2/\text{day}$ | Risser (1972); Wiens and Innis (1972) |
| FMES | Grazing by small mammal population on standing dead plant material | $\text{g/m}^2/\text{day}$ | Pearson (1947); Rood (1958); Golley (1960); McNab (1963); Douglas (1969); Risser (1972) |
| FIES | Grazing by insect population on standing dead plant material | $\text{g/m}^2/\text{day}$ | Blocker and Reed (1971); Risser (1972) |
| RLITT | Litter respiration | $\text{g/m}^2/\text{day}$ | Calculation |
| TLITIN | Import of litter material from outside the system | $\text{g/m}^2/\text{day}$ | Field measurement |
| FDM | Transfer of litter to the decomposers for grazing and breakdown | $\text{g/m}^2/\text{day}$ | Calculation |
| RBR1 | Bird population respiration of live plant material from grazing | $\text{g/m}^2/\text{day}$ | Risser (1972) |
| RBR2 | Bird population respiration of standing dead plant material from grazing | $\text{g/m}^2/\text{day}$ | Risser (1972) |
| RBR3 | Bird population respiration of mammals from predation | $\text{g/m}^2/\text{day}$ | None |
| RBR4 | Bird population respiration of insects from predation | $\text{g/m}^2/\text{day}$ | Risser (1972) |
| RBR5 | Bird population respiration of decomposers from predation | $\text{g/m}^2/\text{day}$ | None |
| EXB | Bird population excretion | $\text{g/m}^2/\text{day}$ | Risser (1972) |
| DBMOR | Bird population mortality | $\text{g/m}^2/\text{day}$ | None |
| GBREP | Bird population reproduction | $\text{g/m}^2/\text{day}$ | None |
| TBOUT | Bird population emigration | $\text{g/m}^2/\text{day}$ | None |
| TBIN | Bird population immigration | $\text{g/m}^2/\text{day}$ | None |
| RMRI | Mammal population respiration of live plant material from grazing | $\text{g/m}^2/\text{day}$ | Risser (1972) |
| RMR2 | Mammal population respiration of standing dead plant material from grazing | $\text{g/m}^2/\text{day}$ | Risser (1972) |

TABLE VII. (contd.)

| SYMBOLS (FORTRAN) | SYMBOL MEANING | UNITS OF MEASUREMENT | DATA SOURCE |
|----------------------|--|-------------------------|--|
| RMR3 | Mammal population respiration of insects from predation | g/m ² /day | Risser (1972) |
| RMR4 | Mammal population respiration of decomposers from predation | g/m ² /day | None |
| FBEM | Predation by bird population on mammals | g/m ² /day | None |
| EXM | Mammal excretion | g/m ² /day | Golley (1960) |
| DMMOR | Mammal mortality | g/m ² /day | None |
| GMREP | Mammal reproduction | g/m ² /day | None |
| TMOUT | Mammal emigration | g/m ² /day | None |
| TMIN | Mammal immigration | g/m ² /day | None |
| RIR1 | Insect population respiration of live plant material from grazing | g/m ² /day | Risser (1972) |
| RIR2 | Insect population respiration of standing dead plant material from grazing | g/m ² /day | Risser (1972) |
| RIR3 | Insect population respiration of decomposers from predation | g/m ² /day | Risser (1972) |
| FMEI | Predation by mammal population on insects | g/m ² /day | Pearson (1947); Rood (1958); Golley (1960); McNab (1963); Douglas (1969); Risser (1972) |
| FBEI | Predation by bird population on insects | g/m ² /day | Risser (1972) |
| EXI | Insect population excretion | g/m ² /day | Van Hook (1969) |
| DIMOR | Insect population mortality | g/m ² /day | None |
| GIREP | Insect reproduction | g/m ² /day | Calculation |
| TIOUT | Insect emigration | g/m ² /day | Calculation |
| TIIN | Insect immigration | g/m ² /day | None |
| RDRI | Decomposer population respiration on litter from grazing | g/m ² /day | Calculation |
| FBED | Predation by bird population on decomposers | g/m ² /day | None |
| FMED | Predation by mammal population on decomposers | g/m ² /day | None |
| FIED | Predation by insect population on decomposers | g/m ² /day | None |
| EXD | Decomposer excretion | g/m ² /day | None |
| DDMOR | Decomposer mortality | g/m ² /day | None |
| GDREP | Decomposer reproduction | g/m ² /day | None |
| TSOM | Transfer (breakdown) of matter from decomposers to soil organic matter | g/m ² /day | Calculation |

Producer Compartment; 2) transfer functions, i.e. grazing; 3) forcing functions, i.e. solar energy; and 4) parameters, i.e. photosynthetic efficiency.

The flow of energy (organic matter) through each compartment in the system was represented as a series of losses or gains by the receiving compartment. The losses or gains were expressed as fractional units of either the donor or the recipient compartment. The net change per unit of time in the compartment was the difference between income and loss. In a simplified form, this may be written as the differential equation:

$$\frac{dX}{dt} = I - X \sum_{ij} c_{ij} \quad (1)$$

or the net rate of change with respect to time, $\frac{dX}{dt}$, is equal to income, I , minus loss, $X \sum_{ij} c_{ij}$. Here c_{ij} is the fractional transfer from the i -th compartment (whose change is being considered) to the j -th compartment. This partial transfer function describes how material was lost by one compartment and partitioned to others. Further discussions of mathematical models appear in Kelly (1969), Odum (1971), and Patten (1971).

By assuming that the transfer of energy from the "donor" compartment to the "receiving" compartment was directly proportional to the amount of energy contained in the donor compartment, and by collecting all the energy inputs and losses of each compartment expressed as transfer functions, the system was defined by the set of equations in Table VIII. The FORTRAN mnemonic name has been used in the equations to symbolize the various compartments and processes defined in Table VII. The mathematical model having been formulated, it became necessary to obtain numerical solutions to the equations for use in studying the dynamics of the system with respect to time.

TABLE VIII. Mathematical equations developed for compartmental computations.

| | |
|------------------------------|--|
| Producer Compartment | $DXPROD/dt = GPG + SPROD * XSTAD - ((RPROD + TPTR + DPROD + FBEP + FMEP + FIEP) * GPG)$ |
| Standing Dead Compartment | $DXSTAD/dt = DPROD * GPG - ((RSTAD + TSTIT + GSPROD + FBES + FMES + FIES) * XSTAD)$ |
| Litter Compartment | $DXLITT/dt = (TSTIT * XSTAD + (EXB * (FBEP * GPG)) + (EXB * (FBES * XSTAD)) + (EXB * (FBEM * XM)) + (EXB * (FBEI * XI)) + (EXB * (FBED * XDECO)) + (DBMOR * XB) + (EXM * (FMEP * GPG)) + (EXM * (FMES * XSTAD)) + (EXM * (FMEI * XI)) + (EXM * (FMED * XDECO)) + (DMMOR * XM) + (EXI * (FIEP * GPG)) + (EXI * (FIES * XSTAD)) + (EXI * (FIED * XDECO)) + (DIMOR * XI) + (EXD * (TDM * XLITT)) + (DDMOR * XDECO) + TLITIN) - ((FDM + RLITT) * XLITT)$ |
| Bird Compartment | $DXXB/dt = (FBEP * GPG + FBES * XSTAD + FBEM * XM + FBEI * XI + FBED * XDECO + GBREP * XB + TBIN) - ((EXB * (FBEP * GPG)) + (EXB * (FBES * XSTAD)) + (EXB * (FBEM * XM)) + (EXB * (FBEI * XI)) + (EXB * (FBED * XDECO)) + (DBMOR * XB) + (RBR1 * (FBEP * GPG)) + (RBR2 * (FBES * XSTAD)) + (RBR3 * (FBEM * XM)) + (RBR4 * (FBEI * XI)) + (RBR5 * (FBED * XDECO)) + TBOUT)$ |
| Mammal Compartment | $DXXM/dt = (FMEP * GPG + FMES * XSTAD + FMEI * XI + FMED * XDECO + GMREP * XM + TMIN) - ((EXM * (FMEP * GPG)) + (EXM * (FMES * XSTAD)) + (EXM * (FMEI * XI)) + (EXM * (FMED * XDECO)) + (DMMOR * XM) + (RMRI * (FMEP * GPG)) + (RMR2 * (FMES * XSTAD)) + (RMR3 * (FMEI * XI)) + (RMR4 * (FMED * XDECO)) + (FBEM * XM) + TMOUT)$ |
| Insect Compartment | $DXXI/dt = (FIEP * GPG + FIES * XSTAD + FIED * XDECO + GIREP + TIIN) - ((EXI * (FIEP * GPG)) + (EXI * (FIES * XSTAD)) + (EXI * (FIED * XDECO)) + (DIMOR * XI) + (RIR1 * (FIEP * GPG)) + (RIR2 * (FIES * XSTAD)) + (RIR3 * (FIED * XDECO)) + (FBEI + FMEI) * XI + TIOUT)$ |
| Decomposer Compartment | $DXDECO/dt = (FDM * XLITT + GDREP * XDECO) - ((FBED + FMED + FIED) * XDECO + (EXD * (FDM * XLITT)) + (DDMOR * XDECO) + (RDRI + TSOM) * XLITT)$ |

COMPUTER PROGRAM

Numerical solutions were calculated directly by a computer algorithm (the digital computer program). The computer program appears in Appendix I. A copy of this program was placed on file in the Division of Biology, Emporia State University. In developing the computer program a series of logical statements about the structure of the system was made in progression that mimicked the systems behavior in some salient form.

Initially, time was set to zero in the program (card 0001). For purposes of simulation, the year was divided into 365 days. The interaction interval used in the current program (card 0023) is daily. Daily time intervals were chosen for simulation of the study community principally for the ability to approximate the field data on mass/area and the production rates and patterns that occurred between successive sampling periods.

Compartment size or standing crop (g/m^2) were initially defined (cards 0002-0008) for each of the seven compartments of the model. The initial standing crop of each compartment reflects the biomass of the first day of the nominal simulation which began on 1 January 1973.

Before the DO LOOP, which allowed values to be placed on the transfer functions and forcing functions per defined unit of time, the column headings for the printout (computed state of each compartment) were programmed (cards 0009-0010). The column headings were spaced horizontally across the page. The state of each compartment heading ($\text{g}/\text{m}^2/\text{day}$) was printed under the applicable heading after each computation of the differential equations (cards 0051-0052).

Transfer functions and forcing functions (cards 0012-0018) were variable throughout the three basic time periods in the model (cards 0024-0026). The DO LOOP (card 0011) incorporated in the program enabled a transfer function or forcing function to be varied or changed with respect to time during these specified time periods by a set of sub-time periods. It actually would read a set of values assigned to the functions on cards for a specified number of days within the three basic time periods. The values assigned these functions mimicked the rate that processes were occurring during different times during the three basic time periods.

A DO LOOP to calculate the states of the system on the basis of the activity of the forcing function was programmed (card 0022). For purposes of simulation, the year was divided into three time periods (cards 0024-0026). The pregrowth period of the plant community (card 0024) was established from direct field measurements. The growth period (card 0025) was established from the date of initial growth to the date of the first killing frost determined from air temperature measurements. The post-growing season made up the remainder of the year (card 0026).

Two sets of differential equations were incorporated into the program to simulate compartment behavior during the growing season (card 0025) and the non-growing season (cards 0024 and 0026). The Producer Compartment was considered to be the controlling compartment for the behavior of the community influencing the interacting rates of energy flows in and between compartments. During the non-growing season the system had no external forcing function being applied to it. The compartments merely interacted within the system to maintain themselves.

The set of equations used during the non-growing season, for each compartment, are contained in cards 0027-0033. The change in the compartment is computed in these equations per unit of time. The state of each compartment was computed by gains or losses to the previous computed state of the compartment by a series of algebraic equations (cards 0044-0050) and then printed under the appropriate compartment heading (card 51).

During the growing season (card 0025) a forcing function was applied to the system in the form of solar radiation. Solar radiation affected every compartment of the model to some degree, but had its primary effect upon the Producer Compartment in the photosynthetic process. A subroutine (SUBROUTINE PHOTO) was placed in the computer program to mimic the photosynthetic process by using solar radiation intensity as the forcing function (card 0036) used to calculate the gross production of the Producer Compartment. Photosynthesis was computed on a daily basis (24 hours) in the subroutine. A photoperiod of twelve hours was assumed for the growing season. A series of IF Statements were placed in the subroutine (cards 0006-0008) to mimic the photoperiod and aid in the calculation of daily solar intensities.

Hourly solar energy values were generated ($\text{kcal/m}^2/\text{hr}$) by the sinusoidal equation (card 0009) for the photoperiod (card 0007) and then summed (card 0010) for the day. Solar energy ($\text{kcal/m}^2/\text{day}$) was converted into moles of glucose and converted into biomass ($\text{g/m}^2/\text{day}$) in the photosynthetic equation (card 0011) and reentered the main computer program (card 0015) with a computed value for gross production, which was in turn used in the second set of equations of the main program (cards 0037-0043). The computed state of each compartment was

calculated in the same manner as it was for the equations in the non-growing season.

The computer program was used to obtain numerical solutions of the system, given a particular initial state and set of inputs. The numerical solutions are the states of the computed model and were used in the process of systems analysis to determine whether or not the model was a realistic representation of the natural community from which it was derived. The numerical solutions of the model are presented in Appendix II.

DERIVATION OF VALUES AND DISCUSSION OF

MODEL OPERATION

The solution of the mathematical equations in the computer program reproduced the standing crops of the various biological species comprising the biotic compartments of the grassland community by simulating the biological activity within and between each of the compartments with respect to time. The biotic species contained in the various compartments of the community were not divided into their taxonomic units. The purpose of the study was to assess community behavior at the compartment level and not individual species behavior within each compartment comprising the community. Approximating the behavior of the community with respect to time can best be discussed compartment by compartment. For each of the compartments named below, the FORTRAN mnemonic name used in the model and initial dry biomass of the compartment are indicated in parenthesis and a brief description is given.

PRODUCERS (XPROD, 0.00000 g/m²)

The Producer Compartment, composed of 55 plant species (Table II), was perhaps the most important compartment influencing community behavior. Estimates of production and standing crops were measured by biomass increases or decreases during the year beginning on 1 January 1973.

The objective was to sample the plant community as closely as possible to the time of significant phenological events occurring in it. The major sampling periods were defined as: the pre-growing season, the period of rapid vegetative growth and flowering, the late growing season, and the post-growing season. A 0.1 m² sampling square was used to obtain the standing crop in the field. Samples were taken only within designated

portions of the total study area, which were a set of ten 10 m^2 areas arranged in a randomized design within the study area (Figure 1). Blindfolded, the researcher threw the sampling square into one of the designated sampling areas. The vegetation rooted within the boundaries of the sampling square was then clipped to ground level and placed in plastic bags. Five replicate samples were taken for each sampling date from either the odd or even numbered 10 m^2 sampling areas identified in Figure 1. Sampling areas were alternated for each sampling date. Clipped herbage was sorted in the laboratory into live and standing dead plant material using the criteria of Harris (1966). Sorted plant material was then oven dried at 60 C for 72 hours. Dry masses were determined to the nearest 0.01 g . The five replicate samples were then combined and an average dry biomass (g/m^2) was calculated for the sample date (Table IX).

Biomass measurements on the first sampling date indicated that little growth was occurring in the plant community. Air temperatures are normally below 0 C during January and inhibit growth. Although some biomass production was occurring as a result of photosynthetic process on warm days it was a negligible quantity and not accurately measurable. Therefore, the initial state of the Producer Compartment was considered to be zero and would remain constant until initial green plant growth was observed.

Initial green plant growth was observed on 15 February, the second sampling date. New grass shoots and dormant plant growth comprised the standing crop on this sampling date. The period between initial sampling on 1 January and the observance of initial green plant growth on 15 February was designated as the pre-growing season.

On the third sampling date, 21 April, the standing crop had again increased. During the time period from initial plant growth to the third

TABLE IX. Producer Compartment standing crop biomass mean for five replicate samples per sampling date.

| Sampling Date 1973 | Standing Crop Dry Weight (g/m ²) |
|-----------------------|--|
| 01 January | 0.00000 |
| 15 February | 0.65248 |
| 21 April | 57.34793 |
| 06 June | 184.26276 |
| 30 July | 196.86419 |
| 20 September | 145.70978 |
| 09 October | 92.37967 |
| 04 November | 0.06541 |
| 15 December | 0.00000 |

sampling date the plant community had grown at a daily rate of 0.87 g/m^2 . Between the third and fifth sampling dates when the peak biomass of the Producer Compartment was observed, the daily rate of plant growth had increased to 1.21 g/m^2 . However, the greatest rate of growth occurred between the third and fourth sampling dates. The average daily rate of growth was 1.39 g/m^2 . From the date of peak biomass to the sixth sampling date, 20 September, the standing crop of the Producer Compartment had decreased, indicating that production rates were decreasing and some green plant material was being transferred to the Standing Dead Compartment. A further decrease in biomass was measured between the sixth and seventh sampling dates. On 29 October the first killing frost occurred, and a marked reduction in biomass was measured on the eighth sampling date on 4 November. Between the eighth and final sampling date on 15 December, the standing crop of the Producer Compartment had decreased to an unmeasurable quantity and was assumed to be zero. The post-growing season was designated as occurring from the first killing frost to the end of the year on 31 December.

In the computer program, the pre- and post-growing seasons were classified as the non-growing season for the plant community. The growing season of the plant community was designated as the intermediate time period between initial green plant growth and the first killing frost, a total of 257 days. The average growing season as reported by Flora (1948) is 187 days. Flora based his growing season on the frost-free period of the year and not as was done in the present study. The frost-free period of 1973 lasted a total of 199 days.

The state of the Producer Compartment, as well as the state for all other compartments, for any given interval of time was affected by

quantities of energy entering (inputs) and leaving (outputs) the compartment. For each of the inputs and outputs named below, the FORTRAN mnemonic name used in the model is indicated in parantheses and a brief description is given.

Inputs

There were two inputs identified as affecting the Producer Compartment. One a forcing function, solar energy, and the second a transfer function, dormancy.

Solar Energy (XSE). It is known that photosynthetic activity is variable throughout the year and throughout the photoperiod of a given day, depending upon the available light energy (Odum, 1971). During the non-growing season solar intensities did not have a measurable effect on the plant community through the photosynthetic process as standing crop measurements indicated. For purposes in the computer program the non-growing season of the Producer Compartment remained a constant at 0.00 g/m².

An Eppley pyrhelimeter Model 10 and a Bristols Model 570, 64 A-1ph wide strip dynamaster recorder and a portable Weather Measure Corporation solar radiation recorder Model R 401 were used to record solar insolation intensities (gm-cal/cm²/min) on a strip of calibrated paper. Malfunctions with the recording instruments prevented this researcher from obtaining enough reliable data for use in the study. Mean monthly insolation values (gm-cal/cm²/min) were obtained from Osborne (1968) and utilized in the current study. Solar insolation reported by Osborne were converted to kcal/m²/hr (Table X). Reported solar insolation values varied from season to season. As solar insolation values increased during the growing season,

TABLE X. Mean monthly solar insolation received in the study community (after Osborne, 1968).

| Month | Monthly Mean Insolation g-cal/cm ² /min | kcal/m ² /hr |
|-----------|--|-------------------------|
| January | 0.55 | 330 |
| February | 0.80 | 480 |
| March | 1.15 | 690 |
| April | 1.25 | 750 |
| May | 1.26 | 756 |
| *June | 1.24 | 744 |
| July | 1.13 | 678 |
| August | 1.02 | 612 |
| September | 0.84 | 504 |
| October | 0.78 | 468 |
| November | 0.49 | 294 |
| December | 0.27 | 162 |

*Value reported for June was an assumed value.

so did the standing crop of the Producer Compartment.

Solar insolation was used as the forcing function in the computer program to mimic the photosynthetic process. A subroutine (SUBROUTINE PHOTO) was used in the computer program to calculate daily gross primary production of the plant community on an hour by hour, day by day basis, depending upon insolation received.

Mean monthly solar insolation values reported in Table X were assumed to be the maximum intensities received per day throughout the month and would occur during the mid-point of the daily photoperiod. Although the photoperiod varied from 8 to 16 hours per day during the growing season, a constant 12 hour photoperiod was utilized in the subroutine. Varying the photoperiod in future models would be a possible refinement of the present program. Daily solar insolation was assumed to follow a sinusoidal curve during the photoperiod. Mean monthly solar insolation values were entered into the computer program data bank as XSE. In equation 1 of the subroutine:

$$XLIGHT = XSE * SIN (1.5708*(1.-ABS((T-12.)/6.0))) \quad (1)$$

XSE represents the maximum value of solar insolation in kcal/m²/hr input as the mid-point of the sinusoidal curve. SIN is an internal function of the computer telling it to take the sin function of 1.5708 (which is ½ of pi) and multiply it by 1.0 minus ABS (absolute value of the hourly time indexed for each hour during the photoperiod) T minus 12 (the length of the photoperiod divided by 6.0 or midpoint of the photoperiod. In this manner hourly values for the photoperiod (kcal/m²/hr) were calculated and expressed as XLIGHT. For each hour during the photoperiod XLIGHT was summed in equation 2:

$$GTOTXL = GTOTXL + XLIGHT \quad (2)$$

This gives a total for the photoperiod expressed as GTOTXL ($\text{kcal/m}^2/\text{photoperiod}$).

