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Structure and Function of North American Desert Grassland Ecosystems

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This volume is dedicated to the memory of George M. Van Dyne, Robert Packard and Eugene Staffeldt for their contributions to our understanding of Desert Grassland Ecosystems.

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STRUCTURE AND FUNCTION OF NORTH AMERICAN DESERT GRASSLAND ECOSYSTEMS

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PREFACE

It became obvious during the preparation of this volume that many gaps exist in our knowledge of Desert Grassland ecosystems. The research conducted under the Grassland Biome of the International Biological Program, and summarized in this volume, barely scratched the surface. This volume, however, presents some new information and unique analysis for desert grasslands.

The primary purpose of the volume is not to present a finished, definitive analysis of desert grassland ecosystems, but rather to summarize the current state of the art. The authors are painfully aware of the shortcomings of the volume. We hope that this material will serve as a base for future studies on desert grasslands. In addition, information from this volume will contribute to a better understanding of grasslands in general and aid in comparisons among North American grasslands.

The authors contributed to different sections of the volume. Pieper was overall coordinator, and with Herbel, worked on abiotic and primary producer sections. Anway was responsible for the modeling aspects as well as general review. Mark Ellstrom and Gordon Watts contributed the sections on invertebrates. Stuart Pimm and Ralph Raitt conducted the avian studies and reviewed other sections of the manuscript. Robert Packard was responsible for the material on small mammals. Eugene Staffeldt contributed the information on decomposers.

In addition to the authors, others also made major contributions to the volume. Dr. Walt Whitford generously contributed the sections on reptiles from his Desert Biome work and assisted in many other ways.

Personnel at the Natural Resource Ecology Laboratory at Colorado State University provided services without which the completion of the volume would not have been possible. We make special acknowledgement to the following: Dave Swift, Norm French, George M. Van Dyne, Marilyn Campion, Charles Van Baker, Robin Andrews, Jai Singh, Freeman Smith, Mel Dyer, and Francis Clark. Also editors of volumes on other grassland types, Tex Lewis, Paul Risser, Tad Weaver, Don Duncan, and Bill Rickard made important contributions.

Rex D. Pieper
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INTRODUCTION

The classification and the terminology of the North American Desert Grassland have been treated differently by different authors. Some have considered it a relatively stable climax grassland (Clements 1920, Whitfield and Beutner 1938, Whitfield and Anderson 1938, Campbell 1929, and Gardner 1951). Shreve (1917) considered it a transition between the midwestern grasslands and the desert succulents to the west. More recently, Brown (1950) assessed the area not as a grassland climax, but as a grassland maintained by some factor(s) that prevented the invasion of shrubs. The delineation of Chihuahuan and Sonoran deserts and desert grassland has always been questionable. Sites that once supported grassland now support mainly desert shrubs, such as mesquite (*Prosopis juliflora*) or creosotebush (*Larrea tridentata*) (Canfield 1948, Branscomb 1956, York and Dick-Peddie 1969, and Buffington and Herbel 1965). Once the shrubs become established, they maintain their dominance more or less permanently (Herbel, Dittberner, and Bickle 1970) or at least through the life-span of the shrubs.

The desert grassland was termed the "desert plains grassland" by Clements (1920), Weaver and Clements (1938), Whitfield and Anderson (1938); "semidesert grassland" by Buffington and Herbel (1965) and Herbel, Dittberner, and Bickle (1970); and "desert-grassland transition" by Shreve (1917). The "desert plains grassland" of Weaver and Clements (1938) was considered a grassland dominated by *Bouteloua* and *Aristida*, which extended from southwestern Texas, across southern New Mexico and Arizona and into northern Mexico. Whitfield and Beutner (1938) divided that association into a *Bouteloua-Hilaria* faciation, with *B. eriopoda* and *H. mutica* as the dominants, and a *Hilaria-Bouteloua* faciation with *H. belangeri* and *B. gracilis* as the dominants. The *Bouteloua-Hilaria* faciation ranged from 0 to 1330 m in elevation and was generally warmer and south of the *Hilaria-Bouteloua* faciation, which ranged from 1800 to 1700 m in elevation. The map of Shreve (1917) shows the desert grassland transision occurring extensively in northwestern Texas, eastern New Mexico, southwestern New Mexico, and north-central Arizona.

The areas of desert grassland to be included in this volume were selected somewhat arbitrarily and the following types (Kuchler 1964) are included here as desert grassland:

1. Grama--galleta steppee
2. Grama--tobosa prairie
3. Galleta--three awn
4. Grama--tobosa shrub steppe
5. Trans--Pecos shrub savannah

The region discussed in this volume is shown in figure 1. The volume includes vegetation in New Mexico related to shortgrass vegetation with a blue grama (*Bouteloua gracilis*) dominance and the main part of the range of galleta (*Hilaria jamesii*) (West et al. 1972). Most of the data presented are from the Grassland Biome Comprehensive Site located at the Jornada Experimental Range in southern New Mexico.

This volume was prepared as a part of the United States contribution to the Analysis of Ecosystem portion of the International Biological Program. The overall objective of the IBP is to examine "the biological basis of productivity in human welfare" (Van Dyne 1971). Consequently, this volume will emphasize the various facets of

Figure 1. Area covered by desert grassland.

productivity in a desert grassland ecosystem.

An integral part of the US/IBP efforts was to gain understanding of the functioning of entire ecosystems. Major emphasis was placed on the measurement of abiotic and biotic variables and their interactions over the three-year period. In general, the approach here will be to present data from as many sources as possible, including the Jornada comprehensive site on the Experimental Range, and then to concentrate on comparable Jornada field data. All data presented will be made as comparable as possible and presented in a systems context.

The ecosystem is viewed as an open system with certain abiotic driving variables or inputs such as water, solar radiation, wind speed, and air temperature controlling the system variables, such as soil water, primary productivity, decomposition, etc. (Innis 1973). The systems approach in grasslands involves collecting information about the system over a period of time and using this information to develop models that may illustrate new insights into the systems and may be used in management decisions.

Several terms will be used throughout the following sections. These are defined here (Woodmansee 1974):

Control - Biotic or abiotic factors that influence a process; regulator of the flow of matter or energy from one compartment or state variable to another.

Driving variable - Independent or extrinsic variables that cause the system to respond but are not affected themseleves by the system.

Feedback - Response of a state variable or compartment to a change in its own size or a change in another mutually interactive state variable.

Flow - Movement of matter, energy, or information from one compartment (state variable) to another.

Process - Those events that govern ways in which energy or matter moves from compartment to compartment in the abiotic and biotic portions of the ecosystem; biotic or abiotic factors that control the flow of matter or energy between compartments.

State varible - Sets of numbers that are used to represent the state or condition of a system at any time.

Transfer function - The manner in which conditions at the input are transferred to the output.

Parameter - A quantity in a mathematical model that controls functions in the model but itself does not vary within the simulation exercise in which it is used, as distinguished from a variable, which can assume only those values that the form of the function makes possible.

DESCRIPTION OF DESERT GRASSLAND ECOSYSTEMS

Historical Development of Desert Grasslands

Dix (1964) stated that plant species of the desert grasslands evolved in place, in ancient forests, and suggested that many of the herbaceous species developed from the southern grasslands in the Miocene, while shrubby species were components of the Madro-territory flora in Oligocene-Miocene times. He indicated that the desert grassland is the oldest and most stable grassland, being relatively undisturbed in the Pleistocene glaciation.

Most of the plant and animal species found in the desert grasslands occur over the western United States. Wright (1972) reported that only 0.8% of the plant species found on the Jornada were endemic to New Mexico. About 40% of the species were restricted to the southwestern semi-deserts and 80% to the western United States. Most of the animal species are also widespread in the Southwest and the West.

Many ecologists hold that, before European man arrived, the desert grassland was rather open, with only a scattering of shrubby species, abundant pronghorn antelope, and few bison. Even in those times, however, the area was a transition zone between the Great Plains grasslands to the northeast and the hot deserts to the west. When European man came upon the scene, many sensitive ecological complexes were altered, and the desert grassland has undergone rapid and rather drastic changes with an increase in shrublands and a decrease in grasslands. Evaluation and explanation of the changes are difficult, because few records are available of conditions in the 1500s.

Abiotic Factors

Abiotic factors are the master or driving variables for ecosystem development and determine the final product of the biotic components. Jenny (1961) and Major (1951) considered both abiotic and biotic components as functionally related to soil, vegetation, or ecosystem properties. In their formulation, the abiotic factors were soil parent material, relief or topography, and climate. These are the abiotic factors considered in this section.

Certain abiotic factors impinge directly on all organisms in an ecosystem. The overall climate of an area does not come into operational contact (Mason and Langenheim 1955) with organisms of an ecosystem but does influence the microclimate, which in turn impinges directly on organisms. Microclimate may be changed by organisms, but it is under primary control of the macroclimate. For example, tall plants may intercept solar radiation and reduce wind velocity, and so alter the environment for some smaller plant or animal.

Long-Term Climatic Variables for Desert Grasslands

For several desert grassland sites, climatic records are available for a period of 50 years or more. These records provide a fairly complete picture of the climatic environment of these areas and the spatial and temporal variation in climatic parameters.

Precipitation. Figure 2 shows the seasonal precipitation distribution for several weather bureau stations within the desert grassland as defined in this volume. Several characteristics are apparent from figure 2. All the stations except for Blanding, Utah,

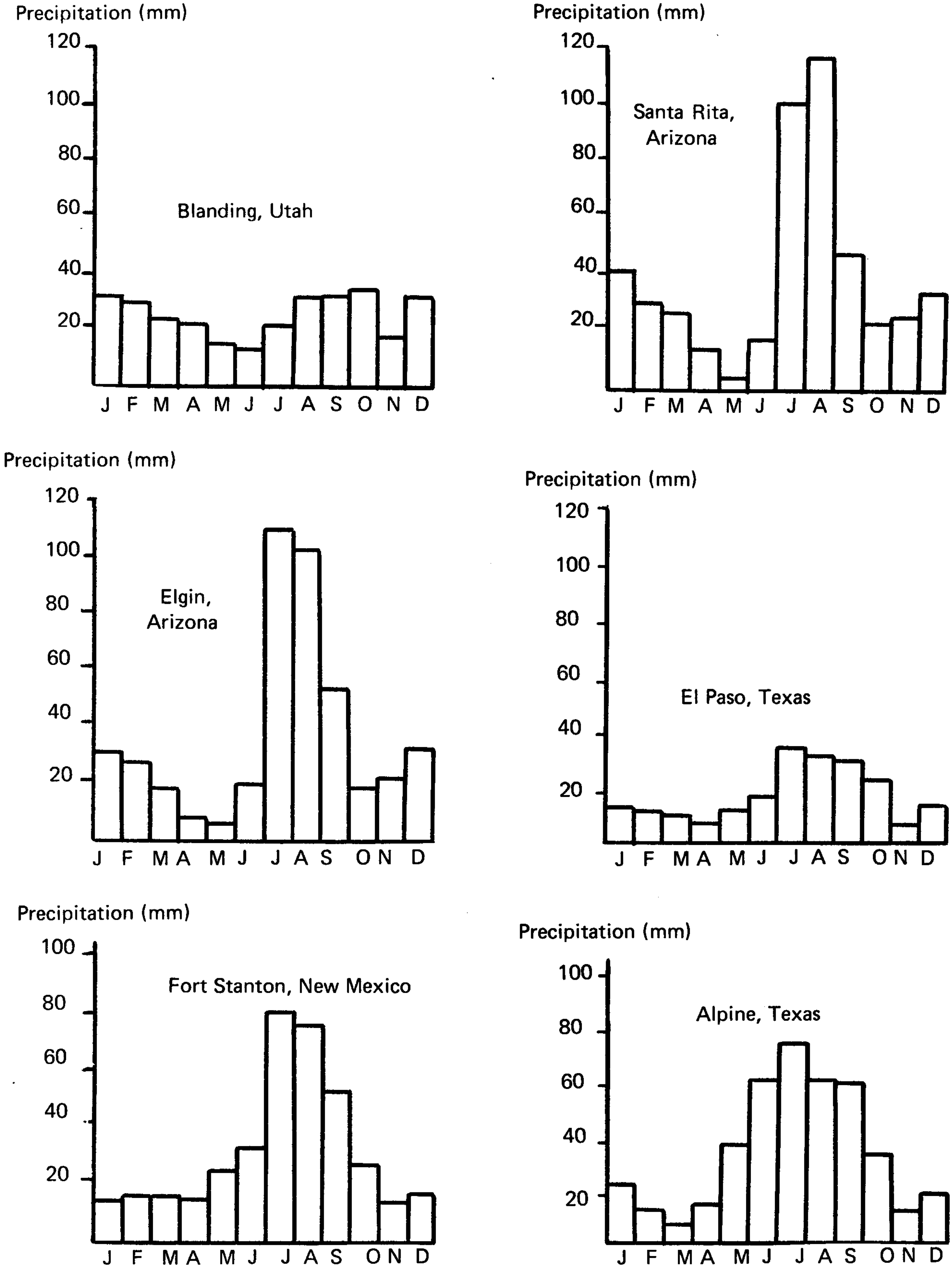

Figure 2. Monthly distribution of precipitation at several stations within the desert grassland. Data from U.S. Weather Bureau except for Elgin, Arizona which is from Nicholson (1972) and is the Average for the Canelo and Fort Huachuca, Arizona Stations.

are characterized by low spring precipitation. At El Paso, Texas, February, March, April and May have less than or just over 10 mm of precipitation per month. In southern Arizona, April and May are dry. At Blanding, Utah, springs are drier than winters, but a larger proportion of the annual precipitation falls in spring there than on sites further south.

Except for Blanding, desert grassland sites are all characterized by summer precipitation maxima (figure 2). In southern Arizona, summer rains begin in July; in western Texas, they begin in June and July. Trewartha (1961) included Blanding and most of Arizona in a precipitation type with summer maxima, but Blanding received considerable winter precipitation, some in the form of snow, and lower amounts in spring and early summer. Monthly variations at Blanding are less pronounced than at some of the other sites. Most of these precipitation patterns are related to maritime moisture sources and wind patterns (Borchert 1950). Southern Utah and all of Arizona are included by Trewartha (1961) in a precipitation zone that is characterized by a summer peak and also a lesser peak in the winter (figure 2). The spring drought is a result of shifting of the cyclonic belt north of this region (Borchert 1950). Winter storms result from Pacific air masses moving across the region. By the time these air masses move into southern New Mexico, most of their moisture has been dissipated, and winters are rather dry. Although Blanding is included in the summer maxima type, it is closely related to that with winter-spring maxima and influenced by the shifting of the Pacific anticyclone northward in June (Trewartha 1961).

Central and southern New Mexico are in a zone characterized by only summer maxima, relatively dry winters, and very dry springs (Trewartha 1961). Precipitation for December, January, and February at El Paso is less than one-third of that received in southern Arizona.

Moisture for summer storms for the desert grassland comes mostly from the Gulf of Mexico. There is some orographic influence as moist air from the Gulf moves westward to the highlands of western Texas, New Mexico, and Arizona. Most of these summer storms are convectional, very intense, and localized. Hence, spatial variation is high. Local mountains and relief also influence these summer storms. The desert mountains have higher precipitation than surrounding areas. For example, the headquarters of the Santa Rita Experimental Range and the Fort Stanton Experimental Range are in mountains, and receive more precipitation than do the surrounding areas at lower elevations (table 1). Bryson et al. (1970) discussed the effects of mountains on local variation in precipitation for the Jornada, which includes some orographic effects and influence on air movement.

Monthly distribution of precipitation for the Jornada Experimental Range follows closely that for El Paso, as expected, since they are approximately 100 km apart. July and August are the only months when precipitation exceeds 40 mm. Sometimes late fall and winter precipitation, when evaporation is low, is sufficient to provide soil water storage for spring growth of cool-season annuals. April has the lowest average precipitation at the Jornada, with gradually increasing amounts in May and June before the large increase in July (figure 3).

Yearly precipitation varies greatly in the desert grasslands, and drought is common (Figure 3). From 1916 to 1972, precipitation was below average in nearly two-thirds of the years at the Jornada. Dry years are roughly twice as common as wet ones. Years with highest total annual precipitation were 1920, 1942, 1958, and 1962, when over 340 mm fell (Herbel and Pieper 1970). The driest years were 1918 and 1956, when just over 90 mm fell. The period of the early 1950's was one of extreme drought throughout many portions of the Southwest. Droughts of such severity occur only once in several hundred years (Herbel, Ares, and Wright 1972).

Temperature. Seasonal temperature patterns are fairly similar throughout the desert grassland region, because of its continental location. Local variations are due to elevational and latitudinal gradients. Generally, temperatures reach a maximum in June, July, or August and a minimum in December and January (figure 4). Average daily temperatures at El Paso approach 18°C during the winter and are a little lower at Marfa, Texas. Otherwise, average daily temperatures were slightly lower at El Paso than at Marfa. The temperatures in southern Arizona are higher than those at El Paso or Marfa.

Temperature extremes are more indicative of temperature ranges and effects than daily means. The average January maximum at Tucson, Arizona, is 17.0°C and the minimum is 2.8°C; at Roswell, New Mexico, the January maximum is 12.8°C and the minimum is -6.3°C (table 2). El Paso extremes for July and January are somewhat intermediate between those at Roswell and Tucson. At another station south of Tucson in southern Arizona, December and January are the only months when the mean minimum temperatures are below freezing (figure 5).

At the Jornada, most temperature measurements follow consistent

Table 1. Yearly total and total precipitation (mm) for June, July, August, and September for selected stations in the desert grassland

Station	Total precipitation for June, July, August, and September	Annual Total
Blanding, Utah	95.7	304
Santa Rita, Arizona	286.1	491
Elgin, Arizona	285.0	452
El Paso, Texas	109.4	200
Fort Stanton, New Mexico	245.1	389
Alpine, Texas	244.4	392

Table 2. Average maximum and minimum temperatures (°C) for three desert grassland stations for January and July.

Station	January		July	
	Maximum	Minimum	Maximum	Minimum
Tucson, Arizona	17.0	2.8	36.9	23.4
Roswell, New Mexico	12.8	-6.3	35.2	16.5
El Paso, Texas	13.5	-1.4	34.9	20.5

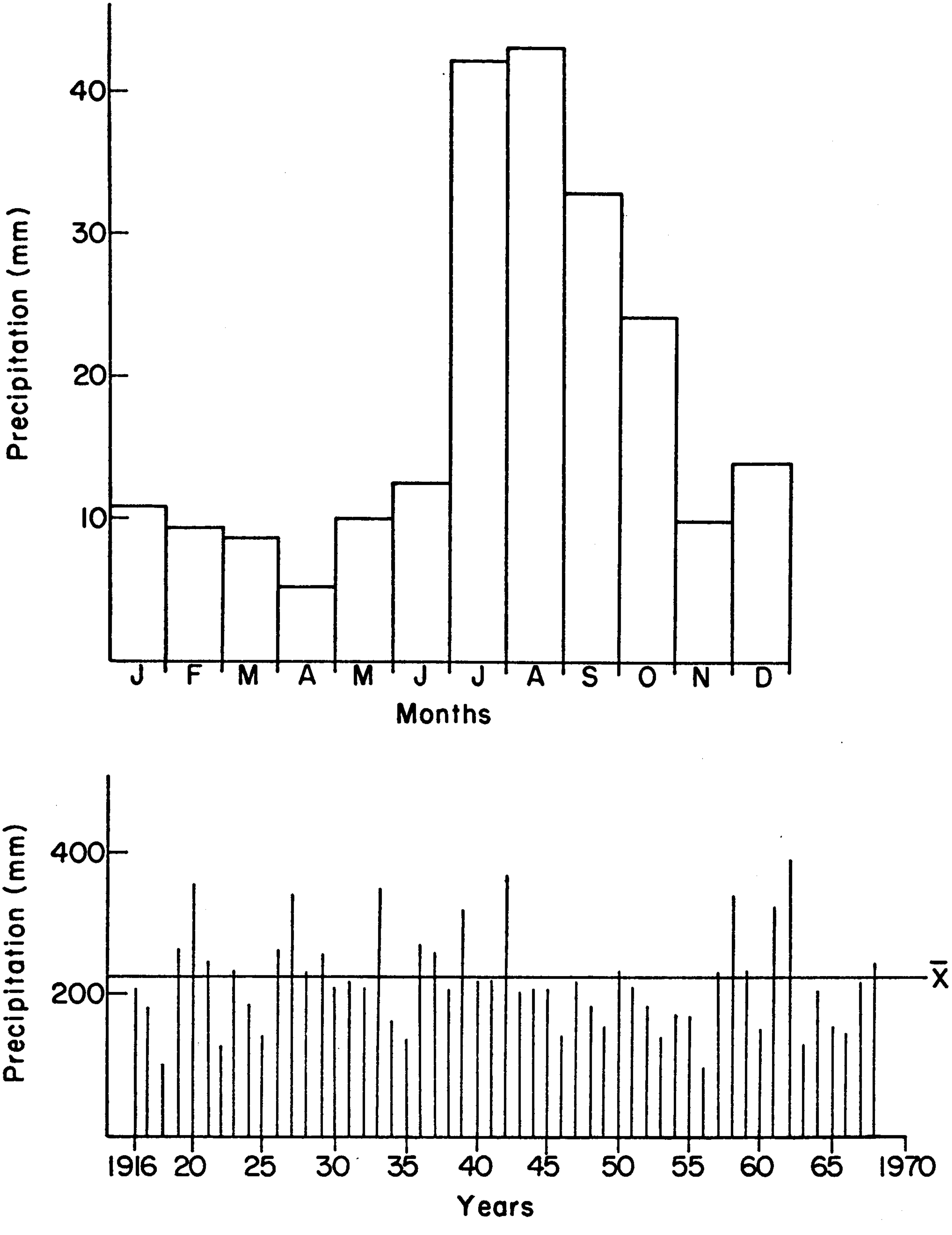

Figure 3. Monthly and yearly precipitation totals at the Jornada Headquarters.

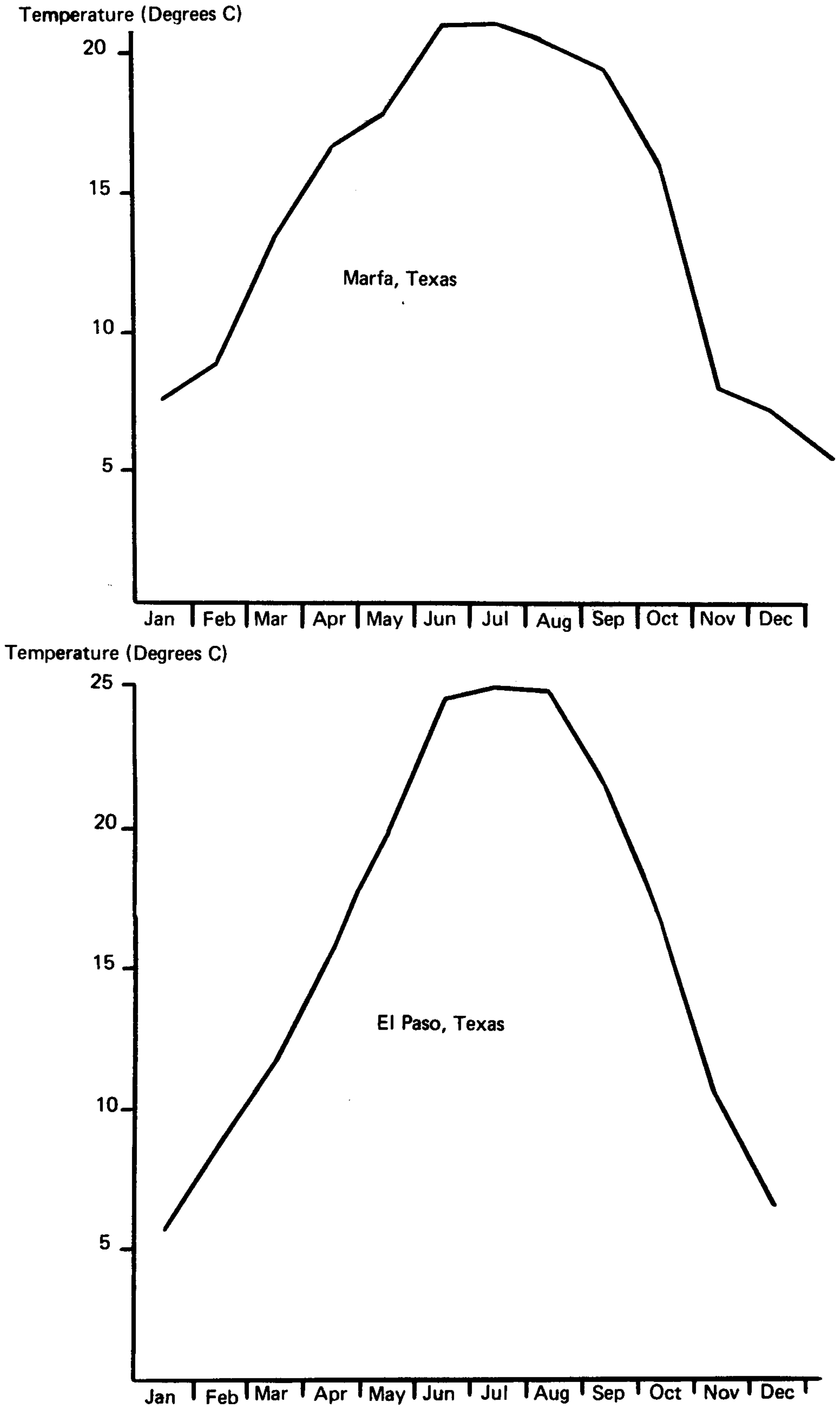

Figure 4. Average monthly temperatures for Marfa and El Paso, Texas. Taken from U.S. Weather Bureau records.