The calculated value for solar insolation for the photoperiod (GTOTXL) was then utilized in the photosynthetic process in which moles of glucose were converted to biomass and entered the system as GPG, gross primary production, in $\text{g/m}^2/\text{photoperiod}$ in equation 3:

$$\text{GPG} = ((\text{GTOTXL}/673.0) * (180.0)) * (\text{PCE}) \quad (3)$$

GTOTXL expressed as $\text{kcal/m}^2/\text{photoperiod}$ is divided by 673.0 to convert it to moles of glucose/ $\text{m}^2/\text{photoperiod}$ and multiplied by 180, the atomic weight of glucose required to manufacture one gram of plant material, and then multiplied by a parameter or constant PCE, which represents photosynthetic efficiency. The value assigned to photosynthetic efficiency, the amount of light available for use in the photosynthetic process from the available light spectrum, was extrapolated from the literature. In an old-field study in Michigan, Golley (1960) was able to measure the total amount of light entering the system. Of the total amount entering only 1.295 per cent of it was in the range of the light spectrum that could be utilized by plants in the photosynthetic process. Macfadyen (1964) reported that the photosynthetic efficiency of a grassland in Britain was approximately 1.32 per cent; however, he failed to discuss the derivation of this value. Odum (1971) estimates photosynthetic efficiency worldwide to range between 1 and 5 per cent. The calculated value for the above equation enters the system daily as GPG or gross primary production in $\text{g/m}^2/\text{photoperiod}$. For no other reason than being a measured value, photosynthetic efficiency was assumed to be 1.295 percent. Although it was realized that photosynthetic efficiency varied

from day to day and month to month it was assigned this constant rate. Varying the photosynthetic efficiency throughout the growing season might be incorporated as a refinement to the current program at some future date. The calculated gross primary production (GPG) values entering the system per photoperiod per month appear in Table XI. As gross primary production increased each month so did the standing crop of the Producer Compartment and visa versa.

Dormancy (GSPROD). While making field measurements on the standing crops of the Producer, Standing Dead, and Litter Compartments it was observed that some of the plant material that had been classified as standing dead during the non-growing season was producing chlorophyll during the initial few weeks of the growing season. Although no actual field measurements were made, it was arbitrarily assumed that approximately 25 per cent of the biomass leaving the Standing Dead Compartment was transferred to the Producer Compartment. Dormancy, is a transfer function or an interaction between compartments, and is dependent upon the state of the donor compartment (or directly proportional to the state of the Standing Dead Compartment) for its flow rate or fractional quantity of material delivered to the receiving Producer Compartment during an interval of time.

In the computer program the first 66 days of the growing season were divided into 4 time units of 14, 15, 16, and 21 days respectively, which represented portions of the months of February, March, and April. Because the state of the donor compartment was variable during these 3 months the flow rate was varied for dormancy. The flow rates were 0.0024834, 0.0029158, 0.0035672, and 0.0048365 for the respective time units of the 3 months. This resulted in an approximate flow rate of 0.35 per cent of

TABLE XI. Gross primary production of the Producer Compartment during the growing season as generated by the computer program.

| Month | Gross Primary Production (g/m ² /photoperiod) |
|-----------|--|
| January | 0.00 |
| *February | 12.63 |
| March | 18.15 |
| April | 19.73 |
| May | 19.89 |
| June | 19.57 |
| July | 17.84 |
| August | 16.10 |
| September | 13.26 |
| **October | 12.31 |
| November | 0.00 |
| December | 0.00 |

*The growing season began 15 February.

**The growing season ended on 29 October.

the daily standing crop of the Standing Dead Compartment for the first 66 days of the growing season or approximately 25 per cent of the energy leaving or output from the Standing Dead Compartment. The biomass of the Producer Compartment was increased approximately $0.35 \text{ g/m}^2/\text{day}$ during this time interval from the transfer.

Outputs

There were six outputs identified as transfer functions affecting the state of the Producer Compartment and all represented flows of energy (biomass) out of the Producer Compartment. They were identified as respiration, translocation, mortality, grazing by birds, grazing by mammals, and grazing by insects. During the non-growing season when the state of the Producer Compartment was constant at 0.00 g/m^2 all of the above transfer functions assumed a zero rate of flow. The above transfer functions were only utilized during the growing season and all were a function of gross primary production entering the compartment.

Respiration (RPROD). Estimates of producer metabolism were based on values obtained from the literature. Lundegardh (1931), in the laboratory, estimated that respiration of live top vegetation was at least 50 per cent of gross primary production during the year. Golley (1965) calculated respiration in an old field broomsedge community to fluctuate between 21.9 and 44.1 per cent of gross primary production during the growing season. Williams and Murdoch (1968) estimated live top respiration of a Festuca and Andropogon community to be 50 per cent of gross primary production for the growing season. In a British grassland, Macfadyen (1964) calculated respiration to be 44 per cent per season of

gross primary production. Risser (1972) calculated respiration in the laboratory from gas exchange rates for Andropogon scoparius, Andropogon gerardi, Sorghastrum nutans, and Panicum virgatum. During the study respiration of the seedlings was calculated to be approximately 41 per cent of gross primary production. An average of the above values indicates that respiration of live plants would be approximately 42 per cent of gross primary production in similar communities.

In the computer program the growing season was divided into 14 time units representing portions of the months February through October. Because the state of photosynthetic input was variable during each of the months and the flow rate for respiration was dependent upon the photosynthetic input for its value, it was varied during these 14 time units. The flow rate for RPROD varied from 33.76 per cent per day of GPG during May to 54.68 per cent per day of GPG during September and had an average value of 47.42 per cent per day of GPG for the growing season. During the growing season approximately $7.93 \text{ g/m}^2/\text{day}$ of GPG was output through metabolic processes.

The 47.42 per cent value assigned to respiration during the growing season was higher than the average 42 per cent reported from the literature. Knowing the standing crop of the Producer Compartment, RPROD was varied in computer manipulations during the 14 time units to allow the computer program to mimic the standing crops of the compartment as measured, and therefore resulted in the fluctuation of flow rates assigned to respiration and the higher average respiration rate for the growing season. Actual values used during the 14 time units and average daily biomass flows are summarized in Table XII for reference.

TABLE XII. *Respiration values, growing season time units, per cent transfer rate, and average daily biomass outflow from the Producer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 48.71052 | 6.1512355 |
| March | 15 | 48.29933 | 8.7677406 |
| March | 16 | 48.30022 | 8.7679022 |
| April | 21 | 48.22563 | 9.5156136 |
| April | 09 | 42.64483 | 8.4144411 |
| May | 31 | 33.76119 | 6.7148636 |
| June | 15 | 43.87900 | 8.5886968 |
| June | 15 | 44.87900 | 8.7844328 |
| July | 31 | 52.43886 | 9.3536342 |
| August | 15 | 50.61005 | 8.1486538 |
| August | 16 | 50.56107 | 8.1407676 |
| September | 15 | 51.04948 | 6.7689328 |
| September | 15 | 54.67557 | 7.2497361 |
| October | 29 | 45.88886 | 5.6495603 |

*The same values were assigned to the translocation (TPTR) transfer function.

Translocation (TPTR). The transfer of energy from aboveground to below-ground plant parts was accomplished through translocation. Values assigned to translocation were sketchy in the literature. Risser (1972) estimated translocation to be approximately 43 per cent of gross primary production. By measuring the standing crop of roots in g/m^2 and using laboratory experiments to calculate root respiration he was able to extrapolate that approximately 43 per cent of incoming energy in the form of gross primary production was necessary to maintain the root system by assuming that 75 per cent of the root system was alive.

In the computer program the growing season was divided into 14 time units representing portions of the months February through October as was done for respiration. Translocation was assumed to be directly related to respiration and therefore the same flow rates were used for translocation as were for respiration (Table XII). The flow rate varied the same for translocation as it did for respiration with an average 47.42 per cent per day of gross primary production being transferred to the root system.

Mortality (DPROD). By measuring the standing crop of the Standing Dead Compartment (XSTAD), the amount of live plant material transferred, or input, to the Standing Dead Compartment could be calculated per unit of time. The method of measurement was identical to that used in obtaining the standing crop of the Producer Compartment as previously described. Applying the criteria of Harris (1966) to the field samples, live plant material and standing dead plant material were separated for each sampling date and reported as g/m^2 (Table XIII). An increase in the state of the

TABLE XIII. Standing Dead Compartment standing crop biomass mean for five replicate samples per sampling date.

| Sampling Date 1973 | Standing Crop Dry Weight (g/m ²) |
|-----------------------|--|
| 01 January | 209.27253 |
| 15 February | 147.62195 |
| 21 April | 56.43752 |
| 06 June | 60.55315 |
| 30 July | 61.82467 |
| 20 September | 66.93350 |
| 09 October | 75.27010 |
| 04 November | 180.32971 |
| 15 December | 137.81435 |

Standing Dead Compartment was considered as an input from the Producer Compartment through mortality.

In the computer program, 10 of the 14 time units during the growing season showed mortality as an input into the Standing Dead Compartment. During the first four time units dormancy (GSPROD) was used as an input to the Producer Compartment as mortality was assumed to be zero. The flow rate of mortality was a function of the donor Producer Compartment and gross primary production (GPG) entering the system. By calculating the increase in the state of the Standing Dead Compartment per sampling date the rate of flow from the Producer Compartment to the Standing Dead Compartment as a function of gross primary production was calculated. Actual values used during the 14 time units and average daily biomass outflows from the Producer Compartment are summarized in Table XIV for reference. During the 14 time units of the growing season, Producer Compartment mortality (DPROD) averaged 5.68 per cent of daily gross primary production entering the compartment, or approximately $0.87 \text{ g/m}^2/\text{day}$ of biomass.

Grazing By Birds (FBEP). Estimates of grazing on green plants by the bird population were obtained from a single literature source. Risser (1972) used grazing estimates based upon procedures of bioenergetic estimation developed by Wiens and Innis (1972). It was estimated that the bird population grazed on green plant material and seeds at the rate of $0.00033 \text{ g/m}^2/\text{day}$ during the growing season which was the equivalent of 0.00145 per cent of daily gross primary production entering the system and was used in the computer program as the value for bird grazing, an outflow from the Producer Compartment and an inflow to the Bird Compartment.

TABLE XIV. *Mortality rates, growing season time units, per cent transfer rate, and average daily biomass outflow from the Producer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0 | 0 |
| March | 15 | 0 | 0 |
| March | 16 | 0 | 0 |
| April | 21 | 0 | 0 |
| April | 09 | 0.47144 | 0.0930219 |
| May | 31 | 18.23874 | 3.6275573 |
| June | 15 | 7.00000 | 1.3701515 |
| June | 15 | 5.00000 | 0.9786796 |
| July | 31 | 0.69692 | 0.1243111 |
| August | 15 | 0.79755 | 0.1284124 |
| August | 16 | 0.74962 | 0.1206952 |
| September | 15 | 1.24179 | 0.1646558 |
| September | 15 | 4.44462 | 0.5893367 |
| October | 29 | 40.86065 | 5.0309438 |

*Mortality was an input to the Standing Dead Compartment (XSTAD).

It was assumed that the bird population would graze on the Producer Compartment at a relatively constant rate during the growing season regardless of its standing crop. Therefore, bird grazing remained constant at 0.00145 per cent of gross primary production, an average flow rate of biomass of $0.0002447 \text{ g/m}^2/\text{day}$ during the growing season and a total of $0.628879 \text{ g/m}^2/\text{growing season}$. In theory, it was believed that as gross primary production increased during the year more food would be available to the bird population as it too was increasing. Although grazing did fluctuate with the bird population and standing crop of the Producer Compartment throughout the growing season, it probably did not fluctuate enough to accurately mimic grazing by the bird population (Table XV). Instead of being a function of gross primary production, it probably should have been a function of the standing crop of the Producer Compartment in order to more closely mimic the grazing process. This could be used as a possible refinement in future modeling attempts to improve on the current program.

Grazing By Mammals (FMEP). Estimates of grazing on green plants by the mammal population were obtained from literature sources. Golley (1960) calculated the energy transfers through a vegetation-vole-weasel food chain in a Michigan old-field and estimated that voles grazed on vegetation at the rate of 1.58 per cent of the standing crop of vegetation which was equivalent to 0.07845 per cent of gross primary production. Odum, Connell and Davenport (1962), calculated that Microtus consumed approximately 1.6 per cent of the standing crop of vegetation in a study of population energy flows of three primary components of old-field ecosystems. This was equivalent to 0.072 per cent of gross primary

TABLE XV. *Grazing by the bird populations, growing season time units, per cent transfer rate, and average daily biomass outflow from the Producer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0.00145 | 0.0001831 |
| March | 15 | 0.00145 | 0.0002632 |
| March | 16 | 0.00145 | 0.0002632 |
| April | 21 | 0.00145 | 0.0002861 |
| April | 09 | 0.00145 | 0.0002861 |
| May | 31 | 0.00145 | 0.0002883 |
| June | 15 | 0.00145 | 0.0002838 |
| June | 15 | 0.00145 | 0.0002838 |
| July | 31 | 0.00145 | 0.0002586 |
| August | 15 | 0.00145 | 0.0002334 |
| August | 16 | 0.00145 | 0.0002334 |
| September | 15 | 0.00145 | 0.0001922 |
| September | 15 | 0.00145 | 0.0001922 |
| October | 29 | 0.00145 | 0.0001785 |

*Grazing was an input to the Bird Compartment (XB).

production. Fleharty and Choate (1972) reported that Sigmodon hispidus grazed at less than 1.0 per cent on the standing crop of vegetation throughout the year or the equivalent of approximately 0.1 per cent of gross primary production. Risser (1972) used consumption rates derived from Golley (1960) for Microtus, McNab (1963) for Reithrodontomys, Pearson (1947) and Rood (1958) for Blarina, and Douglas (1969) for Spermophilus. Grazing reported by Risser (1972) was at the rate of 0.03309 g/m²/day during the growing season or 0.14643 per cent of daily gross primary production. Although the grazing rate reported by Risser (1972) was almost twice the other available reported literature values it was used as the rate for grazing by the mammals, representing the outflow from the Producer Compartment as a function of gross primary production, and an inflow to the Mammal Compartment (XM).

In the computer program it was assumed that the mammal population would graze on the Producer Compartment at a constant rate during the growing season regardless of its standing crop, as did the bird population. Therefore, mammal grazing remained constant at 0.14643 per cent of gross primary production, an average flow rate of biomass of 0.0247156 g/m²/day during the growing season and a total of 6.351910 g/m²/growing season. It was believed that as gross primary production increased during the year more food would be available to the mammal population as it too was increasing and becoming more active. Although mammal grazing did fluctuate in the same manner as for bird grazing, it probably did not actually mimic grazing by the mammal population (Table XVI). Instead of being a function of gross primary production, mammal grazing probably should have been a function of the standing crop of the Producer Compartment as was suggested for bird grazing.

TABLE XVI. *Grazing by the mammal populations, growing season time units, per cent transfer rate, and average daily biomass outflow from the Producer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0.14643 | 0.0184913 |
| March | 15 | 0.14643 | 0.0265813 |
| March | 16 | 0.14643 | 0.0265813 |
| April | 21 | 0.14643 | 0.0288927 |
| April | 09 | 0.14643 | 0.0288927 |
| May | 31 | 0.14643 | 0.0291238 |
| June | 15 | 0.14643 | 0.0286616 |
| June | 15 | 0.14643 | 0.0286616 |
| July | 31 | 0.14643 | 0.0261190 |
| August | 15 | 0.14643 | 0.0235764 |
| August | 16 | 0.14643 | 0.0235764 |
| September | 15 | 0.14643 | 0.0194159 |
| September | 15 | 0.14643 | 0.0194159 |
| October | 29 | 0.14643 | 0.0180291 |

*Grazing was an input to the Mammal Compartment (XM).

Grazing by Insects (FIEP). Estimates of grazing on green plants by the insect population were obtained from literature sources. Teal (1962) studied the energy flow in a salt marsh ecosystem dominated by Spartina in Georgia. Smalley (1960) estimated that Orchelimum fidicinium consumed 2 per cent of net primary production of a similar salt marsh ecosystem. Teal (1962) utilized this value for grazing in his study which was the equivalent of 0.49843 per cent of gross primary production. Risser (1972) estimated insect grazing from previous studies of Blocker and Reed (1971) in which the insect population consumed approximately 7.625206 g/m^2 of net primary production during the growing season for an approximate rate of $0.0381239 \text{ g/m}^2/\text{day}$, equivalent to 0.16869 per cent of daily gross primary production. Because of the similarities between the composition of the Oklahoma study site and this site, the value utilized for insect grazing in the study was chosen to be 0.16869 per cent of gross primary production. This value then represented the outflow from the Producer Compartment as a function of gross primary production, and an inflow to the Insect Compartment (XI).

In the computer program, it was assumed that the insect population would graze on the Producer Compartment at a constant rate during the growing season regardless of its standing crop, as did the bird and mammal populations. Grazing by insects (FIEP) remained constant at 0.16869 per cent of gross primary production, an average flow rate of biomass of $0.0284728 \text{ g/m}^2/\text{day}$ during the growing season and a total of $7.31751 \text{ g/m}^2/\text{growing season}$. This was probably an underestimate of insect grazing. Grazing by insects, a function of gross primary production, was believed to fluctuate accurately enough as gross primary production

(GPG) fluctuated in the model to allow it to accurately mimic the grazing process as was assumed for the birds and mammals. However, it probably did not accurately mimic grazing by the insects (Table XVII). Instead of being a function of gross primary production, grazing probably should have been a function of the standing crop of the Producer Compartment as was suggested for bird and mammal grazing.

STANDING DEAD
(XSTAD, 209.27253 g/m²)

As taxonomically diverse as the Producer Compartment (Table II), the Standing Dead Compartment represents the transitional state between live plant matter and ground litter. The method of measurement was identical to that used in obtaining the standing crop of the Producer Compartment. Estimates of standing crop of standing dead plant material were measured by biomass increases or decreases during the year (Table XIII).

The major sampling periods of the year were the same for the Standing Dead Compartment as for the Producer Compartment (Table IX). Biomass measurements on the first sampling date indicated that a large amount of organic matter existed in the form of standing dead plant material (209.27253 g/m²). Between the first and second sampling date the standing crop of this compartment decreased by 61.65058 g/m² or an average of 1.37001 g/m²/day. Standing dead plant material changed states after being grazed upon by the consumer population and transferred to ground litter.

The standing crop decreased 91.18443 g/m² between the second and third sampling date, an average of 1.40284 g/m²/day. During the initial weeks of the growing season some plant material that had been classified as standing dead plant material began producing chlorophyll. This resulted

TABLE XVII. *Grazing by the insect populations, growing season time units, per cent transfer rate, and average daily biomass outflow from the Producer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0.16869 | 0.0213024 |
| March | 15 | 0.16869 | 0.0306221 |
| March | 16 | 0.16869 | 0.0306221 |
| April | 21 | 0.16869 | 0.0332849 |
| April | 09 | 0.16869 | 0.0332849 |
| May | 31 | 0.16869 | 0.0335512 |
| June | 15 | 0.16869 | 0.0330186 |
| June | 15 | 0.16869 | 0.0330186 |
| July | 31 | 0.16869 | 0.0300896 |
| August | 15 | 0.16869 | 0.0271605 |
| August | 16 | 0.16869 | 0.0271605 |
| September | 15 | 0.16869 | 0.0223675 |
| September | 15 | 0.16869 | 0.0223675 |
| October | 29 | 0.16869 | 0.0207698 |

*Grazing was an input into the Insect Compartment (XI).

in an input to the Producer Compartment of approximately 23.1 g/m^2 during the initial 66 days of the growing season. The remainder of the biomass decrease was attributed to grazing by the consumers and a transfer of matter to the Litter Compartment. The standing crop increased by 18.83258 g/m^2 between the third and seventh sampling date, or approximately $0.11013 \text{ g/m}^2/\text{day}$. Little live plant material was being transferred from the Producer Compartment to the Standing Dead Compartment during this period. However, between the seventh sampling date and the eighth, during which time the first killing frost occurred, an average of $4.04075 \text{ g/m}^2/\text{day}$ of biomass was transferred into the compartment. This increase was attributed to Producer mortality. Between 4 November and 15 December, the Standing Dead Compartment decreased 42.51536 g/m^2 , or $1.03696 \text{ g/m}^2/\text{day}$. This indicated that plant material was being transferred to the Litter Compartment and also lost through some grazing by consumers.

Inputs

An increase in the state (biomass) of the Standing Dead Compartment was considered as an input from the Producer Compartment through mortality.

Mortality (DPROD). The amount of material transferred to the Standing Dead Compartment from the Producer Compartment was in the section of Producer Compartment Outputs.

Outputs

A decrease in the state of the Standing Dead Compartment was considered as an outflow of material through transfer functions identified

as dormancy, respiration, grazing by birds, grazing by mammals, grazing by insects, and a transfer to the Litter Compartment.

Dormancy (GSPROD). The function of dormancy was discussed in the section on the Producer Compartment Outputs.

Respiration (RSTAD). Using the criteria of Harris (1966) some plant material classified as standing dead material contained chlorophyll and metabolism was occurring. Although respiration measurements were not made and no respiration rates were utilized from the literature, the transfer function was assumed to be a viable feature to the model. A zero rate of metabolism was assigned to the transfer function for the year.

Grazing By Birds (FBES). Estimates of grazing on standing dead plant material by the bird population were obtained from a single literature source. Risser (1972) used grazing estimates based upon procedures of bioenergetic estimation developed by Wiens and Innis (1972). It was estimated that the bird population grazed on standing dead plant material and seeds at the rate of 0.00003 per cent of the standing crop of the Standing Dead Compartment, and was used in the computer program as the value for bird grazing.

It was assumed that the bird population would graze on the Standing Dead Compartment at a relatively constant rate throughout the year regardless of the compartment's standing crop. Bird grazing remained constant at 0.00003 per cent of the standing crop of the Standing Dead Compartment, an average flow rate of $0.0000305 \text{ g/m}^2/\text{day}$ during the year and a total of $0.0111325 \text{ g/m}^2/\text{year}$. In theory, it was believed that as the Standing Dead Compartment increased during the year more food would be available

to the bird population. As anticipated, grazing by the bird population did fluctuate with the standing crop of the Standing Dead Compartment (Table XVIII).

Grazing By Mammals (FMES). Estimates of grazing on standing dead plant material by the mammal population were obtained from a single literature source. Risser (1972) used consumption rates derived from Golley (1960) for Microtus, McNab (1963) for Reithrodontomys, Pearson (1947) and Rood (1958) for Blarina, and Douglas (1969) for Spermophilus. Grazing reported by Risser (1972) was at the rate of $0.01031 \text{ g/m}^2/\text{day}$ throughout the year or 0.00289 per cent of the standing crop of the Standing Dead Compartment. This value was used in the computer program as the value for mammal grazing which represented an outflow from the Standing Dead Compartment and an inflow to the Mammal Compartment.