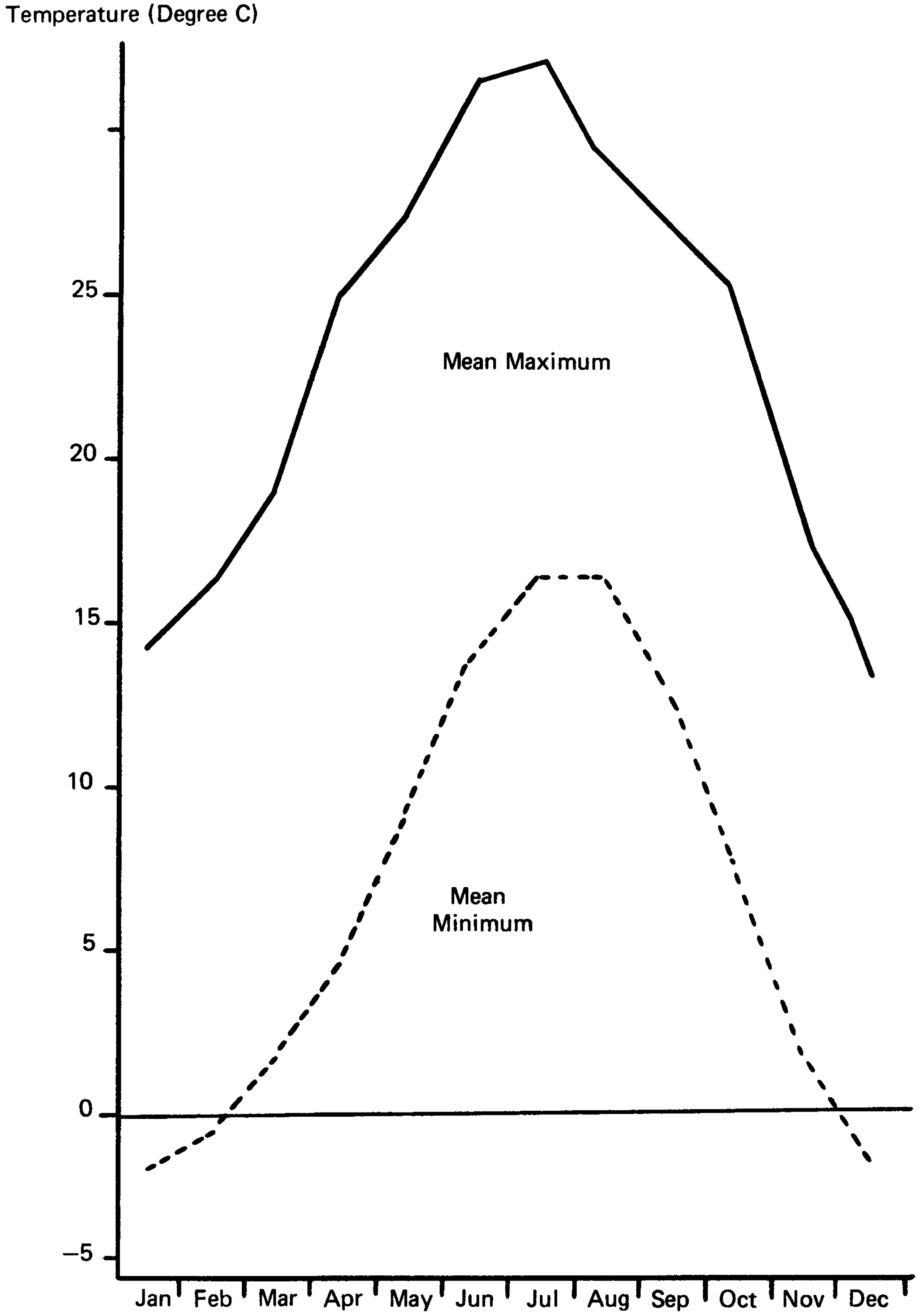

Figure 5. Monthly mean maximum and minimum temperatures at for Elgin, Arizona (From Nicholson 1972).

monthly patterns (figure 6) and are similar to those at El Paso. These patterns indicate maximum values in June-July and lowest values in December-January.

Solar Radiation

Solar radiation is high for most desert grassland areas because cloud cover is low during most seasons; elevation and particles in the atmosphere are the principal factors controlling the amount of solar radiation falling on the surface. The maximum amount of sunshine falls below 75% for Tucson only during October and December. During the spring and summer, 85% to 90% of maximum possible sunshine occurs. Both El Paso and Tucson have 85% of maximum sunshine annually. Cloud cover is below 40% during April, May, and June and in September and October. Cloud cover ranges from 43% to 48% for the rest of the year.

Most desert grasslands lie above 1000 m elevation, and the wavelengths absorbed and reflected are a function of distance traveled through the atmosphere. For 1970, total solar radiation at the Jornada was about 1.9 million kcal/m^2 (Sims and Singh 1971).

Geology, Soils, and Topography

The desert grassland area lies in three physiographic provinces (Fenneman 1931). Northern Arizona, southern Utah, and northwestern New Mexico are included in the Colorado Plateau (figure 7). Southern Arizona and southern New Mexico are in a southern extension of the Basin and Range Province. Eastern New Mexico and part of western Texas are included in the southern portion of the Great Plains Province.

The Colorado Plateau is characterized by deep canyons and plateaus.

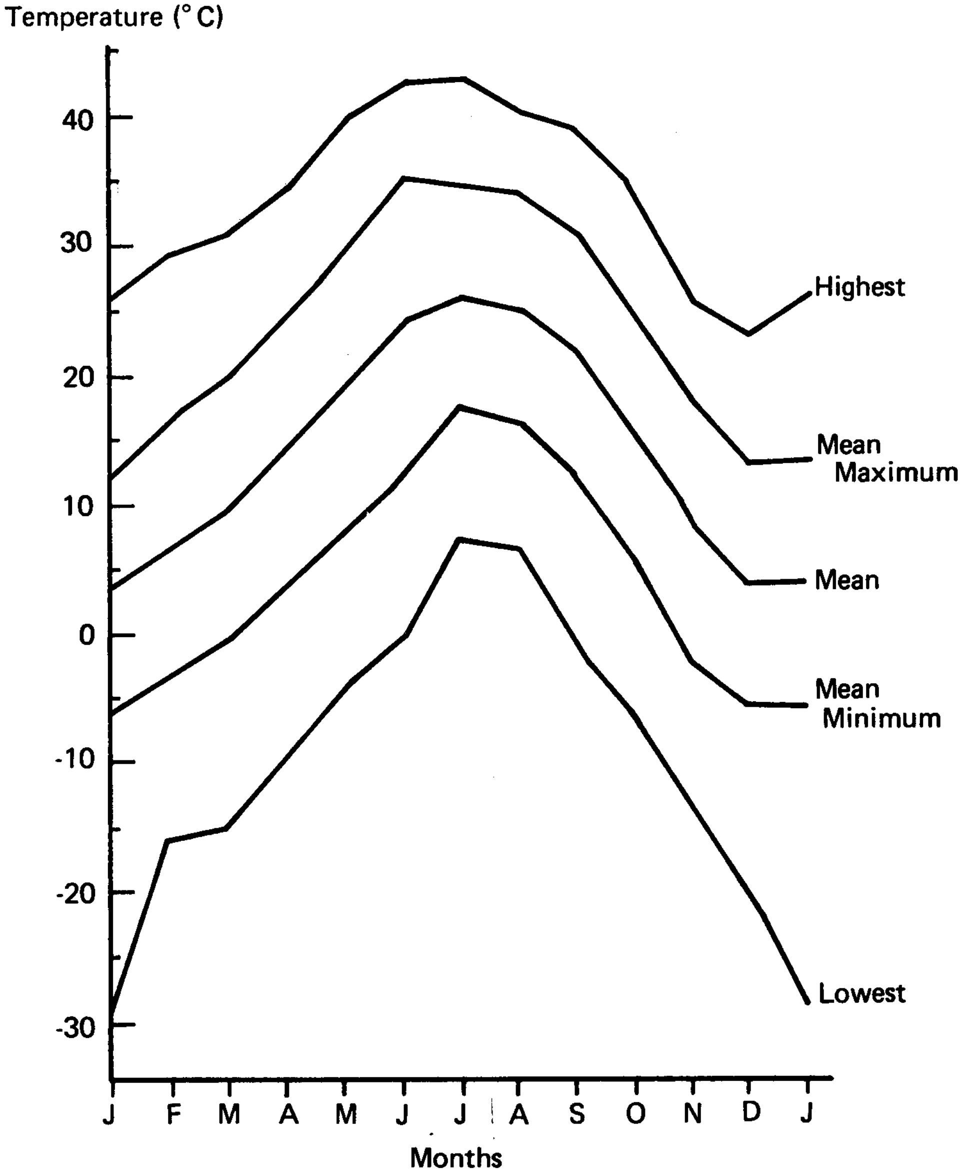

Figure 6. The annual trend of temperature at the Jornada Experimental Range (from Bryson et al. 1970).

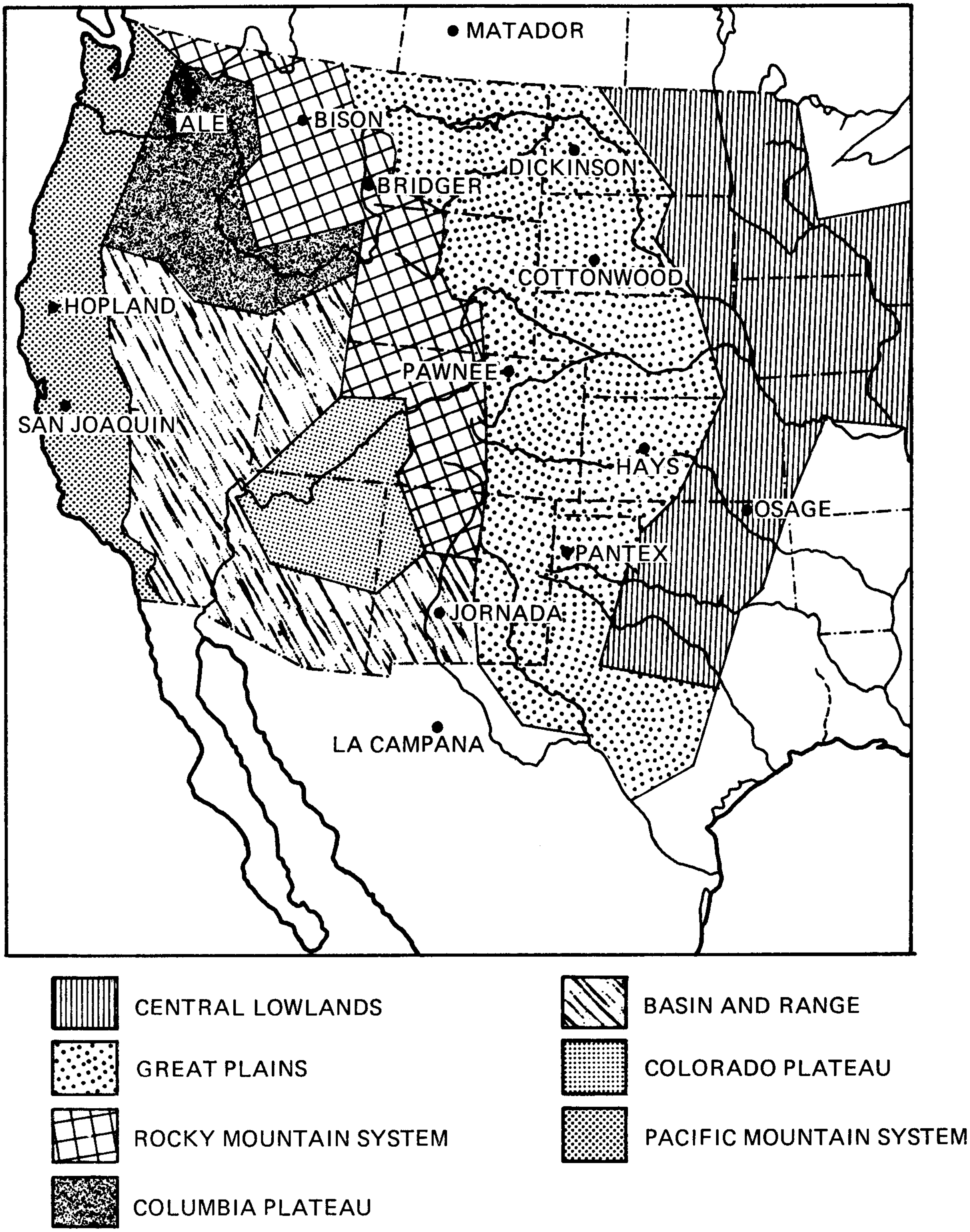

Figure 7. Geomorphic provinces of the western United States (From Smith 1973)

Much of the parent material is sedimentary limestone, although there are extensive igneous formations of volcanic nature (Fenneman 1931). Along the Grand Canyon there are 11 distinct strata of limestone, sandstone, shale, and schist, ranging to the Cambrian in age. Most of the formations are characterized by uplifting and folding in the Cretaceous, followed by extensive erosion and deposition in the Eocene, followed by further uplifting and erosion.

The Basin and Range Province is characterized by fairly level basins with gentle slopes up to the mountains and steep, narrow mountain ranges separating the valleys. These mountain ranges are often 80 to 120 km long (Fenneman 1931). Parent materials of this province are sedimentary, with some that are partially metamorphosed. The region was characterized by folding, faulting, and erosion. Some of the mountain ranges in southern New Mexico and western Texas, such as the San Andres, Caballos, Franklins, and Ord mountains were centers of volcanic activities. Many of the basins are closed with no external drainage.

The Great Plains Province is characterized by gentle topography, with some areas nearly flat and others gently rolling. Parent materials of this province include sandstones, shales, limestone, and igneous rocks. Erosion and deposition have been a continuous facet of the physiographic development.

The Jornada plain is a fairly level area between the San Andres Mountains and the Rio Grande. The soil parent material is mostly alluvial sediments from the San Andres and Dona Ana mountains (Herbel, Dittberner, and Bickle 1970). The San Andres Mountains are dominated by sedimentary rocks, especially limestone (Herbel and Gile 1973). The

Dona Ana Mountains are more complex, containing igneous rocks, primarily monzonite, rhyolite andesite, and latite, with some sedimentary rocks (Kottlowski 1960).

More than 22 soil types have been delineated for the Jornada Experimental Range by the Soil Conservation Service (Buffington and Herbel 1965, Herbel and Gile 1973).

Biotic Factors

Vegetation

The desert grassland probably follows Shreve's transitional type more closely than other classification systems. There are ecotonal problems with the shortgrass type to the east and north, the Chihuahuan and Sonoran deserts to the south and west, and the Great Basin or cool-desert types to the north and west.

Species Composition of Desert Grassland

An extensive area is shown in figure 1 as being desert grassland, but many other vegetational types are interspersed with desert grassland throughout the Southwest. Including Kuchler's (1964) types (grama-galleta steppe, grama-tobosa prairie, galleta-threeawn, grama-tobosa shrub steppe, and the trans-Pecos shrub savannah) as desert grassland, Van Dyne and Dyer (1973) calculated that the desert grassland covers 206,565 km^2, or 7% of the grasslands in the United States.

Humphrey (1958) listed three characteristic grass genera for the desert grassland: *Bouteloua*, *Hilaria*, and *Aristida*. Secondary genera were *Andropogon*, *Eragrostis*, *Heteropogon*, *Leptochloa*, and *Trichachne*.

One important grass genus, not included by Humphrey, is *Sporobolus*. Most desert grasslands are not pure stands of herbaceous species but include a conspicuous component of shrubs. Important shrubby genera listed by Humphrey included *Opuntia, Prosopis, Acacia, Yucca, Flourensia,* and *Happlopappus*. In New Mexico and Texas, *Gutierrezia (Xanthocephalum)* is also important.

The two most important species of *Bouteloua* are probably blue grama (*B. gracilis*) and black grama (*B. eriopoda*). Blue grama, much more widely distributed than black grama, grows from Canada to Mexico and from the Great Basin to the eastern deciduous forests. Black grama is restricted to the Southwest, where it grows best on fairly coarse soils. Blue grama is resistant to grazing (Bement 1969), but black grama is fairly susceptible (Valentinte 1970, Paulsen and Ares 1962).

Other gramas such as sideoats (*B. curtipendula)* and hairy grama (*B. hirsuta*) are also important, but somewhat more restricted in distribution. In southern Arizona, several other gramas are important in open grassland types. These include *B. rothrockii, B. eludens, B. chrondiosiodes,* and *B. filiformis*. All these species, plus black, sideoats, hairy, and blue grama were correlated with topography, elevation, aspect, and soil properties (Nicholson 1972, Wallmo 1955, and Haase and Schreiber 1972). Certain species exhibited greater abundance on some sites than others.

The three important species of *Hilaria* are galleta (*H. jamesii*), tobosa (*H. mutica*), and curly mesquite (*H. belangeri*). Galleta is found mostly in southern Utah, northern Arizona, and New Mexico (West et al. 1972). Tobosa is morphologically similar to galleta, but generally occurs further south although there is some overlap in their ranges (West et al. 1972). Curly mesquite is important in western Texas and southern Arizona, but not so abundant in southern New Mexico.

Several species of *Aristida* (three-awns) are important. Humphrey (1958) lists *A. divaricata, A. hamulosa, A. glabrata,* and *A. longiseta* as important three-awn species. In addition, there are many widely distributed annual species.

Table 3 shows the vegetational composition of several representative desert grassand areas. The vegetation at Fort Stanton, which is in the foothills at about 2200 to 2500 m elevation, is similar to the grasslands of the San Augustin Plains of western New Mexico, with blue grama the dominant herbaceous species. Ute Mountain in northern New Mexico is dominated by galleta with other Great Basin species. The area near Tombstone, Arizona, is dominated by several species of grama grasses (table 3).

In general, taller species that require relatively high levels of soil water such as *Andropogon, Trichachne,* and *Leptochloa,* occur in southern Arizona and western Texas rather than southern New Mexico. The drier zone in central New Mexico, with precipitation increasing both eastward and westward is probably responsible for vegetation differences.

The vegetation is considerably different on the Santa Rita Experimental Range in southern Arizona and the Jornada in southern New Mexico. On the Santa Rita area, perennial grass distribution is related to elevation and rainfall (Martin and Reynolds 1973). At lower and middle elevations, Santa Rita three awn (*A. glabrata*) and rothrock

Table 3. Vegetational composition of several grassland areas included within the desert grassland.

	Ft. Stanton[a/] Composition (%)	Ute Mt.[b/] Composition (%)	San Augustin[c/] Plains Composition (%)	Tombstone[d/] Frequency (%)
Grasses				
Bouteloua gracilis	69		43	10
Bouteloua curtipendula	26			38
Hilaria jamesii		33		
Lycurus phleaides	1			
Sporobolus airoides		13		
Oryzopsis hymenoides		9		
Bouteloua chondrosoides				20
Bouteloua hirsuta	Tr			16
Bouteloua eriopoda	Tr			75
Aristida spp.	Tr			28
Munroa squarrosa			11	
Aristida adscenionis			2	
Aristida divaricata			1	
Sporobolus cryptandrus	71		5	
Tridens puchellus				20
Tridens muticus				21
Forbs				
Salsola kali			20	
Amaranthus spp.			4	
Aster arenosus			3	
Sphaeralcea coccinea	Tr		2	
Zinnia grandiflora	Tr		1	
Psilostrophe spp.			1	
Artemisia caruthii	>1			
Calliandra spp.				21
Croton corymbulosus				32
Other forbs	2	1		
Annuals		41		
Shrubs				
Gutierrezia sarothrae		>1		
Atriplex confertifolia		2		
Atriplex canescens		>2		

[a/] From Pieper, Montoya, and Groce 1971.

[b/] From West et al. 1972.

[c/] From Potter 1957.

[d/] From Haase and Schrieber 1972.

grama are common. Bush muhly (*Muhlenbergia porteri*) is also abundant at middle elevations. At the higher elevations black grama, slender grama (*B. filiformis*), sideoats (*B. curtipendula*), sprucetop (*B. chondrosioides*), and hairy (*B. hirsuta*) grama comprise more than 60% of the cover. Arizona cottontop (*Digitaria californica*) is abundant at all elevations (Martin and Reynolds 1973). *Aristida hamulosa* and *A. ternipes* (considered tall three awns) are common at all elevations.

At the Jornada, black grama is the dominant grass species on upland sites in good condition, along with mesa dropseed (*S. flexuosus*) and three awns (*A. purpurea* and *A. longiseta*). On the flood plains tobosa (*H. mutica*) and burrograss (*Scleropogon brevifolius*) are dominant (Herbel and Pieper 1972, Little and Campbell 1943). Soaptree yucca (*Y. elata*) is a conspicuous component of even good condition grassland.

A large variety of forbs occur at both stations. Some of the annual grasses, such as six-weeks grama (*B. barbata*), needle grama (*B. aristidoides*), and six-weeks three awn are common to both stations.

Shrub invasion into grassland areas has been a widespread phenomenon over the past 100 years in the West, especially in the Southwest. In southern Arizona, creosotebush (*Larrea divaricata*), burroweed (*H. tenuisectus*), cholla cactus (*Opuntia supp.*), and mesquite have increased considerably (Humphrey and Mehrohoff 1958, Brown 1950, Glendening 1952, Glendening and Paulsen 1955, and Martin and Reynolds 1973). According to Humphrey and Mehrhoff (1952), the most rapid increase occurred between 1904 and 1934. Cholla cactus and burroweed populations seem somewhat lower than they were 5 to 15 years ago (Martin and Reynolds 1973). Burroweed populations seem to increase during periods of dry winters (Cable 1969) and to be related to soil characteristics, including pH (Meyer 1973). Causes for shifts in cholla populations appear more complicated.

Invasion by mesquite and creosotebush seems to be more permanent. Changes in shrubby species have been followed by careful evaluation of old survey reports on the Jornada Experimental Range (Buffington and Herbel 1965). These authors studied invasion of mesquite, creosotebush, and tarbush (*Flourensia cernua*) by soil type. Areas with 55% to 100% mesquite increased from just over 2500 ha in 1858 to 26,771 ha in 1963 (table 4). Dense stands of creosotebush increased from 0 to 5,013 ha, and dense stands of tarbush increased from 0 to over 1,775 ha. Over half the area was considered free from brush in 1858, but none was considered free from brush in 1963 (table 4).

Humphrey listed possible factors involved in the invasion of shrubs into desert grassland as: (1) increase of livestock grazing, (2) climatic change, (3) increased competition among species, (4) rabbits and rodents, and (5) more effective fire control. Several workers indict livestock grazing as responsible for brush increase (Gardner 1950, Gardner 1951, and Dick-Peddie 1965). Certainly, livestock have had a dramatic impact on other desert grassland components and are probably the distributing agent for mesquite. However, Buffington and Herbel (1965) pointed out that many long-term exclosures have been invaded by shrubby species. Climatic records have been kept for a relatively short time and no discernible drying trend is evident for the last 100 years (Humphrey 1958, Buffington and Herbel 1965).

Small rodents and rabbits have a great impact on some desert

Table 4. Areas (ha) with various degrees of brush composition on the Jornada Experimental Range (from Buffington and Herbel 1965).