It was assumed that the mammal population would graze on the Standing Dead Compartment at a relatively constant rate throughout the year regardless of the compartment's standing crop. Mammal grazing remained constant at 0.00289 per cent of the standing crop of the Standing Dead Compartment which yielded an average flow rate of $0.0029323 \text{ g/m}^2/\text{day}$ during the year and a total of $1.0702895 \text{ g/m}^2/\text{year}$. It was believed that as the Standing Dead Compartment increased during the year more food would be available to the mammal population. As anticipated, grazing by the mammal population did fluctuate with the standing crop of the Standing Dead Compartment (Table XIX).

Grazing By Insects (FIES). Estimates of grazing on standing dead plant material by the insect population were obtained from a single literature source. Risser (1972) estimated insect grazing from previous studies of

TABLE XVIII. *Grazing by the bird populations, yearly time units, per cent transfer rate, and average daily biomass outflow from the Standing Dead Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|------------------|----------------------|---------------------------|--|
| January | 31 | 0.00003 | 0.0000560 |
| February | 14 | 0.00003 | 0.0000470 |
| February | 14 | 0.00003 | 0.0000412 |
| March | 15 | 0.00003 | 0.0000352 |
| March | 16 | 0.00003 | 0.0000287 |
| April | 21 | 0.00003 | 0.0000208 |
| April | 09 | 0.00003 | 0.0000170 |
| May | 31 | 0.00003 | 0.0000177 |
| June | 15 | 0.00003 | 0.0000181 |
| June | 15 | 0.00003 | 0.0000184 |
| July | 31 | 0.00003 | 0.0000188 |
| August | 15 | 0.00003 | 0.0000193 |
| August | 16 | 0.00003 | 0.0000195 |
| September | 15 | 0.00003 | 0.0000199 |
| September | 15 | 0.00003 | 0.0000207 |
| October | 29 | 0.00003 | 0.0000400 |
| October-November | 17 | 0.00003 | 0.0000530 |
| November | 15 | 0.00003 | 0.0000459 |
| December | 31 | 0.00003 | 0.0000414 |

*Grazing was an input to the Bird Compartment (XB).

TABLE XIX. *Grazing by the mammal populations, yearly time units, per cent transfer rate, and average daily biomass outflow from the Standing Dead Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|------------------|----------------------|---------------------------|--|
| January | 31 | 0.00289 | 0.0053971 |
| February | 14 | 0.00289 | 0.0045282 |
| February | 14 | 0.00289 | 0.0039683 |
| March | 15 | 0.00289 | 0.0033857 |
| March | 16 | 0.00289 | 0.0027610 |
| April | 21 | 0.00289 | 0.0020024 |
| April | 09 | 0.00289 | 0.0016415 |
| May | 31 | 0.00289 | 0.0017051 |
| June | 15 | 0.00289 | 0.0017419 |
| June | 15 | 0.00289 | 0.0017722 |
| July | 31 | 0.00289 | 0.0018136 |
| August | 15 | 0.00289 | 0.0018541 |
| August | 16 | 0.00289 | 0.0018811 |
| September | 15 | 0.00289 | 0.0019121 |
| September | 15 | 0.00289 | 0.0019942 |
| October | 29 | 0.00289 | 0.0038493 |
| October-November | 17 | 0.00289 | 0.0051037 |
| November | 15 | 0.00289 | 0.0044181 |
| December | 31 | 0.00289 | 0.0039857 |

*Grazing was an input to the Mammal Compartment (XM).

Blocker and Reed (1971) in which the insect population consumed 2.374794 g/m² of standing dead plant material throughout the year for an approximate rate of 0.0065062 g/m²/day. This was equivalent to 0.00333 per cent of the daily standing crop of the Standing Dead Compartment. The value used in the computer program to simulate insect grazing was 0.00333 per cent of the daily standing crop of the Standing Dead Compartment, and an inflow to the Insect Compartment.

In the computer program it was assumed that the insect population would graze on the Standing Dead Compartment at a constant rate throughout the year as did the bird and mammal populations. Insect grazing remained constant at 0.00333 per cent of the standing crop of the Standing Dead Compartment and yielded an average flow of 0.0033788 g/m²/day for a total of 1.233262 g/m²/year. It was believed that as the Standing Dead Compartment increased during the year more food would be available to the insect population. As anticipated, grazing by the insect population did fluctuate with the standing crop of the Standing Dead Compartment (Table XX).

Transfer To The Litter Compartment of Standing Dead Plant Material (TSTIT).

Standing dead plant material was continually being transferred to the Litter Compartment throughout the year. A decrease in the state of the Standing Dead Compartment meant that more material was being transferred out of the compartment than was incoming. By measuring the standing crop of the Standing Dead Compartment (XSTAD) per unit of time (Table XIII), the amount of material transferred from the compartment could be calculated.

During the non-growing season, material was being lost from the Standing Dead Compartment without inputs into the compartment. The

TABLE XX. *Grazing by the insect populations, yearly time units, per cent transfer rate, and average daily biomass outflow from the Standing Dead Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|------------------|----------------------|---------------------------|--|
| January | 31 | 0.00333 | 0.0062188 |
| February | 14 | 0.00333 | 0.0052176 |
| February | 14 | 0.00333 | 0.0045725 |
| March | 15 | 0.00333 | 0.0039012 |
| March | 16 | 0.00333 | 0.0031814 |
| April | 21 | 0.00333 | 0.0023073 |
| April | 09 | 0.00333 | 0.0018914 |
| May | 31 | 0.00333 | 0.0019648 |
| June | 15 | 0.00333 | 0.0020071 |
| June | 15 | 0.00333 | 0.0020420 |
| July | 31 | 0.00333 | 0.0020898 |
| August | 15 | 0.00333 | 0.0021363 |
| August | 16 | 0.00333 | 0.0021675 |
| September | 15 | 0.00333 | 0.0022032 |
| September | 15 | 0.00333 | 0.0022978 |
| October | 29 | 0.00333 | 0.0044353 |
| October-November | 17 | 0.00333 | 0.0058807 |
| November | 15 | 0.00333 | 0.0050908 |
| December | 31 | 0.00333 | 0.0045925 |

*Grazing was an input to the Insect Compartment (XI).

amount of material lost per defined unit of area and time ($\text{g}/\text{m}^2/\text{day}$) was transferred to the Bird, Mammal, and Insect Compartments through grazing, to the Producer Compartment through dormancy, and to the Litter Compartment through a change of state in the plant material. The transfer rate of material to the Litter Compartment was calculated as the difference of material lost from the Standing Dead Compartment after grazing by the bird, mammal, and insect populations and dormancy (Table XXI). During the non-growing season, (time units 1, 2, 18, and 19), the average rate of transfer of standing dead plant material to the Litter Compartment was 0.6937225 per cent of the Standing Dead Compartment or $1.1243375 \text{ g}/\text{m}^2/\text{day}$.

During the growing season when the state of the Standing Dead Compartment was decreasing (time units 3 through 7), the amount of material transferred to the Litter Compartment was calculated as being the difference between the amount of plant material entering the compartment minus bird, mammal, and insect grazing. The average rate of transfer to the Litter Compartment was calculated as 0.828198 per cent of the standing crop or $0.815142 \text{ g}/\text{m}^2/\text{day}$.

When the state of the Standing Dead Compartment was increasing (time units 8 through 17), the amount of material transferred to the Litter Compartment was calculated as being the difference between the amount of plant material entering the compartment necessary to increase the compartment to the levels the field measurements indicated (Table XIV), minus bird, mammal, and insect grazing (Table XXI). The average rate of transfer to the Litter Compartment during this time was calculated as 1.20019 per cent of the standing crop or $0.867349 \text{ g}/\text{m}^2/\text{day}$.

TABLE XXI. *Transfer to the Litter Compartment, yearly time units, per cent transfer rate, and average daily biomass outflow from the Standing Dead Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|------------------|----------------------|---------------------------|--|
| January | 31 | 0.72569 | 1.35523 |
| February | 14 | 0.87064 | 1.36418 |
| February | 14 | 0.74506 | 1.02307 |
| March | 15 | 0.87476 | 1.02482 |
| March | 16 | 1.07020 | 1.02245 |
| April | 21 | 1.45097 | 1.00537 |
| April | 09 | 0.00000 | 0.00000 |
| May | 31 | 6.02840 | 3.55696 |
| June | 15 | 2.14887 | 1.29534 |
| June | 15 | 1.47764 | 0.90613 |
| July | 31 | 0.09564 | 0.06002 |
| August | 15 | 0.09668 | 0.06203 |
| August | 16 | 0.08934 | 0.05815 |
| September | 15 | 0.12099 | 0.08005 |
| September | 15 | 0.42314 | 0.29198 |
| October | 29 | 0.74243 | 0.98888 |
| October-November | 17 | 0.77806 | 1.37405 |
| November | 15 | 1.01939 | 1.55842 |
| December | 31 | 0.15917 | 0.21952 |

*Transfer to the Litter Compartment from the Standing Dead Compartment was an input to the Litter Compartment (XLITT).

LITTER
(XLITT, 323.40664 g/m²)

The Litter Compartment was as taxonomically diverse as the Producer and Standing Dead Compartments (Table II), and represented the "sink" of material that was undergoing decomposition. Grasses and forbs were lumped together in the plant portion of the compartment, while animal fecal matter and animal carcasses comprised the animal portion of the compartment. Estimates of ground litter standing crops were measured by biomass increases or decreases throughout the year (Table XXII). The method of measurement was identical to that used in obtaining the standing crops of the Producer and Standing Dead Compartments, except ground litter was collected by raking the sample area free of organic matter rather than by clipping herbage. Each of the five replicate samples were placed in a Berlese funnel for 72 hours for collection of debris dwelling invertebrates. Then the litter was freed of soil contamination by hand and placed in drying ovens at 60 C for 24 hours. Dry weights were then determined for each of the five replicate samples to the nearest 0.01 g. The five replicate samples were then combined and an average dry weight per defined unit area (g/m²) was assigned for the sample date (Table XXII).

The major sampling periods of the year were the same for the Litter Compartment as for the Producer and Standing Dead Compartments. Biomass measurements on the first sampling date indicated that a large amount of organic matter existed in the form of ground litter in the community (323.40664 g/m²). Between the first and second sampling date, the standing crop of the Litter Compartment increased by 37.47449 g/m² at an average of 0.8146628 g/m²/day due to inputs from the Standing Dead Compartment and the Bird, Mammal, and Insect Compartments.

TABLE XXII. Litter Compartment standing crop biomass mean for five replicate samples per sampling date.

| Sampling Date 1973 | Standing Crop Dry Weight (g/m ²) |
|-----------------------|--|
| 01 January | 323.40664 |
| 15 February | 360.88113 |
| 21 April | 63.42732 |
| 06 June | 628.93116 |
| 30 July | 436.84165 |
| 20 September | 251.88847 |
| 09 October | 202.38055 |
| 04 November | 262.91373 |
| 15 December | 305.09876 |

Between the second and third sampling date, the standing crop decreased an average of $4.5068759 \text{ g/m}^2/\text{day}$. This indicated that a considerable amount of organic matter was being transferred from the Litter Compartment. It was assumed that most of this matter was being rapidly processed by decomposer organisms and returned to the soil. Between the third and fourth sample dates, the state of the Litter Compartment increased by 565.50384 g/m^2 . This increase was primarily due to the import of matter into the study community by heavy precipitations. The Litter Compartment decreased 426.55061 g/m^2 between the fourth and seventh sampling date. Ground litter was being transferred out of the Litter Compartment by decomposition and by precipitation trends during September when more than normal precipitation fell and litter was observed to be washed out of the study community. Between the seventh and ninth sampling dates, the state of the Litter Compartment increased by 102.71821 g/m^2 . This increase was primarily due to the transfer of matter from the Standing Dead Compartment to the Litter Compartment.

Inputs

The increase in the Litter Compartment was influenced by the input of material by 18 transfer functions from the Standing Dead, Bird, Mammal, Insect, and Decomposer Compartments, and from the physical transfer of litter from outside the system into it.

Transfer To The Litter Compartment of Standing Dead Plant Material

(TSTIT). The amount of material transferred to the Litter Compartment from the Standing Dead Compartment was discussed in the section on Standing Dead Compartment Outputs.

Bird Population Excretion (EXB). Estimates of excretion by birds used in this study were obtained from a single literature source. Risser (1972) calculated a digestive efficiency of 70 per cent of food intake for the bird population. The remaining 30 per cent of the avian food intake was contributed to the litter via egestion of undigested food and excretion.

It was assumed that bird excretion would not vary with the food source but would remain constant throughout the year. Therefore, bird excretion remained a constant 30 per cent of food source intake which was divided between live plant material, standing dead plant material, mammals, insects, and decomposers (Table XXIII). The amount of excretion was directly proportional to the food intake of each of the food sources during the year. As food intake increased so did the amount of excretion input to the Litter Compartment.

Bird Mortality (DBMOR). Bird mortality was felt to be a viable feature of the model used as a way to input bird carcasses into the decomposition process via the Litter Compartment. In this study it was assumed that biomass lost through mortality would be replaced by reproduction and therefore a zero transfer rate was assigned this function. The function remains in the model for use in future modeling attempts.

Mammal Population Excretion (EXM). Estimates of excretion by mammals used in this study were obtained from a single literature source. In a study of the energy dynamics of a food chain in an old-field community, Golley (1960) calculated that the contribution of small mammals to litter was mainly through losses in feces and urine on the order of 19 per cent of the total energy intake of the small mammals.

TABLE XXIII. *Bird excretion rates per food source, yearly time units, per cent transfer rate, and average daily biomass input the Litter Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Input (g/m ²) | | | | | All Food Sources |
|-----------|----------------------|---------------------------|--|------------------------|--------|-----------|------------|---------------------|
| | | | Live Plant | Standing Dead Plant | Mammal | Insect | Decomposer | |
| January | 31 | 30.00000 | 0 | 0.0000168 | 0 | 0 | 0 | 0.0000168 |
| February | 14 | 30.00000 | 0 | 0.0000141 | 0 | 0 | 0 | 0.0000141 |
| February | 14 | 30.00000 | 0.0000549 | 0.0000123 | 0 | 0 | 0 | 0.0000672 |
| March | 15 | 30.00000 | 0.0000789 | 0.0000105 | 0 | 0 | 0 | 0.0000894 |
| March | 16 | 30.00000 | 0.0000789 | 0.0000086 | 0 | 0 | 0 | 0.0000878 |
| April | 21 | 30.00000 | 0.0000858 | 0.0000062 | 0 | 0.0022984 | 0 | 0.0023904 |
| April | 09 | 30.00000 | 0.0000858 | 0.0000051 | 0 | 0.0036532 | 0 | 0.0037441 |
| May | 31 | 30.00000 | 0.0000864 | 0.0000053 | 0 | 0.0059447 | 0 | 0.0060364 |
| June | 15 | 30.00000 | 0.0000851 | 0.0000054 | 0 | 0.0077882 | 0 | 0.0078787 |
| June | 15 | 30.00000 | 0.0000851 | 0.0000055 | 0 | 0.0093401 | 0 | 0.0094307 |
| July | 31 | 30.00000 | 0.0000775 | 0.0000056 | 0 | 0.0112491 | 0 | 0.0113322 |
| August | 15 | 30.00000 | 0.0000700 | 0.0000057 | 0 | 0.0127675 | 0 | 0.0128432 |
| August | 16 | 30.00000 | 0.0000700 | 0.0000058 | 0 | 0.0141248 | 0 | 0.0142006 |
| September | 15 | 30.00000 | 0.0000576 | 0.0000059 | 0 | 0.0126012 | 0 | 0.0126647 |
| September | 15 | 30.00000 | 0.0000576 | 0.0000062 | 0 | 0.0088612 | 0 | 0.0089250 |
| October | 29 | 30.00000 | 0.0000535 | 0.0000120 | 0 | 0 | 0 | 0.0000655 |
| October- | | | | | | | | |
| November | 17 | 30.00000 | 0 | 0.0000159 | 0 | 0 | 0 | 0.0000159 |
| November | 15 | 30.00000 | 0 | 0.0000137 | 0 | 0 | 0 | 0.0000137 |
| December | 31 | 30.00000 | 0 | 0.0000124 | 0 | 0 | 0 | 0.0000124 |

*Bird excretion was an output from the Bird Compartment (XB).

It was assumed that mammal excretion would not vary with the food source and would remain constant throughout the year as it had for bird excretion. Therefore, mammal excretion remained a constant 19 per cent of food source intake which was divided between live plant material, standing dead plant material, insects and decomposers (Table XXIV). The amount of excretion contributed to the Litter Compartment was directly proportional to the food intake of each of the food sources during the year as it had been with the bird population.

Mammal Mortality (DMMOR). Mammal mortality was felt to be a viable feature of the model, as was bird mortality, and was used as a way to input mammal carcasses into the decomposition process via the Litter Compartment. As was done for bird mortality, a zero transfer rate was assigned this function. This function remains in the model for use in future modeling attempts.

Insect Population Excretion (EXI). Estimates of insect contributions to the Litter Compartment were obtained from a search of the available literature. Van Hook (1969) found that approximately 61 per cent of the food intake of the adult stages of three species of dominant grassland arthropod Conocephalus fasciatus, Pteronemobius fasciatus, and Lycosa spp., was contributed to the litter through the process of egestion. Risser (1972) found that approximately 62 per cent of food ingested by insects was contributed to the litter. He reported that literature values indicated that 50 per cent of insect food intake went directly to the litter. Because of the similarities between the study site in Oklahoma and this study site, the transfer rate assigned to insect excretion was 62 per cent of food

TABLE XXIV. *Mammal excretion rates per food source, yearly time units, per cent transfer rate, and average daily biomass input to the Litter Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Input (g/m ²) | | | | For All Food Sources |
|-----------------------|----------------------|------------------------------|---|------------------------|-----------|------------|-------------------------|
| | | | Live Plant | Standing Dead Plant | Insect | Decomposer | |
| January | 31 | 19.00000 | 0 | 0.0010254 | 0 | 0 | 0.0010254 |
| February | 14 | 19.00000 | 0 | 0.0008603 | 0 | 0 | 0.0008603 |
| February | 14 | 19.00000 | 0.0035133 | 0.0007539 | 0 | 0 | 0.0042672 |
| March | 15 | 19.00000 | 0.0050504 | 0.0006432 | 0 | 0 | 0.0056936 |
| March | 16 | 19.00000 | 0.0050504 | 0.0005245 | 0 | 0 | 0.0055749 |
| April | 21 | 19.00000 | 0.0054896 | 0.0003804 | 0.0004075 | 0 | 0.0062775 |
| April | 09 | 19.00000 | 0.0054896 | 0.0003118 | 0.0006478 | 0 | 0.0064492 |
| May | 31 | 19.00000 | 0.0055335 | 0.0003239 | 0.0010541 | 0 | 0.0069115 |
| June | 15 | 19.00000 | 0.0054457 | 0.0003309 | 0.0013811 | 0 | 0.0071577 |
| June | 15 | 19.00000 | 0.0054457 | 0.0003367 | 0.0016563 | 0 | 0.0074387 |
| July | 31 | 19.00000 | 0.0049626 | 0.0003445 | 0.0019901 | 0 | 0.0072972 |
| August | 15 | 19.00000 | 0.0044795 | 0.0003522 | 0.0022640 | 0 | 0.0070957 |
| August | 16 | 19.00000 | 0.0044795 | 0.0003574 | 0.0025047 | 0 | 0.0073416 |
| September | 15 | 19.00000 | 0.0036890 | 0.0003632 | 0.0022346 | 0 | 0.0062868 |
| September | 15 | 19.00000 | 0.0036890 | 0.0003788 | 0.0015713 | 0 | 0.0056391 |
| October | 29 | 19.00000 | 0.0034255 | 0.0007313 | 0 | 0 | 0.0041568 |
| October - November | 17 | 19.00000 | 0 | 0.0009697 | 0 | 0 | 0.0009697 |
| November | 15 | 19.00000 | 0 | 0.0008394 | 0 | 0 | 0.0008394 |
| December | 31 | 19.00000 | 0 | 0.0007572 | 0 | 0 | 0.0007572 |

*Mammal excretion was an output from the Mammal Compartment (XM).

intake and was divided between live plant material, standing dead plant material, and decomposer organisms (Table XXV). The amount of excretion was directly proportional to the food intake of each of the food sources during the year. As food intake increased so did the amount of excretion input to the Litter Compartment.

Insect Mortality (DIMOR). Insect mortality was felt to be a viable feature of the model used as a way to input insect carcasses into the decomposition process via the Litter Compartment. A transfer rate for mortality was not assigned in this study, but remains in the model for use in future modeling efforts.

Decomposer Population Excretion (EXD). Because excretion was felt to be a viable process of the decomposer organisms it was placed in the model. Although it was evident that the decomposers contributed excretion to the Litter Compartment, a value for excretion was not assigned. It was felt that as more reliable data becomes available a value for decomposer excretion would be assigned this function. It remains in the model for use in future modeling attempts.

Decomposer Mortality (DDMOR). Mortality was felt to be a viable feature of the model but it was not assigned a transfer rate. The function remains in the model for use in future modeling attempts.