Vegetation Type	Brush Composition (%)	Year			
		1858	1915	1928	1963
Grassland, no brush		33,843	14,350	13,287	0
Mesquite	1-15	303	6,125	8,413	5,972
	16-55	8,933	4,407	6,014	4,368
	56-100	2,536	13,053	12,009	26,771
Mesquite-creosotebush	1-15	0	51	125	0
	16-55	3,737	0	153	26
	56-100	0	255	0	723
Creosotebush	1-15	0	0	0	0
	16-55	260	0	472	0
	56-100	0	375	756	5,013
Creosotebush-tarbush	1-15	0	149	641	0
	16-55	102	10,955	1,338	473
	56-100	0	981	3,005	1,973
Tarbush	1-15	1,096	1,295	1,746	1,112
	16-55	2,573	2,941	3,741	1,907
	56-100	0	290	560	1,775
Tarbush-mesquite	1-15	0	17	166	957
	16-55	203	300	165	811
	56-100	0	0	410	699
Tarbush-mesquite-creosotebush	1-15	231	173	293	71
	16-55	3,876	1,152	2,665	0
	56-100	775	1,600	2,509	5,816
Total		58,468	58,468	58,468	58,468

grassland components (Wood 1969), but there seems to be no evidence that these animals are increasing. Most observers feel that deteriorated range attracts these animals, but that the animals are not directly responsible for the reduction in grass cover or the increase in shrubs (Humphrey 1958, and Buffington and Herbel 1965). In some instances competition from grasses may be a factor in suppressing brush invasion. Grazing would give the advantage to the brush over the grass.

Humphrey (1958, 1962) considered fire the principal mechanism for suppressing shrub invasion into grassland areas. He considered the desert grassland a fire disclimax. Fire frequencies have been reduced by improved detection and better control. Some areas of desert grassland, however, probably support insufficient fuel to carry a fire. Results from accidental burns and controlled fires have been variable (Wright 1974). Most mature shrubs are fairly resistant to fire, but small seedlings are much more susceptible. Fires in desert grassland were undoubtedly a historic factor, and the reduction of their frequency has probably had pronounced effects, but these are difficult to evaluate.

It is likely that all five of these factors, along with others, have been responsible for vegetational shifts (Buffington and Herbel 1965). Any one factor is unlikely to be the controlling one over the whole area.

Animals

Animals exhibit many adaptations to the hot, dry conditions found in desert grasslands. Many of these adaptations result from water balance problems since most desert grasslands are characterized by definite wet and dry seasons with overall aridity the norm. Chief among these are the physiological ability to conserve water in time of drought stress.

Large Mammals

The pronghorn antelope (*Antilocapra americana*) was perhaps the major large herbivore in desert grasslands before cattle were brought to North America (bison occurrence was sporadic in the eastern part of the desert grasslands area). Yoakum (1968) estimated that there were 35 million pronghorn antelope in North America in 1805. Within 75 years, there were only about 20,000 individuals. From 1924 to 1964, pronghorns increased about 100%. The original pronghorn distribution included western Texas and all of Arizona and New Mexico (Einarsen 1948, Yoakum 1972) (figure 8).

Of the principal desert grassland states, New Mexico has the largest range and greatest numbers of pronghorn (Yoakum 1972) (table 5). Arizona and Texas each had about 10,000 head of pronghorn in 1964. Numbers apparently have stabilized somewhat in the past 10 to 15 years. In Texas, there is a Panhandle and trans-Pecos herd and a small herd in the Permian Basin (Hailey and De Arment 1972, De Arment 1966). The Texas population has fluctuated from a high of 12,000 head in 1961 to a low of about 5,000 head in 1964.

Small Mammals

Desert grasslands are well known for the presence of a large variety and number of small mammals. Among the rodents, most are in

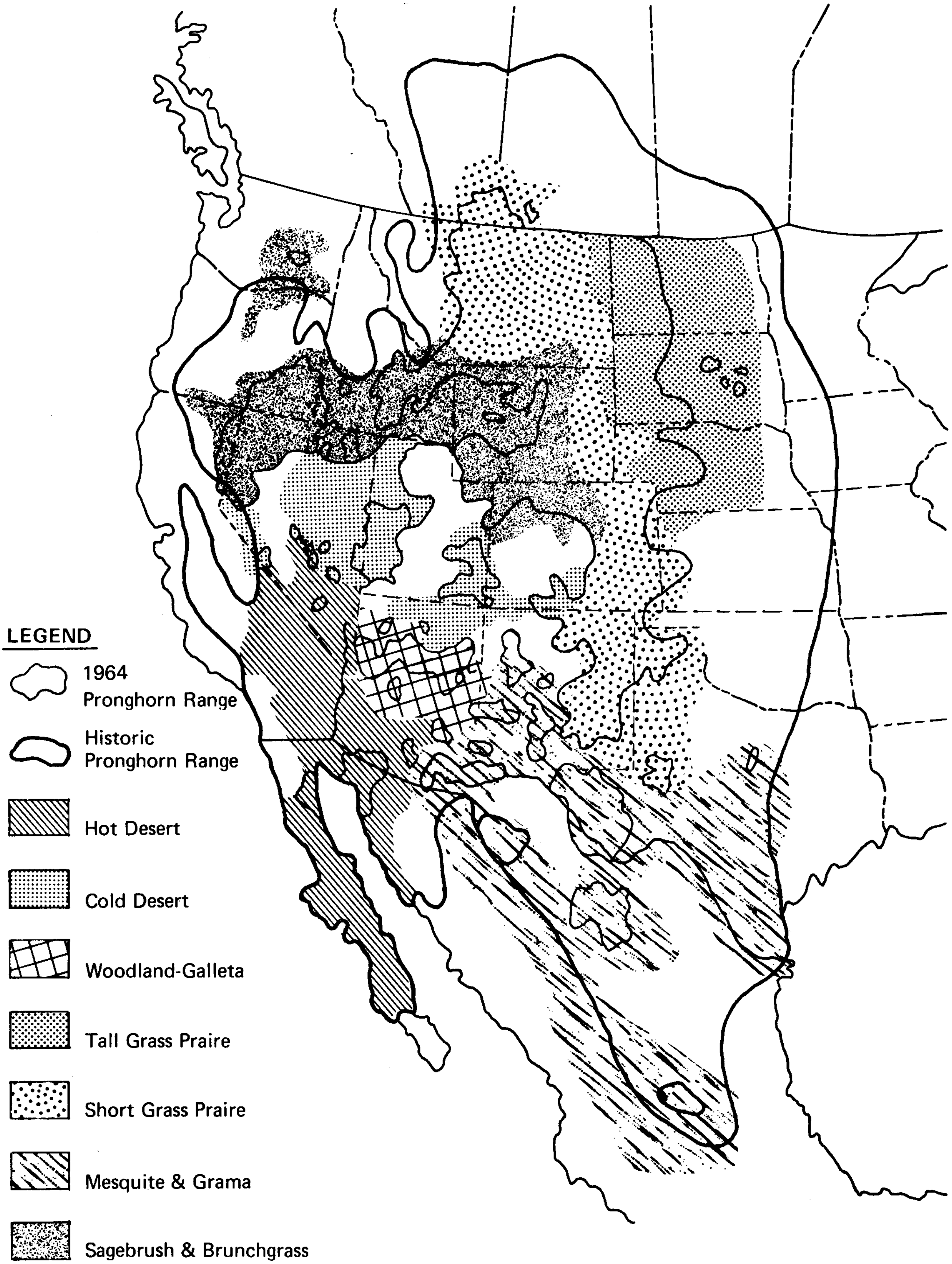

Figure 8. Pronghorn antelope distribution in desert grasslands (From Yoakum 1972).

Table 5. Pronghorn antelope population numbers[a] in Arizona, New Mexico, and Texas for various years

State	1924	1958	1964	Range (km^2)
Arizona	650	8,500	10,000	2,714
New Mexico	1,680	25,000	22,500	23,206
Texas	2,410	11,000	9,380	1,448

[a] Numbers for 1924 and 1964 are from Yoakum (1968); numbers for 1958 are from Buechner (1960).

the family Heteromyidae with a few species of Cricetidae and one of Sciuridae. Many of these are also well distributed in the Chihuahuan and Sonoran deserts. Rodents are likely the most important small mammals in terms of numbers and biomass. In terms of number of species, bats are second only to the rodents. Their occurrence in large concentrations in warmer months around playa lakes and stock ponds doubtlessly has considerable impact on local food webs.

Several species of kangaroo rats, such as Ord's (*Dipodgmys ordii*), Merriam's (*D. merrian*), and the banner-tailed kangaroo rat (*D. spectabilis*), are common in desert and desert grassland conditions (table 6). The table indicates those species found on the Jornada as well as those also listed for the Santa Rita (Martin and Reynolds 1973) and for trans-Pecos area of Texas (Davis 1966). Additional species listed for the Santa Rita included the gray-tailed antelope squirrel (*Spermophilus tereticaudus*), Bailey pocket mouse (*Perognathus baileyi*), Merriam pocket mouse (*Peromyscus merriam*), ringtail (*Bassariscus astutus*), and the hog-nosed skunk (*Conepatus mesoleucus*). The antelope jackrabbit (*Lepus alleni*) also occurs in relatively high numbers on the Santa Rita Experimental Range and throughout southern Arizona. Buechner (1950b) also listed the prairie dog (*Cynomys ludovicianus*) and pocket gopher (*Thomomys bottae*) for Trans-Pecos, Texas. These are not intended to be inclusive lists, but rather to indicate the general mammalian species present on these areas.

The black-tailed jackrabbit (*Lepus californica*) is the principal species of jackrabbit in the desert grassland (figure 9). It occurs throughout western Texas, New Mexico, and Arizona (Taylor 1948, Davis

Table 6. List of mammals present on grassland areas on Jornada Experimental Range (from Rogers 1965, Packard 1971).

Common Name	Scientific Name		
Bats			
California myotis	*Myotis californicus*		
Yuma myotis	*Myotis yumanensis*		
Cave myotis	*Myotis velifer*		
Fringed myotis	*Myotis thysanodes*		
Western pipistrelle	*Pipistrellus hesperus*		
Townsend's big-eared bat	*Plecotus townsendii*		
Pallid bat	*Antrozous pallidus*		
Brazilian free-tailed bat	*Tadarida brasiliensis*		
Rodents			
Ord's kangaroo rat	*Dipodomys ordii*		
Merriam's kangaroo rat	*Dipodomys merriami*	S[a/]	
Banner-tailed kangaroo rat	*Dipodomys spectabilis*	S	T[b/]
White-throated wood rat	*Neotoma albigula*	S	
Southern plains wood rat	*Neotoma micropus*		
Silky pocket mouse	*Perognathus flavus*	S	
Apache pocket mouse	*Perognathus apache*		
Peniciliate pocket mouse	*Perognathus penicillatus*	S	
Grasshopper mouse	*Onychomys leucogaster*		
White-footed mouse	*Peromyscus maniculatus*		
Spotted ground squirrel	*Spermophilus spilosoma*		T
Cotton rat	*Sigmodon hispidus*		
Harvest mouse	*Reithrodontomys megalotis*	S	
Lagomorphs			
Desert cottontail	*Sylvilagus auduboni*		T
Black-tailed jackrabbit	*Lepus californicus*	S	
Artiodactylas			
Pronghorn antelope	*Antilocapra americana*		T
Carnivores			
Coyote	*Canis latrans*		T
Bobcat	*Lynx rufus*	S	
Badger	*Taxidea taxus*	S	T
Desert fox	*Vulpes macrotis*		
Striped skunk	*Mephitis mephitis*	S	
Gray fox	*Urocyon cinereoargenteus*	S	
Long-tailed weasel	*Mustela frenata*		

[a/] S indicates that the species were also listed for the Santa Rita Experimental Range by Martin and Reynolds (1973).

[b/] T indicates that the species were listed by Davis (1966) for the trans-Pecos, Texas, area.

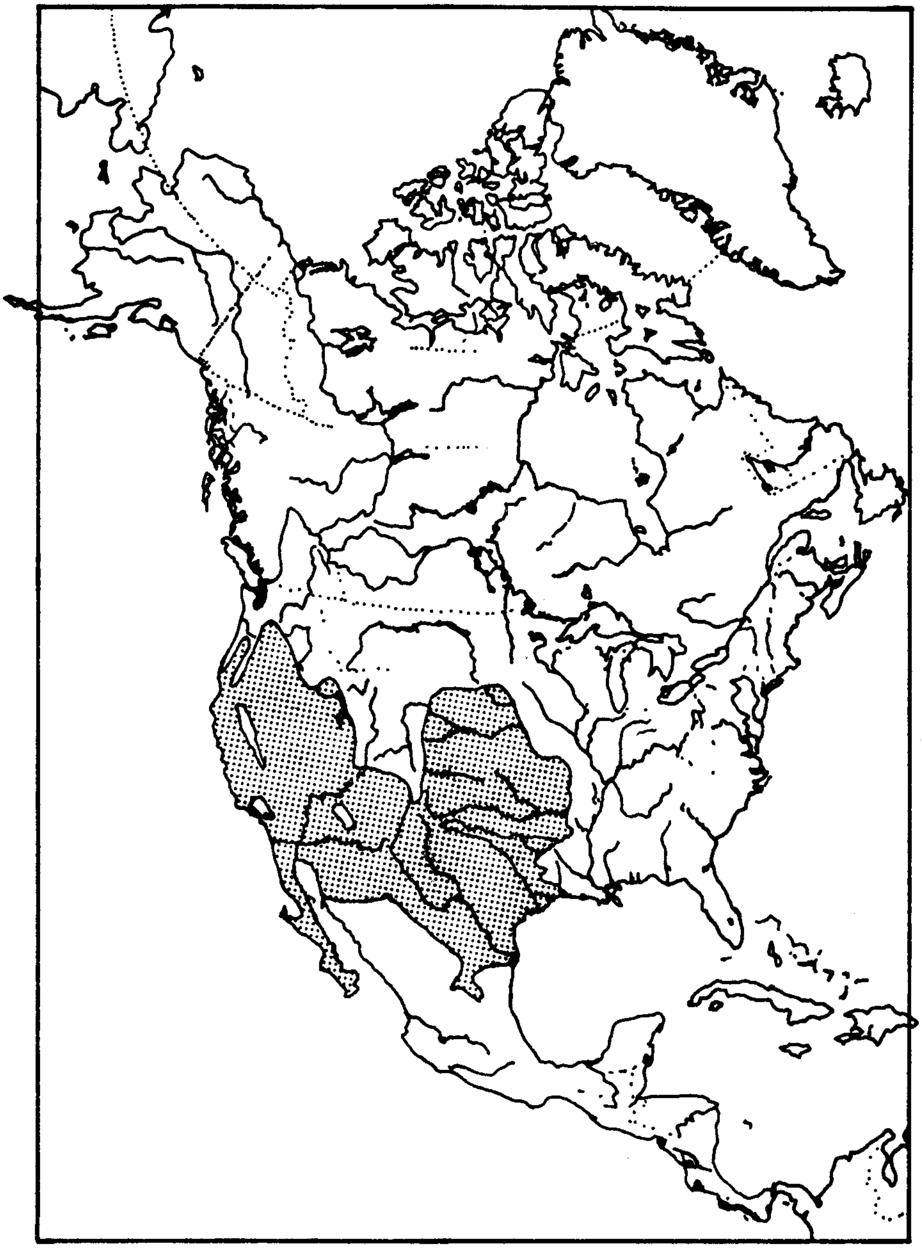

Figure 9. The distribution of the black-tailed jackribbit in North America (From Hansen and Flinders 1969).

and Robertson 1944). Both the antelope jackrabbit and Gaillard's jackrabbit (*Lepus gaillardii*) are found in limited areas in northern Mexico and Arizona (Hansen and Flinders 1969, Palmer 1954).

Species of the genus *Dipodomys* are distributed throughtout the arid and semi-arid regions of the western United States. Merriam's kangaroo rat is distributed throughout lower elevation areas in Arizona, southern California, Nevada, New Mexico, and Texas. Ord's kangaroo rat is found not only in the Southwest, but also in the cool deserts of the Great Basin into southern Idaho (Johnson 1961). The bannertailed kangaroo rat is found in western Texas and along the Rio Grande and Pecos River and in northwestern New Mexico (Monson and Kessler 1940, Bailey 1931) and in southern Arizona.

The white-throated wood rat (*Neotoma albigula*) occurs in most of Arizona, New Mexico, western Texas, and in the states of Sonora, Chihuahua, and Coahuila, Mexico (Vorhies and Taylor 1940).

Except for the jackrabbit, most of these small mammals do not exhibit a regular cyclic pattern, but apparently respond to weather variations and changes in food supply. In southern Nevada, rodent numbers and reproduction seems to be directly related to winter annuals (Beatley 1969).

The impact of rodents and rabbits on western rangelands has received wide study. Most authors feel that small mammals are not primarily responsible for range deterioration but find some lower stage of secondary succession a more suitable habitat (Norris 1950, Wood 1969, Lewis 1970, Monson and Kessler 1940). On New Mexico State University's College Ranch, adjacent to the Jornada Experimental Range, Norris (1950) found kangaroo rat densities three times greater on mesquite sandhills than on black grama grassland (table 7). Gray wood rat densities were also much higher in mesquite sandhills than in grassland, but ground squirrel populations were low in all vegetational types.

Coyotes appear to be the major carnivore throughout the desert grassland region, although several other predators may be important locally.

Birds

The dominant species of birds on several desert-grassland areas, two representative grassland communities, and two representative desert communities are listed in table 8. Desert grassland avifaunas are intermediate in several ways between those of grasslands and deserts; the intermediate species diversity is apparent from the table. The faunistic similarities may be evaluated from figure 10, which shows the ordination of the passerine data from table 8 by the method of principal components analyses. The closer the positions in the ordinations of the locations, the more similar are the avifaunas of those locations. Desert grasslands tend to be intermediate between deserts and grasslands rather than having any well defined species of their own. There is a tendency for the desert grassland sites to be similar to the desert shrub community nearby. Thus, the desert grassland at the Santa Rita IBP site shares a variety of species with the nearby Sonoran Desert site at Silver Bell, and the Jornada desert grassland shares a variety of species with the nearby Chihuahuan Desert IBP shrub site--the Bajada. The danger of considering only summer data is apparent in the affinities

Table 7. Density of rodents and rodent dens on different vegetational types in southern New Mexico (from Norris 1950).

Rodent	Grassland		Snakeweed-grass[a]		Mesquite Sandhills	
	No. Dens per ha	No. Rodents[b]	No. Dens per ha	No. Rodents	No. Dens per ha	No. Rodents
Kangaroo rats	4.3	44.0	5.3	55.0	34.3	131.0
Miscellaneous mice[c]	4.5	0.0	11.0	4.0	43.0	1.0
Ground squirrel	2.3	1.0	3.5	0.0	5.0	1.0
Wood rat	0.5	2.0	1.3	3.0	1.3	18.0
Total	11.6	47.0	11.1	62.0	83.6	159.0

[a] This type also included some creosotebush areas for den density.

[b] Rodent numbers are for seven lines each with ten snap traps run for five nights for each vegetational type.

[c] Included, grasshopper mouse, harvest mouse, and pocket mouse.

Table 8. Bird species occurring on various **desert grassland and related sites.**

Common Name	Scientific Name	Desert Gasslands						Grasslands		Deserts	
		Jornada		Santa Rita		Mixed-grass	Short-grass				
		Summer	Winter	Summer	Winter			Short	Tall	Chihuahuan	Sonoran
Turkey Vulture	*Cathartes aura*	1		1		1	1			1	
Swainson's Hawk	*Buteo swainsoni*	1									
Ferruginous Hawk	*Buteo regalis*		1						1		
Hen Harrier	*Circus cyaneus*		1						1		
Prairie Falcon	*Falco mexicanus*	1	1				1	1			
Scaled Quail	*Callipepela squamata*	1	1		1		1				
Gambel's Quail	*Lophortyx gambelli*			1	1					1	1
Bobwhite Quail	*Colinus virginianus*								1		
Upland Sandpiper	*Batramia longicauda*								1		
Killdeer Plover	*Charadruius vociferus*								1		
White-winged Dove	*Zenaida asiatica*			1							1
Mourning Dove	*Zenaida macroura*	1	1	1	1	1	1	1	1	1	1
Roadrunner	*Geococcyx californianus*	1	1	1	1	1	1				
Burrowing Owl	*Speotyto cunicularia*	1									
Gilded Flicker	*Colaptes chysoides*			1	1						1
Gila Woodpecker	*Centurus uropygialis*			1	1						1
Nighthawk sp.	*Chordeiles minor/ accutipennis*	1	1			1	1			1	1
Ladder-backed Woodpecker	*Dendrocopus scalaris*			1	1		1				1
Western Kingbird	*Tyrannus verticalis*	1				1					
Ash-throated Flycatcher	*Myiarchus cinerascens*	1		1		1	1				1
Wied's Crested Flycatcher	*Myiarchus*										1
Say's Phoebe	*Sayornis saya*		1				1				
White-necked Raven	*Corvus cryptoleucus*	1					1				
Horned Lark	*Eremophila alpestris*		1					1	1		
Verdin	*Auriparus flaviceps*			1	1	1	1			1	1
Cactus Wren	*C. brunneicapillus*	1	1	1	1	1	1			1	1
Mockingbird	*Mimus polyglottus*	1				1				1	
Curve-billed Thrasher	*Toxostoma curvirostre*			1	1						1
Crissal Thrasher	*Toxostoma dorsale*									1	
Black-tailed Gnatcatcher	*Polioptila melanura*			1	1		1			1	1
Loggerhead Shrike	*Lanius ludovicianus*	1	1			1	1	1	1	1	
Meadowlark species	*Sturnella magna/ neglecta*	1	1			1					
Scott' Oriole	*Icterus parisorum*	1				1	1			1	
Cowbird	*Molotrus ater*			1	1		1			1	1
Blue Crosbeak	*Guirica caerula*					1					
Pyrrhuloxia	*Pyrrhuloxia pyrrhuloxia*						1				1
Dickcissel	*Spiza americana*								1		
House finch	*Carpodacus mexicanus*							1		1	
Brown Towhee	*Pipilo fuscus*			1	1		1				1
Lark Bunting	*Calamospiza melanocorys*		1					1			
Grasshopper	*Passerculus sandwichensis*										
Vesper Sparrow	*Pooectes gramineus*		1								
Cassin's Sparrow	*Aimophila cassini*				1						
Rufous-winged Sparrow	*Aimophila carpalis*			1	1						
Rufous-crowned Sparrow	*Aimophila ruficleps*						1				
Black-throated Sparrow	*Amphispiza bilineata*				1	1	1			1	1
Sage Sparrow	*Amphispiza belli*		1								
Brewer's Sparrow	*Spizellu breweri*		1		1						
McCown's Longspur	*Calcarius mccownii*							1			
Chestnut-collared Longspur	*Calcarius ornatus*		1					1			

*1 (not defined).

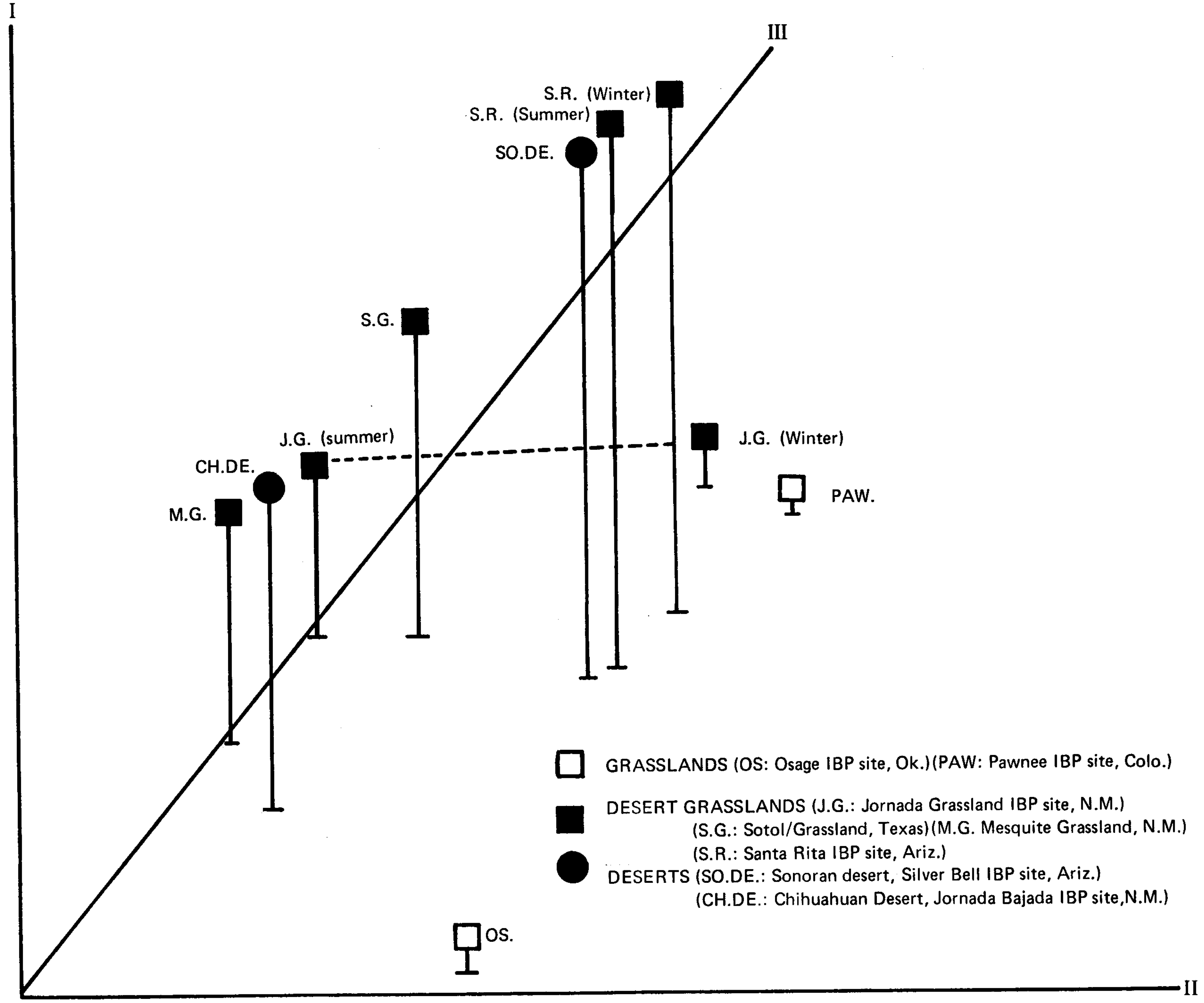

Fig. 10. Ordination of desert and grassland avifaunas along first three principal components (I, II & III).

of the Jornada. In summer the fauna is dominated by insectivores, many of which it shares with the Bajada; in winter the fauna is dominated by granivores, which are many times more numerous than the insectivores and which originate largely in shortgrass prairie regions further north. For example, during the winter, the Jornada has many faunal similarities with the region typified by the Pawnee grassland site.

On the Jornada some of the breeding species are yearlong residents, such as the loggerhead shrike and cactus wren, but the majority appear to be summer visitors, such as the western kingbird, mockingbird, and Scott's oriole. Of the larger seedeaters, quail are resident but mourning doves, though present usually all year round, fluctuate dramatically in numbers as migrants arrive and leave. The smaller seedeaters such as lark buntings, brewer's sparrows, sage sparrows, and horned larks tend to be non-breeding season visitors from July until mid-May, although occasionally some horned larks remain and breed on areas dominated by tobosa grass.

In summer the most important species of raptor is the Swainson's hawk--the only raptor that nests in any numbers on the area. In winter more species are present; marsh hawks are perhaps the commonest, with lesser numbers of red-tailed and ferruginous hawks and golden eagles.

Reptiles

A list of the lizard fauna of the Jornada desert grasslands is presented in table 9 with an indication of the relative density. The most abundant species in Chihuahuan desert grasslands are *Cnemidophorus tigris* and *Phrynosoma cornutum*. These species prey preferentially on social insects. *Cnemidophorus tigris* feeds primarily on termites when

Table 9. Species composition of the lizard fauna of the Jornada desert grasslands in southern New Mexico. In the first column, the number of +'s indicates relative abundance of the species which are characteristic of desert grasslands, an * indicates those species which occur infrequently in deserts. Species reported common in other desert grasslands are indicated in the second column (data furnished by Walter G. Whitford, Desert Biome, IBP).

Species	Relative Abundance	
Cnemidophorus tigris	++++	
Cnemidophorus tesselatus	++	
Cnemidophorus inornatus	*	
Crotaphytus wislizenii	+	
Eumeces obsoletus	*	
Holbrookia maculata	+	+++[a]
Phrynosoma cornutum	+++	
Phrynosoma modestum	+	
Sceloporus magister	+	
Uta stansburiana	+	+++[b]

[a] Gennaro 1972.

[b] Tinkle 1967.

these are available (Milstead and Tinkle 1969, Echternacht 1967, Pianka 1970), and *Phrynosoma cornutum* preferentially feeds on harvester ants. High densities of social insect predators probably reflect the greater predictability and availability of these arthropods than other arthropod groups.

Invertebrates

Although little has been done concerning the biology and ecology of desert grassland invertebrates as a group, a sizeable effort has gone toward evaluation of the economically destructive species. Grasshoppers, potentially the most damaging group, have received considerable attention because they may consume a vast amount of valuable forage and thus compete with livestock and wildlife for food. A list of potentially damaging species by geographical area may be found in Hewitt et al. (1974). Nerney (1960) measured populations of four dominant grasshopper species on the San Carlos Indian Reservation in eastern Arizona in 1953 to 1955. Densities of *Aulocara elliotii*, *Melanoplus bilitauratus*, *M. cuneatus*, and *Hadrotettix tritrasciatus* varied from $7.5/m^2$ to about $23/m^2$ with an average of about $10/m^2$. During severe outbreak conditions, densities may be much higher, on the order of $50/m^2$ or more.

Harvester ants are probably second in importance to grasshoppers in the desert grassland. In the spring, the activities of these ants involve cutting off and removing emerging seedlings as well as established grasses and forbs in the area surrounding the mound of the colony. The result, through time, is an increasing area of bare soil around the mound. In the San Augustin Plains of New Mexico, Race (1966) found an average of 42 colonies of the western harvester ant (*Pogonomyrmex occidentalis* Cresson) per hectare. The area of vegetation cleared away per colony ranged from 3.58 m2 to 7.29 m^2.

Harvester ants also gather seed and move soil throughout the various horizons in the construction of their chambers and tunnels. Seed gathering is of questionable importance as to its effects on stands of grasslands, especially perennial grasses, which reproduce primarily by stolons (Hewitt et al. 1974). Soil movement is considered beneficial because of its effects on soil aeration.

Among other chewing insects of importance to the desert grassland is the range caterpillar (*Hemileuca oliviae* Cockerell), whose distribution is limited primarily to elevations between 1,740 and 2,440 m in northeastern and east-central New Mexico, although it may occasionally extend into extreme southern Colorado and the western fringe of the Texas Panhandle. The range caterpillar consumes grasses, feeding often down to the crown and leaving unconsumed portions of the blades. It also restricts grazing because the larvae posses urticarial spines that irritate the tender skin around the mouths of cattle. At times, densities of the range caterpillar have been observed to exceed 200/m^2 (Hewitt et al. 1974).

Additional chewing insects of regional significance in the desert grassland include the termites and white grubs. Among the termites, *Gnathamitermes tubiformans* occurs in New Mexico, Texas, Arizona, and northern Mexico (Snyder 1949, Light 1946). This termite constructs tubular mud galleries around the stems of plants on which it feeds; it may disturb large areas of growing vegetation on grazing lands (Weesner 1970). Other termites on the New Mexico desert grassland have been observed to utilize *Lepus californicus* fecel pellets, *Ephedra trifurca* stems, *Prosopis grandulosa* branches, dry basal shoots of *Hilaria mutica*, and an occasional fallen stalk of *Yucca elata* as food sources (Walter G. Whitford, Desert Biome, IBP, unpublished reference).

White grubs (Scarabaeidae:Phyllophaga spp.), the larval stage of June beetles, may drastically disturb large areas of range vegetation by root feeding. Densities may exceed $200/m^2$ (Hewitt et al. 1974), and their activities can completely kill vegetation. Their role in the desert grassland, however, needs further elucidation.

Sucking insects attract comparatively little attention as economic pests of grasslands, but that is not necessarily a fair measure of their importance in grassland functioning. The economic impact by the Pseudococcidae, or mealybugs, could easily be the most underestimated of any grassland pest, perhaps the best known of which is the rhodesgrass scale (*Antonina graminis* (Mushell)). The King Ranch in Texas lost 40,500 ha of pasture to this insect between 1945 and 1949 (Chada and Wood 1960). In South Dakota mealybugs were calculated to consume about 1 g of phloem per month per individual, and the total consumption of a heavy population would equal that of livestock (Anonymous 1971).

Black grass bugs, including several species of *Labops* and *Irbisia*, are recognized as major pests in restricted areas of most western states. As many as 800 to 1000 of these gregarious grass bugs have been found on a single clump of grass, and 4,050 ha were heavily damaged in Nevada in 1972 (Haws et al. 1973).

The western flower thrips (*Frankliniella occidentalis* (Pergande)) is present in virtually all black grama flowers and may reach incalculable numbers in some. In flowers, they appear to be primarily pollen feeders, so they are presumed to do little damage to range vegetation.

Few attempts have been made to elucidate the general composition of the invertebrate fauna of the New Mexico desert grasslands.

Many of the invertebrates collected during the study for this volume were found in close association with the larger perennial shrubs such as mesquite and yucca. On mesquite the Homoptera were well represented by the Psyllidae, Membracidae, and Cicadellidae. Other common groups were the Geometridae, Cerambycidae, Thripidae, and Pompilidae.

Yucca supports a wide variety of invertebrates, with a spatial stratification of populations on the plant. During the spring and summer, when the yucca plant sends up its flowering stalk, aphids and thrips are numerous on the developing stems and in the flowers. Predaceous lady beetles (Coccinellidae) and honeydew-seeking ants are also common at this time (table 10). During the summer two species of Pentatomidae, *Chlorochroa sayi* Stal and *C. ligata* Stal are found on the green sword-like leaves of the yucca plant.

The denser undergrowth of the yucca, often with one or more dead stalks, supports the greatest diversity of invertebrates on the yucca plant (table 10). Adult darkling beetles, *Eleodes* spp., are found nestled under the dead leaves near the main stem, often in large numbers (i.e., $40/m^2$). Termites are even more abundant, having been recorded at nearly $200/m^2$ on one occasion (Ellstrom 1973). Other groups commonly found in association with yucca are the lygaeids

Table 10. Partial list of invertebrates found in association with yucca plants (excluding flowers) in August 1972.

Order	Family	Life Stage	Density (Numbers/m^2)	
			August 8	August 30
Hemiptera	Lygaeidae	Adult	32	14
		Nymph	12	18
Coleoptera	Tenebrionidae	Adult	44	14
Isoptera	Termitidae	Nymph	182	68
Orthoptera	Gryllidae	Nymph	42	36
	Blattidae	Nymph	2	6
Araneida	Lycosidae	Adult	2	4
		Immature	32	10
	Thomisidae	Adult	22	2
		Immature	16	0
Collembola		All	4	18
Hymenoptera	Formicidae	Adult	16	12

(*Lygaeus* sp.), crickets (Gryllidae), springtails (Collembola), and the "daddy-long-legs" (Phalangiala). Yucca is also one of the few plants on which oribatid mites were captured during the study.

During the three years of the IBP sampling, 19 invertebrate orders and representatives from 118 families were collected from the Jornada site (Ellstorm 1973) (table 11). Most of these were collected by the standard quick trap but some by pitfalls, sweep nets, etc.

Table 11. List of orders and families collected at the Jornada Site from 1970 to 1972.

Order	Family	Order	Family
Thysanura	Lepismatidae	Coleoptera	Carabidae
		(Continued)	Silphidae
Collembola	Sminthuridae		Pselaphidae
	Entomobryidae		Cantharidae
	Poduridae		Cleridae
			Elateridae
Thysanoptera	Phlaeothripidae		Cebrionidae
	Thripidae		Mordellidae
			Nitidulidae
Neuroptera	Chrysopidae		Erotylidae
	Myrmeleontidae		Phalacridae
			Coccinellidae
Isoptera	Termitidae		Meloidae
			Tenebrionidae
Orthoptera	Acrididae		Bostrichidae
	Blattidae		Scarabaeidae
	Gryllidae		Trogidae
	Gryllacrididae		Histeridae
	Mantidae		Chrysomelidae
	Phasmidae		Bruchidae
	Tettigonilidae		Curculionidae
Homoptera	Aphididae	Diptera	Asilidae
	Cixiidae		Bombyliidae
	Coccidae		Pipunculidae
	Cicadidae		Syrphidae
	Cicadellidae		Chloropidae
	Cercopidae		Anthomyidae
	Fulgoridae		Muscidae
	Membracidae		Tachinidae
	Psyllidae		Calliphoridae
			Sarcophagidae
Hemiptera	Coreidae		Sciaridae
	Corizidae		Mycetophilidae
	Cydnidae		
	Corimelaenidae	Lepidoptera	Pieridae
	Lygaeidae		Lycaenidae
	Miridae		Nymphalidae
	Nabidae		Sphingidae
	Pentatomidae		Geometridae
	Phymatidae		Arctiidae
	Reduviidae		Noctuidae
	Tingidae		Pyromorphidae
			Pyralidae
Coleoptera	Burprestidae		Tortricidae
	Cerambycidae		
	Cicindelidae		

Table 11. Continued.

Order	Family	Order	Family
Hymenoptera	Baraconidae	Araneida	Lycosidae
	Ichneumonidae		Salticidae
	Eulophidae		Thomisidae
	Encyrtidae		Teridiidae
	Euchartidae		Argiopidae
	Chalcididae		Linyphiidae
	Eurytomidae		Gnaphosidae
	Ceraphronidae		Agelenidae
	Chrysididae		Dictynidae
	Cynipidae		Theraphosidae
	Tiphiidae		
	Mutillidae	Phalangida	Phalangiidae
	Formicidae		
	Pompilidae	Chelonethida	Chermetidae
	Vespidae		
	Sphecidae	Solpugida	
	Andrenidae		
	Apidae	Scorpionida	Buthidae
	Xylocopidae		
		Scolopendromorpha	
Acarina	Caeculidae		
	Oribatulidae	Class Diplopoda	
	Tetranychidae		
	Trombidiidae		

Decomposers

Little work has been done on decomposer organisms in arid regions. Barkley (1964) found that areas receiving less than 4 cm annual precipitation had similar species composition and distribution of microorganisms, providing that sufficient plant cover was available for microbial populations to develop. Clark (1969) listed bacteria, actimomycetes, fungi, algae, and lichens as microorganisms present in grassland soils. On the Jornada fungi and bacteria are probably the main types of decomposing microorganisms (Pieper et al. 1971), although blue green, nitrogen-fixing algae are common in desert soils (Cameron and Fuller 1960). Of the bacteria, the genus *Bacillus* seems to be fairly common in desert soils (Staffeldt 1967). Other important genera are listed in table 12.

Table 12. Genera of decomposers found at Jornada IBP Grassland Site.

Fungi (Primary)	Bacteria (Secondary)
Fusarium	Bacillus
Aspergillus	Pseudomonas
Trichoderma	Achromobacter
Sclerotium	Vibrio
Penicillium	Azotobacter
Pythium	
Rhizopus	
Alternaria	
Myrotherium	
Chaetomium	

STRUCTURE OF DESERT GRASSLAND ECOSYSTEMS

Methods

Most of the methods used in this study followed closely those outlined for the Grassland Biome of the IBP (French 1970; French 1971; and French and Swift 1972). Any deviations from these general procedures are described below.

Field Design

The basic design, which was followed at the comprehensive network sites, was two contrasting treatments. An ungrazed treatment was provided by the construction of a permanent, 10-ha livestock exclosure in the spring of 1970 on a remnant of good condition rangeland dominated by *Bouteloua eriopoda* that had been lightly grazed in previous years. A grazed treatment was located about 200 m east of the permanent exclosure on a deteriorated black grama rangeland with less *Bouteloua eriopoda* and more bare gound than in the permanent exclosure. This cover had been reduced primarily by drought, but perhaps also by past grazing pressure. Each year, a temporary, 2-ha livestock exclosure was erected on a new portion of the grazed treatment, so that ungrazed herbage could be collected. Thus, the grazing treatment was removed during the year that measurements were made. No attempt was made to reduce consumers other than cattle. Two replications per treatment were used for all three years of the study.

Most measurements were taken in both treatments, but small mammal sampling and decomposer work were conducted only in the ungrazed treatment. Avian censuses were conducted in much larger plots in comparable areas.

Driving Variables

Precipitation

During the three years of the IBP study, precipitation on the Jornada was below average in two years and above average in one. The two dry years came in succession, and the second dry year, 1971, probably exerted harsher conditions on the biotic components of the system than a single dry year would have, in a series of average or above average years.

The year 1970 was actually the driest years; only in July was there any substantial precipitation (figure 11). However, little precipitation fell from August 1970 to July 1971. None was recorded in February, March, or May 1971. Consequently, the range was dry when precipitation was received in late July and early August 1971. Relatively large amounts of precipitation fell in late fall of 1971 and early winter of 1972 even though the spring of 1972 was dry.

Rainfall was heavy in the summer of 1972 (figure 11). The total received during June, July, August, and September was 200 mm, nearly double the annual total for 1970 and equal to that for 1971. June, August, and October received peak amounts, with slightly less during July and September.

Soil Water

Soil water levels followed storm periods closely. Soil water

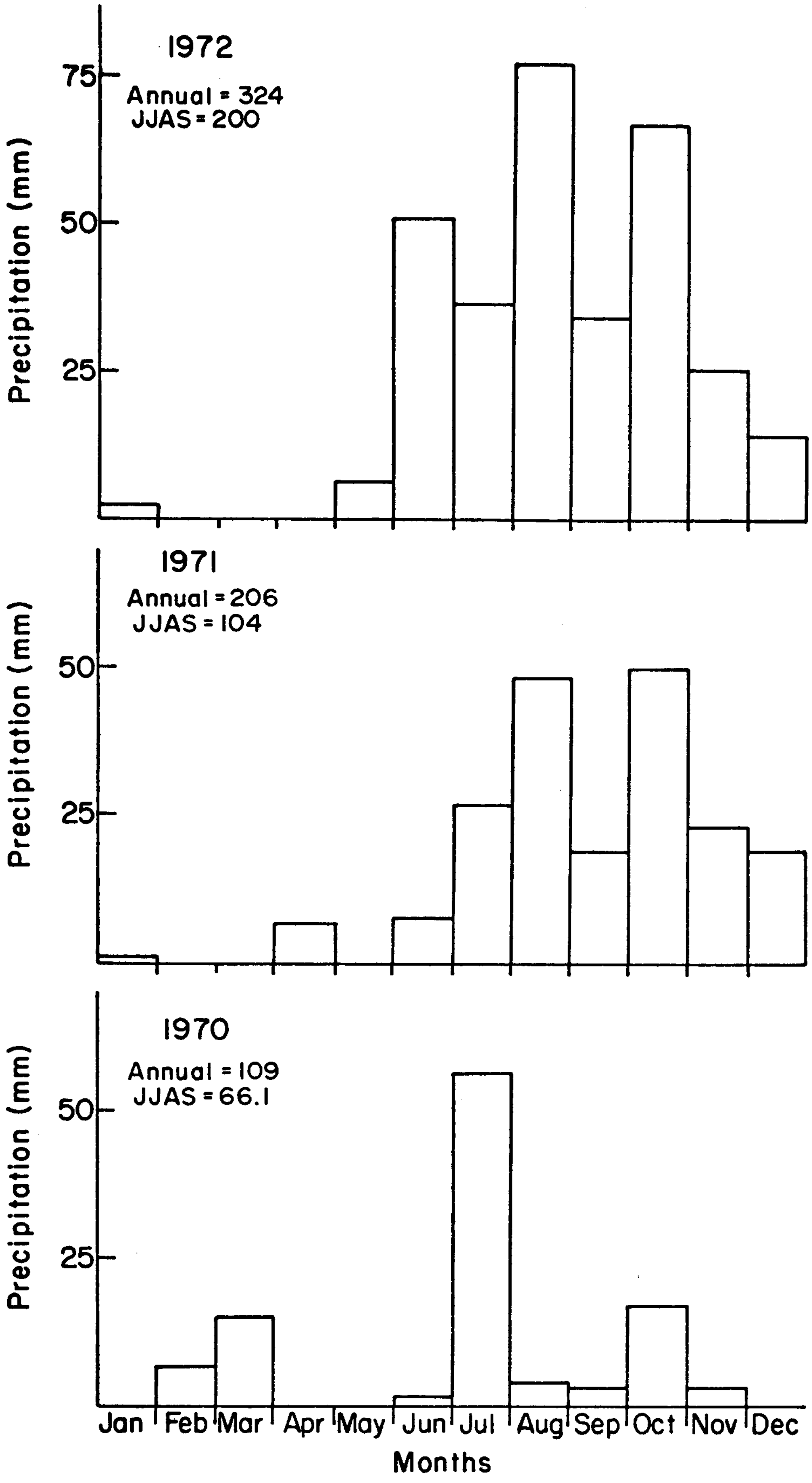

Fig. 11. Monthly precipitation at IBP site for the three years of the study. Totals for the period January through June 1970 were taken from records for the Jornada headquarters since the rain gauge was not established at the IBP site until June.

values shown in figure 12 were obtained from an area about a mile from the IBP grassland site but with similar soils. In 1970 soil water was held at tensions of less than 1 bar for only a short time in early August at depths down to 40 cm. At the 53 cm depth, soil water tensions were never lower than -5 bars (figure 12). During the peirod of July 19 through July 28, 57 mm of rain fell. Bailey (1967) found that 25 mm of simulated rainfall penetrated to a depth of 19 cm and 38 mm of simulated rain penetrated to a depth of 23 cm on soils similar to those at the IBP site. Herbel, Dittberner, and Bickle (1970) reported that 30 to 37 mm of rainfall were required to reduce soil water tensions to less than -1 bar at the 10 and 25 cm depth on sandy soils.

The dip in the soil water tensions at the 10 cm depth to -16 bars followed by the increase to -1 bar in 1970 probably represents drying of the surface soil, followed by a light shower that recharged the surface.

In 1971 soil water tensions were lower than -1 bar again during only a short period in late July and early August (figure 12). From July 22 to July 30, 28 mm of rainfall were recorded, and on August 2, 14 mm and on August 6, 31 mm were recorded. This represented most of the rainfall available for plant growth during 1971.

Soil water tensions were low during the spring of 1972. Little precipitation was received during this period, so the soil water recorded must have been stored from fall storms (figure 12). Soil water was available during this period for cool-season plants.

This close relationship between precipitation and soil water is shown in figure 13 for three exclosures on the Jornada. Data for a clay loam, tobosa-burrograss site indicated that 75% to 90% of the

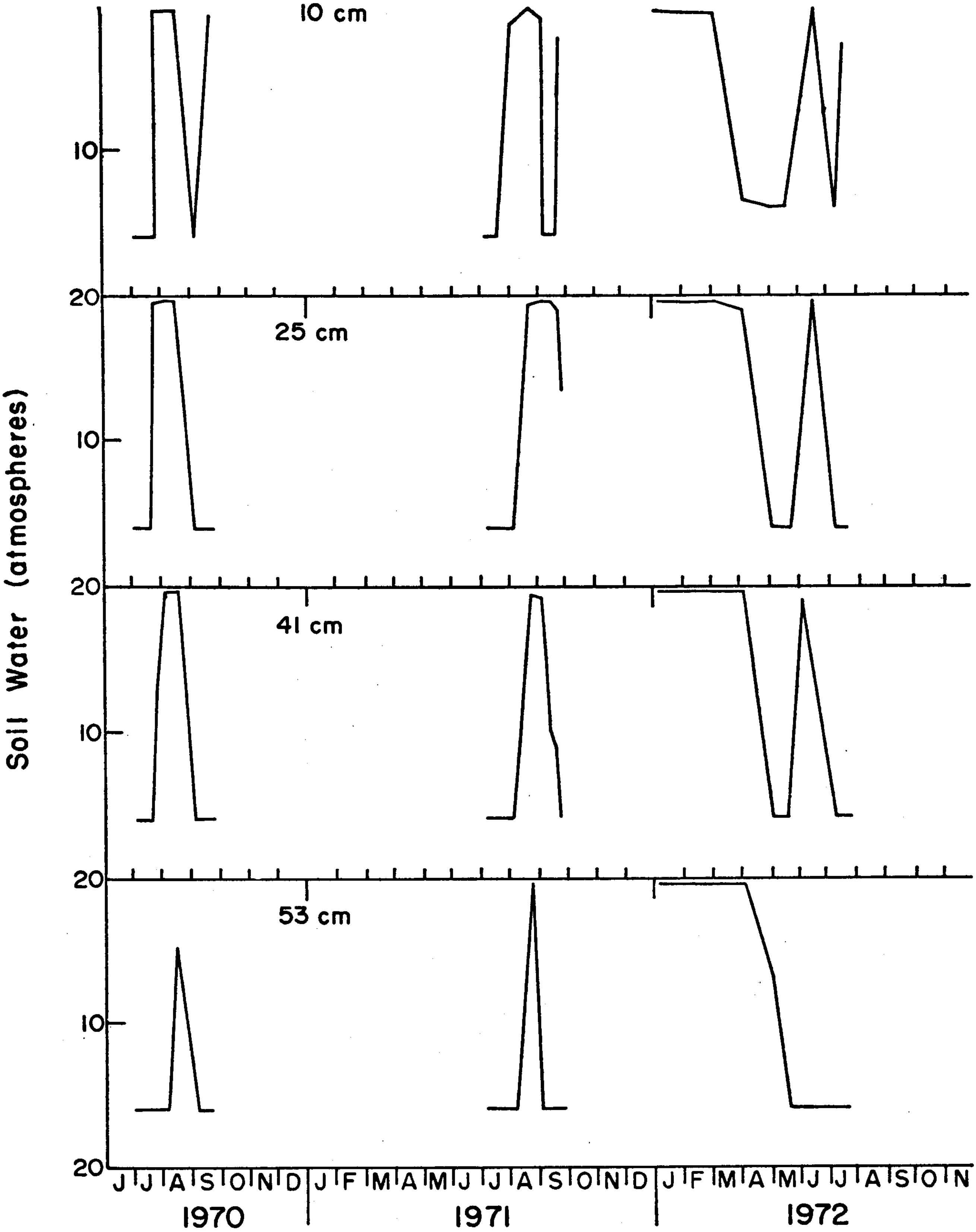

Fig. 12. Soil water at four depths at a site similar to and about one mile from the IBP site.