Import of Litter (TLITIN). An import transfer of litter material from outside the system was an important source of litter build-up during this study. Heavy precipitation occurred at different periods during the study causing litter to be washed into the sample plots and resulted in increases in litter biomass. Heavy precipitation during the week prior

TABLE XXV. *Insect excretion rates per food source, yearly time units, per cent transfer rate, and average daily biomass input to the Litter Compartment generated by the computer program.

| Month | Time Units in Days | Per Cent Transfer Rate | Live Plant | Average Daily Biomass Input (g/m ²) | | |
|-----------|-----------------------|------------------------------|---------------|---|-------------|-------------------------|
| | | | | Standing Dead Plant | Decomposers | For All Food Sources |
| January | 31 | 62.00000 | 0 | 0.0038556 | 0 | 0.0038556 |
| February | 14 | 62.00000 | 0 | 0.0032349 | 0 | 0.0032349 |
| February | 14 | 62.00000 | 0.0132074 | 0.0028349 | 0 | 0.0160423 |
| March | 15 | 62.00000 | 0.0189857 | 0.0024187 | 0 | 0.0214044 |
| March | 16 | 62.00000 | 0.0189857 | 0.0019724 | 0 | 0.0209581 |
| April | 21 | 62.00000 | 0.0206366 | 0.0014305 | 0 | 0.0220671 |
| April | 09 | 62.00000 | 0.0206366 | 0.0011726 | 0 | 0.0218092 |
| May | 31 | 62.00000 | 0.0208017 | 0.0012181 | 0 | 0.0220198 |
| June | 15 | 62.00000 | 0.0204715 | 0.0012444 | 0 | 0.0217159 |
| June | 15 | 62.00000 | 0.0204715 | 0.0012660 | 0 | 0.0217375 |
| July | 31 | 62.00000 | 0.0186555 | 0.0012956 | 0 | 0.0199511 |
| August | 15 | 62.00000 | 0.0168395 | 0.0013245 | 0 | 0.0181640 |
| August | 16 | 62.00000 | 0.0168395 | 0.0013438 | 0 | 0.0181833 |
| September | 15 | 62.00000 | 0.0138678 | 0.0013659 | 0 | 0.0152337 |

TABLE XXV. (contd.)

| Month | Time Units in Days | Per Cent Transfer Rate | Live Plant | Average Daily Biomass Input (g/m ²) | | |
|------------------|-----------------------|------------------------------|---------------|---|-------------|-------------------------|
| | | | | Standing Dead Plant | Decomposers | For All Food Sources |
| September | 15 | 62.00000 | 0.0138678 | 0.0014246 | 0 | 0.0152924 |
| October | 29 | 62.00000 | 0.0128772 | 0.0027498 | 0 | 0.0156270 |
| October-November | 17 | 62.00000 | 0 | 0.0036460 | 0 | 0.0036460 |
| November | 15 | 62.00000 | 0 | 0.0031562 | 0 | 0.0031562 |
| December | 31 | 62.00000 | 0 | 0.0028473 | 0 | 0.0028473 |

*Insect excretion was an output from the Insect Compartment (XI).

to 6 June washed an average of 434.80539 g/m^2 of litter into the plots sampled. In the computer program the addition of this material was accomplished by adding $28.9870260 \text{ g/m}^2/\text{day}$ to the Litter Compartment during the ninth time period containing 15 days.

Outputs

A decrease in the state of the Litter Compartment was considered as an outflow of material through transfer functions identified as respiration and organic breakdown by the decomposer organisms.

Litter Respiration (RLITT). No data were available for litter respiration from literature sources. The value utilized for litter respiration in this study was calculated as the difference between the organic breakdown of litter by the decomposer organisms and the other inputs previously discussed. In this manner the state of the Litter Compartment was actually manipulated to correspond to field measurements. Values used for litter respiration have been included in Table XXVI. It is hoped that in future modeling efforts the arbitrary values assigned respiration can be replaced with documented values

Transfer To The Decomposer Compartment (FDM). The transfer rate utilized in the transfer of matter to the Decomposer Compartment for organic breakdown in this study was calculated as the difference between litter respiration and the other inputs previously discussed. By measuring the standing crop of the Litter Compartment the amount of litter lost to the system or transferred to the decomposers could be calculated per unit of time. This loss was then expressed as a transfer rate for each of the 19 time units of the study in the computer program. In this manner the state of the Litter Compartment could be manipulated to correspond to field measurements in which a loss of matter from the compartment was measured (Table XXVII).

TABLE XXVI. Litter respiration, yearly time units, per cent transfer rate, and average daily biomass output from the Litter Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|------------------|----------------------|---------------------------|--|
| January | 31 | 0.47692 | 1.3579324 |
| February | 14 | 0.58482 | 1.3675578 |
| February | 14 | 0.51901 | 1.0423745 |
| March | 15 | 0.63096 | 1.0501698 |
| March | 16 | 0.80688 | 1.0449241 |
| April | 21 | 1.20276 | 1.0136145 |
| April | 09 | 0.04922 | 0.0314893 |
| May | 31 | 0 | 0 |
| June | 15 | 0 | 0 |
| June | 15 | 0.16159 | 0.9451886 |
| July | 31 | 0.02099 | 0.1019022 |
| August | 15 | 0.02542 | 0.1041380 |
| August | 16 | 0.02760 | 0.0975721 |
| September | 15 | 0.04134 | 0.1177869 |
| September | 15 | 0.13505 | 0.3214316 |
| October | 29 | 0 | 0 |
| October-November | 17 | 0 | 0 |
| November | 15 | 0 | 0 |
| December | 31 | 0 | 0 |

TABLE XXVII. Transfer to the Decomposer Compartment, yearly time units, per cent transfer rate, and average daily biomass outflow from the Litter Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|------------------|----------------------|---------------------------|--|
| January | 31 | 0.81579 | 2.3227956 |
| February | 14 | 0.99918 | 2.3365077 |
| February | 14 | 1.16169 | 2.3331268 |
| March | 15 | 1.40191 | 2.3333390 |
| March | 16 | 1.79112 | 2.3195326 |
| April | 21 | 2.66094 | 2.2424819 |
| April | 09 | 0 | 0 |
| May | 31 | 0 | 0 |
| June | 15 | 0 | 0 |
| June | 15 | 0.97079 | 5.6784434 |
| July | 31 | 0.72825 | 3.5355079 |
| August | 15 | 0.74972 | 3.0713764 |
| August | 16 | 1.12880 | 3.9905588 |
| September | 15 | 1.64986 | 4.7008220 |
| September | 15 | 0.72726 | 1.7309467 |
| October | 29 | 0 | 0 |
| October-November | 17 | 0 | 0 |
| November | 15 | 0 | 0 |
| December | 31 | 0 | 0 |

BIRDS
(XB, 0.018 g/m²)

A census of the bird population was made to determine the species present within the study community (Table III). Each time a visit was made to the study area field observations of the birds frequenting the area were made from observation blinds constructed in the study area.

Ten species of birds were classified as permanent year round residents of the area and 11 species classified as summer migrants. The biomass of an average adult was calculated for each species after Goodrich (1946). The biomass was then averaged for permanent and summer residents separately. By assuming that the standing crop of the Bird Compartment would be equal to the average biomass of the permanent residents at any one time during the year for the 1.42 ha study community, the average permanent resident biomass was converted to units of g/m² for use in the computer program (0.0176985 g/m²). It was further assumed that the bird population would increase in response to the arrival of the migrant species beginning on 15 March and peaking on 15 June (0.0212804 g/m²). The standing crop for summer residents was estimated in the same manner as discussed for the permanent residents and converted to g/m² for use in the computer program (0.0032563 g/m²). The standing crop of the Bird Compartment decreased from 15 June to 15 September as the summer residents migrated from the area. On 15 September the standing crop of the Bird Compartment approximated the standing crop of the permanent residents of the study community as originally calculated (0.0176985 g/m²). The standing crop of the Bird Compartment as utilized in the computer program appears in Table XXVIII. The state of the compartment approximated the calculated states for the population as previously discussed.

TABLE XXVIII. Bird Compartment standing crop biomass generated by the computer program during the year.

| Date | Standing Crop Biomass per unit area (g/m ²) |
|--------------|---|
| 01 January | 0.0180000 |
| 01 February | 0.0180000 |
| 01 March | 0.0180000 |
| 15 March | 0.0180000 |
| 01 April | 0.0181189 |
| 01 May | 0.0188358 |
| 01 June | 0.0200480 |
| 15 June | 0.0220269 |
| 01 July | 0.0200382 |
| 01 August | 0.0189376 |
| 01 September | 0.0181432 |
| 15 September | 0.0180446 |
| 01 October | 0.0180447 |
| 01 November | 0.0180447 |
| 01 December | 0.0180447 |
| 31 December | 0.0180447 |

Even though the compartment state remained relatively constant, the physiological processes were interacting to maintain the population by allowing the inputs to the compartment to equal the outputs from it.

Inputs

Inputs to the Bird Compartment were attributed to grazing and predation on food sources identified as live plant material, standing dead plant material, mammals, insects, and decomposers, reproduction and immigration.

Grazing on Live Plant Material by Birds (FBEP). Bird grazing on live plant material was discussed in the section on the Producer Compartment, Outputs.

Grazing on Standing Dead Plant Material by Birds (FBES). Bird grazing on standing dead plant material was discussed in the section on the Standing Dead Compartment, Outputs.

Predation on Mammals by Birds (FBEM). It was assumed that little, if any, carnivory upon mammals was occurring in the study community. The food preferences of the species comprising the bird population were primarily herbivorous, insectivorous, and spermivorous. It was further assumed that Buteo borealis preyed little on small mammals within the study community. Therefore, it was assumed that no predation was taking place and the transfer rate assigned to predation was zero for the entire length of the study. Predation on small mammals was felt to be a viable feature of the model and therefore was not deleted from it. Possibly in future modeling attempts or refinements a transfer rate can be assigned this transfer function.

Predation on Insects by Birds (FBEI). Estimates of predation on the insect population were obtained from a single literature source. Risser (1972) estimated that the bird population preyed upon the standing crop of the insect population at the rate of 2 per cent. The energy intake by each bird species was divided into seed and insect sources according to grams dry weight. Using bioenergetic estimation developed by Wiens and Innis (1972), the 2 per cent predation rate was calculated.

It was thus assumed that the bird population would prey on the Insect Compartment standing crop at a constant rate during that portion of the growing season when the insect population was active. Because temperatures controlled insect productivity, birds preyed on the insect population during April through September when field measurements indicated that insect activity was not restricted by temperature. This resulted in an average flow of $0.0329185 \text{ g/m}^2/\text{day}$ during the growing season and a total of $5.3657278 \text{ g/m}^2/\text{growing season}$ (Table XXIX). During the non-growing season when insect populations were influenced by temperature resulting in minute standing crop biomass, predation by the bird population was assumed to be negligible and a zero transfer rate was utilized in the computer program.

Predation on Decomposers by Birds (FBED). The decomposer organisms of the Decomposer Compartment were an excellent source of food for the birds, but no transfer rate was assigned bird predation in this study. Although the bird population was expected to utilize the decomposers as a food source no reliable estimates of bird predation were found in the literature. Therefore, bird predation was assigned a zero transfer rate for the year. This function remains in the model for utilization in future modeling attempts.

TABLE XXIX. *Predation by the bird populations, growing season time units, per cent transfer rate, and average daily biomass outflow from the Insect Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Outflow (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0 | 0 |
| March | 15 | 0 | 0 |
| March | 16 | 0 | 0 |
| April | 21 | 2.00000 | 0.0076614 |
| April | 09 | 2.00000 | 0.0121774 |
| May | 31 | 2.00000 | 0.0198159 |
| June | 15 | 2.00000 | 0.0259609 |
| June | 15 | 2.00000 | 0.0311339 |
| July | 31 | 2.00000 | 0.0374971 |
| August | 15 | 2.00000 | 0.0425584 |
| August | 16 | 2.00000 | 0.0470827 |
| September | 15 | 2.00000 | 0.0420043 |
| September | 15 | 2.00000 | 0.0295375 |
| October | 29 | 0 | 0 |

*Predation was an input to the Bird Compartment (XB).

Bird Reproduction (GBREP). It was felt that bird reproduction would equal bird mortality and was therefore assigned a zero transfer rate in the model. It remains in the model as a viable feature for utilization in future modeling attempts.

Bird Immigration (TBIN). Immigration was the primary manner in which the state of the Bird Compartment increased during the study. As previously discussed, the standing crop of the Bird Compartment increased in response to the arrival of migrant species beginning on 15 March and peaking on 15 June. The standing crop increased by 0.0040269 g/m^2 between 15 March and 15 June (Table XXVIII).

In the computer program the transfer rate assigned to bird immigration should have been equal to the biomass increase noted, but was not. Bird immigration was assigned a zero rate of transfer throughout the year. Increases in the standing crop of the Bird Compartment were manipulated by allowing the inputs to exceed outputs from the Bird Compartment without utilizing a transfer rate for immigration directly. In this indirect manner the state of the Bird Compartment fluctuated in the same manner as if a transfer rate for immigration had been employed. Increases in the state of the compartment should not have been calculated in this manner. This was a programming error attributed to the programmer. In future attempts in modeling, this mistake should be corrected to reflect population fluctuations attributable to immigration.

Outputs

Outflows of energy from the Bird Compartment were attributable to transfer functions identified as excretion, respiration for each of the

food sources identified as live plant material, standing dead plant material, mammals, insects, and decomposers, emigration, and mortality.

Bird Excretion (EXB). Bird population excretion was discussed in the section on the Litter Compartment, Inputs.

Bird Respiration (RBR1, RBR2, RBR3, RBR4, RBR5). Metabolism was assumed to be a function of food intake from the various food sources throughout the year. Each category of food intake was assigned a respiratory transfer rate. Estimates of the respiratory transfer rate followed Risser (1972) in which the respiratory rate was calculated by the difference (Respiration = Food Intake - Egestion). Since egestion was 30 per cent of the food intake per food source, respiration was calculated to be 70 per cent of the food intake per food source. In order to mimic the standing crop of the bird population in the community, the respiratory rate fluctuated per food source during the 19 time units of the year in the computer program. This allowed biomass increases and decreases in the Bird Compartment to be directly responsive to gains and losses of body weights of the bird population. However, as previously discussed, the state of the Bird Compartment was influenced by immigration and emigration more than gains or losses in body weights of the population and should have been programmed to reflect such. However, it was not and the assigned respiratory rate was manipulated to reflect the state of the compartment per time unit during the year per food source (Table XXX). The respiratory rate should have been utilized to mimic body weight fluctuations of the standing crop of the compartment. Any future modeling attempts should reflect this.

TABLE XXX. Bird respiration per food source, yearly time units, per cent transfer rate, and average daily biomass outflow from the Bird Compartment generated by the computer program.

| Per Cent Transfer Rate and Average Daily Biomass Outflow (g/m ²) | | | | | | | |
|--|----------------------|-----------------------|----------------------------------|------------------|-----------------------|----------------------|-------------------------|
| Month | Time Unit in Days | Live Plant (RBR1) | Standing Dead Plant (RBR2) | Mammal (RBR3) | Insect (RBR4) | Decomposer (RBR5) | For All Food Sources |
| January | 31 | 0 | 70.00000 0.0000392 | 0 | 0 | 0 | 0.0000392 |
| February | 14 | 0 | 70.00000 0.0000329 | 0 | 0 | 0 | 0.0000329 |
| February | 14 | 70.00000 0.0001281 | 70.00000 0.0000288 | 0 | 0 | 0 | 0.0001569 |
| March | 15 | 70.00000 0.0001842 | 70.00000 0.0000246 | 0 | 0 | 0 | 0.0002088 |
| March | 16 | 69.00000 0.0001816 | 53.41614 0.0000153 | 0 | 0 | 0 | 0.0001969 |
| April | 21 | 69.00000 0.0001974 | 60.00000 0.0000143 | 0 | 69.96027 0.0053599 | 0 | 0.0055716 |
| April | 09 | 69.00000 0.0001974 | 69.00000 0.0000117 | 0 | 69.47520 0.0084602 | 0 | 0.0086693 |
| May | 31 | 69.00000 0.0001989 | 69.00000 0.0000122 | 0 | 69.81368 0.0138342 | 0 | 0.0140453 |
| June | 15 | 69.00000 0.0001958 | 69.00000 0.0000124 | 0 | 69.49961 0.0180427 | 0 | 0.0182509 |
| June | 15 | 70.00000 0.0001986 | 70.00000 0.0000128 | 0 | 70.43000 0.0219276 | 0 | 0.0221390 |
| July | 31 | 70.00000 0.0001810 | 70.00000 0.0000131 | 0 | 70.09567 0.0262225 | 0 | 0.0264166 |
| August | 15 | 70.00000 0.0001633 | 70.00000 0.0000135 | 0 | 70.10964 0.0298375 | 0 | 0.0300143 |
| August | 16 | 70.00000 0.0001633 | 70.00000 0.0000136 | 0 | 70.01319 0.0329641 | 0 | 0.0331410 |
| September | 15 | 70.00000 0.0001345 | 70.00000 0.0000139 | 0 | 70.01545 0.0294094 | 0 | 0.0295578 |

TABLE XXX. (contd.)

| Month | Time Unit in Days | Per Cent Transfer Rate and Average Daily Biomass Outflow (g/m ²) | | | | | |
|-----------------------|----------------------|--|----------------------------------|------------------|-----------------------|----------------------|-------------------------|
| | | Live Plant (RBR1) | Standing Dead Plant (RBR2) | Mammal (RBR3) | Insect (RBR4) | Decomposer (RBR5) | For All Food Sources |
| September | 15 | 70.00000 0.0001345 | 70.00000 0.0000144 | 0 | 70.00000 0.0206762 | 0 | 0.0208251 |
| October | 29 | 70.00000 0.0001249 | 70.00000 0.0000280 | 0 | 0 | 0 | 0.0001529 |
| October - November | 17 | 0 | 70.00000 0.0000371 | 0 | 0 | 0 | 0.0000371 |
| November | 15 | 0 | 70.00000 0.0000321 | 0 | 0 | 0 | 0.0000321 |
| December | 31 | 0 | 70.00000 0.0000289 | 0 | 0 | 0 | 0.0000289 |

Bird Emigration (TBOUT). Emigration was the primary manner in which the Bird Compartment decreased during the study. As previously discussed, the standing crop of the Bird Compartment decreased in response to the departure of migrant species beginning on 15 June and ending on 15 September. The standing crop decreased by 0.0039823 g/m^2 between 15 June and 15 September (Table XXVIII).

In the computer program the transfer rate assigned to bird emigration should have been equal to the biomass decrease noted, but was not. As was done for bird immigration, bird emigration was assigned a zero rate of transfer throughout the year. Decreases in the standing crop of the Bird Compartment were manipulated by allowing outputs to exceed inputs from the Bird Compartment without utilizing a value for emigration directly. In this indirect manner the state of the Bird Compartment fluctuated in the same manner as if a value for emigration had been employed. Decreases in the state of the compartment should not have been calculated in this manner. This was a programming error attributable to the programmer. In future attempts in modeling, this mistake should be corrected to reflect population fluctuations attributable to emigration.

Bird Mortality (DBMOR). Bird population mortality was discussed in the section on the Litter Compartment, Inputs.

MAMMALS
(XM, 0.004 g/m^2)

Biomass estimates of the small mammal population were calculated from data reported by Johnson (1968). For each of the 24 trap-nights reported, all small mammals by species were summed. Biomass, in grams,

of an average adult was computed for each species after Hall (1955) and totaled and converted to biomass for the sample date. Assuming that the 45 trapping stations were dispersed through the 3.8 ha trapping area to representatively sample the population within the entire area, the biomass reported was converted to g/m^2 for the entire 3.8 ha area for each sample date. The standing crop of small mammals calculated by the preceding method was probably an underestimate of the actual standing crop of the mammal population, however values reported were utilized in the computer program as a basis for the standing crop of the Mammal Compartment. In the computer program the initial standing crop of the Mammal Compartment was assumed to be equal to the minimum standing crop calculated for 10 March, 0.0035054 g/m^2 , rounded to 0.004 g/m^2 . The standing crop was assumed to remain constant until the spring. Beginning on 15 March, the mammal standing crop began increasing, peaking on 15 June. The maximum standing crop of the Mammal Compartment on 15 June corresponded to the maximum trap-line standing crop reported for 18 May, 0.0280217 g/m^2 . The mammal standing crop decreased between 15 June and 15 September when it approximated the initial standing crop of the Mammal Compartment (0.0040255 g/m^2). The cyclic behavior of the mammal standing crop was an assumed characteristic for programming purposes only. It may not actually reflect the true mammal population of the study community. The cyclic behavior of the state of the compartment was attained by manipulating the inputs and outputs to and from the compartment to correspond to the assumed state of it (Table XXXI).

Inputs

Inputs to the Mammal Compartment were attributed to grazing and predation on food sources identified as live plant material, standing

TABLE XXXI. Mammal Compartment standing crop biomass generated by the computer program during the year.

| Date | Standing Crop Biomass Per Unit Area (g/m ²) |
|--------------|---|
| 01 January | 0.0040000 |
| 01 February | 0.0040000 |
| 01 March | 0.0040002 |
| 15 March | 0.0040003 |
| 01 April | 0.0040939 |
| 01 May | 0.0091090 |
| 01 June | 0.0210356 |
| 15 June | 0.0280217 |
| 01 July | 0.0190218 |
| 01 August | 0.0095235 |
| 01 September | 0.0041246 |
| 15 September | 0.0040255 |
| 01 October | 0.0040256 |
| 01 November | 0.0040257 |
| 01 December | 0.0040259 |
| 31 December | 0.0040260 |

dead plant material, insects, and decomposers, reproduction and immigration.

Grazing on Live Plant Material by Mammals (FMEP). Mammal grazing on live plant material was discussed in the section on the Producer Compartment, Outputs.

Grazing on Standing Dead Plant Material by Mammals (FMES). Mammal grazing on standing dead plant material was discussed in the section on the Standing Dead Compartment, Outputs.

Predation on Insects by Mammals (FMEI). Estimates of predation on the insect population were obtained from a single literature source. Risser (1972) estimated that the mammal population preyed upon the standing crop of the insect population at the rate of 0.56 per cent. Derivation of this value was based on consumption rates for various species of the mammal population of the Oklahoma study; Golley (1960) for Microtus, McNab (1963) for Reithrodontomys, Pearson (1947) and Rood (1958) for Blarina, and Douglas (1969) for Spermophilus.