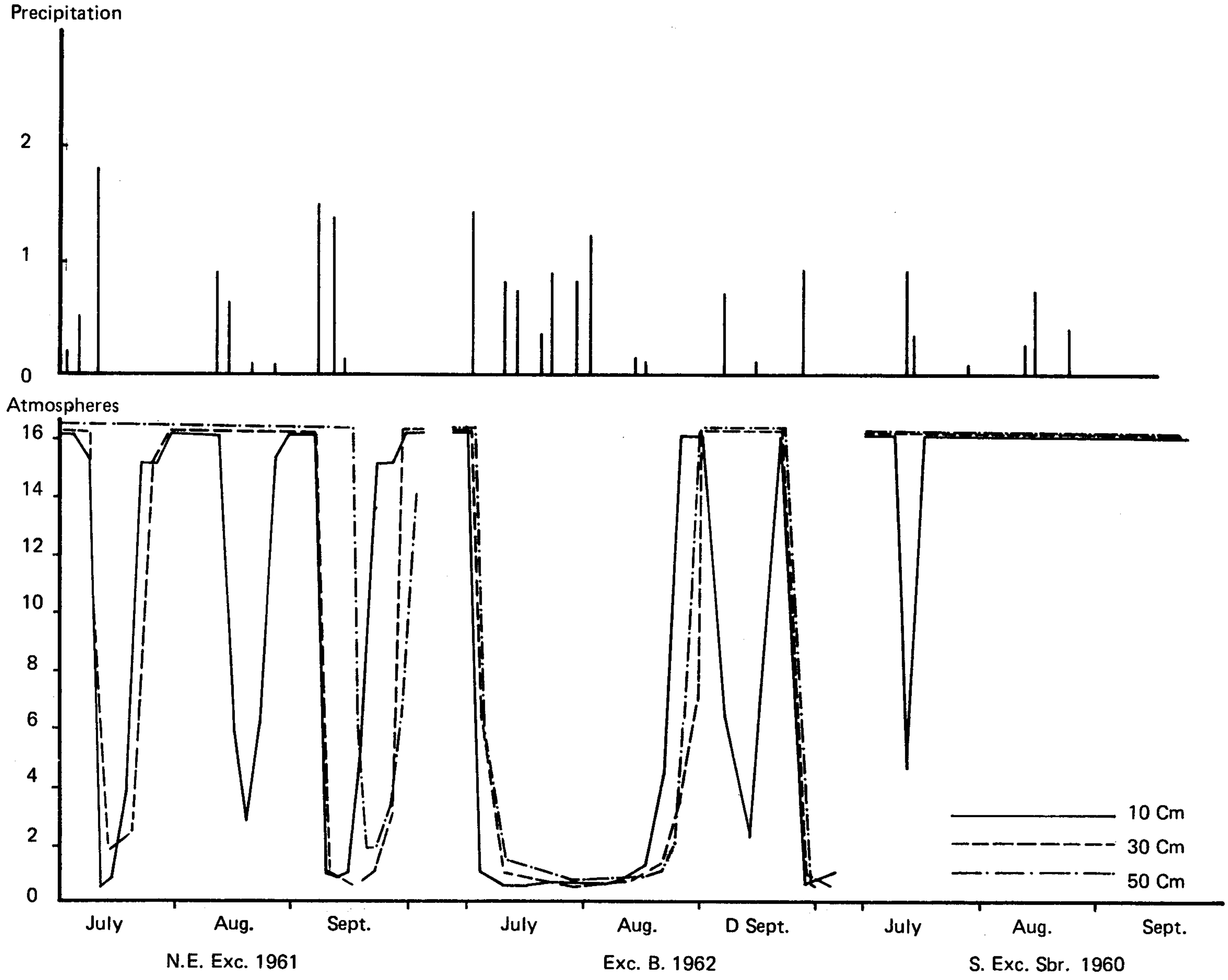

Fig. 13. Precipitation and soil moisture at selected sites.

available soil water may be contributed by run-in water (Herbel, Dittberner, and Bickle 1970). Calculations by Bryson et al. (1970) also illustrate the importance of run-in water for the low-lying areas (table 13). During July and August 38 mm of run-in water were present and largely accounted for all water storage. On both a dune area and the tobosa-burrograss area, soil water storage occurred only during the summer.

Table 14 shows some relationships between precipitation and soil water for two sites on the Jornada. Site F is on a slight slope, and Site G is similar to the IBP site (Herbel and Gile 1973), except that the depth to the petrocalcic layer is greater. On both sites, the number of days when soil water tensions were between 0 and -15 bars decreased with depth. Many light showers influence the surface layers but not the deeper layers. For the Petrocalcic Paleargid, the correlation coefficients for the regression of precipitation on number of days when soil water tensions were less than -15 bars varied from 0.51 at the 10 cm depth to 0.71 at the 90 cm depth (table 14). These correlation coefficients are higher than for the Typic Haplargid (Site F).

The petrocalcic layer impedes water percolation and holds more soil water in the areas available to plants (Herbel and Gile 1973). At Site G, soil water was also stored for longer periods of time due to the coarse texture of the surface soil and low evaporative loss because of reduced capillary movement of water (table 15). Bailey (1967) also documented the greater amount of water in upper horizons of soil with petrocalcic horizons than in deeper soils.

Table 13. Water budgets in mm for soil-air interface on a dune and tobosa-burrograss area on Jornada (from Bryson et al. 1970).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
						Dune Area						
Precipitation	9.0	8.3	8.0	4.9	8.9	11.4	40.1	41.0	33.4	21.2	13.0	17.4
Evaporation	11.1	10.5	10.2	7.6	10.1	11.9	34.7	36.5	30.5	20.6	12.6	17.4
Runoff	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Soil Storage	-1.9	-1.8	-2.2	-2.7	-1.2	-0.5	5.4	4.5	2.9	0.5	-2.9	0.3
						Tobosa-Burrogras Area						
Precipitation	7.4	6.8	7.1	5.0	8.0	11.3	37.8	37.1	33.8	20.7	8.9	11.1
Evaporation	8.8	8.6	9.0	7.1	9.5	18.9	73.1	71.1	40.1	19.6	10.4	10.6
Runoff	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Soil Storage	-1.4	-1.8	-1.9	-2.1	-1.5	-1.2	2.8	4.1	2.8	1.1	-1.5	0.5

Table 14. Precipitation and soil water at two Sites in the Jornada basin floor (from Herbel and Gile 1973).

	Site F	Site G[a]
Precipitation (cm)[b]		
Mean	19.3	18.9
Range	10.8-29.8	11.5-34.9
Soil water (days)[c]	at stated depths	
10 cm		
Mean	192.0	193.9
Range	97-301	64-321
25 cm		
Mean	173.5	212.2
Range	62.318	99-336
40 cm		
Mean	121.9	158.5
Range	0-312	32-333
60 cm		
Mean	90.2	116.8
Range	0-319	0-350
90 cm		
Mean	18.7	96.5
Range	0-179	0-278

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[a]

[b]

[c]

Table 15. Soil morphology (in part)[a] at two Sites in the Jornada basin floor (from Herbel and Gile 1973).

Site F		Site G	
Typic Haplargid, Coarse-loamy, Mixed, Thermic		Petrocalcic Paleargid, Coarse-loamy, Mixed Thermic	
Horizon and Depth (cm)	Morphology[a]	Horizon and Depth (cm)	Morphology[a]
B2t, 0-18	Fine sandy loam, blocky, slightly hard	C, 0-5	Sand, loose, soft, single grain, massive
B31t, 18-34	Fine sandy loam, massive, slightly hard	A2, 5-10	Fine sandy loam, massive, soft
B32t, 34-44	Loamy sand, massive, soft	B1t, 10-23	Fine sandy loam, massive, slightly hard
B1tcab, 44-60	Sandy loam, prismatic, blocky, hard	B21t 23-36	Fine sandy loam, massive, slightly hard
B21tcab, 60-76	Sandy clay, loamy, prismatic, blocky, hard	B22tca, 36-46	Fine sandy loam, massive, slightly hard
B22tcab, 76-90	Sandy clay loam, prismatic, blocky, hard	B3ca 46-71	Sandy loam, blocky, slightly hard
B23tcab, 90-103	Sandy clay loam, prismatic, blocky, hard	K1, 71-79	Very gravelly sandy loam, crumb, loose
K2b, 103-126	Sandy clay loam, blocky, very hard	K2m, 79-90	Carbonate-cemented material, massive, extremely hard

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[a]

Soil and Air Temperatures

Average monthly maximum and minimum air temperatures for 1970, 1971, and 1972 are given in table 16. These data illustrate the fairly typical patterns for seasonal changes in air temperatures, with the winter and early spring minimum temperatures being below freezing. For all three years, minimum temperatures below freezing extended from November through March. Summer minimums and maximums were slightly lower during 1972 than during the other two years, possibly a result of more cloud cover. The mean annual temperature was also slightly lower in 1972 than in the other two years (table 17), although the mean growing season temperature was lowest for 1970.

Although soil temperatures were not measured, there is a close relationship between air temperature and soil temperatures. Surface soil temperatures are dependent on air temperatures, soil water content, solar radiation, and texture and amount of litter or standing vegetation (Herbel, Dittberner, and Bickle 1969). Soil surface temperatures are higher than air temperatures and reach very high temperatures if they are bare (Herbel 1972). Soil surface temperatures without cover may be 30°C higher than those under heavy cover (figure 14).

Evaporation

Evaporation from a weather bureau pan is approximately 10 times precipitation on the Jornada (Herbel, Dittberner, and Bickle 1969, Herbel and Pieper 1970). The potential thermal growing season is only a month or two short of the entire year, so the actual evapotranspiration for the growing season was nearly equal to that for the year

Table 16. Mean monthly maximum and minimum air temperatures at Jornada headquarters (degrees centigrade).

	1970		1971		1972	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
January	-7.6	14.5	-7.2	15.0	-5.8	15.2
February	-3.1	16.5	-5.1	17.0	-5.6	17.9
March	-1.2	17.7	-2.4	22.3	-2.5	19.1
April	1.1	23.8	3.0	23.8	0.8	25.1
May	7.4	30.4	7.2	28.7	5.1	26.4
June	12.9	33.9	12.8	34.8	14.8	33.0
July	17.9	35.8	18.0	36.6	16.6	33.0
August	16.1	33.9	16.4	32.2	14.3	28.4
September	11.3	30.3	12.8	30.5	12.4	29.0
October	2.0	21.9	5.5	22.8	4.7	19.4
November	-3.8	19.4	-0.2	18.0	-3.9	15.7
December	-4.7	16.0	-3.1	12.5	-4.5	13.8

Table 17. Certain abiotic parameters for the Jornada Site during 1970, 1971, 1972.

Paramerter	1970	1971	1972
Growing season[a]			
Beginning and ending (Julian)	23-357	70-349	32-354
Days	335	280	333
Average temperature (°C)			
Annual	14.3	14.7	13.5
Growing season	15.3	17.7	16.7
Precipitation (mm)			
Annual	166	186	345
Growing season	166	183	324
Actual evapotranspiration (mm)			
Annual	166	186	345
Growing season	166	183	324
Potential evapotranspiration (mm)			
Annual	788	803	845
Growing season	781	771	838
Solar radiation (kcal/m^2)			
Total incident			
Annual	1,883,400	1,857,850	1,795,190
Usable growing season	800,131	687,933	775,181
Daily during growing season	2,388	2,457	2,328

[a] Growing season based on number of consecutive days with a 15-day running mean air temperature greater than or equal to 4.4°C (from Smith 1973).

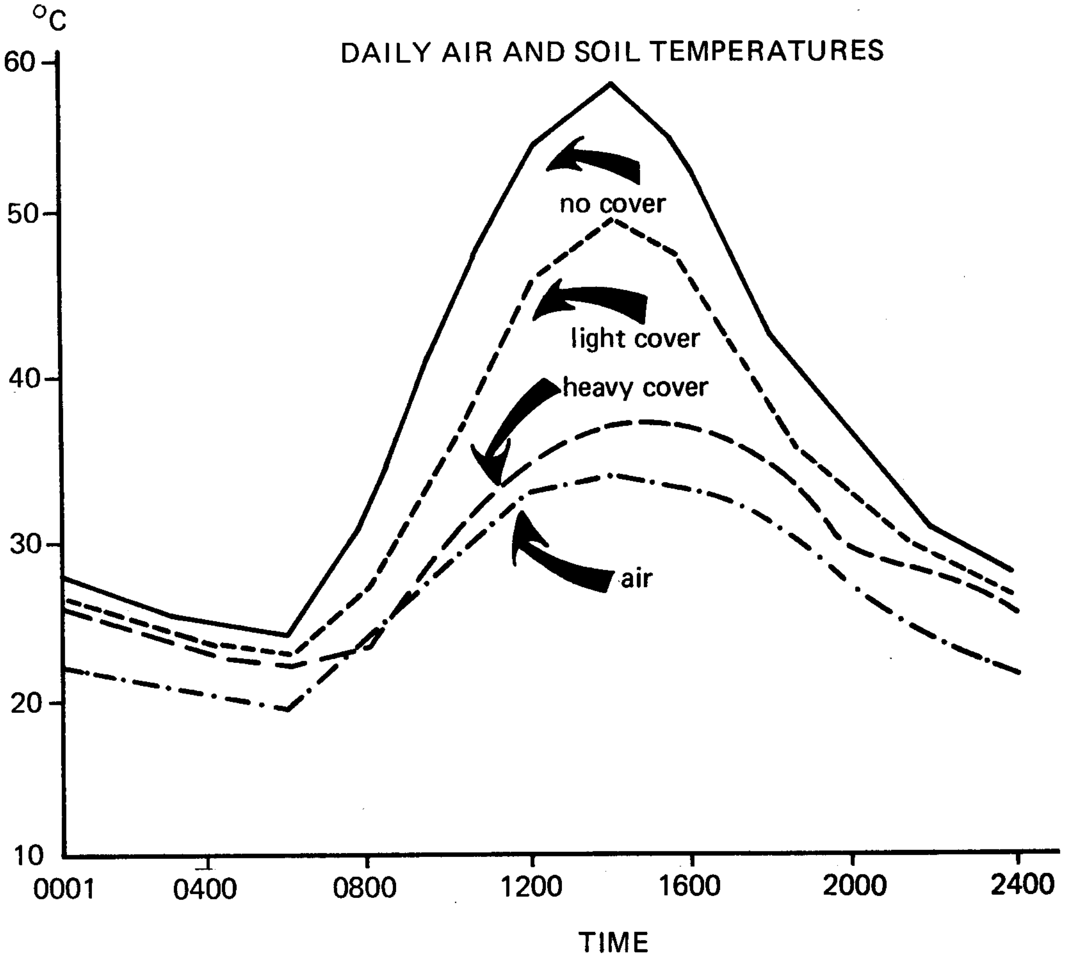

Fig. 14. Average daily soil temperatures (°C) at the 1.3-cm. depth with light and heavy brush cover, without surface cover, and air temperature 10 cm. above the surface of the soil for the period July 28–August 15, 1964, on the Jornada Experimental Range (Herbel 1972). Light brush cover = one dead tarbush (Flourensia cernua) plant; heavy brush cover = three dead tarbush plants.

(table 17). Potential evapotranspiration was highest in 1972 and lowest in 1970. Since there was no runoff or deep percolation, all the precipitation received was accounted for by evapotranspiration.

State Variables

Primary Producers

Phenology. Phenological observations were made on the major species at each sampling date in 1971 and 1972. Because of the limited amount of precipitation in 1971 all species developed in a similar pattern (figure 15). Mesa dropseed developed a little earlier than the other species, but there was little difference in phenological development among black grama, Russian thistle, and broom snakeweed. All species completed their growth cycle almost entirely during August, September, and early October. In 1972, with soil water available over a much longer time, phenological development was markedly different among the species. Cryptantha (*Cryptantha crassisepala*), a cool-season annual forb, began growth in February, was in mid-bloom in May, and had ripe seed in June (figure 16). Broom snakeweed, which is classified as a warm-season shrub, started growth early in the spring, but was still in prebud stage in late July. Most of its phenological development past the flowering stage actually occurred during the same period as that of mesa dropseed and black grama, both warm-season grasses. Although broom snakeweed can grow in the spring at relatively low temperatures if soil water is available, most of the growth occurs during the summer. Russian thistle completed its life cycle at a somewhat earlier date than the perennial grasses. Annual plants often complete their life

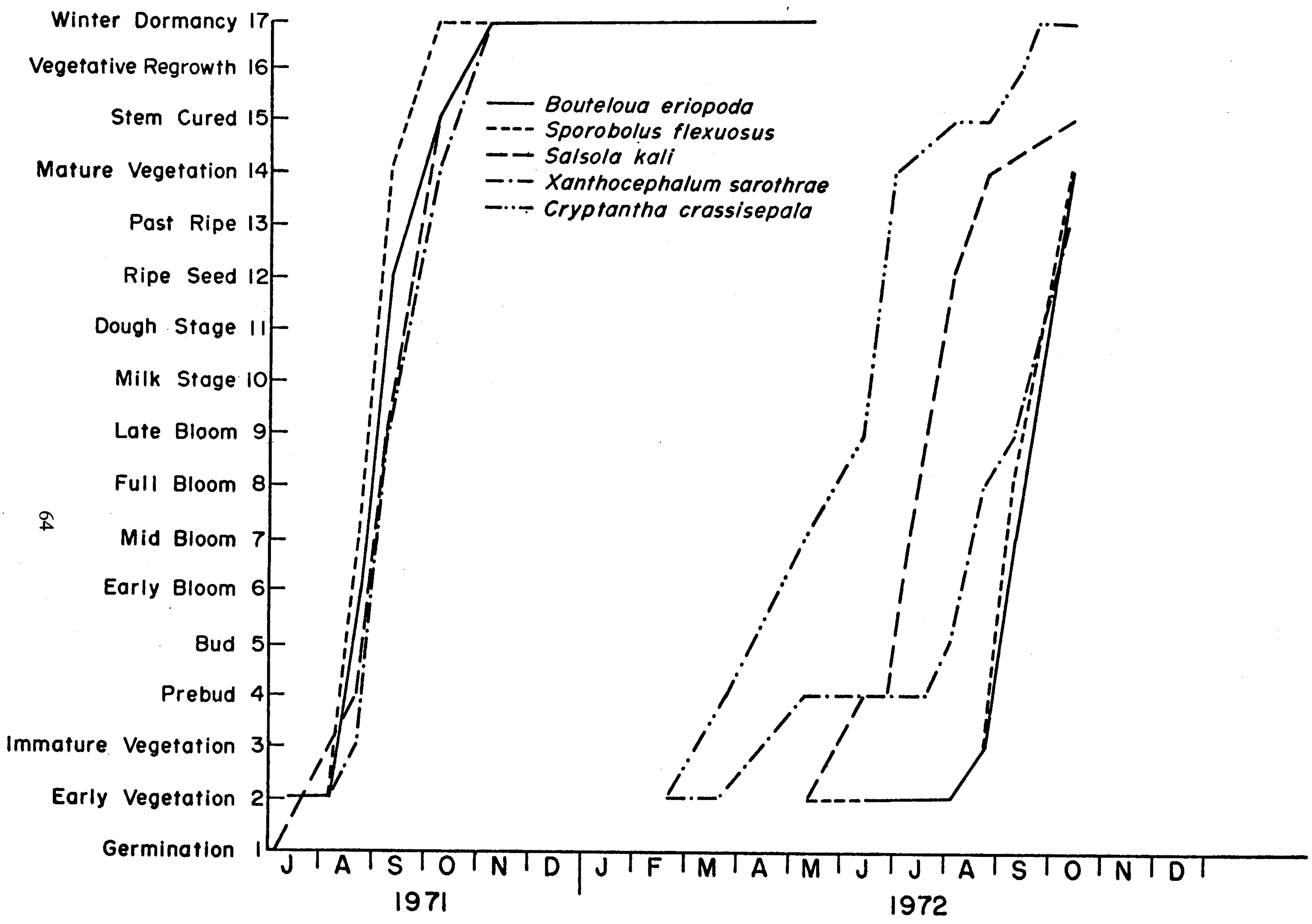

Fig. 15. Phenological development of five important species during 1971 and 1972.

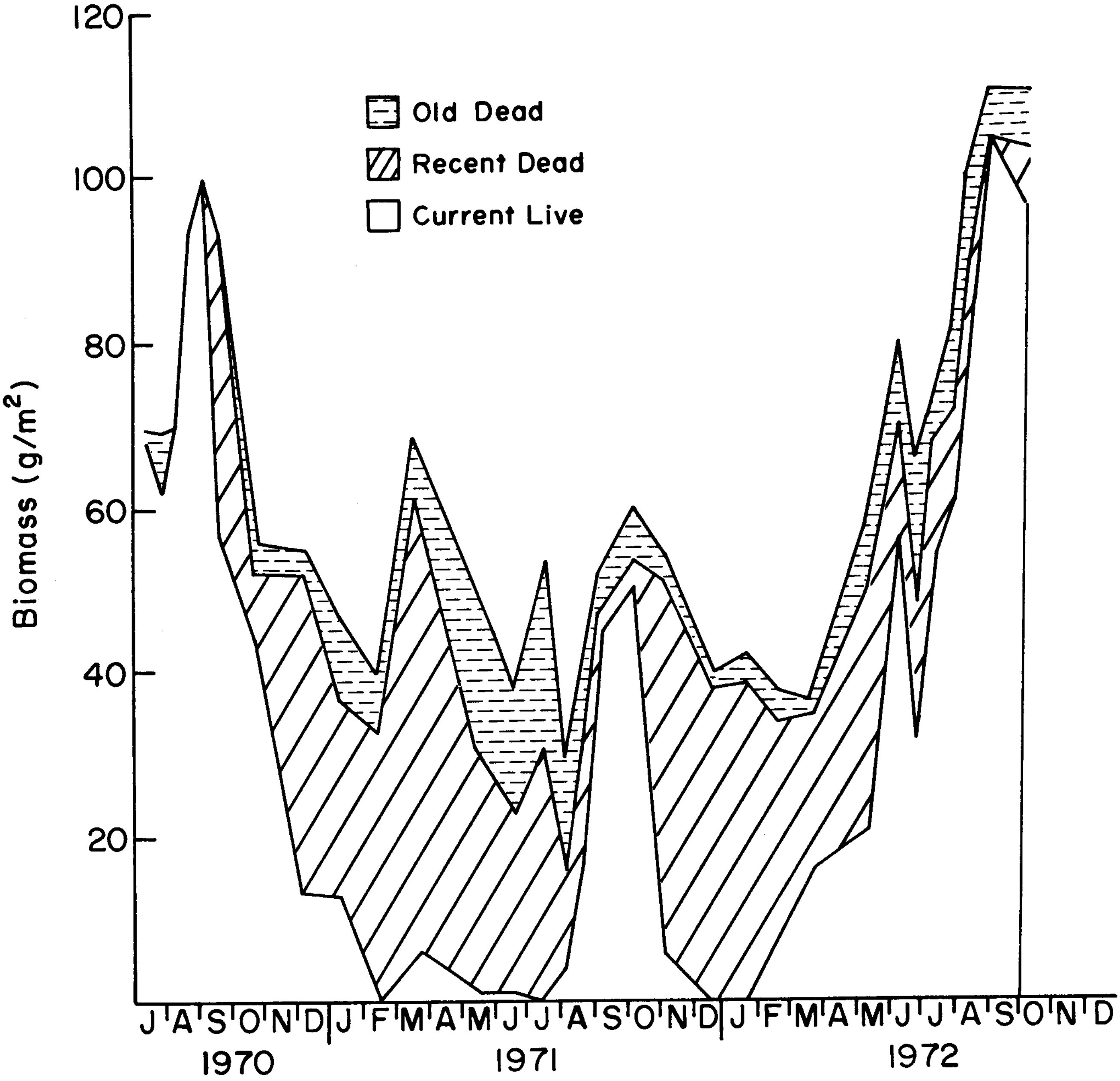

Fig. 16. Aboveground standing crop of all species on the ungrazed area during all three years of the study.

cycle on a limited amount of precipitation but may put on additional vegetative growth if soil water becomes available.

Total aboveground biomass changes. These data do not include biomass of scattered shrubs yucca (Engelm.) and mesquite because of sampling problems discussed later.

The analysis of variance for all three years showed a significant difference ($P < .01$ or $.05$) between the grazed and ungrazed treatments in amounts of current-live and recent-dead categories (Appendix table 1). However, there were no differences between treatments in the old-dead category, possibly because of high variability in old-dead and differential rates of transfer to the litter category.

There was also a significant difference ($P < .01$ or $.05$) among dates for all years and ecological categories (live, recent dead, old dead, and litter) except for the old-dead and current-live compartments in 1972 (Appendix table 1). The date x treatment interaction was also significant for recent-dead for all years and for current-live in 1970 and 1972. This interaction indicates that treatment differences were not consistent on all dates. Early in the growing season, biomass differences were not so great between treatments as later in the season.

Seasonal changes in current live biomass follow a build-up phase, a short period of maximum biomass, and a rapid decline (figures 16 and 17). The rapid decline in standing live material represents a transfer to recent dead. For example, the current live material declined from 100 on September 1, 1970 to 56 on Septebmer 26, 1970, while recent dead biomass increased from 0 to 34 (figure 16) on the ungrazed

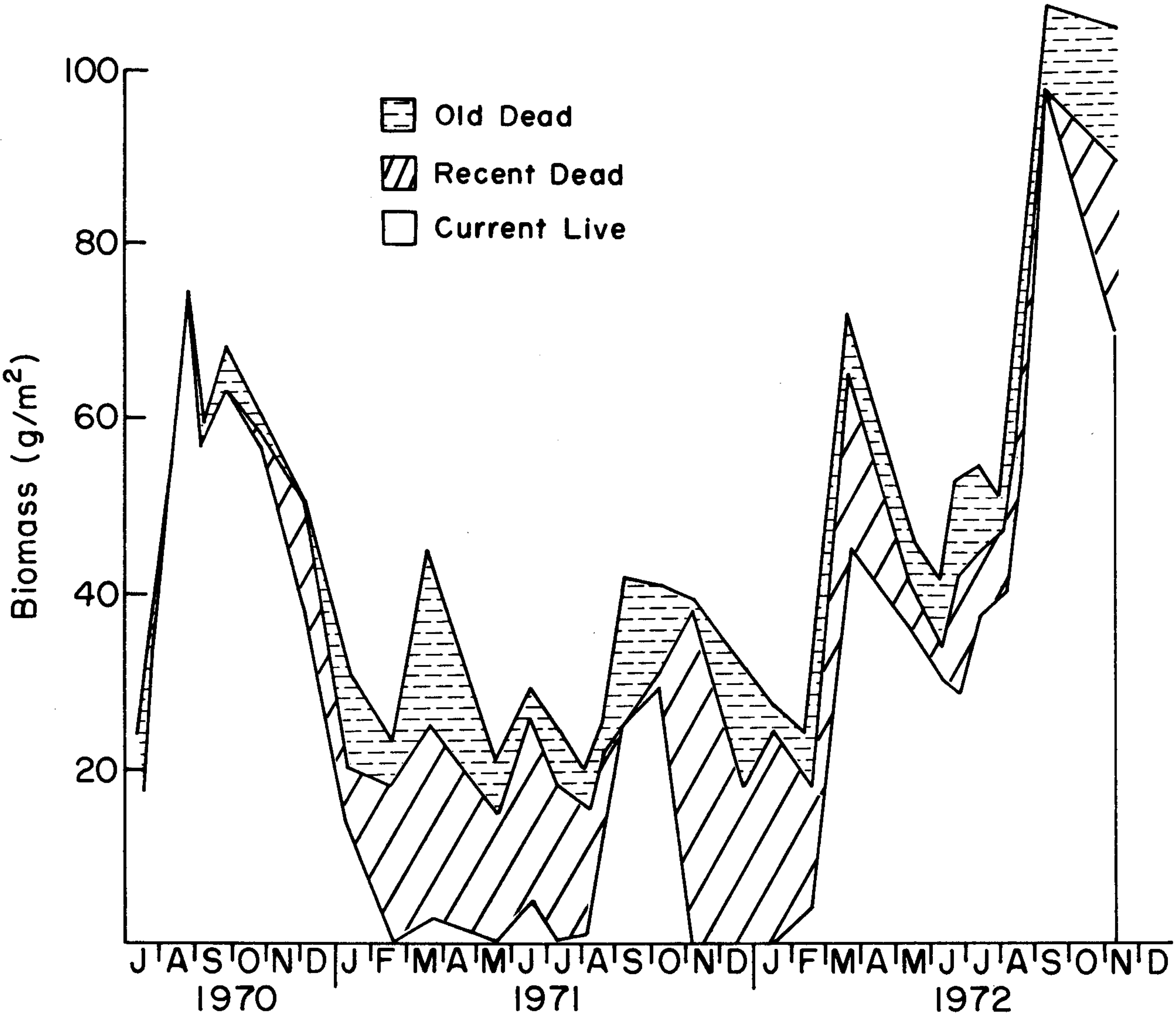

Fig. 17. Aboveground standing crop of all species on the grazed area during all three years of the study.

treatment. On both treatments, recent dead material generally declined slowly during the dormant season as it turned grey or black and was classified as old dead material (figures 16 and 17). The old dead standing crop was more uniform throughout the year, with higher values on the ungrazed than on the grazed treatment. There was no discernible increase in old dead biomass as the recent dead material was added to the old dead. Apparently, old dead was detached and became part of the litter at about the same rate as the recent dead was added to old dead.

Although precipitation in 1970 was much lower than in 1972, peak community standing crop was only slightly higher in 1972 than in 1970 on the ungrazed treatment (figure 16). On the grazed treatment, however, peak community standing crop was about 25 g/m^2 greater in 1972 than in 1970. These differences could probably be explained by a decrease in basal area of black grama plants during the dry years of 1970 and 1971. Such reductions in black grama cover during drought periods are typical in the Southwest (Herbel, Ares, and Wright 1972, Lohmiller 1963, and Valentine 1970). Therefore, there probably were not enough black grama clumps to take advantage of the additional soil water in 1972, and annual forbs and grasses added some biomass but not so much as black grama. Parker (1963) showed that black grama cover was a major factor in effective utilization of soil water. Black grama responds slowly to wet years because it reproduces mainly by stolens.

In both 1970 and 1971, the live standing crop in the ungrazed treatment greatly exceeded that of the grazed treatment (figures 16 and 17). The analysis of variance indicates a significant ($P<.01$)

difference between treatments for the current live compartment for all years (Appendix table 1). These differences reflect the greater vegetational cover and higher range condition in the ungrazed treatment. In 1972, however, the peak biomass was nearly as great in the grazed as ungrazed treatment. Species compositional differences probably account for these different reactions.

Data on aboveground standing crop from other areas may not be as variable as those on the Jornada. Figures 18 and 19 indicate that the standing crop curves at Fort Stanton are rather smooth. As at the Jornada, the peak standing crop for both the fertilized and unfertilized treatment occurred in September and was followed by a rather sharp decline through October and November and stable conditions during the rest of the dormant season (Pieper, Dwyer, and Banner 1975, Pieper el al. 1971). Blue grama contributed most of the standing crop; other grasses and forbs contributed minor amounts. Fertilization nearly doubled the peak standing crop over the unfertilized treatment; however, fertilization had little effect on forb biomass.

Most aboveground biomass data for desert grasslands were collected once a year, usually in the fall at the end of the growing season. Tables 18 and 19 show that the highest peak biomass of these locations was at Fort Stanton, where blue grama is the dominant species. However, data from Paulsen and Ares (1962) included only perennial grass, and that from Valentine (1970) included only black grama. Consequently, these values considerably underestimate total peak aboveground biomass. On the Santa Rita, annual grasses contributed more than twice the biomass that perennial grasses contributed, but with considerable

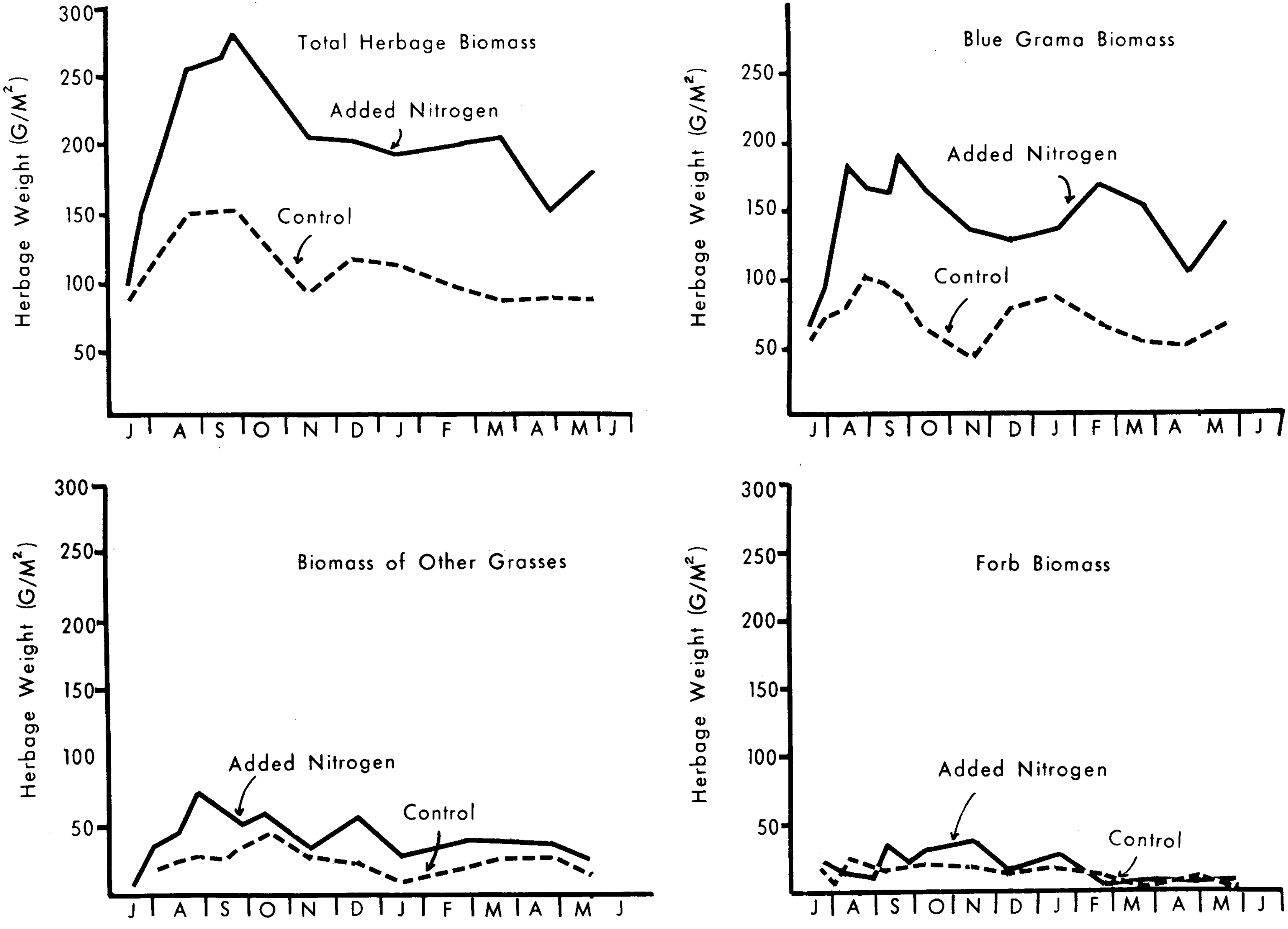

Fig. 18. Average dry weight biomass for blue grama, forbs other grasses and total herbage during 1967-1968 at Fort Stanton under two soil levels (from Pieper, Dwyer and Banner 1974).

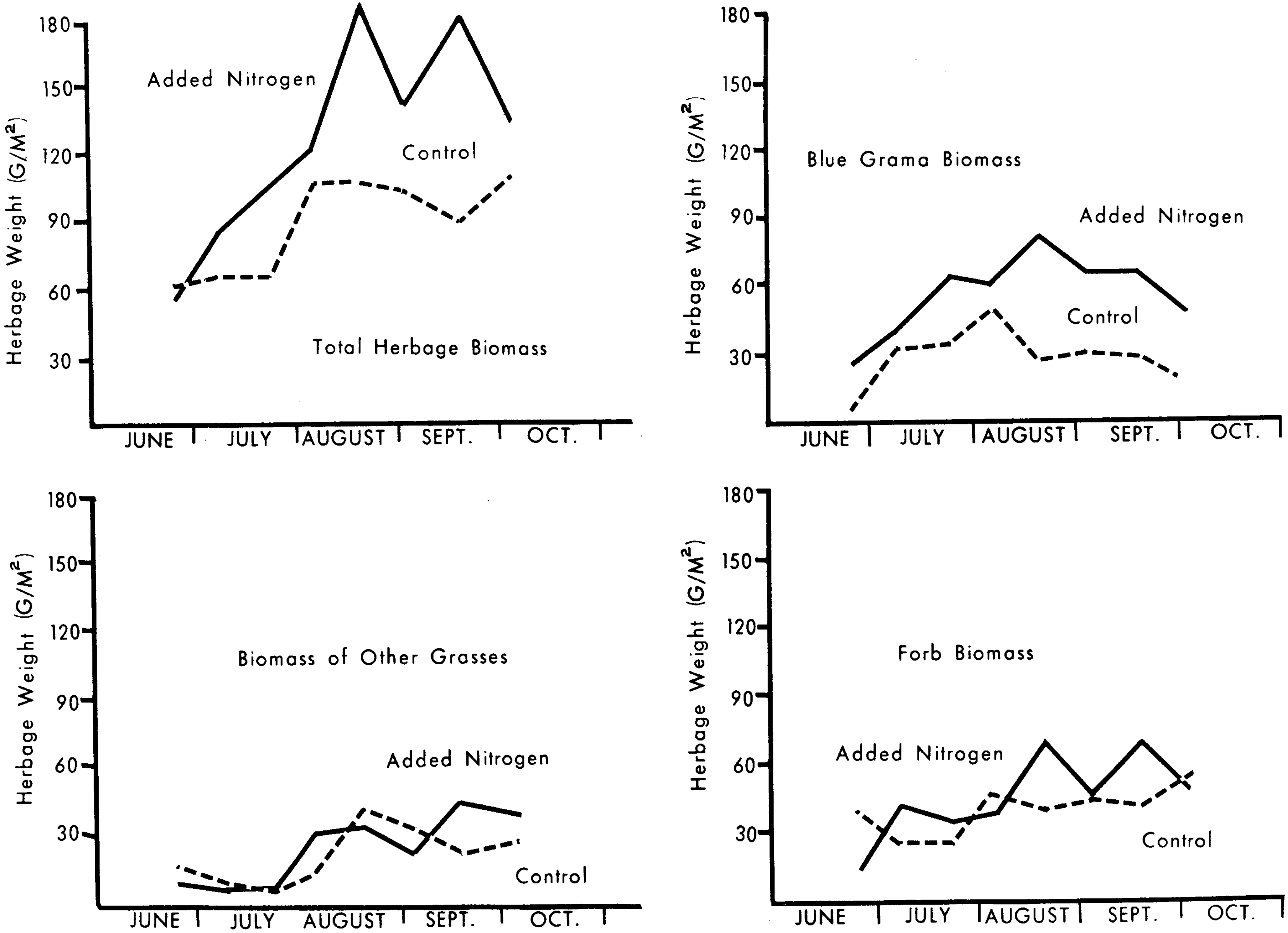

Fig. 19. Average dry weight biomass for blue grama, forbs, other grasses and total herbage during the 1968 growing season at Fort Stanton under two soil nitrogen levels (from Pieper, Dwyer and Banner 1974).

Table 18. End-of-season aboveground standing crop for various desert grassland locations.

Location	n[a]	Dominant Species	Peak Biomass		Author
			g/m^2	± SE	
Southwestern Colorado-Northwestern New Mexico	4	*Hilaria jamesii*	51	9	West et al. 1972
Fort Stanton, New Mexico	36	*Bouteloua gracilis*	113	12	Pieper et al. 1971
Jornada Experimental Range, New Mexico	15	*Bouteloua eriopoda*	58[b]	20	Paulsen and Ares 1962
New Mexico State College Range	3	*Bouteloua eriopoda*	12[c]	15	Valentine 1970

[a] Includes the number of years and locations included in the average used.

[b] Includes only perennial grasses.

[c] Includes only black grama biomass determined in 1964 from three locations grazed at a proper stocking rate.

Table 19. End-of-season standing crop of grasses on the Santa Rita Experimental Range in southern Arizona (from Martin and Cable 1974).

Species	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	Average
Perennial grasses											
Aristida glabrata	0.2	0.7	0.3	0.3	0.2	0.1	0.2	0.6	0.9	0.7	0.4
A. ternipes & hamolosa	0.2	1.3	1.1	1.1	0.7	0.2	0.4	0.9	1.2	1.1	0.8
Bouteloua rothrockii	0.2	0.8	0.4	0.2	0.2	0.1	0.2	1.0	1.6	0.7	0.5
Muhlenbergia porteri	0.3	1.1	1.0	0.7	0.7	0.3	0.7	0.9	0.8	0.7	0.7
Trichachne californica	1.1	3.2	2.7	2.0	2.2	0.7	1.5	3.1	2.7	2.2	2.1
Bouteloua eriopoda	0.3	0.7	0.8	0.6	0.6	0.3	0.3	0.6	0.9	0.8	0.6
Other	0.2	0.8	0.7	0.4	0.6	0.1	0.4	1.0	1.1	1.5	0.7
Total	2.5	8.6	7.0	5.3	5.2	1.8	3.7	8.1	9.2	7.7	5.8
Annual grass	3.4	22.8	30.6	5.7	20.9	1.6	25.7	20.4	4.5	8.9	14.4
Total Grass	5.9	31.4	37.6	11.0	26.1	3.4	29.4	28.5	13.7	16.6	20.2

yearly variation (table 19). On the ungrazed IBP treatment on the Jornada, perennial grasses contributed only about 45% of the total aboveground biomass for 1970 through 1972 (Pieper and Herbel, 1982). Black grama contributed about 40% of the peak biomass on the ungrazed treatment and less than 5% on the grazed treatment.

The mulch data were quite variable, and seasonal trends were difficult to discern (figure 20). The quadrats used were not well suited for sampling mulch on desert grasslands. During the windy season most of the fine and moderately fine mulch is redistributed and tends to be concentrated at the base of shrubs and within shrub crowns. Where there are fences, Russian thisles collect and prevent accumulation of other mulch. Consequently, there are many nearly bare areas and other areas with concentrations of mulch. Differential size of mulch material also contributed to high variability in wieght among quadrats. Pieces of shrubs such as soaptree yucca, mesquite, or broom snakeweed may contribute much weight in certain quadrats and none in others. The large differences in mulch between two consecutive sampling dates shown in figure 20 probably reflect considerable sampling variation.

Generally, litter biomass was greater on the ungrazed treatment than on the grazed treatment, and the amount of mulch decreased during the three years of the study (table 20). Since aboveground herbage was generally higher on the ungrazed treatment than on the grazed treatment, it is not surprising that litter biomass was also greater. The reduction in mulch biomass from 1971 to 1972 was probably due to the low production in 1971.

These mulch values agree, although on the lower side, with those

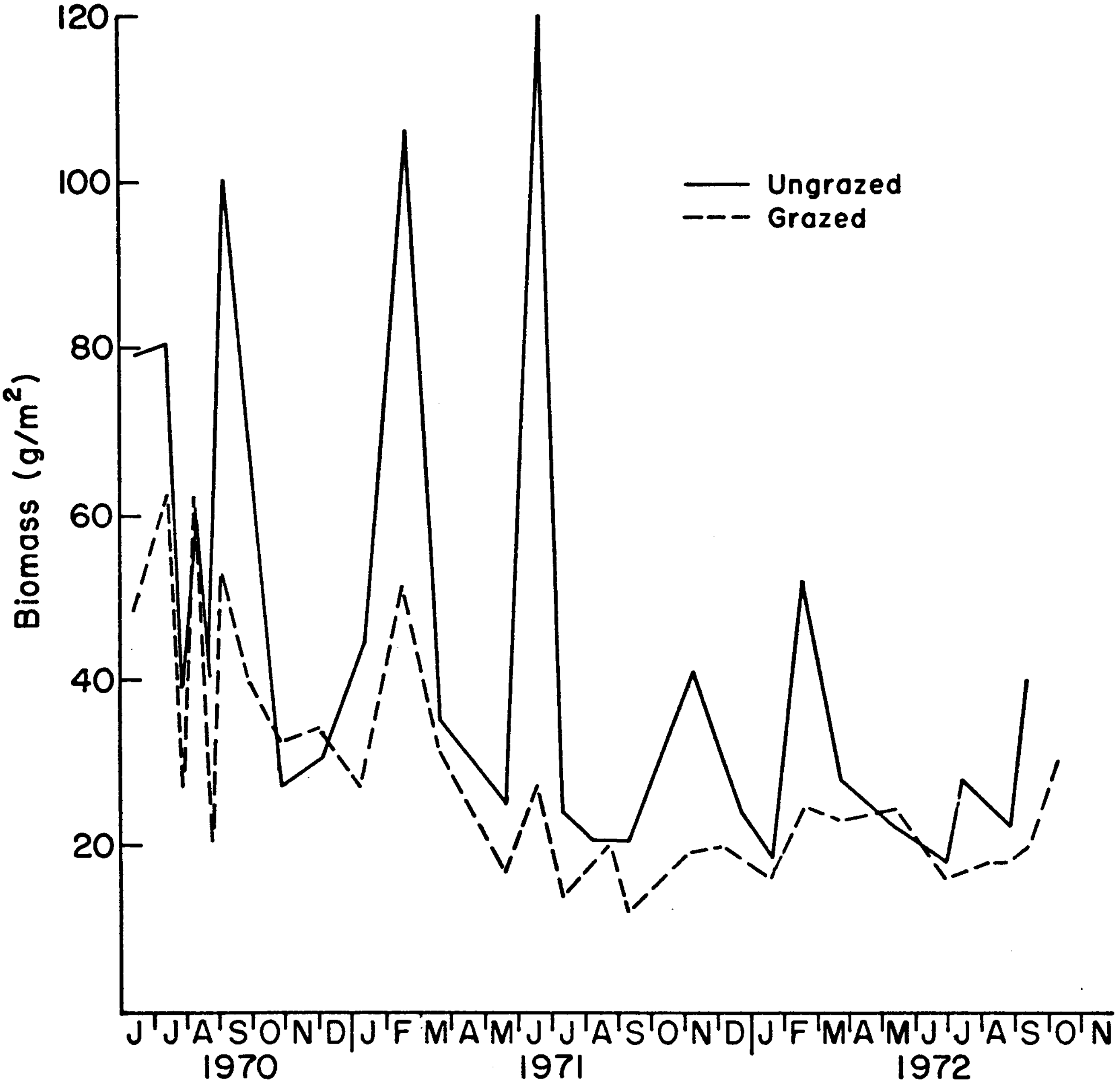

Fig. 20. Standing crop of mulch on grazed and ungrazed treatments.

Table 20. Standing crop of mulch averaged over all dates for each of the three years of the study on grazed and ungrazed treatments. Means with same large letters are not significantly different ($P<.05$) among years within treatments while those means with the same small letter are not significantly different ($P<.05$) within a year between treatments.

Treatment	1970	1971	1972	Average
Ungrazed	A 58.2a	B 46.4a	C 28.1a	44.
Grazed	A 40.1b	B 24.0b	C 21.3	28.5
Average	A 49.1	B 35.2	C 24.7	

reported by Tomanek (1969) for the Northern Great Plains. The lowest mulch standing crop reported by Tomanek (1969) was 33 in South Dakota and the highest over 2500 g/m^2 in Kansas. Few data are available for other desert grassland areas.

Seasonal changes in ecological groups and individual species: Two shrubby species, soaptree yucca and mesquite were difficult to sample because of their scattered distribution and large size. The rectangular and circular quadrats used in the study encompassed only a few of these species. When they were in a quadrat, the biomass would often be from 100 to 1000 times the average quadrat biomass. Distinctions between current live and perennial live material were also difficult to make. Because of these difficulties, sampling variation with yucca and mesquite included was very large. Changes in yucca and mesquite biomass from one sampling period to another were predominantly a reflection of the number of quadrats containing these plants, rather than growth or loss of biomass.