It was assumed that the mammal population would prey on the Insect Compartment standing crop during that portion of the growing season when the insect population was active. Temperature was the controlling factor influencing insect productivity. Mammals preyed on the insect population during April through September when field measurements indicated that insect activity was not restricted by temperature. This resulted in an average flow of $0.0092171 \text{ g/m}^2/\text{day}$ during the growing season and a total of $1.5023952 \text{ g/m}^2/\text{growing season}$ (Table XXXII). During the non-growing season, when insect populations were influenced

TABLE XXXII. *Predation by the mammal populations, growing season time units, per cent transfer rate, and average daily biomass inputs to the Mammal Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Input (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0 | 0 |
| March | 15 | 0 | 0 |
| March | 16 | 0 | 0 |
| April | 21 | 0.56000 | 0.0021451 |
| April | 09 | 0.56000 | 0.0034096 |
| May | 31 | 0.56000 | 0.0055484 |
| June | 15 | 0.56000 | 0.0072690 |
| June | 15 | 0.56000 | 0.0087174 |
| July | 31 | 0.56000 | 0.0104747 |
| August | 15 | 0.56000 | 0.0110163 |
| August | 16 | 0.56000 | 0.0131831 |
| September | 15 | 0.56000 | 0.0117612 |
| September | 15 | 0.56000 | 0.0082705 |
| October | 29 | 0 | 0 |

*Mammal predation was an output from the Insect Compartment (XI).

by temperature resulting in minute standing crops, predation by the mammal population was assumed to be negligible and a zero transfer rate was utilized in the computer program.

Predation on Decomposers by Mammals (FMED). Undoubtedly the small mammal population did utilize the decomposer organisms as a food source; however, estimates of small mammal predation on decomposers were not found in the available literature. Therefore, mammal predation was assigned a zero transfer rate for the year. This function remains in the model for utilization in future modeling attempts.

Mammal Reproduction (GMREP). It was felt that mammal reproduction would equal mammal mortality and was therefore assigned a zero transfer rate in the model. In the study, however, biomass increases in the mammal population were probably influenced by reproduction. Spring reproduction probably resulted in an increased population and increased activity, reaching a peak in early to mid-summer, and declining through mortality or emigration in the fall and winter. Although assigned a zero transfer rate in this study, it would appear to be a viable feature of the model and should be utilized in future modeling attempts.

Mammal Immigration (TMIN). It was assumed that little immigration into the study area by small mammals took place during the year. A relatively stable population of mammals existed within the confines of the study community. Therefore, a zero transfer rate was utilized in the model for immigration. However, the immigration transfer function remained in the model for future use.

Outputs

Outflows of energy from the Mammal Compartment were attributable to transfer functions identified as excretion, respiration for each of the food sources identified as live plant material, standing dead plant material, insects, and decomposers, emigration, predation by birds, and mortality.

Mammal Excretion (EXM). Mammal population excretion was discussed in the section on the Litter Compartment, Inputs.

Mammal Respiration (RMR1, RMR2, RMR3, RMR4). As previously discussed for bird respiration, mammal metabolism was assumed to be a function of food intake from the various food sources throughout the year. Each category of food intake was assigned a respiratory transfer rate. Estimates of the respiratory transfer rate followed Risser (1972) in which the respiratory rate was calculated by the difference (Respiration=Food Intake-Egestion). Since egestion was 19 per cent of the food intake per food source, respiration was calculated to be 81 per cent of the food intake per food source. In order to mimic the standing crop of the mammal population in the community, the respiratory rate fluctuated per food source during the 19 time units of the year in the computer program. This allowed biomass increases and decreases in the state of the Mammal Compartment to be directly responsive to gains and losses of body weights of the mammal population. However, as previously discussed, the state of the Mammal Compartment was probably influenced by reproduction and mortality more than gains and losses of body weights of the population and should be programmed in the future to reflect this fact.

However, it was not done in this study and the assigned respiratory rate for each of the 19 time units of the computer program were manipulated to reflect the state of the compartment per time unit during the year per food source (Table XXXIII).

Mammal Emigration (TMOU). It was assumed that little emigration from the study area took place during the year. A relatively stable population of mammals existed within the confines of the study community. Therefore, a zero transfer rate was utilized in the model for emigration. However, the emigration transfer function remains in the model for future use.

Predation by Birds on Mammals (FBEM). Predation by the bird population on the standing crop of the Mammal Compartment was discussed in the section on the Bird Compartment, Inputs.

Mammal Mortality (DMMOR). Mammal population mortality was discussed in the section on the Litter Compartment, Inputs.

INSECTS
(XI, 0.0001 g/m²)

Invertebrate sampling was conducted to obtain quantitative estimates of number and biomass of major groups. Distinction between vegetative dwelling and debris dwelling invertebrates was necessary for compartmentalization. Those insects which were predominantly vegetative dwelling were placed in the Insect Compartment (Table V). Those insects that derived their energy from their activity in the debris were placed in the Decomposer Compartment (Table VI).

TABLE XXXIII. Mammal respiration per food source, yearly time units, per cent transfer rate, and average daily biomass outflow from the Mammal Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate and Average Daily Biomass Outflow (g/m ²) | | | | |
|----------|----------------------|--|----------------------------------|-----------------------|-----------------------|-------------------------|
| | | Live Plant (RMR1) | Standing Dead Plant (RMR2) | Insects (RMR3) | Decomposers (RMR4) | For All Food Sources |
| January | 31 | 0 | 81.00000 0.0043716 | 0 | 0 | 0.0043716 |
| February | 14 | 0 | 81.00000 0.0036678 | 0 | 0 | 0.0036678 |
| February | 14 | 81.00000 0.0149779 | 81.00000 0.0032143 | 0 | 0 | 0.0181922 |
| March | 15 | 81.00000 0.0215308 | 81.00000 0.0027424 | 0 | 0 | 0.0242732 |
| March | 16 | 80.98851 0.0215277 | 80.90000 0.0022336 | 0 | 0 | 0.0237613 |
| April | 21 | 80.99416 0.0234013 | 80.90000 0.0016199 | 80.90000 0.0017353 | 0 | 0.0267565 |
| April | 09 | 79.29061 0.0229091 | 80.00000 0.0013132 | 80.00000 0.0027276 | 0 | 0.0269499 |
| May | 31 | 79.92329 0.0232766 | 80.00000 0.0013640 | 80.00000 0.0044387 | 0 | 0.0290793 |
| June | 15 | 79.68745 0.0228396 | 80.00000 0.0013935 | 80.00000 0.0058152 | 0 | 0.0300483 |
| June | 15 | 83.09340 0.0238158 | 81.00000 0.0014354 | 81.00000 0.0070610 | 0 | 0.0323122 |
| July | 31 | 82.17313 0.0214627 | 81.00000 0.0014690 | 81.00000 0.0084845 | 0 | 0.0314162 |
| August | 15 | 82.49860 0.0194501 | 81.00000 0.0015018 | 81.00000 0.0096522 | 0 | 0.0306041 |
| August | 16 | 81.02636 0.0191030 | 81.00000 0.0015236 | 81.00000 0.0106783 | 0 | 0.0313049 |

TABLE XXXIII. (contd.)

| Per Cent Transfer Rate and Average Daily Biomass Outflow (g/m ²) | | | | | | |
|--|----------------------|----------------------|----------------------------------|-------------------|-----------------------|-------------------------|
| Month | Time Unit in Days | Live Plant (RMR1) | Standing Dead Plant (RMR2) | Insects (RMR3) | Decomposers (RMR4) | For All Food Sources |
| September | 15 | 81.03410 | 81.00000 | 81.00000 | 0 | 0.0268087 |
| | | 0.0157334 | 0.0015488 | 0.0095265 | | |
| September | 15 | 81.00000 | 81.00000 | 81.00000 | 0 | 0.0240412 |
| | | 0.0157268 | 0.0016153 | 0.0066991 | | |
| October | 29 | 81.00000 | 81.00000 | 0 | 0 | 0.0177214 |
| | | 0.0146035 | 0.0031179 | | | |
| October- November | 17 | 0 | 81.00000 | 0 | 0 | 0.0041339 |
| | | | 0.0041339 | | | |
| November | 15 | 0 | 81.00000 | 0 | 0 | 0.0035786 |
| | | | 0.0035786 | | | |
| December | 31 | 0 | 81.00000 | 0 | 0 | 0.0032284 |
| | | | 0.0032284 | | | |

Temperature was the predominant environmental factor affecting the invertebrates and was utilized as the controlling mechanism for the state of the Insect Compartment in the computer model. Temperature was the limiting factor prior to 15 March and after 29 October for the insect standing crop. The standing crop approached zero during this time interval (0.0001 g/m^2). Although the population was not sampled during this time interval, it was assumed that the population was in a dormant state and were few in numbers and biomass. Prior field sampling the previous year indicated a standing crop of approximately 0.0001 g/m^2 during this time interval in an adjacent study plot (Raines, 1972). It was assumed that the insect standing crop of this study community would be similar and thus the state of the Insect Compartment was initially input as 0.0001 g/m^2 in the computer model.

Between 15 March and 29 October the standing crop of the Insect Compartment was estimated from periodic samples. Insect populations were sampled with a 40 cm diameter sweep net along a 100 m transect line. Insects were collected by taking 20 sweeps at 5 m intervals along the transect with the 40 cm diameter sweep net. An area of approximately 3 m^2 was covered for each sample. Eight transects were collected during each sampling date. The insects were placed in paper bags and returned to the laboratory. The insects were killed by "freezing" at approximately 6 C and then sorted into orders and families. Species were assigned to a compartment on the basis of gross morphology. After identification, samples were recombined, and dried at 80 C for 24 hours. They were then weighed on an analytical balance to determine total dry weight biomass. Standing crops of the Insect Compartment and Decomposer

Compartment were sampled for five of the dates litter samples were taken. Each of the five replicate litter samples were placed in a Berlese funnel for 72 hours for collection of invertebrates. The invertebrates were collected in vials containing a 70 per cent alcohol solution. After 72 hours the vials were removed and the insects were sorted into orders and families. After identification, samples were recombined, and dried at 60 C for 24 hours. They were then weighed on an analytical balance to determine total dry weight biomass and assigned to a compartment. Standing crops of the Insect Compartment and Decomposer Compartment appear in Table XXXIV for each of the sample dates.

In the computer program the state of the Insect Compartment was approximated for the sample dates identified. The insect standing crop increased between 15 March, peaking on 1 September. Increases in the standing crop were attributed to reproduction and changes in developmental stages of the insects. The standing crop of this compartment increased by $0.0144665 \text{ g/m}^2/\text{day}$ for a total of 2.4448385 g/m^2 for the 169 days between 15 March and 1 September. Between 1 September and the first killing frost on 29 October the standing crop decreased by $0.0414362 \text{ g/m}^2/\text{day}$ or a total of 2.4447415 g/m^2 for the 59 days between 1 September and 29 October. Decreases were attributable to insect emigration and temperature. Increases in the state of the compartment were attributed to reproduction and changes in the developmental states of the insects, and decreases to emigration and the effects of temperature on the population. Internal physiological processes were important in maintaining the population and were utilized in the computer program to mimic the fluctuation of the population.

TABLE XXXIV. Insect and Decomposer Compartment standing crops for eight replicate samples per sampling date and Berlese funnel samples per sampling date.

| Sampling Date 1973 | Standing Crop Dry Weight (g/m ²) | |
|-----------------------|---|-------------|
| | Insects | Decomposers |
| 01 January | *0.0001 | *0.0500 |
| 20 March | 0.0700 | 0.1600 |
| 21 April | 0.5100 | 0.8000 |
| 06 June | 1.2600 | 0.2600 |
| 20 June | 1.3500 | 0.2200 |
| 30 July | 1.9700 | 0.2200 |
| 31 August | 2.4600 | 0.4000 |
| 20 September | 1.9600 | 0.4000 |
| 01 October | 1.7200 | 0.4000 |
| 09 October | 0.8500 | 0.4000 |
| 01 November | *0.0001 | 0.4000 |
| 01 December | *0.0001 | *0.0500 |

*Estimate of standing crops without field measurement.

Inputs

Inputs to the Insect Compartment were attributed to grazing and predation on food sources identified as a live plant material, standing dead plant material, and decomposers, reproduction, and immigration.

Grazing on Live Plant Material by Insects (FIEP). Insect grazing on live plant material was discussed in the section on the Producer Compartment, Outputs.

Grazing on Standing Dead Plant Material by Insects (FIES). Insect grazing on standing dead plant material was discussed in the section on the Standing Dead Compartment, Outputs.

Predation on Decomposers by Insects (FIED). Herbivory was the predominant source of energy for the insect population. Although some predatory species were included in the Insect Compartment (Table V) it was assumed that little predation on decomposers occurred. Predation on decomposers was assigned a zero transfer rate for the study. The predatory function remains in the model for future use because it was believed that the function was a viable feature to the model.

Insect Reproduction (GIREP). Biomass increases within the insect population were attributed to reproduction. As new individuals were produced and developed through their life stages to adults, the standing crop of the compartment increased. The state of the Insect Compartment approximated the field measurements by utilizing reproduction to input biomass changes. Biomass changes through reproduction were input in the computer program as transfer rates which were dependent on the standing crop of the Insect Compartment between 15 March and 29 October. The

standing crop of the Insect Compartment reproduced at the rate of $0.0684107 \text{ g/m}^2/\text{day}$ for a total of 12.5875720 g/m^2 between 15 March and 29 October (Table XXXV). Reproduction was temperature dependent prior to 15 March and after 29 October and was not a factor in compartment functioning, and a zero transfer rate was assumed.

Insect Immigration (TIIN). Immigration of insects into the study community was not assumed to have a major effect upon the insect population. The sparse floral diversity of the vegetative community accounted for the low species diversity of the insect population. If the study community had had a more diverse floral composition, immigration may have played a more important role in the model. Immigration transfer rates were not employed within the computer program, thereby assuming a zero transfer rate. The function remains in the model for future use.

Outputs

Outflows of energy from the Insect Compartment were attributable to transfer functions identified as excretion, respiration for each of the food sources identified as live plant material, standing dead plant material, and decomposers, emigration, predation by birds, predation by mammals, and mortality.

Insect Excretion (EXI). Insect population excretion was discussed in the section on the Litter Compartment, Inputs.

Insect Respiration (RIR1, RIR2, RIR3). As previously discussed for bird and mammal respiration, insect metabolism was assumed to be a function of food intake from the various food sources throughout the year. Each category of food intake was assigned a respiratory transfer rate.

TABLE XXXV. Insect reproduction, growing season time units, per cent transfer rate, and average daily biomass inputs generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate | Average Daily Biomass Input (g/m ²) |
|-----------|----------------------|---------------------------|--|
| February | 14 | 0 | 0 |
| March | 15 | 0 | 0 |
| March | 16 | 1.34009 | 0.0014744 |
| April | 21 | 2.27968 | 0.0087327 |
| April | 09 | 3.62471 | 0.0220699 |
| May | 31 | 4.00938 | 0.0397248 |
| June | 15 | 4.62628 | 0.0600512 |
| June | 15 | 5.93291 | 0.0923573 |
| July | 31 | 5.67154 | 0.1060853 |
| August | 15 | 7.07734 | 0.1506004 |
| August | 16 | 7.23664 | 0.1703603 |
| September | 15 | 1.24100 | 0.0260637 |
| September | 15 | 0 | 0 |
| October | 29 | 0 | 0 |

Estimates of the respiratory transfer rate followed Risser (1972) in which the respiratory rate was calculated by the difference (Respiration= Food Intake-Egestion). Since egestion was 62 per cent of the food intake per food source, respiration was calculated to be 38 per cent of the food intake per food source. In order to mimic the responses of the insect population to growth in the community, the respiratory rate fluctuated per food source during the 19 time units of the year in the computer program. In this manner the insect population was responsive to growth and changes in insect life cycles to better mimic the real life phenomena (Table XXXVI).

Insect Emigration (TIOUOUT). Emigration of insects out of the study area was utilized as the primary means to decrease the standing crop of the Insect Compartment between 15 September and 29 October in the computer program. Undoubtedly insects emigrated from the study area, but the decrease in the state of the Insect Compartment was probably associated with temperature more than emigration. As temperatures approached 0 C, insect mortality probably reduced the standing crop of insects. However, in this model, emigration was assigned a transfer rate to allow the computer simulation to approximate the state of the Insect Compartment. The model should be refined to reflect the decreases associated with temperature to be assigned to mortality of insects. Between 15 September and 30 September the transfer rate for emigration (0.26773 per cent) decreased the insect population by 0.0039540 g/m²/day for a total of 0.05931 g/m² for the time period. Between 1 October and 29 October, the date of the first killing frost, the emigration transfer rate (4.12805 per cent) decreased the insect population by 0.0247132 g/m²/day, for a total of 0.7166828 g/m² for the time period.

TABLE XXXVI. Insect respiration per food source, yearly time units, per cent transfer rate, and average daily biomass outflow from the Insect Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate and Average Daily Biomass Outflow (g/m ²) | | | |
|-----------------------|----------------------|---|----------------------------------|-----------------------|-------------------------|
| | | Live Plant (RIR1) | Standing Dead Plant (RIR2) | Decomposers (RIR3) | For All Food Sources |
| January | 31 | 0 | 38.00000 0.0023631 | 0 | 0.0023631 |
| February | 14 | 0 | 38.00000 0.0019826 | 0 | 0.0019826 |
| February | 14 | 38.00000 0.0080949 | 38.00000 0.0017375 | 0 | 0.0098324 |
| March | 15 | 38.00000 0.0116363 | 38.00000 0.0014824 | 0 | 0.0131187 |
| March | 16 | 37.00000 0.0013298 | 37.00000 0.0011771 | 0 | 0.0125069 |
| April | 21 | 37.00000 0.0123154 | 37.00000 0.0008537 | 0 | 0.0131691 |
| April | 09 | 37.00000 0.0123154 | 37.00000 0.0006998 | 0 | 0.0130152 |
| May | 31 | 37.00000 0.0124139 | 37.00000 0.0007269 | 0 | 0.0131408 |
| June | 15 | 37.00000 0.0122168 | 37.00000 0.0007426 | 0 | 0.0129594 |
| June | 15 | 37.00000 0.0122168 | 37.00000 0.0007555 | 0 | 0.0129723 |
| July | 31 | 37.00000 0.0111331 | 37.00000 0.0007732 | 0 | 0.0119063 |
| August | 15 | 37.00000 0.0100493 | 37.00000 0.0007904 | 0 | 0.0108397 |
| August | 16 | 37.00000 0.0100493 | 37.00000 0.0008019 | 0 | 0.0108512 |
| September | 15 | 37.00000 0.0082759 | 37.00000 0.0008151 | 0 | 0.0090910 |
| September | 15 | 38.00000 0.0084996 | 38.00000 0.0008731 | 0 | 0.0093727 |
| October | 29 | 38.00000 0.0078925 | 38.00000 0.0016854 | 0 | 0.0095779 |
| October - November | 17 | 0 | 38.00000 0.0022346 | 0 | 0.0022346 |
| November | 15 | 0 | 38.00000 0.0019345 | 0 | 0.0019345 |
| December | 31 | 0 | 38.00000 0.0017451 | 0 | 0.0017451 |

Predation by Birds on Insects (FBEI). Predation by the bird population on the standing crop of the Insect Compartment was discussed in the section on the Bird Compartment, Inputs.

Predation by Mammals on Insects (FMEI). Predation by the mammal population on the standing crop of the Insect Compartment was discussed in the section on the Mammal Compartment, Inputs.

Insect Mortality (DIMOR). Insect mortality was discussed in the section on the Litter Compartment, Inputs.

DECOMPOSERS
(XD, 0.05 g/m²)

Invertebrate sampling has been discussed in the Insect Compartment. Those insects that derived their energy from their activity in the debris were placed in the Decomposer Compartment (Table VI). The initial state of the Decomposer Compartment was taken from a previous year sampling in an adjacent study area where the standing crop of the decomposers approximated 0.05 g/m² (Raines, 1972). It was assumed that the decomposer standing crop of this study community would be similar and thus the state of the Decomposer Compartment was initially input as 0.05 g/m² in the computer program. Standing crops of the decomposers, as sampled in the field, appear in Table XXXIV for each of the sample dates.

The trend of the decomposers followed a seasonal variance. Their standing crop was low during the winter months. In the early spring their standing crop increased as well as their activity peaking on 21 April. Environmental conditions probably decreased their standing crop to a relatively stable population during the summer. In the fall the population again increased to a relatively steady state, again

probably due to more favorable environmental conditions. With the first killing frost on 29 October, the population began to decrease to approximate its initial state.

In the computer program, the field data collected were approximated by allowing the decomposer population to fluctuate on a seasonal basis. The Decomposer Compartment remained relatively constant at 0.05 g/m^2 until 15 March. Between 15 March and 15 April the population increased from 0.05 g/m^2 to 0.7956793 g/m^2 , and then decreased to 0.2210361 g/m^2 on 15 June simulating field measurements. The population remained relatively constant until 15 August when population increased to a steady state on 1 September. The decomposers began decreasing on 15 November until they approximated the initial state of the compartment on 1 December, thereby completing the seasonal variance programmed.

Increases and decreases in the state of the Decomposer Compartment were assumed to be dependent upon environmental factors and not physiological processes. After reviewing the data, reproduction probably accounted for the increases and mortality the decreases. Environmental conditions seemed to control these processes. However, in this model, increases and decreases of the standing crop of decomposers were manipulated by the respiratory rate and organic transfer function, and not reproduction and mortality.

Inputs

Inputs to the Decomposer Compartment were attributed to reproduction and a transfer of litter to the decomposers for grazing and organic breakdown.

Decomposer Reproduction (GDREP). It was assumed that decomposer reproduction would equal decomposer mortality and was therefore assigned a zero rate of transfer. This was probably a misconception of the programmer as it related to decomposers. Increases in the standing crop of the decomposers should have been attributed to reproduction as it had been in the Insect Compartment.

Transfer of Litter to the Decomposers for Grazing and Organic Breakdown (FDM). The transfer of litter to the decomposers for grazing and organic breakdown was discussed in the section on the Litter Compartment, Outputs.

Outputs

Outflows of energy from the Decomposer Compartment were attributable to transfer functions identified as excretion, mortality, predation by the bird, mammal, and insect populations, respiration, and contributions to the soil organic matter.

Decomposer Excretion (EXD). Decomposer excretion was discussed in the section on the Litter Compartment, Inputs.

Decomposer Mortality (DDMOR). Decomposer mortality was discussed in the section on the Litter Compartment, Inputs.

Predation by Birds, Mammals, and Insects on Decomposers (FBED, FMED, FIED). Predation on decomposers by birds, mammals, and insects were discussed in the sections on the Bird, Mammal, and Insect Compartments, Inputs.

Decomposer Respiration (RDR1). Increases and decreases of the standing crop of decomposers were manipulated by the respiratory rate and the organic transfer rate. Neither an estimated nor a literature value for

respiration were utilized in this model. The rate assigned to respiration was dependent upon the amount of energy flowing into the compartment. The respiratory rate was calculated to be approximately 50 per cent of the energy entering the compartment per unit of time. In order for the standing crop to fluctuate as field measurements indicated, the rate was varied with the organic transfer rate to be greater than or less than the total energy entering the compartment. This function was utilized to also mimic the loss of litter from the Litter Compartment, as measured in the study community. Litter was being transferred to the decomposers for breakdown and return to the soil organic matter. To account for this disappearance, the respiratory and organic transfer rates were utilized in conjunction with the biomass estimates for the decomposer standing crop to simulate the state of the Decomposer Compartment per unit of time as well as the disappearance of litter from the community (Table XXXVII). The respiratory rate accounted for the transfer of 1.1419731 g/m²/day or 328.88828 g/m²/year of matter from the system.

Matter Breakdown Transferred to the Soil Organic Matter (TSOM). As previously discussed for the respiratory rate, the transfer rate of matter to soil organic matter by action of the decomposers was manipulated to simulate the state of the Decomposer Compartment per unit of time as well as the disappearance of litter from the community (Table XXXVIII). The matter transfer rate was calculated to be approximately 50 per cent of the energy entering the compartment per unit of time. The rate was varied to fluctuate as field measurements indicated to be greater than or less than the total amount of energy entering the compartment. The Decomposer Compartment standing crop was simulated and the loss of litter from the Litter Compartment was returned to the soil in the form of organic matter.

TABLE XXXVII. Decomposer respiration, yearly time units, per cent transfer rate, and average daily biomass outflow from the Decomposer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate (RIR1) | Average Daily Biomass Output (g/m ²) |
|------------------|----------------------|-------------------------------------|--|
| January | 31 | 0.40789 | 1.1613836 |
| February | 14 | 0.49959 | 1.1682538 |
| February | 14 | 0.58084 | 1.1665533 |
| March | 15 | 0.70095 | 1.1666611 |
| March | 16 | 0.88791 | 1.1498594 |
| April | 21 | 1.31881 | 1.1114145 |
| April | 09 | 0.01313 | 0.0084001 |
| May | 31 | 0.00516 | 0.0061340 |
| June | 15 | 0.00041 | 0.0016492 |
| June | 15 | 0.48539 | 2.8391924 |
| July | 31 | 0.36412 | 1.7677297 |
| August | 15 | 0.37486 | 1.5356882 |
| August | 16 | 0.56281 | 1.9896584 |
| September | 15 | 0.82493 | 2.3504110 |
| September | 15 | 0.36363 | 0.8654733 |
| October | 29 | 0 | 0 |
| October-November | 17 | 0 | 0 |
| November | 15 | 0.00401 | 0.0116426 |
| December | 31 | 0 | 0 |

TABLE XXXVIII. Decomposer breakdown to soil organic matter, yearly time units, per cent transfer rate, and average daily biomass outflow from the Decomposer Compartment generated by the computer program.

| Month | Time Unit in Days | Per Cent Transfer Rate (TSOM) | Average Daily Biomass Output (g/m ²) |
|------------------|----------------------|-------------------------------------|--|
| January | 31 | 0.40790 | 1.1614120 |
| February | 14 | 0.49959 | 1.1682538 |
| February | 14 | 0.58085 | 1.1665734 |
| March | 15 | 0.70096 | 1.1666778 |
| March | 16 | 0.88791 | 1.1498594 |
| April | 21 | 1.31881 | 1.1114145 |
| April | 09 | 0.01314 | 0.0084065 |
| May | 31 | 0.00516 | 0.0061340 |
| June | 15 | 0.00042 | 0.0016984 |
| June | 15 | 0.48540 | 2.8392509 |
| July | 31 | 0.36413 | 1.7677782 |
| August | 15 | 0.37486 | 1.5356882 |
| August | 16 | 0.56282 | 1.9896937 |
| September | 15 | 0.82493 | 2.3504110 |
| September | 15 | 0.36363 | 0.8654733 |
| October | 29 | 0 | 0 |
| October-November | 17 | 0 | 0 |
| November | 15 | 0.00402 | 0.0116716 |
| December | 31 | 0 | 0 |

This transfer function accounted for the return of 1.1419921 g/m²/day or 328.89373 g/m²/year of matter to the soil organic matter.

SUMMARY

Systems analysis techniques were utilized in the derivation and operation of a computer model of a grassland community undergoing secondary succession, and in predicting community structure through time during the period from January 1, 1973, through December 31, 1973, on the Ross Natural History Reservation, Lyon County, Kansas.

A seven-compartment model was designed to simulate the structure and controlling ecological processes and interactions of the study community. A series of mathematical functions related to biological or environmental phenomena were developed to mimic the quantified structure and controlling ecological processes and interactions of the study community. The computer program was written, utilizing the mathematical functions, to simulate the redistribution of matter (biomass) through the system. Finally, the computer model was tested, utilizing data values derived from separate studies or abstracted from the literature, and results utilized to make predictions concerning community structure through time.

The computer simulation was successful in approximating the structure of the study community by manipulating the controlling ecological processes and interactions of the community through time as related to biological or environmental phenomena. Community structure was expressed as biomass per unit of measure per day ($\text{g/m}^2/\text{day}$) for live plant material, standing dead plant material, litter, birds, mammals, insects, and decomposers.

A copy of the FORTRAN program of the model was placed on file in the Division of Biology of Emporia State University.

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APPENDIX

APPENDIX I

THE COMPUTER PROGRAM LISTING

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C GRASSLAND MODEL FOR 7 COMPARTMENTS-RAINFS-5/7/74
C TIME FUNCTIONS FOR 365 DAYS AND SUBROUTINE
C SET TIME TO ZERO
0001      T=0.
C INITIALIZE COMPARTMENT SIZE AT TIME ZERO
0002      XPROD = 0.0
0003      XSTAD = 209.27253
0004      XLITT = 323.40664
0005      XDFOO = 0.05
0006      XB = 0.018
0007      XM = 0.004
0008      XI = 0.0001
C WRITE TABLE HEADINGS FOR DAILY PRINT OUT
0009      WRITE (6,7)
0010      7 FORMAT (2X,3HDAY,3X,8HPRODUCER,6X,9HSTD. DEAD,7X,6HLITTER,7X,
110HDECOMPOSER,5X,5HBIRDS,9X,7HMAMMALS,7X,7HINSECTS,7X,3HGGP)
C READ DATA CARDS FOR VARYING COMPARTMENTAL FUNCTIONS IN DO LOOP
0011      DO 85 J =1,19
0012      READ (5,1) XSE,GPG,RPROD,TPTR,DPROD,GSPROD,FBEP,FMEP,FIFP,NDA
0013      READ (5,5) RSTAD,TSTIT,FBES,FMES,FIES,RBR3,RBR4,RBR5,NDA
0014      READ (5,5) RLITT,FOM,RDR1,TSOM,TBIN,TBOUT,TLITIN,RIR3,NDA
0015      READ (5,5) EXO,DMOR,GDREP,FBED,FMED,FIED,RMR3,RMR4,NDA
0016      READ (5,4) GBREP,RBR1,RBR2,EXB,DBMOR,FBEM,FBFI,NDA
0017      READ (5,5) GMREP,RMR1,RMR2,TMIN,TMOUT,EXM,DMOR,FMEI,NDA
0018      READ (5,5) GIPFP,RIR1,RIR2,TIIN,TIOUT,EXI,DI MOR,PCE,NDA
0019      1 FORMAT (2F3.0,7F9.7,12)
0020      4 FORMAT (7F9.7,12)
0021      5 FORMAT (8F9.7,12)
C ESTABLISH DO LOOP FOR CALCULATIONS
0022      DO 85 I =1,NDA
C INCREMENT TIME
0023      T=T+1.
C TIME PERIODS FOR CALCULATIONS
0024      IF (T-45.) 20,20,201
0025      201 IF (T-302.) 21,21,202
0026      202 IF (T-365.) 20,20,206
C CALCULATE COMPARTMENT SIZE FOR TIME PERIODS
0027      20 NXPROD = GPG+GSPROD*XSTAD-((RPROD+TPTR+DPROD+FBEP+FMEP+FIFP)*GPG)
0028      20 XSTAD = DPROD*GPG-((RSTAD+TSTIT+GSPROD+FBES+FMES+FIES)*XSTAD)
0029      20 XLITT = (TSTIT)*XSTAD+(EXB*(FBEP*GPG))+(EXB*(FBES*XSTAD))+(EXB*(FB
1FM*XM))+(EXB*(FBFI*XI))+(EXB*(FBED*XDECO))+(DMOR*XB)+(EXM*(FMEP*G
2PG))+(EXM*(FMES*XSTAD))+(EXM*(FMEI*XI))+(EXM*(FMED*XDECO))+(DMOR*
3XM)+(EXI*(FIFP*GPG))+(EXI*(FIES*XSTAD))+(EXI*(FIED*XDECO))+(DI MOR*
4XI)+(EXO*(FOM*XLITT))+(DMOR*XDECO)+TLITIN)-((FOM+RLITT)*XLITT)

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0030      DXDECO = (FDM*XLITT+GDREP*XDECO)-((FBFD+FMED+FIED)*XDECO+(EXD*(FDM
1*XLITT)+(DIMOR*XDECO)+(RMR1+TSM)*XLITT)
0031      DXXB = (FBFP*GPG+FBFS*XSTAD+FBFM*XM+FBFI*XI+FBED*XDECO+GBREP*XB+TB
1IN)-((EXB*(FBFP*GPG))+EXB*(FBES*XSTAD))+EXB*(FBEM*XM))+EXB*(FBE
2I*XI))+EXB*(FBFD*XDECO))+((DBMOR*XB)+(RBR1*(FBFP*GPG))+RBR2*(FBES
3*XSTAD))+RBR3*(FBEM*XM))+RBR4*(FBFI*XI))+RBR5*(FBED*XDECO))+TBO
4UT)
0032      DXXM = (FMFP*GPG+FMES*XSTAD+FMEI*XI+FMED*XDECO+GMREP*XM+TMIN)-((EX
1M*(FMFP*GPG))+EXM*(FMES*XSTAD))+EXM*(FMEI*XI))+EXM*(FMED*XDECO)
2)+(DIMOR*XM)+(RMR1*(FMFP*GPG))+RMR2*(FMES*XSTAD))+RMR3*(FMEI*XI)
3)+(RMR4*(FMED*XDECO))+FBEM*XM)+TMOUT)
0033      DXXI = (FIEP*GPG+FIES*XSTAD+FIED*XDECO+GIREP+TIIN)-((EXI*(FIEP*GPG
1))+EXI*(FIES*XSTAD))+EXI*(FIED*XDECO))+((DIMOR*XI)+(RIR1*(FIEP*GP
2G))+RIR2*(FIES*XSTAD))+RIR3*(FIED*XDECO))+((FBEI+FMEI)*XI+TIOUT)

0034      GO TO 31
0035      21 CONTINUE
C CALL SUBROUTINE TO CALCULATE GROSS PRODUCTION FROM LIGHT ENTERING
0036      CALL PHOTO (XSE,GPG,PCE)
C CALCULATION SET EQUATIONS FOR TIME PERIODS
0037      DXPROD = GPG+GSPROD*XSTAD-((RPROD+TPTR+OPROD+FBFP+FMED+FIED)*GPG)
0038      DXSTAD = OPROD*GPG-((RSTAD+TSTIT+GSPROD+FBFS+FMES+FIES)*XSTAD)
0039      DXLITT = (TSTIT*XSTAD+(EXB*(FBFP*GPG))+EXB*(FBES*XSTAD))+EXB*(FB
1FM*XM))+EXB*(FBFI*XI))+EXB*(FBFD*XDECO))+((DBMOR*XB)+(EXM*(FMFP*G
2PG))+EXM*(FMES*XSTAD))+EXM*(FMEI*XI))+EXM*(FMED*XDECO))+((DIMOR*
3XM))+EXI*(FIEP*GPG))+EXI*(FIES*XSTAD))+EXI*(FIED*XDECO))+((DIMOR*
4XI)+(EXD*(FDM*XLITT))+((DIMOR*XDECO)+TLITIN)-((FDM+RLITT)*XLITT)
0040      DXDECO = (FDM*XLITT+GDREP*XDECO)-((FBED+FMED+FIED)*XDECO+(EXD*(FDM
1*XLITT)+(DIMOR*XDECO)+(RMR1+TSM)*XLITT)
0041      DXXB = (FBFP*GPG+FBES*XSTAD+FBFM*XM+FBFI*XI+FBED*XDECO+GBREP*XB+TB
1IN)-((EXB*(FBFP*GPG))+EXB*(FBES*XSTAD))+EXB*(FBEM*XM))+EXB*(FBE
2I*XI))+EXB*(FBFD*XDECO))+((DBMOR*XB)+(RBR1*(FBFP*GPG))+RBR2*(FBES
3*XSTAD))+RBR3*(FBEM*XM))+RBR4*(FBFI*XI))+RBR5*(FBED*XDECO))+TBO
4UT)
0042      DXXM = (FMFP*GPG+FMES*XSTAD+FMEI*XI+FMED*XDECO+GMREP*XM+TMIN)-((EX
1M*(FMFP*GPG))+EXM*(FMES*XSTAD))+EXM*(FMEI*XI))+EXM*(FMED*XDECO)
2)+(DIMOR*XM)+(RMR1*(FMFP*GPG))+RMR2*(FMES*XSTAD))+RMR3*(FMEI*XI)
3)+(RMR4*(FMED*XDECO))+FBEM*XM)+TMOUT)
0043      DXXI = (FIEP*GPG+FIES*XSTAD+FIED*XDECO+GIREP+TIIN)-((EXI*(FIEP*GPG
1))+EXI*(FIES*XSTAD))+EXI*(FIED*XDECO))+((DIMOR*XI)+(RIR1*(FIEP*GP
2G))+RIR2*(FIES*XSTAD))+RIR3*(FIED*XDECO))+((FBEI+FMEI)*XI+TIOUT)
C CALCULATE COMPARTMENT SIZE FOR TIME PERIODS
0044      31 XPROD = XPROD+DXPROD
0045      XSTAD = XSTAD+DXSTAD
0046      XLITT = XLITT+DXLITT
0047      XDECO = XDECO+DXDECO

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0048      XB = XB+DXXB
0049      XM = XM+DXXM
0050      XI = XI+DXXI
          C  WRITE COMPARTMENT SIZE FROM PREVIOUS CALCULATIONS
0051      WRITE (6,9) T,XPRDD,XSTAD,XLITT,XDFCO,XR,XM,XI,GPG
0052      8 FORMAT (F5.0,8(2X,F12.7))
0053      85 CONTINUE
0054      206 STOP
0055      END

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          C  THIS SUBPROGRAM BELONGS TO RICHARD R. RAINES
          C  GROSS PRODUCTION CALCULATION FROM INCOMING LIGHT
          C  READ DATA CARDS FROM VARIABLES IN MAIN PROGRAM FOR GPG
0001      SUBROUTINE PHOTO (XSE,GPG,PCE)
0002      T=0.
0003      GTOTXL = 0.0
          C  DO LOOP TP CALCULATE LIGHT ENTERING (KCAL/M2/24 HOUR PERIOD
0004      DO 15 I =1,24
0005      T =T+1.
          C  TIME PERIODS FOR CALCULATIONS PER DAY
0006      IF (T.LT.6.) GO TO 13
0007      IF (T.GE.6..AND.T.LE.18.) GO TO 14
0008      IF (T.GT.18.) GO TO 13
          C  CALCULATION FOR PHOTO PERIOD
0009      14 XLIGHT = XSE*SIN(1.5708*(1.-ABS((T-12.)/6.0)))
          C  CALCULATION TO TOTAL THE LIGHT ENTERING/DAY
0010      GTOTXL = GTOTXL+XLIGHT
          C  CONVERTS LIGHT IN PHOTOSYNTHESIS TO G/M2/DAY GROSS PRODUCTION
0011      GPG = ((GTOTXL/673.0)*(180.0))*PCE
0012      GO TO 15
0013      13 XLIGHT =0.0
0014      15 CONTINUE
          C  RETURNS TO MAIN PROGRAM WITH VALUE FOR GPG CALCULATED
0015      RETURN
0016      END

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APPENDIX II

THE NUMERICAL SOLUTIONS TO THE MODEL

| DAY | PRODUCER | STD. DEAN | LITTER | DECOMPOSER | BIRDS | MAMMALS | INSECTS | GPG |
|-----|-----------|--------------|--------------|------------|-----------|-----------|-----------|------------|
| 1. | 0.0 | 237.7407634 | 320.7497559 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 2. | 0.0 | 206.2722301 | 318.1162109 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 3. | 0.0 | 204.7109154 | 315.5056152 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 4. | 0.0 | 203.2124491 | 312.9179699 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 5. | 0.0 | 201.7250319 | 310.3527932 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 6. | 0.0 | 200.2485352 | 307.8099145 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 7. | 0.0 | 193.7323369 | 305.2990625 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 8. | 0.0 | 197.3279656 | 302.7902332 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 9. | 0.0 | 195.8935449 | 300.3132324 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 10. | 0.0 | 194.4697933 | 297.8576560 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 11. | 0.0 | 193.0461099 | 295.4233399 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 12. | 0.0 | 191.6136780 | 293.0100000 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 13. | 0.0 | 190.2111316 | 290.6176759 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 14. | 0.0 | 188.8133392 | 288.2463934 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 15. | 0.0 | 187.4353996 | 285.8950195 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 16. | 0.0 | 186.0647567 | 283.5642090 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 17. | 0.0 | 184.7033667 | 281.2536621 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 18. | 0.0 | 183.3511595 | 279.9624906 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 19. | 0.0 | 182.0091249 | 278.6919945 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 20. | 0.0 | 180.6763257 | 277.4406739 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 21. | 0.0 | 179.3544769 | 276.2087402 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 22. | 0.0 | 178.0417073 | 274.9963933 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 23. | 0.0 | 176.7395406 | 273.8026902 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 24. | 0.0 | 175.4469159 | 272.6276855 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 25. | 0.0 | 174.1607666 | 271.4716797 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 26. | 0.0 | 172.8863168 | 270.3339844 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 27. | 0.0 | 171.6205092 | 269.2148839 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 28. | 0.0 | 170.3644257 | 268.1137675 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 29. | 0.0 | 169.1174622 | 267.0309229 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 30. | 0.0 | 167.8792734 | 265.9657135 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 31. | 0.0 | 166.6509331 | 264.9182739 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 32. | 0.0 | 165.4303335 | 263.8900173 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 33. | 0.0 | 164.21607515 | 262.89069051 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 34. | 0.0 | 162.9951147 | 261.9161199 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 35. | 0.0 | 161.7813455 | 261.0028534 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 36. | 0.0 | 159.5717799 | 259.5902863 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 37. | 0.0 | 157.3727091 | 258.2036133 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 38. | 0.0 | 155.1845845 | 256.8425273 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 39. | 0.0 | 153.0126063 | 255.5067444 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 40. | 0.0 | 150.8506936 | 254.1959534 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 41. | 0.0 | 152.6035927 | 252.9099815 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 42. | 0.0 | 151.2625427 | 251.6482733 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 43. | 0.0 | 149.9361267 | 250.4107056 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 44. | 0.0 | 148.6213531 | 249.1970527 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 45. | 0.0 | 147.3191070 | 248.0069733 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 0.0 |
| 46. | 0.6515473 | 145.8454235 | 246.8411664 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 47. | 1.2924613 | 144.3974317 | 245.7071436 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 48. | 1.9437122 | 142.9641071 | 244.6064623 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 49. | 2.5943992 | 141.5515172 | 243.5272259 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 50. | 3.2215376 | 140.1305075 | 242.4691577 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 51. | 3.8551626 | 138.6999069 | 241.4200409 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 52. | 4.4853096 | 137.3134766 | 240.37990199 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 53. | 5.1120129 | 135.9409112 | 239.3409580 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |
| 54. | 5.7353177 | 134.5819797 | 238.3030269 | 0.0500000 | 0.0190000 | 0.0040000 | 0.0001000 | 12.6281462 |