Table 21 shows that yucca biomass was higher than that of mesquite and a larger sampling problem. The average biomass for yucca was much higher on the ungrazed than on the grazed treatment, even though it was encountered on only one or two quadrats per replication. In 1971 the highest biomass recorded for yucca was 191 g/m^2, and it occurred on only a few quadrats. The greatest biomass for mesquite was 46 g/m^2 in 1971 and 48 g/m^2 in 1972 on ungrazed treatment. Neither mesquite nor yucca contributed as much biomass in 1972 as the previous two years. Consequently, yucca and mesquite data were not included in any of the later analyses discussed.

Table 21. Aboveground live standing crop (g/m^2) of *Yucca elata* and *Prosopis juliflora* averaged over all sample dates and the range in values among sample dates.

Treatment	and Year	*Yucca elata*	*Prosopis juliflora*
Ungrazed	1970		
	Mean	12.6	1.1
	Range	0–38	0–7.3
	1971		
	Mean	31.3	4.9
	Range	0–191	0–46
	1972		
	Mean	1.4	4.4
	Range	0–14	0–48
Grazed	1970		
	Mean	5.0	0.1
	Range	0–20	0–1
	1971		
	Mean	3.0	0.1
	Range	0–11	0–1
	1972		
	Mean	2.7	1.2
	Range	0–30	0–10

The analysis of variance showed a significant difference ($P<.01$) in biomass among ecological categories (warm-season perennial grasses, warm-season annual grasses, warm-season perennial forbs, warm-season annual forbs, cool-season perennial forbs, cool-season annual forbs, shrubs, and succulents) for all compartments except for current live in 1972. Many of the interactions involving ecological categories such as the treatment x ecological category and the date x ecological category as well as the three-way interaction of date x treatment x ecological category were significant for most categories (Appendix table 1). These interactions indicate that biomass was high for some dates and treatments and low for others. For example, biomass of cool-season annual forbs was low in 1970 and 1971 and was the highest during the spring of 1972 on both treatments.

Biomass of perennial warm-season grasses was higher in 1970 than in 1972 on the ungrazed treatment, but lower on the grazed treatment (figure 21). These differences may have been a result of black grama mortality and a reduction in vigor on the ungrazed areas and establishment of new seedlings of mesa dropseed on the grazed area. The standing crop curves for black grama and mesa dropseed support these views. In 1970 the peak standing crop of black grama was over 50 g/m^2 on the ungrazed area compared to less than 30 in 1971 and only 36 g/m^2 in 1972 (figure 22). Black grama never contributed much biomass on the grazed area. The current live biomass of black grama was significantly lower on the grazed treatment than on the ungrazed treatment every year (table 21). However, there was no significant difference in biomass among dates for 1971 and only at $P<.10$ in 1970. Even mesa dropseed

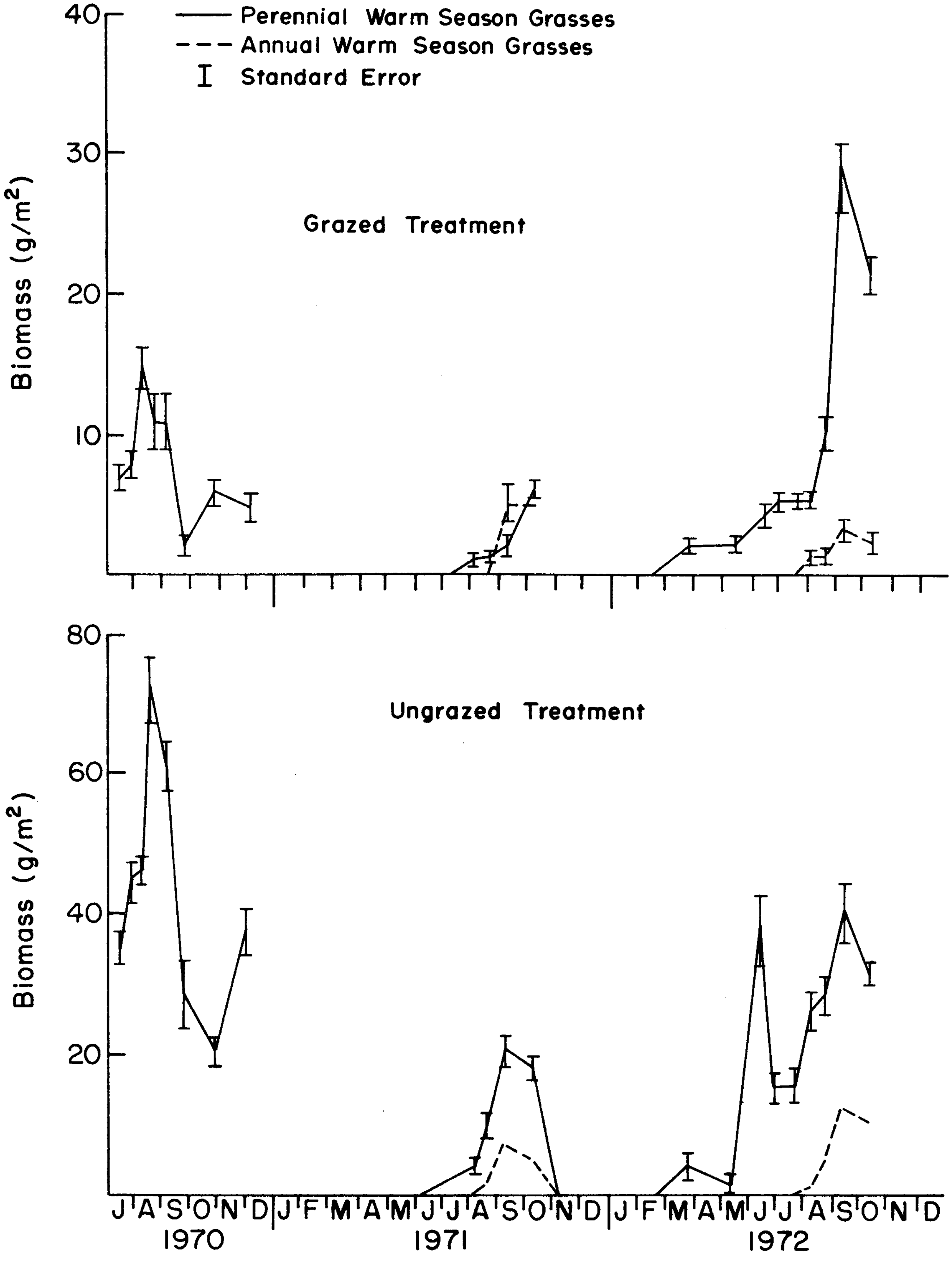

Fig. 21. Above ground current live standing crop for perennial and annual warm season grasses on ungrazed and grazed treatments.

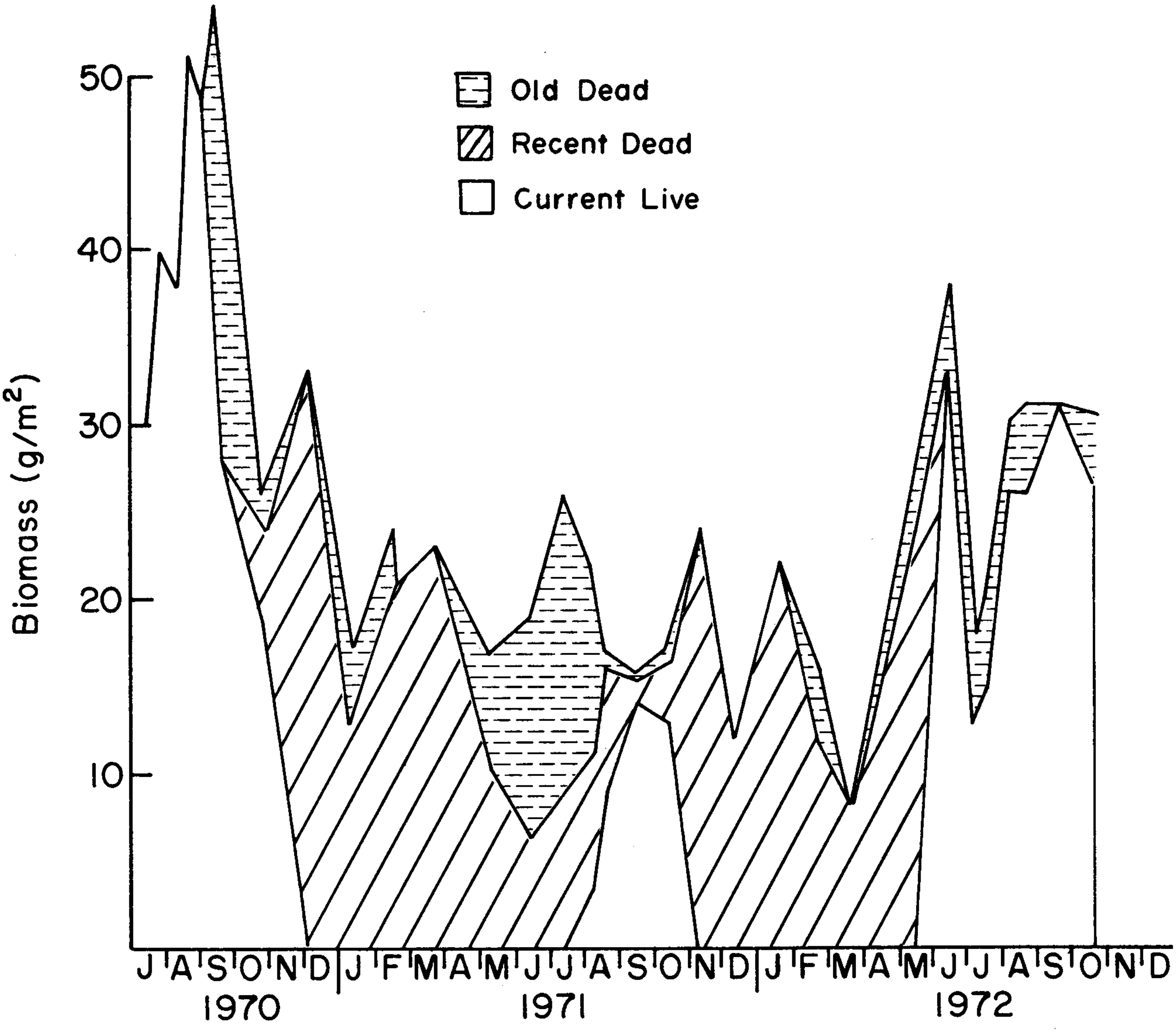

Fig. 22. Standing crop of *Bouteloua eriopoda* on the ungrazed area during all three years of the study.

production was considerably lower in 1972 than in 1970 on the ungrazed area (figure 23), which also suggests mortality and loss of vigor. On the grazed area, however, the peak standing crop of mesa dropseed was over twice as large in 1972 as in 1970. Much of this increase may have been contributed by seedlings established during the summer of 1972 which was favorable for plant growth. Besides open spaces for seedling establishment in the grazed area, reasons for the greater increase in mesa dropseed on the grazed area are not clear. There was no significant difference in current live biomass for sand dropseed between treatments, but there was among dates for all years (table 21). Annual warm-season grasses were not encountered in 1970 and were only a small part of the standing live material in 1971 and 1972 (figure 21). Perennial warm-season grasses contributed about 50% of the peak current live biomass on the ungrazed treatment and less than 30% on the grazed treatment (table 22). No grasses classified as a cool-season species were found, but some grasses may grow in the spring if soil water is available. Mesa dropseed and several species of *Aristida* often produced new leaves during the cool spring weather. During most years, however, the bulk of mesa dropseed growth is made during the summer (figure 23 and 24).

Annual warm-season forbs were an important component of the standing crop of vegetation throughout the study. On the grazed area, the biomass of annual warm-season forbs seemed directly related to the precipitation; the lowest production occurred in 1971 and the greatest in 1972 (figure 25). On the ungrazed treatment, production of annual warm-season forbs was greater in 1971 than in 1970. Apparently the

Table 22. Percentage contribution to peak aboveground standing live by various categories.

Category	1970		1971		1972	
	G	U	G	U	G	U
Perennial						
Warm-season grasses	14.5	62.7	36.7	47.1	32.8	50.1
Warm-season forbs	3.5	1.1	4.3	1.8	13.1	2.9
Annual						
Warm-season forbs	33.8	11.4	51.3	45.7	42.4	44.3
Shrubs	48.2	24.8	6.5	5.0	11.7	2.7
Succulents	0.0	0.0	1.2	0.4	0.0	0.0
Total	100.0	100.0	100.0	100.0	100.0	100.0

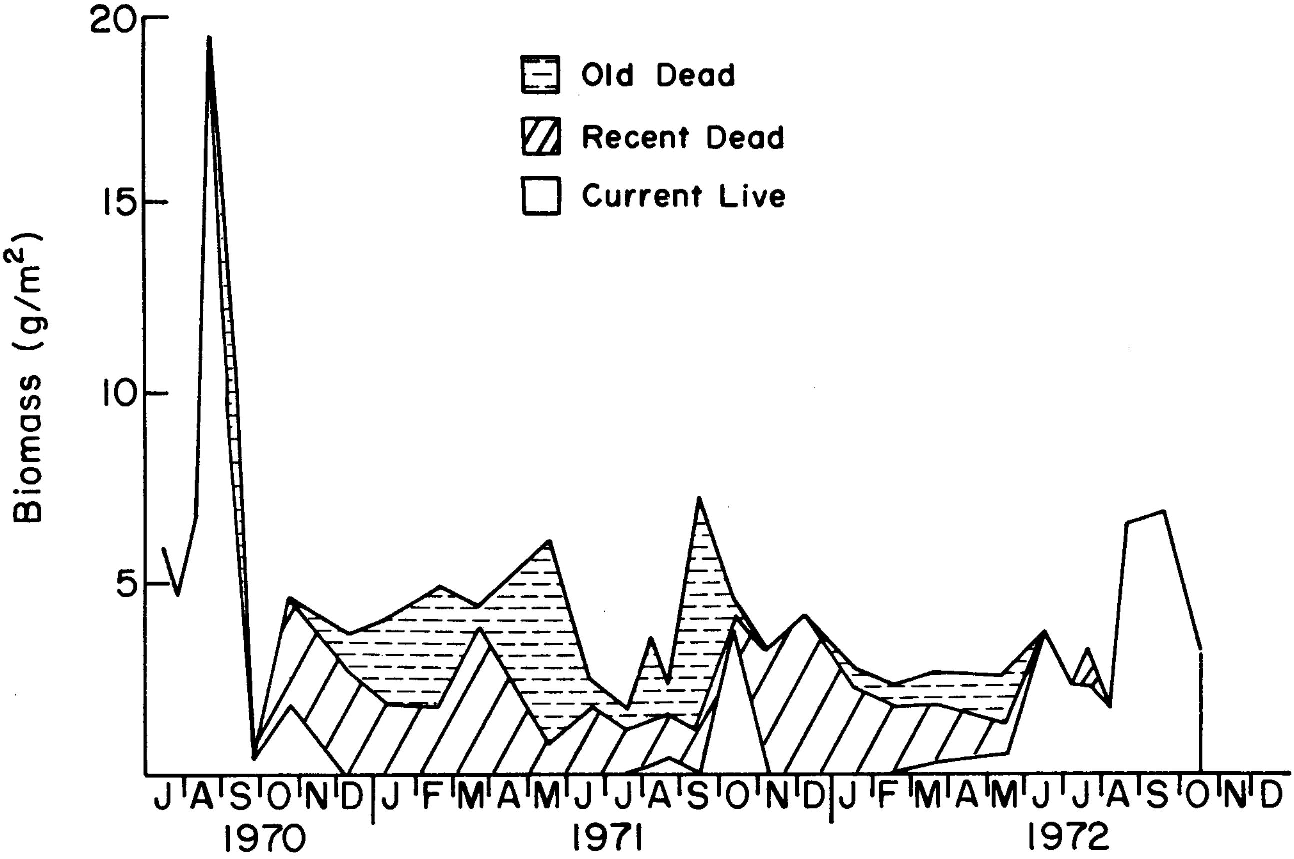

Fig. 23. Standing crop of *Sporobolus flexuosus* on the ungrazed area during all three years of the study.

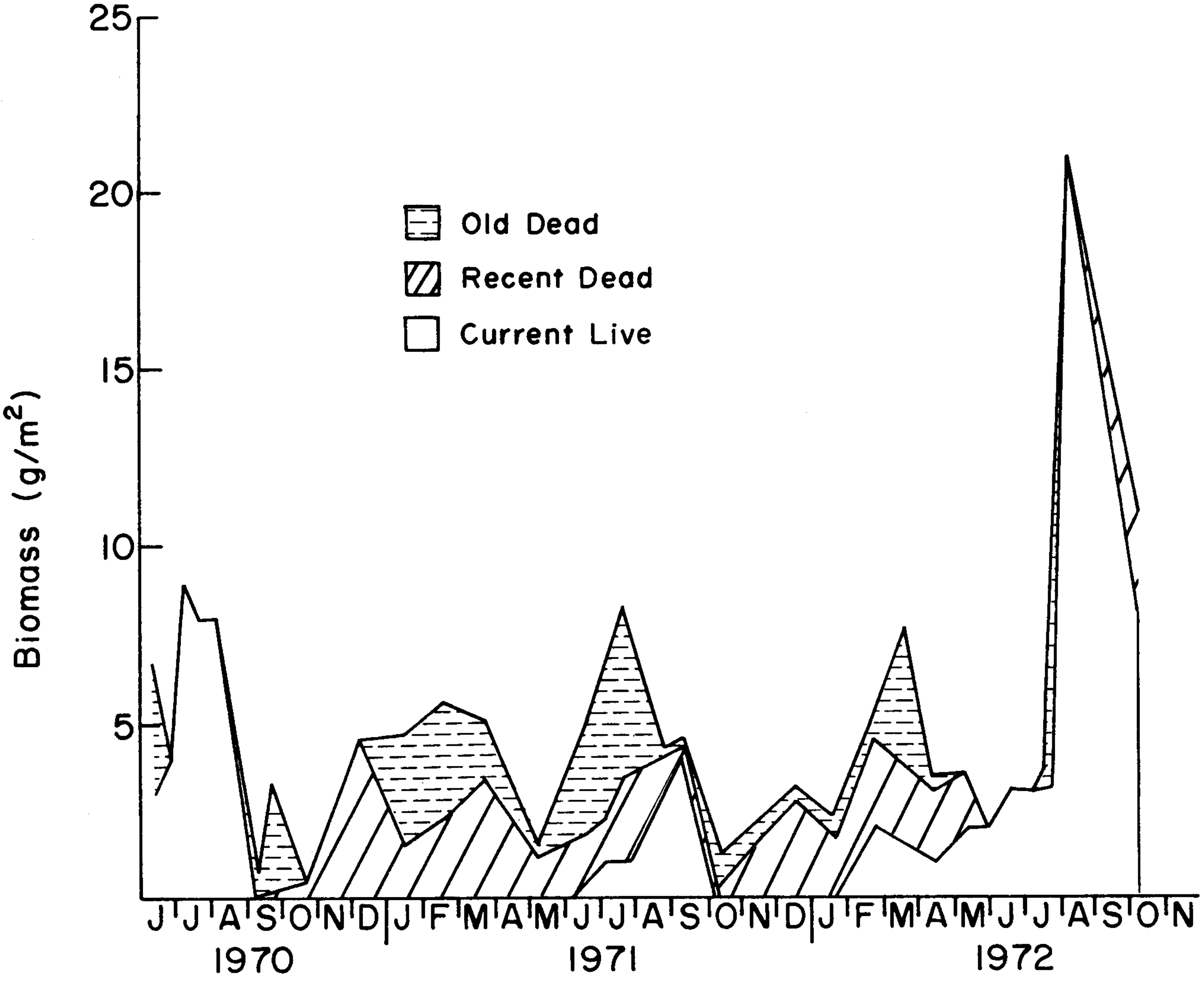

Fig. 24. Standing crop of *Sporobolus flexuosus* on grazed area for all three years of the study.

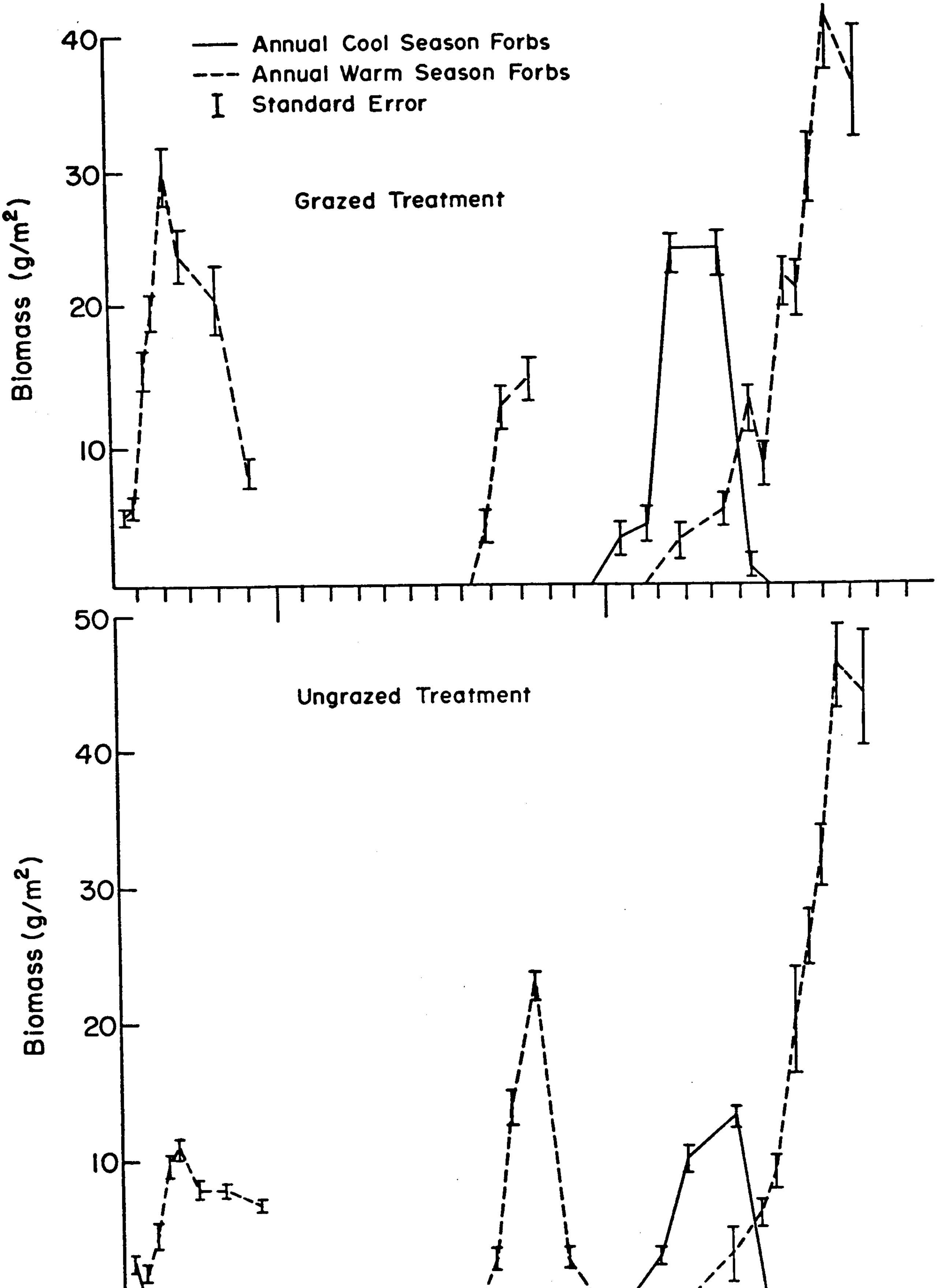

Fig. 25. Aboveground current live standing crop for annual warm- and cool-season forbs on the ungrazed and grazed treatment.

annual forbs were able to utilize the available soil water in 1970 before the perennial grasses could. Annual warm-season forbs contributed 42.5% of the current live biomass on the grazed area and 33.8% on the ungrazed area over the three years of the study (table 22). The most important annual warm-season forb was Russian thistle, which followed similar growth patterns on both treatments in 1971 and 1972 (figures 26 and 27). In 1970, the Russian thistle peak standing live biomass was much greater on the grazed area than on the ungrazed. Competition from perennial grasses, which were fairly vigorous in 1970, may have reduced Russian thistle productivity on the ungrazed area. Current live biomass of the species was significantly higher on the grazed treatment in 1970, but not in 1971 and 1972 (figure 26). All differences among dates for Russian thistle were significant ($P<.01$) for the current live category.