| | | | | | | | | |
|------|------------|-------------|-------------|-----------|-----------|-----------|-----------|------------|
| 55. | 6.3552275 | 133.2365245 | 193.9292450 | 0.0500133 | 0.0190000 | 0.0060002 | 0.0001002 | 12.6291462 |
| 56. | 6.9714065 | 131.9366173 | 191.6424309 | 0.0500133 | 0.0190000 | 0.0060002 | 0.0001003 | 12.6291462 |
| 57. | 7.5957732 | 130.5964291 | 190.4662181 | 0.0500133 | 0.0190000 | 0.0060002 | 0.0001003 | 12.6291462 |
| 58. | 8.1950750 | 129.2976244 | 189.2730255 | 0.0500133 | 0.0190000 | 0.0060002 | 0.0001003 | 12.6291462 |
| 59. | 8.8919333 | 127.9992560 | 188.1089220 | 0.0500133 | 0.0190000 | 0.0060002 | 0.0001003 | 12.6291462 |
| 60. | 9.7364939 | 126.4974974 | 187.4929352 | 0.0500133 | 0.0190000 | 0.0060002 | 0.0001003 | 18.1529236 |
| 61. | 10.6637940 | 125.0763330 | 187.9169769 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 62. | 11.5882530 | 123.5385132 | 177.3893711 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 63. | 12.5096343 | 122.0897049 | 174.8924615 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 64. | 13.4244041 | 120.6592794 | 172.4226227 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 65. | 14.3361931 | 119.2634540 | 170.0092299 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 66. | 15.2438522 | 117.8452149 | 167.6146693 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 67. | 16.1476457 | 116.4433636 | 165.2653351 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 68. | 17.0467971 | 115.0977173 | 162.9516649 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001003 | 18.1529236 |
| 69. | 17.9425912 | 113.7480927 | 160.6730042 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001004 | 18.1529236 |
| 70. | 18.8362245 | 112.4142914 | 159.4289483 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001004 | 18.1529236 |
| 71. | 19.7219940 | 111.0961304 | 156.2186127 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001004 | 18.1529236 |
| 72. | 20.6059760 | 109.7936245 | 154.0417329 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001004 | 18.1529236 |
| 73. | 21.4897077 | 109.5351967 | 151.9976993 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001004 | 18.1529236 |
| 74. | 22.3623657 | 107.2336578 | 149.7852344 | 0.0500133 | 0.0190000 | 0.0060003 | 0.0001004 | 18.1529236 |
| 75. | 23.3245522 | 105.6064070 | 147.0690309 | 0.0729311 | 0.0190000 | 0.0060003 | 0.0139632 | 18.1529236 |
| 76. | 24.2412415 | 104.1919916 | 144.4062195 | 0.0954330 | 0.0190159 | 0.0060126 | 0.0275855 | 18.1529236 |
| 77. | 25.1725311 | 102.6933495 | 141.7963409 | 0.1175259 | 0.0190237 | 0.0060197 | 0.0413274 | 18.1529236 |
| 78. | 26.0936955 | 101.2171733 | 139.2392507 | 0.1392219 | 0.0190314 | 0.0060267 | 0.0550697 | 18.1529236 |
| 79. | 27.0192139 | 99.7465559 | 136.7309197 | 0.1605251 | 0.0190391 | 0.0060307 | 0.0698095 | 18.1529236 |
| 80. | 27.9367334 | 98.3367310 | 134.2729727 | 0.1814449 | 0.0190467 | 0.0060366 | 0.0825498 | 18.1529236 |
| 81. | 28.8451996 | 96.9273997 | 131.8636475 | 0.2019999 | 0.0190542 | 0.0060425 | 0.0962996 | 18.1529236 |
| 82. | 29.7506124 | 95.5382538 | 129.5013005 | 0.2221530 | 0.0190616 | 0.0060494 | 0.1109290 | 18.1529236 |
| 83. | 30.6510650 | 94.1690216 | 127.1864014 | 0.2419775 | 0.0190690 | 0.0060562 | 0.1237630 | 18.1529236 |
| 84. | 31.5465309 | 92.9196122 | 124.9164734 | 0.2616372 | 0.0190763 | 0.0060630 | 0.1375064 | 18.1529236 |
| 85. | 32.4373232 | 91.4391510 | 122.6910640 | 0.2805499 | 0.0190836 | 0.0060697 | 0.1512465 | 18.1529236 |
| 86. | 33.3234170 | 90.1773440 | 120.5091553 | 0.2993219 | 0.0190909 | 0.0060764 | 0.1649820 | 18.1529236 |
| 87. | 34.2047474 | 89.0855439 | 119.3693893 | 0.3177622 | 0.0190979 | 0.0060771 | 0.1797192 | 18.1529236 |
| 88. | 35.0814667 | 87.8116639 | 118.2723399 | 0.3358705 | 0.0191049 | 0.0060827 | 0.1924559 | 18.1529236 |
| 89. | 35.9536639 | 86.3660333 | 116.2156047 | 0.3536703 | 0.0191119 | 0.0060883 | 0.2061921 | 18.1529236 |
| 90. | 36.8213571 | 85.1183229 | 114.1993373 | 0.3711355 | 0.0191199 | 0.0060939 | 0.2199290 | 18.1529236 |
| 91. | 37.6737733 | 83.6663564 | 109.1288452 | 0.3973225 | 0.0191237 | 0.0060993 | 0.2374553 | 19.7314453 |
| 92. | 38.9122009 | 81.9463745 | 106.1535797 | 0.4227493 | 0.0191297 | 0.0061047 | 0.2545344 | 19.7314453 |
| 93. | 39.9659078 | 80.2573430 | 103.2698364 | 0.4475049 | 0.0191339 | 0.0061102 | 0.2711751 | 19.7314453 |
| 94. | 40.9717132 | 79.7071363 | 100.4765331 | 0.4715979 | 0.0191371 | 0.0061157 | 0.2873824 | 19.7314453 |
| 95. | 41.9991970 | 77.1726625 | 97.7667095 | 0.4950397 | 0.0191445 | 0.0061213 | 0.3031991 | 19.7314453 |
| 96. | 43.0317986 | 75.6744352 | 95.1374969 | 0.5179192 | 0.0191500 | 0.0061269 | 0.3185819 | 19.7314453 |
| 97. | 44.0704953 | 74.2060952 | 92.5901337 | 0.5407045 | 0.0191556 | 0.0061326 | 0.3335810 | 19.7314453 |
| 98. | 45.0014954 | 72.7659396 | 90.1199493 | 0.5615956 | 0.0191614 | 0.0061383 | 0.3491956 | 19.7314453 |
| 99. | 45.9911904 | 71.3535461 | 87.7243652 | 0.5826128 | 0.0191672 | 0.0061441 | 0.3624356 | 19.7314453 |
| 100. | 46.9760295 | 69.9486594 | 85.4009094 | 0.6030710 | 0.0191732 | 0.0061498 | 0.3763177 | 19.7314453 |
| 101. | 47.9501901 | 68.6196547 | 83.1471863 | 0.6229875 | 0.0191792 | 0.0061557 | 0.3909830 | 19.7314453 |
| 102. | 48.9137673 | 67.2790720 | 80.9609070 | 0.6423776 | 0.0191854 | 0.0061615 | 0.4030229 | 19.7314453 |
| 103. | 49.8829123 | 65.9732756 | 78.8399285 | 0.6612595 | 0.0191917 | 0.0061674 | 0.4158390 | 19.7314453 |
| 104. | 50.8327527 | 64.6927620 | 76.7914146 | 0.6796443 | 0.0191979 | 0.0061734 | 0.4284341 | 19.7314453 |
| 105. | 51.7903920 | 63.4371339 | 74.7847920 | 0.6975505 | 0.0192045 | 0.0061793 | 0.4405297 | 19.7314453 |
| 106. | 52.7369549 | 62.2759221 | 72.8667712 | 0.7149904 | 0.0192111 | 0.0061853 | 0.4526029 | 19.7314453 |
| 107. | 53.6735637 | 60.9935657 | 70.9659051 | 0.7319792 | 0.0192177 | 0.0061914 | 0.4636917 | 19.7314453 |
| 108. | 54.6163395 | 59.8146515 | 69.1400604 | 0.7485292 | 0.0192244 | 0.0061974 | 0.4752440 | 19.7314453 |
| 109. | 55.5333962 | 58.6537170 | 67.3677216 | 0.7646520 | 0.0192313 | 0.0062035 | 0.4862273 | 19.7314453 |

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| 110. | 54.4543197 | 57.8151148 | 65.6670642 | 0.7193519 | 0.7192392 | 0.0062795 | 0.4949290 | 19.7314453 |
| 111. | 57.3707423 | 56.3990173 | 63.0764097 | 0.7956773 | 0.0192451 | 0.0062157 | 0.5073564 | 19.7314453 |
| 112. | 60.1178236 | 56.4895121 | 63.0761963 | 0.7798637 | 0.0193714 | 0.0067564 | 0.5309668 | 19.7314453 |
| 113. | 62.8649139 | 56.5777877 | 63.0761505 | 0.7529571 | 0.0193502 | 0.0052963 | 0.5635727 | 19.7314453 |
| 114. | 65.6119795 | 56.6674652 | 63.0762573 | 0.7452506 | 0.0194214 | 0.0059356 | 0.5743897 | 19.7314453 |
| 115. | 68.3579351 | 56.7564327 | 63.0763220 | 0.7294449 | 0.0194349 | 0.0063781 | 0.5922329 | 19.7314453 |
| 116. | 71.1041797 | 56.8464050 | 63.0763952 | 0.7115371 | 0.0194507 | 0.0070219 | 0.61795170 | 19.7314453 |
| 117. | 73.8532562 | 56.9354673 | 63.0765391 | 0.6949395 | 0.0194698 | 0.0074670 | 0.6402562 | 19.7314453 |
| 118. | 76.6003618 | 57.0253224 | 63.0782719 | 0.6790235 | 0.0194890 | 0.0080132 | 0.6606665 | 19.7314453 |
| 119. | 79.3474276 | 57.1147765 | 63.0791417 | 0.6612156 | 0.0195061 | 0.0085605 | 0.6801555 | 19.7314453 |
| 120. | 82.0945129 | 57.2042216 | 63.0801636 | 0.6444992 | 0.0195258 | 0.0091090 | 0.6993424 | 19.7314453 |
| 121. | 84.8435712 | 57.2935977 | 67.4615173 | 0.6374995 | 0.0199660 | 0.0094783 | 0.7219975 | 19.992975 |
| 122. | 87.6324274 | 57.3845862 | 70.2536133 | 0.6309664 | 0.0199949 | 0.0099449 | 0.7439555 | 19.992975 |
| 123. | 90.4216375 | 57.4799539 | 74.4558105 | 0.6235229 | 0.0199257 | 0.0102208 | 0.7652613 | 19.992975 |
| 124. | 93.1774658 | 57.5845104 | 77.0674998 | 0.6159331 | 0.0199571 | 0.0105939 | 0.7961191 | 19.992975 |
| 125. | 95.9199761 | 57.6911031 | 81.4881136 | 0.6079913 | 0.0199896 | 0.0109682 | 0.8264430 | 19.992975 |
| 126. | 98.7033623 | 58.1106431 | 85.0171204 | 0.5993922 | 0.0199228 | 0.0113438 | 0.8524665 | 19.992975 |
| 127. | 101.4779235 | 58.2317317 | 88.5540161 | 0.5906094 | 0.0199566 | 0.0117204 | 0.8745433 | 19.992975 |
| 128. | 104.2469738 | 58.3441266 | 92.0983429 | 0.5814494 | 0.0199912 | 0.0120982 | 0.8963661 | 19.992975 |
| 129. | 107.0167370 | 58.4513702 | 95.6496429 | 0.5719659 | 0.0199265 | 0.0124770 | 0.91826675 | 19.992975 |
| 130. | 109.7950952 | 58.5515900 | 99.2075043 | 0.5622960 | 0.0199624 | 0.0128569 | 0.9395200 | 19.992975 |
| 131. | 112.5541536 | 58.6457520 | 102.7715302 | 0.5519557 | 0.0199991 | 0.0132379 | 0.960154 | 19.992975 |
| 132. | 115.3232117 | 58.7342177 | 106.3413696 | 0.5412497 | 0.0199233 | 0.0136198 | 0.9348656 | 19.992975 |
| 133. | 118.0922699 | 58.8173929 | 109.9166565 | 0.5302752 | 0.0199742 | 0.0140027 | 0.9513919 | 19.992975 |
| 134. | 120.8613231 | 58.9055078 | 113.4977971 | 0.5193119 | 0.0199128 | 0.0143866 | 0.9674754 | 19.992975 |
| 135. | 123.6303956 | 58.9699178 | 117.0823212 | 0.5072199 | 0.0199359 | 0.0147714 | 0.9831569 | 19.992975 |
| 136. | 126.3994666 | 59.0377029 | 120.6721039 | 0.4951350 | 0.0199716 | 0.0151571 | 0.9994369 | 19.992975 |
| 137. | 129.1685029 | 59.1027222 | 124.2661591 | 0.4826826 | 0.0199319 | 0.0155437 | 1.0133257 | 19.992975 |
| 138. | 131.9375610 | 59.1636353 | 127.8642273 | 0.4699593 | 0.0199472 | 0.0159311 | 1.0279330 | 19.992975 |
| 139. | 134.7066193 | 59.2207970 | 131.4660665 | 0.4566677 | 0.0199541 | 0.0163193 | 1.0419693 | 19.992975 |
| 140. | 137.4756775 | 59.2745429 | 135.0714562 | 0.4431953 | 0.0199550 | 0.0167084 | 1.0557432 | 19.992975 |
| 141. | 140.2447357 | 59.3251931 | 138.6801910 | 0.4291559 | 0.0199594 | 0.0170982 | 1.0691643 | 19.992975 |
| 142. | 143.0137939 | 59.3726654 | 142.2929685 | 0.4149442 | 0.0199643 | 0.0174888 | 1.0822420 | 19.992975 |
| 143. | 145.7828522 | 59.4172321 | 145.9067061 | 0.4001595 | 0.0199637 | 0.0178802 | 1.0949850 | 19.992975 |
| 144. | 148.5519104 | 59.4592133 | 149.5245207 | 0.3851929 | 0.0199786 | 0.0182723 | 1.1074918 | 19.992975 |
| 145. | 151.3209686 | 59.4985115 | 153.1447601 | 0.3696710 | 0.0199729 | 0.0186650 | 1.1195011 | 19.992975 |
| 146. | 154.0900269 | 59.5356291 | 156.7674561 | 0.3539665 | 0.0199377 | 0.0190585 | 1.1312994 | 19.992975 |
| 147. | 156.8590851 | 59.5704193 | 160.3924713 | 0.3376880 | 0.0199829 | 0.0194527 | 1.1427784 | 19.992975 |
| 148. | 159.6281433 | 59.6031036 | 164.0196533 | 0.3211355 | 0.0199986 | 0.0198475 | 1.1539717 | 19.992975 |
| 149. | 162.3972015 | 59.6333136 | 167.6488953 | 0.3042997 | 0.0199546 | 0.0202329 | 1.1549788 | 19.992975 |
| 150. | 165.1662599 | 59.6625740 | 171.2800598 | 0.2867973 | 0.0200911 | 0.0206190 | 1.1755966 | 19.992975 |
| 151. | 167.9353180 | 59.6907339 | 174.9130402 | 0.2692312 | 0.0200499 | 0.0210356 | 1.1959625 | 19.992975 |
| 152. | 168.4994161 | 59.7735643 | 175.2186432 | 0.2577794 | 0.0201497 | 0.0214755 | 1.2121170 | 19.5735931 |
| 153. | 169.3635121 | 59.8564933 | 235.5261688 | 0.2669761 | 0.0202930 | 0.0219563 | 1.2179556 | 19.5735931 |
| 154. | 170.9276062 | 59.9356342 | 245.3354492 | 0.2641212 | 0.0204199 | 0.0224197 | 1.2333979 | 19.5735931 |
| 155. | 171.7917923 | 60.0141449 | 296.1466844 | 0.2619167 | 0.0205544 | 0.0228806 | 1.2484755 | 19.5735931 |
| 156. | 172.7557993 | 60.0909110 | 326.4594727 | 0.2594567 | 0.0206724 | 0.0233441 | 1.2630787 | 19.5735931 |
| 157. | 173.7193266 | 60.1667339 | 356.7741699 | 0.2567471 | 0.0208118 | 0.0238094 | 1.2773541 | 19.5735931 |
| 158. | 174.6830945 | 60.2395325 | 397.0905762 | 0.2537858 | 0.0209327 | 0.0242735 | 1.2912633 | 19.5735931 |
| 159. | 175.6493955 | 60.3114471 | 417.4086916 | 0.2505729 | 0.0210649 | 0.0247394 | 1.3049248 | 19.5735931 |
| 160. | 176.6121926 | 60.3819154 | 447.7285156 | 0.2471034 | 0.0211986 | 0.0252061 | 1.3180342 | 19.5735931 |
| 161. | 177.5762787 | 60.4505541 | 479.0499067 | 0.2433922 | 0.0213335 | 0.0256736 | 1.3309950 | 19.5735931 |
| 162. | 178.5433749 | 60.5192206 | 509.3729027 | 0.2396244 | 0.0214697 | 0.0261418 | 1.3436667 | 19.5735931 |
| 163. | 179.5044709 | 60.5893233 | 539.6972655 | 0.2352060 | 0.0216072 | 0.0266108 | 1.3556671 | 19.5735931 |

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| 165. | 190.4535650 | 60.6444770 | 569.0231734 | 0.2277335 | 0.2217459 | 0.02273056 | 1.3675747 | 19.5735931 |
| 165. | 191.4326633 | 60.7115021 | 579.3505859 | 0.2260107 | 0.0214459 | 0.02275507 | 1.7791771 | 19.5735931 |
| 166. | 192.3067590 | 61.7732721 | 629.6794434 | 0.2210361 | 0.0220269 | 0.02297217 | 1.3904829 | 19.5735931 |
| 167. | 193.3573551 | 60.9507977 | 623.4843750 | 0.2219389 | 0.0219973 | 0.02276217 | 1.6145569 | 19.5735931 |
| 169. | 194.1249512 | 60.9258170 | 617.3608399 | 0.2210403 | 0.0217356 | 0.02259217 | 1.4380322 | 19.5735931 |
| 169. | 195.2933472 | 61.0004272 | 611.3078613 | 0.2210437 | 0.0216629 | 0.02262217 | 1.4609074 | 19.5735931 |
| 170. | 195.2531633 | 61.0737135 | 605.3247070 | 0.2210445 | 0.0215354 | 0.02256717 | 1.6431772 | 19.5735931 |
| 171. | 187.2172194 | 61.1463165 | 599.6106445 | 0.2210485 | 0.0216038 | 0.02250217 | 1.5049866 | 19.5735931 |
| 172. | 199.1913354 | 61.2175514 | 593.5646973 | 0.2210594 | 0.0212794 | 0.02246717 | 1.5262910 | 19.5735931 |
| 173. | 199.1656315 | 61.2977191 | 587.7861328 | 0.2210532 | 0.0211482 | 0.02237218 | 1.5466537 | 19.5735931 |
| 174. | 190.1395276 | 61.3571472 | 592.0742188 | 0.2210552 | 0.0210152 | 0.02232218 | 1.5667391 | 19.5735931 |
| 175. | 171.0735237 | 61.4253540 | 576.4282227 | 0.2210571 | 0.0209804 | 0.02226218 | 1.5443094 | 19.5735931 |
| 175. | 172.0377107 | 61.4925595 | 579.7471537 | 0.2210599 | 0.0207449 | 0.02220218 | 1.6795791 | 19.5735931 |
| 177. | 193.0019158 | 61.5597311 | 565.3305664 | 0.2210618 | 0.0206160 | 0.02216218 | 1.6230695 | 19.5735931 |
| 174. | 193.0659119 | 61.6232471 | 559.9774414 | 0.2210637 | 0.0204653 | 0.02208219 | 1.6427063 | 19.5735931 |
| 179. | 194.0370079 | 61.6991355 | 554.5873947 | 0.2210655 | 0.0203251 | 0.02202218 | 1.6597789 | 19.5735931 |
| 190. | 195.4941060 | 61.7516301 | 547.1591797 | 0.2210675 | 0.0201824 | 0.02196218 | 1.6768999 | 19.5735931 |
| 181. | 196.3592031 | 61.8139275 | 543.9023360 | 0.2210695 | 0.0200387 | 0.02190218 | 1.6936592 | 19.5735931 |
| 182. | 195.3074361 | 61.8791525 | 537.9135747 | 0.2210705 | 0.0200058 | 0.02184218 | 1.7173298 | 17.8372192 |
| 193. | 194.7554491 | 61.9366166 | 535.0649633 | 0.2210695 | 0.0199731 | 0.02180090 | 1.7206573 | 17.8372192 |
| 194. | 193.7059021 | 61.9976176 | 532.0659984 | 0.2210675 | 0.0199472 | 0.02181076 | 1.7336654 | 17.8372192 |
| 185. | 192.6551351 | 62.0597463 | 528.1562590 | 0.2210655 | 0.0199201 | 0.02177962 | 1.7463097 | 17.8372192 |
| 186. | 191.6043701 | 62.1191200 | 524.2958984 | 0.2210695 | 0.0198737 | 0.02174939 | 1.7586317 | 17.8372192 |
| 187. | 190.5536741 | 62.1803167 | 520.4665996 | 0.2210695 | 0.0198490 | 0.02171834 | 1.7706470 | 17.8372192 |
| 189. | 199.5023391 | 62.2417533 | 516.6623535 | 0.2210695 | 0.0198262 | 0.02168779 | 1.7823553 | 17.8372192 |
| 189. | 199.4529721 | 62.3027529 | 512.9886719 | 0.2210695 | 0.0197701 | 0.02165706 | 1.7937632 | 17.8372192 |
| 190. | 197.4913062 | 62.3535544 | 509.1433105 | 0.2210695 | 0.0197378 | 0.02162642 | 1.8046392 | 17.8372192 |
| 191. | 186.3505432 | 62.4242249 | 505.4226295 | 0.2210695 | 0.0197032 | 0.02159578 | 1.8157110 | 17.8372192 |
| 192. | 185.2997742 | 62.4942243 | 501.7329605 | 0.2210695 | 0.0196685 | 0.02156514 | 1.8262653 | 17.8372192 |
| 193. | 184.2690037 | 62.5645527 | 498.3758835 | 0.2210695 | 0.0196336 | 0.02153450 | 1.8365498 | 17.8372192 |
| 194. | 183.1994222 | 62.6361631 | 494.4418965 | 0.2210695 | 0.0195984 | 0.02150396 | 1.8465710 | 17.8372192 |
| 195. | 192.1474742 | 62.6965555 | 490.9354492 | 0.2210695 | 0.0195631 | 0.02147327 | 1.8563356 | 17.8372192 |
| 196. | 191.0957132 | 62.7271119 | 487.2561735 | 0.2210695 | 0.0195276 | 0.02144258 | 1.8658594 | 17.8372192 |
| 197. | 190.0459442 | 62.7975061 | 483.7039574 | 0.2210695 | 0.0194919 | 0.02141194 | 1.8751211 | 17.8372192 |
| 198. | 179.9951792 | 62.8679394 | 480.1782227 | 0.2210695 | 0.0194561 | 0.02138130 | 1.8841543 | 17.8372192 |
| 199. | 177.9446122 | 62.9081116 | 476.6791992 | 0.2210695 | 0.0194200 | 0.02135066 | 1.8929567 | 17.8372192 |
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| 202. | 174.7921143 | 63.0995520 | 466.3393555 | 0.2210695 | 0.0193109 | 0.02127874 | 1.9180355 | 17.8372192 |
| 203. | 173.7413493 | 63.1695971 | 462.9445891 | 0.2210695 | 0.0192742 | 0.02125810 | 1.9259710 | 17.8372192 |
| 204. | 172.6905923 | 63.2395571 | 459.5751953 | 0.2210695 | 0.0192374 | 0.02123746 | 1.9337034 | 17.8372192 |
| 205. | 171.6398163 | 63.2995631 | 456.2312012 | 0.2210695 | 0.0192004 | 0.02121682 | 1.9412374 | 17.8372192 |
| 206. | 170.5897503 | 63.3293981 | 452.9123535 | 0.2210695 | 0.0191633 | 0.02119619 | 1.9485739 | 17.8372192 |
| 207. | 169.5392843 | 63.3983920 | 449.6186523 | 0.2210695 | 0.0191260 | 0.02117554 | 1.9557323 | 17.8372192 |
| 208. | 168.4875133 | 63.4674169 | 446.3496096 | 0.2210695 | 0.0190886 | 0.02115490 | 1.9627028 | 17.8372192 |
| 209. | 167.4367573 | 63.5374759 | 443.1092245 | 0.2210695 | 0.0190511 | 0.02113427 | 1.9694948 | 17.8372192 |
| 210. | 166.3859353 | 63.5673774 | 439.8952539 | 0.2210695 | 0.0190134 | 0.02111363 | 1.9761124 | 17.8372192 |
| 211. | 165.3352273 | 63.6365176 | 436.6994531 | 0.2210695 | 0.0189757 | 0.02109299 | 1.9825511 | 17.8372192 |
| 212. | 164.2844543 | 63.6963952 | 433.5179223 | 0.2210695 | 0.0189376 | 0.02107235 | 1.9888449 | 17.8372192 |
| 213. | 163.2336761 | 63.7494761 | 430.32561035 | 0.2210695 | 0.0188990 | 0.02105171 | 1.9949960 | 16.1008606 |
| 214. | 163.1828979 | 63.8111731 | 427.1197754 | 0.2210695 | 0.0188600 | 0.02103106 | 2.0009168 | 16.1008606 |
| 215. | 163.1311199 | 63.8744659 | 423.9093379 | 0.2210695 | 0.0188215 | 0.02101042 | 2.0067639 | 16.1008606 |
| 216. | 162.7913416 | 63.9371195 | 420.6229027 | 0.2210695 | 0.0187826 | 0.02098977 | 2.0125472 | 16.1008606 |
| 217. | 162.4755534 | 63.9997101 | 417.4416699 | 0.2210695 | 0.0187433 | 0.020977569 | 2.0182573 | 16.1008606 |

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| 218. | 162.0227952 | 64.0622476 | 414.3254395 | 0.2212695 | 0.0196696 | 0.0074736 | 2.1022739 | 16.1009606 |
| 219. | 161.6540070 | 64.1267131 | 411.2136230 | 0.2210695 | 0.0196236 | 0.0070503 | 2.1195211 | 16.1009606 |
| 220. | 161.2792299 | 64.1971135 | 409.1259765 | 0.2210695 | 0.0195771 | 0.0066970 | 2.1353277 | 16.1009606 |
| 221. | 160.9024536 | 64.2696537 | 405.0625000 | 0.2210575 | 0.0195303 | 0.0063437 | 2.1527033 | 16.1009606 |
| 222. | 160.5265774 | 64.3117219 | 402.0229492 | 0.2210695 | 0.0194931 | 0.0059704 | 2.1685602 | 16.1009606 |
| 223. | 160.1503062 | 64.3737319 | 399.0970891 | 0.2210695 | 0.0194355 | 0.0055371 | 2.1842079 | 16.1009606 |
| 224. | 159.7751160 | 64.4367309 | 396.0144926 | 0.2210695 | 0.0193976 | 0.0051939 | 2.1993590 | 16.1009606 |
| 225. | 159.3993378 | 64.4991699 | 393.0661426 | 0.2210695 | 0.0193394 | 0.0049305 | 2.2141209 | 16.1009606 |
| 226. | 159.0235596 | 64.5621937 | 390.1003618 | 0.2210695 | 0.0192909 | 0.0045771 | 2.2285051 | 16.1009606 |
| 227. | 158.6477714 | 64.6221313 | 387.1777364 | 0.2210695 | 0.0192420 | 0.0042238 | 2.2425213 | 16.1009606 |
| 228. | 158.2719865 | 64.6810655 | 384.2968750 | 0.2233462 | 0.0192141 | 0.0042176 | 2.2577715 | 16.1009606 |
| 229. | 157.8961915 | 64.7393297 | 378.4670610 | 0.2254727 | 0.0192302 | 0.0042114 | 2.2726316 | 16.1009606 |
| 230. | 157.5203966 | 64.7931931 | 374.1872559 | 0.2254727 | 0.0192242 | 0.0042052 | 2.2871113 | 16.1009606 |
| 231. | 157.1446017 | 64.8574524 | 369.9572754 | 0.2269346 | 0.0192182 | 0.0041990 | 2.3012179 | 16.1009606 |
| 232. | 156.7688068 | 64.9161377 | 365.7763672 | 0.2281069 | 0.0192121 | 0.0041928 | 2.3142691 | 16.1009606 |
| 233. | 156.3930119 | 64.9747772 | 361.6437939 | 0.2292666 | 0.0192060 | 0.0041866 | 2.3283644 | 16.1009606 |
| 234. | 156.0172169 | 65.0333557 | 357.5593262 | 0.2304297 | 0.0191999 | 0.0041804 | 2.3414173 | 16.1009606 |
| 235. | 155.6414220 | 65.0919732 | 353.5222169 | 0.2315965 | 0.0191937 | 0.0041742 | 2.3544365 | 16.1009606 |
| 236. | 155.2656271 | 65.1503464 | 349.5317333 | 0.2327627 | 0.0191875 | 0.0041680 | 2.3665275 | 16.1009606 |
| 237. | 155.0898322 | 65.2087555 | 345.5876665 | 0.2337753 | 0.0191813 | 0.0041618 | 2.3786058 | 16.1009606 |
| 238. | 154.7140373 | 65.2671951 | 341.6892090 | 0.2347927 | 0.0191750 | 0.0041556 | 2.3907372 | 16.1009606 |
| 239. | 154.3382423 | 65.3256099 | 337.8361815 | 0.2358140 | 0.0191687 | 0.0041494 | 2.4028393 | 16.1009606 |
| 240. | 154.0624474 | 65.3840517 | 334.0273320 | 0.2368259 | 0.0191624 | 0.0041432 | 2.4139116 | 16.1009606 |
| 241. | 153.6866525 | 65.4425135 | 330.2636710 | 0.2378394 | 0.0191560 | 0.0041370 | 2.4249977 | 16.1009606 |
| 242. | 153.3108576 | 65.5009765 | 326.5429699 | 0.2388540 | 0.0191497 | 0.0041308 | 2.4360955 | 16.1009606 |
| 243. | 153.0350627 | 65.5594444 | 322.8656795 | 0.2398699 | 0.0191432 | 0.0041246 | 2.4468414 | 16.1009606 |
| 244. | 152.6592678 | 65.6179222 | 319.2309961 | 0.2408869 | 0.0191367 | 0.0041180 | 2.4574997 | 13.2595530 |
| 245. | 152.2834729 | 65.6764132 | 315.6466816 | 0.2419049 | 0.0191283 | 0.0041114 | 2.4680754 | 13.2595530 |
| 246. | 151.9076780 | 65.7349134 | 312.1098001 | 0.2429229 | 0.0191211 | 0.0041048 | 2.4789653 | 13.2595530 |
| 247. | 151.5318831 | 65.7934257 | 308.6222169 | 0.2439409 | 0.0191140 | 0.0040982 | 2.4892650 | 13.2595530 |
| 248. | 151.1560882 | 65.8519380 | 305.1846334 | 0.2449589 | 0.0191069 | 0.0040916 | 2.4999738 | 13.2595530 |
| 249. | 150.7802933 | 65.9104503 | 301.7920500 | 0.2459769 | 0.0190997 | 0.0040850 | 2.5106826 | 13.2595530 |
| 250. | 149.4044984 | 66.0689626 | 297.4444666 | 0.2469949 | 0.0190925 | 0.0040784 | 2.5213914 | 13.2595530 |
| 251. | 149.0287035 | 66.1274749 | 294.0518831 | 0.2480129 | 0.0190853 | 0.0040718 | 2.5321002 | 13.2595530 |
| 252. | 148.6529086 | 66.1859872 | 290.7092997 | 0.2490309 | 0.0190781 | 0.0040652 | 2.5428090 | 13.2595530 |
| 253. | 148.2771137 | 66.2445095 | 287.4167162 | 0.2500489 | 0.0190709 | 0.0040586 | 2.5535178 | 13.2595530 |
| 254. | 147.9013188 | 66.3030318 | 284.1741327 | 0.2510669 | 0.0190637 | 0.0040520 | 2.5642266 | 13.2595530 |
| 255. | 147.5255239 | 66.3615541 | 280.9815492 | 0.2520849 | 0.0190565 | 0.0040454 | 2.5749354 | 13.2595530 |
| 256. | 147.1497290 | 66.4200764 | 277.8389657 | 0.2531029 | 0.0190493 | 0.0040388 | 2.5856442 | 13.2595530 |
| 257. | 146.7739341 | 66.4785987 | 274.7463822 | 0.2541209 | 0.0190421 | 0.0040322 | 2.5963530 | 13.2595530 |
| 258. | 146.3981392 | 66.5371210 | 271.7037987 | 0.2551389 | 0.0190349 | 0.0040256 | 2.6070618 | 13.2595530 |
| 259. | 146.0223443 | 66.5956433 | 268.7112152 | 0.2561569 | 0.0190277 | 0.0040190 | 2.6177706 | 13.2595530 |
| 260. | 145.6465494 | 66.6541656 | 265.7686317 | 0.2571749 | 0.0190205 | 0.0040124 | 2.6284794 | 13.2595530 |
| 261. | 145.2707545 | 66.7126879 | 262.8760482 | 0.2581929 | 0.0190133 | 0.0040058 | 2.6391882 | 13.2595530 |
| 262. | 144.8949596 | 66.7712102 | 260.0334647 | 0.2592109 | 0.0190061 | 0.0040025 | 2.6498970 | 13.2595530 |
| 263. | 144.5191647 | 66.8297325 | 257.2408812 | 0.2602289 | 0.0189989 | 0.0040025 | 2.6606058 | 13.2595530 |
| 264. | 144.1433698 | 66.8882548 | 254.5082977 | 0.2612469 | 0.0189917 | 0.0040025 | 2.6713146 | 13.2595530 |
| 265. | 143.7675749 | 66.9467771 | 251.8357142 | 0.2622649 | 0.0189845 | 0.0040025 | 2.6820234 | 13.2595530 |
| 266. | 143.3917800 | 67.0052994 | 249.2231307 | 0.2632829 | 0.0189773 | 0.0040025 | 2.6927322 | 13.2595530 |
| 267. | 143.0159851 | 67.0638217 | 246.6705472 | 0.2643009 | 0.0189701 | 0.0040025 | 2.7034410 | 13.2595530 |
| 268. | 142.6401902 | 67.1223440 | 244.1779637 | 0.2653189 | 0.0189629 | 0.0040025 | 2.7141498 | 13.2595530 |
| 269. | 142.2643953 | 67.1808663 | 241.7453802 | 0.2663369 | 0.0189557 | 0.0040025 | 2.7248586 | 13.2595530 |
| 270. | 141.8886004 | 67.2393886 | 239.3727967 | 0.2673549 | 0.0189485 | 0.0040025 | 2.7355674 | 13.2595530 |
| 271. | 141.5128055 | 67.2979109 | 237.0602132 | 0.2683729 | 0.0189413 | 0.0040025 | 2.7462762 | 13.2595530 |

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| 272. | 119.5493990 | 70.8865509 | 227.0397454 | 0.4016820 | 0.0180447 | 0.0040256 | 1.2314377 | 13.2595530 |
| 273. | 117.4491975 | 71.1714935 | 225.4095764 | 0.4016820 | 0.0180447 | 0.0040256 | 1.1972351 | 13.2595530 |
| 274. | 113.6116436 | 75.6495962 | 225.9561920 | 0.4016820 | 0.0180447 | 0.0040256 | 1.1559544 | 12.3124418 |
| 275. | 109.5541077 | 80.1341127 | 226.5363159 | 0.4016820 | 0.0180447 | 0.0040256 | 1.1146736 | 12.3124418 |
| 276. | 105.4955558 | 84.5547972 | 227.1497040 | 0.4016820 | 0.0180447 | 0.0040256 | 1.0733929 | 12.3124418 |
| 277. | 101.4370259 | 89.9677921 | 227.7961171 | 0.4016820 | 0.0180447 | 0.0040256 | 1.0321121 | 12.3124418 |
| 278. | 97.3814850 | 93.3275925 | 228.4752834 | 0.4016820 | 0.0180447 | 0.0040256 | 0.9908317 | 12.3124418 |
| 279. | 93.3232441 | 97.6599259 | 229.1869659 | 0.4016820 | 0.0180447 | 0.0040256 | 0.9495512 | 12.3124418 |
| 280. | 89.2664032 | 101.9595710 | 229.9309397 | 0.4016820 | 0.0180447 | 0.0040256 | 0.9082709 | 12.3124418 |
| 281. | 85.2094423 | 106.2272491 | 230.7061197 | 0.4016820 | 0.0180447 | 0.0040256 | 0.8669903 | 12.3124418 |
| 282. | 81.1513214 | 110.4629726 | 231.5147400 | 0.4016820 | 0.0180447 | 0.0040256 | 0.8257098 | 12.3124418 |
| 283. | 77.0937325 | 114.6669221 | 232.3547955 | 0.4016820 | 0.0180447 | 0.0040256 | 0.7844293 | 12.3124418 |
| 284. | 73.0362396 | 114.8392439 | 233.2247772 | 0.4016820 | 0.0180447 | 0.0040256 | 0.7431487 | 12.3124418 |
| 285. | 68.9786997 | 122.9896489 | 234.1265411 | 0.4016820 | 0.0180447 | 0.0040256 | 0.7018682 | 12.3124418 |
| 286. | 64.9211578 | 127.0905477 | 235.0591533 | 0.4016820 | 0.0180447 | 0.0040256 | 0.6605879 | 12.3124418 |
| 287. | 60.8635160 | 131.1791159 | 234.0223999 | 0.4016820 | 0.0180447 | 0.0040257 | 0.6193073 | 12.3124418 |
| 288. | 56.8060760 | 135.2149261 | 237.0160370 | 0.4016820 | 0.0180447 | 0.0040257 | 0.5780268 | 12.3124418 |
| 289. | 52.7485352 | 139.2375723 | 233.9394607 | 0.4016820 | 0.0180447 | 0.0040257 | 0.5367463 | 12.3124418 |
| 290. | 48.6910943 | 143.2262742 | 239.0035422 | 0.4016820 | 0.0180447 | 0.0040257 | 0.4954658 | 12.3124418 |
| 291. | 44.6336534 | 147.1847176 | 240.1779325 | 0.4016820 | 0.0180447 | 0.0040257 | 0.4541853 | 12.3124418 |
| 292. | 40.5759125 | 151.1137095 | 241.2899780 | 0.4016820 | 0.0180447 | 0.0040257 | 0.4129048 | 12.3124418 |
| 293. | 36.5183716 | 155.0132926 | 242.4372057 | 0.4016820 | 0.0180447 | 0.0040257 | 0.3716243 | 12.3124418 |
| 294. | 32.4608307 | 158.8836323 | 243.6034851 | 0.4016820 | 0.0180447 | 0.0040257 | 0.3303438 | 12.3124418 |
| 295. | 28.4032908 | 162.7259924 | 244.8036261 | 0.4016820 | 0.0180447 | 0.0040257 | 0.2890633 | 12.3124418 |
| 296. | 24.3457499 | 166.5377350 | 246.0323334 | 0.4016820 | 0.0180447 | 0.0040257 | 0.2477828 | 12.3124418 |
| 297. | 20.2882090 | 170.3219344 | 247.2894745 | 0.4016820 | 0.0180447 | 0.0040257 | 0.2065023 | 12.3124418 |
| 298. | 16.2306681 | 174.0776062 | 248.5748138 | 0.4016820 | 0.0180447 | 0.0040257 | 0.1652218 | 12.3124418 |
| 299. | 12.1731271 | 177.8052573 | 249.8881225 | 0.4016820 | 0.0180447 | 0.0040257 | 0.1239413 | 12.3124418 |
| 300. | 8.1155921 | 181.5059231 | 251.2292175 | 0.4016820 | 0.0180447 | 0.0040257 | 0.0826608 | 12.3124418 |
| 301. | 4.0590530 | 185.1779430 | 252.5978499 | 0.4016820 | 0.0180447 | 0.0040257 | 0.0413803 | 12.3124418 |
| 302. | 0.0005150 | 188.8371624 | 253.9939917 | 0.4016820 | 0.0180447 | 0.0040257 | 0.0001099 | 12.3124418 |
| 303. | 0.0005150 | 187.3405677 | 255.4982910 | 0.4016820 | 0.0180447 | 0.0040257 | 0.0000999 | 0.0 |
| 304. | 0.0005150 | 185.9713379 | 256.9999669 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0000999 | 0.0 |
| 305. | 0.0005150 | 184.6313573 | 258.4721580 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0000999 | 0.0 |
| 306. | 0.0005150 | 182.9671478 | 259.9421387 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 307. | 0.0005150 | 181.5321194 | 261.4006344 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 308. | 0.0005150 | 180.1093374 | 262.8681455 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 309. | 0.0005150 | 178.6957245 | 264.2844238 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 310. | 0.0005150 | 177.2941495 | 265.7097168 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 311. | 0.0005150 | 175.9036550 | 267.1240236 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0000999 | 0.0 |
| 312. | 0.0005150 | 174.5240173 | 268.5275979 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0000999 | 0.0 |
| 313. | 0.0005150 | 173.1551971 | 269.9201660 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0000999 | 0.0 |
| 314. | 0.0005150 | 171.7971191 | 271.3022661 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 315. | 0.0005150 | 170.4495918 | 272.6735860 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0000999 | 0.0 |
| 316. | 0.0005150 | 159.1129397 | 274.0344239 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0000999 | 0.0 |
| 317. | 0.0005150 | 167.7864685 | 275.3847655 | 0.4016820 | 0.0180447 | 0.0040258 | 0.0001000 | 0.0 |
| 318. | 0.0005150 | 166.4705368 | 276.7248535 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 319. | 0.0005150 | 165.1643560 | 278.0546975 | 0.4016820 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 320. | 0.0005150 | 163.4799557 | 279.7489669 | 0.3793562 | 0.0180447 | 0.0040258 | 0.0001000 | 0.0 |
| 321. | 0.0005150 | 161.7942352 | 281.4240723 | 0.3568976 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 322. | 0.0005150 | 160.1347261 | 283.0930078 | 0.3342920 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 323. | 0.0005150 | 159.4973959 | 284.7250977 | 0.3115474 | 0.0180447 | 0.0040258 | 0.0001000 | 0.0 |
| 324. | 0.0005150 | 156.8653213 | 286.3573613 | 0.2896969 | 0.0180447 | 0.0040258 | 0.0001000 | 0.0 |
| 325. | 0.0005150 | 155.2577346 | 287.9587844 | 0.2657930 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |

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| 326. | 0.0005150 | 153.6655426 | 289.5512695 | 0.2475799 | 0.0180447 | 0.0040258 | 0.0001000 | 0.0 |
| 327. | 0.0005150 | 152.0894775 | 291.1271973 | 0.2193799 | 0.0180447 | 0.0040258 | 0.0001000 | 0.0 |
| 328. | 0.0005150 | 150.5295949 | 292.6870117 | 0.1959513 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 329. | 0.0005150 | 149.9856973 | 294.2309570 | 0.1724495 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 330. | 0.0005150 | 147.4676263 | 295.7597332 | 0.1488218 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 331. | 0.0005150 | 145.9652362 | 297.2714866 | 0.1250723 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 332. | 0.0005150 | 144.4483643 | 298.7685547 | 0.1012014 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 333. | 0.0005150 | 142.9669427 | 300.2502441 | 0.0772192 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 334. | 0.0005150 | 141.5005189 | 301.7167949 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 335. | 0.0005150 | 141.2664470 | 301.9506836 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 336. | 0.0005150 | 141.0177670 | 302.1847920 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 337. | 0.0005150 | 140.7994537 | 302.4172363 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 338. | 0.0005150 | 140.5664536 | 302.6499023 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 339. | 0.0005150 | 140.3340149 | 302.8823242 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 340. | 0.0005150 | 140.1018677 | 303.1142579 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 341. | 0.0005150 | 139.8701919 | 303.3459473 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 342. | 0.0005150 | 139.6387177 | 303.5771494 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 343. | 0.0005150 | 139.4077149 | 303.8078613 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 344. | 0.0005150 | 139.1771935 | 304.0383301 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 345. | 0.0005150 | 138.9463536 | 304.2683105 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 346. | 0.0005150 | 138.7147952 | 304.4980443 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 347. | 0.0005150 | 138.4875133 | 304.7272949 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 348. | 0.0005150 | 138.2569220 | 304.9562989 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 349. | 0.0005150 | 138.0297730 | 305.1843145 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 350. | 0.0005150 | 137.8011363 | 305.4130859 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 351. | 0.0005150 | 137.5734253 | 305.6408691 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 352. | 0.0005150 | 137.3453495 | 305.8694792 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 353. | 0.0005150 | 137.1185371 | 306.0954970 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 354. | 0.0005150 | 136.8919152 | 306.3222656 | 0.0531092 | 0.0180447 | 0.0040259 | 0.0001000 | 0.0 |
| 355. | 0.0005150 | 136.6653595 | 306.5485440 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 356. | 0.0005150 | 136.4392953 | 306.774592 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 357. | 0.0005150 | 136.2135773 | 307.0002441 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 358. | 0.0005150 | 135.9882537 | 307.2255459 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 359. | 0.0005150 | 135.7632974 | 307.4506335 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 360. | 0.0005150 | 135.5397115 | 307.6757493 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 361. | 0.0005150 | 135.3144939 | 307.8997169 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 362. | 0.0005150 | 135.0906525 | 308.1236444 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 363. | 0.0005150 | 134.8671722 | 308.3464355 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 364. | 0.0005150 | 134.6447735 | 308.5695921 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |
| 365. | 0.0005150 | 134.4213477 | 308.7922363 | 0.0531092 | 0.0180447 | 0.0040260 | 0.0001000 | 0.0 |