Annual cool-season forbs were important only during 1972 (figure 25), although some were sampled on the ungrazed area in 1970. Cool-season forbs reached their peak live standing crop in April and May, when the annual warm-season forbs were just beginning growth. One species, *Cryptantha crassisepala*, contributed most of the biomass for cool-season annual forbs (figure 27). The peak biomass of this and other cool-season annual forbs was significantly ($P<.01$) greater on the grazed than on the ungrazed treatment (tables 23 and 24) in 1972.

Perennial warm-season forbs contributed little to community standing live biomass in either 1970 or 1971, but were somewhat more important in 1972, especially on the grazed treatment (figure 28, table 21). The growth patterns of this group were similar on both treatments.

The standing crop of shrubs other than soaptree yucca and mesquite

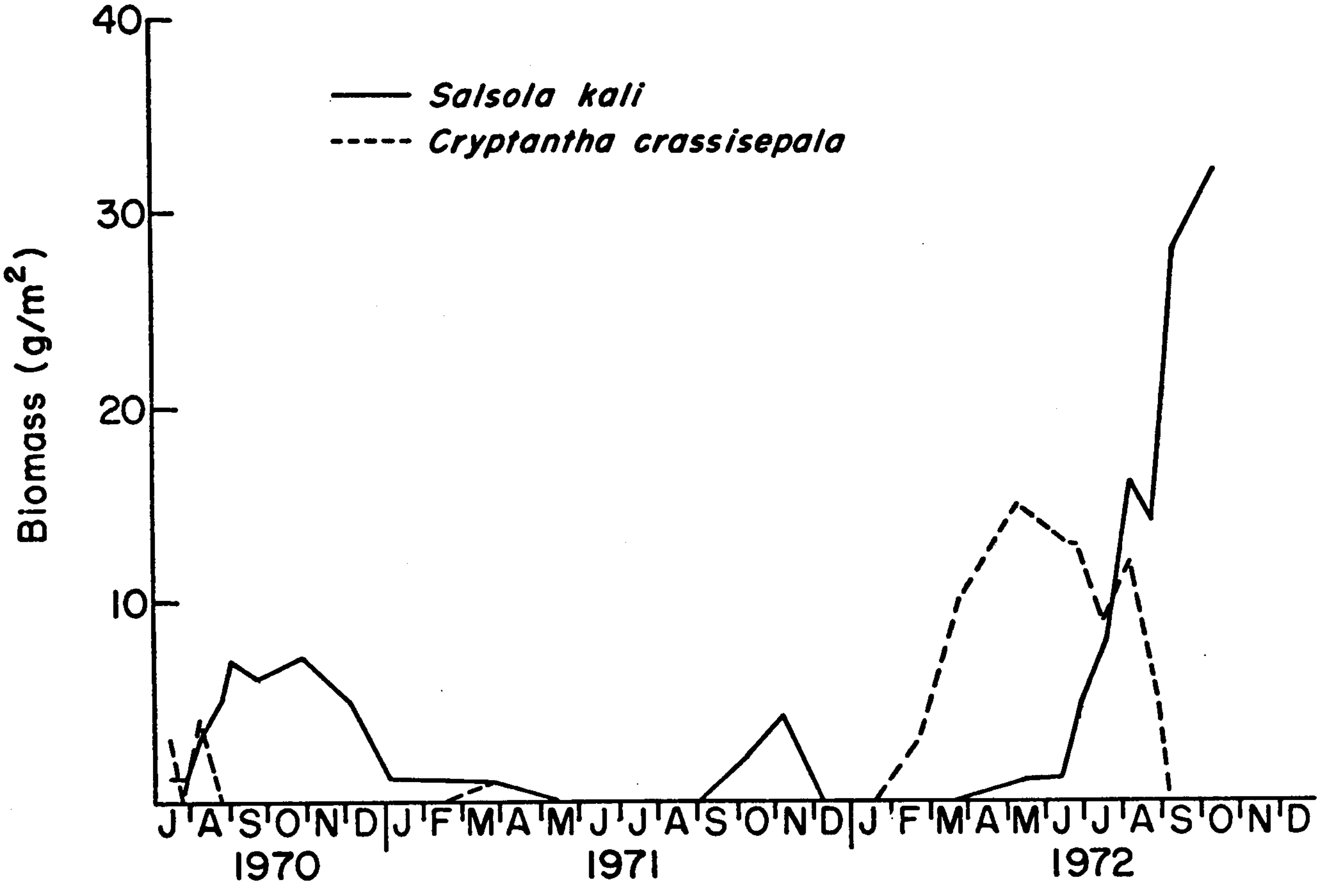

Fig. 26. Standing crop (current live) of Russian thistle (SAKA) and *Cryptantha crassisepala* (CRCR) on the ungrazed area during the study period. Both current live and recent dead were included in graph for *Cryptantha crassisepala.*

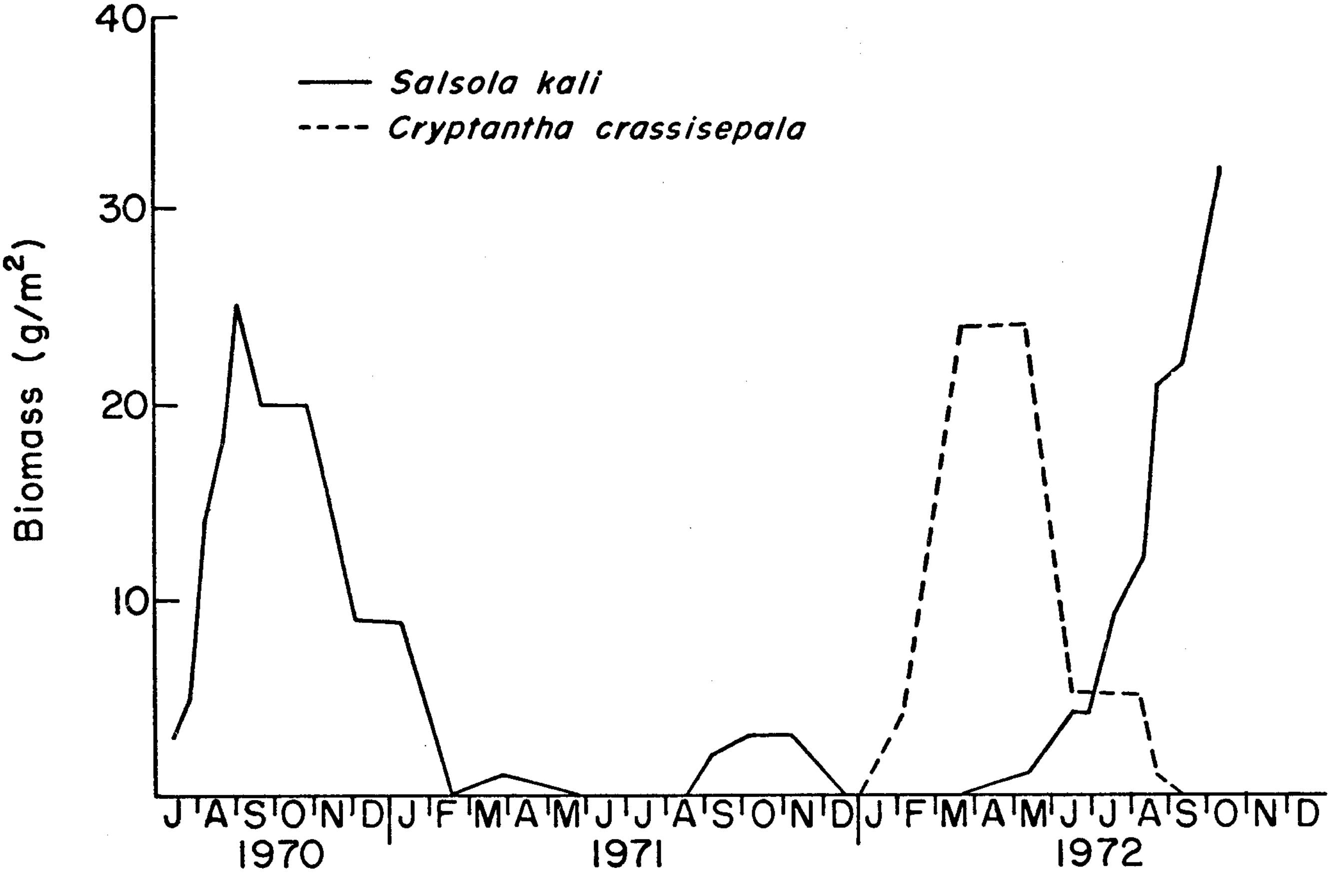

Fig. 27. Standing crop (current live and recent dead) of Russian thistle (Saka) and *Cryptantha crassisepala* (Crcr) on the grazed area during all three years of the study.

Table 23. Peak standing crop of current live material (g/m^2) of important species on the grazed (G) and ungrazed (U) areas during all three years of the study.

Species	1970		1971		1972	
	U	G	U	G	U	G
Bouteloua eriopoda	51	5	27	1	31	1
Sporobolus flexuosus	19	9	5	4	7	21
Gutierrezia sarothrae	19	32	1	3	7	7
Salsola kali	7	25	3	3	37	41
Cryptantha crassisepala	4	1	1	>1	15	24
Croton corymbulosus	4	3	2	2	6	5
Dithyraea wislizeni	0	>1	0	>1	5	7

Table 24. Belowground:aboveground ratios averaged over all sampling dates for each year.[a]

	1970	1971	1972	Average
Ungrazed	1.4a[b]	1.5a	1.3a	1.4a
Grazed	1.7a	2.6a	2.0b	2.0b
Average	A 1.6	B 2.1	A 1.7	

[a] Aboveground biomass includes current live + recent dead + old dead + litter and includes yucca and mesquite.

[b] Means with same small letters are not significantly different (P<.05) within a year, while those with same capital letters are not significantly different (P<.05) among years.

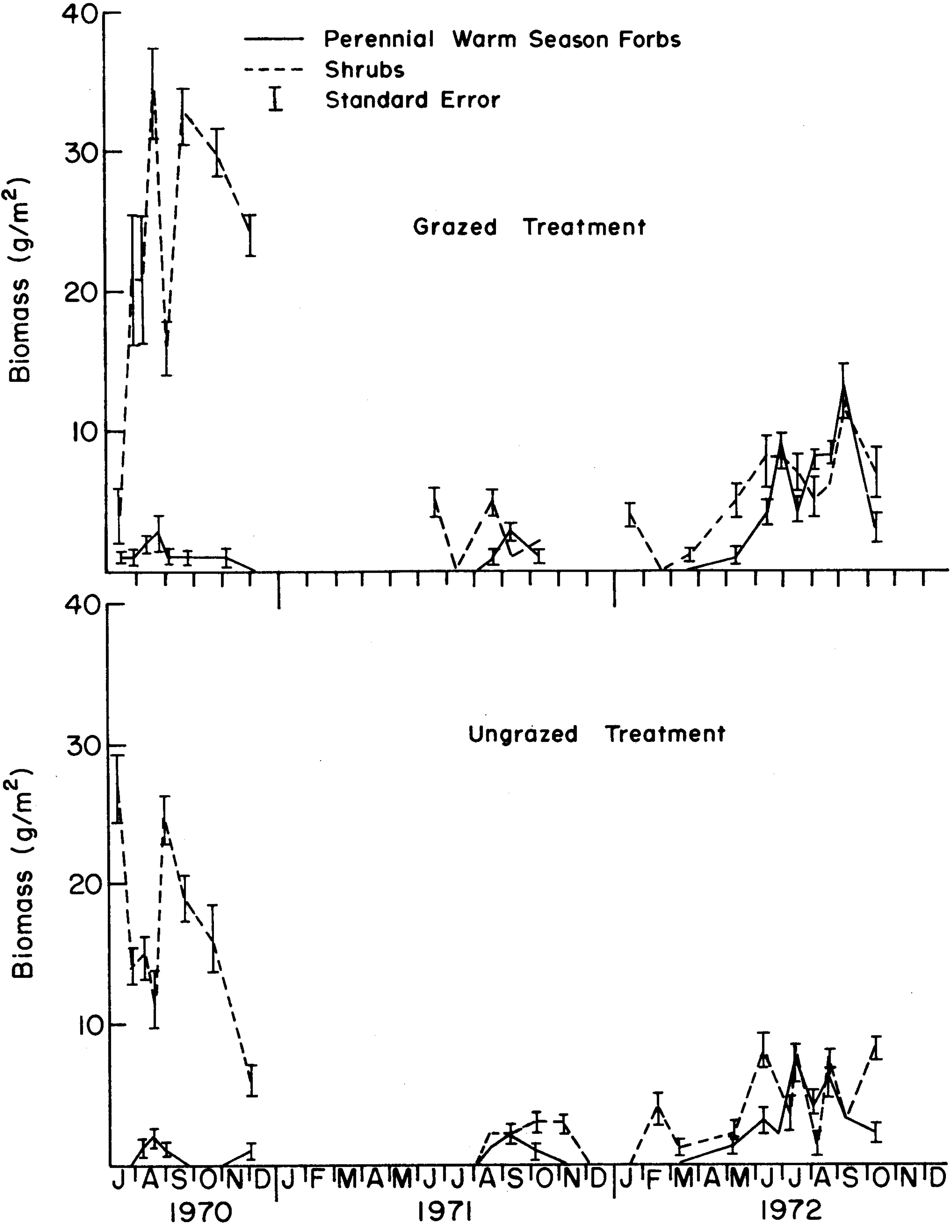

Fig. 28. Aboveground current live standing crop of shrubs and perennial warm season forbs on the ungrazed treatment.

were quite variable from one sampling period to another (figure 28). These variations and relatively large standard errors associated with each mean are probably related to the circular quadrats used and the distribution pattern of the shrubs. The major shrub on both treatments was broom snakeweed (*Gutierrezia sarothrae* [*Xanthocephalum sarothrae*]). Differences in biomass among years were similar for shrubs and broom snakeweed (figures 28 and 29). In 1970 snakeweed populations were high and biomass exceeded 30 g/m^2 on the grazed area and approached 20 g/m^2 on the ungrazed area. During the drought of 1971 snakeweed mortality was high, and its biomass along with that of other shrubs was very low. Many seedlings became established during 1972, but live biomass did not reach the highs of 1971. Standing crop of recent and old dead material of snakeweed were also highly variable and were generally fairly high in early 1971 and much lower in 1972 (figures 29 and 30). Because of the high variation in snakeweed biomass, few significant differences were shown in any compartment for any year (Appendix table 2).

Black grama (*Bouteloua eriopoda*) had the highest peak standing crop of any species on the ungrazed treatment in 1970 and 1971, but was exceeded slightly by Russian thistle in 1972 (table 23). Peak standing crops of mesa dropseed and broom snakeweed were nearly 20 g/m^2 in 1970, but declined considerably in 1971 and 1972. Peak standing crop of broom snakeweed and Russian thistle exceeded that of other species by a large margin on the grazed treatment for 1970, but declined considerably in 1971. In 1972 the peak standing crop exceeded 15 g/m^2 for black grama, Russian thistle, and *Cryptantha crassisepala* on the ungrazed treatment and the latter two species plus mesa dropseed on the grazed

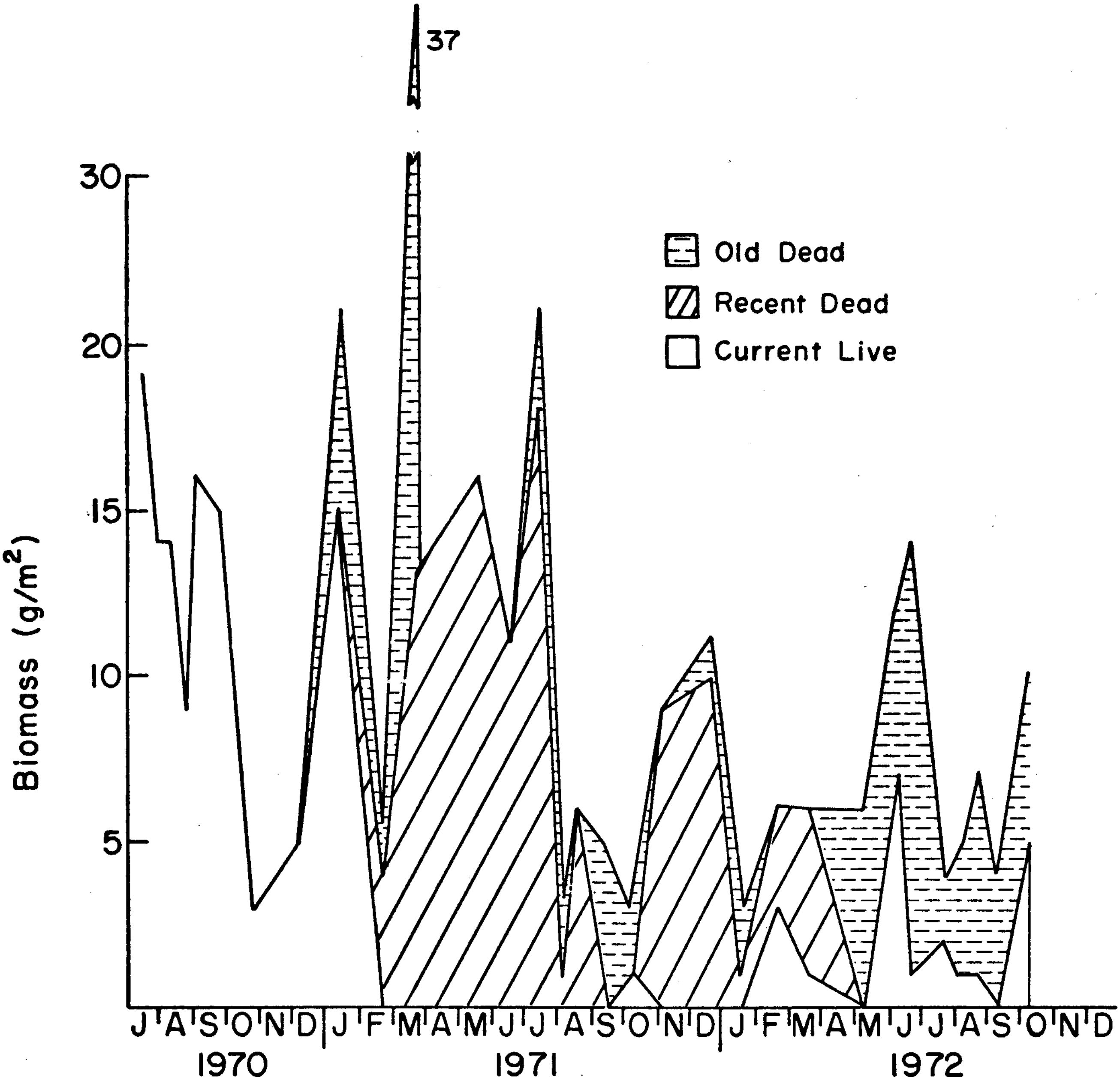

Fig. 29. Standing crop of broom snakeweed on the ungrazed treatment during all three years of the study.

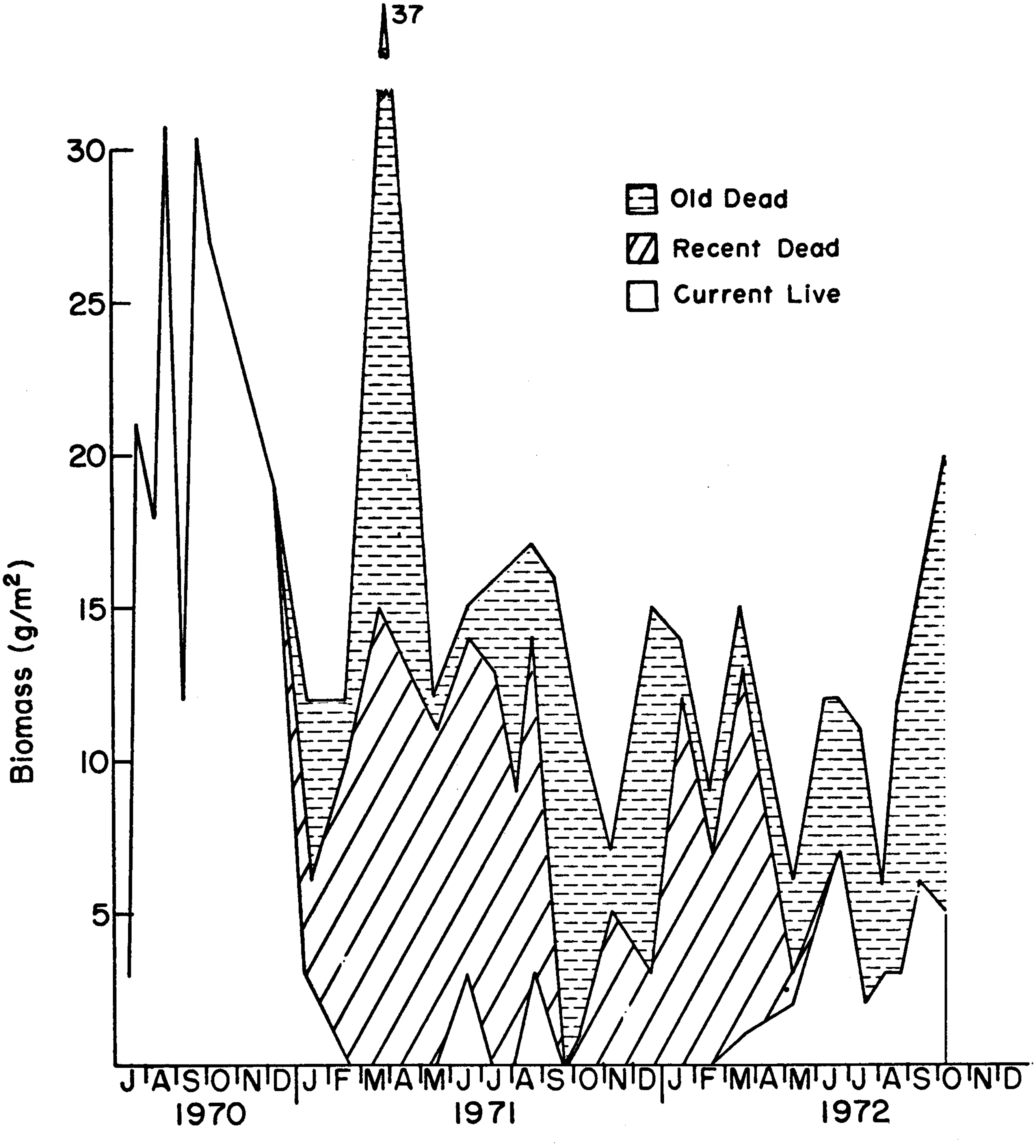

Fig. 30. Standing crop of broom snakeweed on the grazed area during all three years of the study.

treatment.

The major warm-season forb was leatherweed croton (*Croton corymbulosus*). Spectaclepod (*Dithyraea wislizeni*) was fairly abundant in 1972 on the site and more abundant off the site. Black grama was never abundant on the grazed treatment, where the peak standing crop was only 1 g/m^2 in both 1971 and 1972.

The greatest number of species on both areas was found in 1972. Figure 31 shows the composition of the standing live biomass for a date near the peak for that year for both treatments. On the ungrazed treatment, black grama and Russian thistle contributed most of the biomass; Russian thistle and mesa dropseed contributed the most on the grazed treatment. Somewhat surprisingly, the biomass for Russian thistle was greater on the ungrazed treatment than on the grazed treatment (28 g/m^2 compared to 21 g/m^2).

Seasonal dynamics of belowground biomass. Although the data for belowground biomass were quite variable, and large standard errors were associated with the means, some seasonal patterns seemed to repeat themselves during the three years of study. Root respiration may account for some of the decline during the dormant season. In general, seasonal changes followed similar patterns for both treatments, but there were some exceptions. For example, at the 21 to 30 cm depth, belowground biomass declined from 168 to 99 g/m^2 on the grazed treatment, but increased from 146 to 178 g/m^2 on the ungrazed treatment from February to May 1971. There also appeared to be a general increase in belowground biomass during the growing season, probably due to root growth and perhaps also translocation to belowground storage organs.

Since root crowns were included in the belowground samples, storage of carbohydrates may have been important, but no measure of new root development or carbohydrate storage was possible.

Belowground biomass was consistently higher on the ungrazed than on the grazed treatment in the 0 to 10 cm depth (figures 32 and 33). Over the three-year study, there was 16 g/m^2 more belowground biomass on the ungrazed treatment than on the grazed treatment. In the other depths, only small and inconsistent differences were found in belowground biomass between treatments (figures 31 and 32). Differences in belowground biomass between treatments are probably a reflection of differences in species composition. Fibrous rooted perennial grasses were more abundant on the ungrazed area, while a half shrub, broom snakeweed, was more abundant on the grazed treatment.

There was little difference in belowground biomass between 1970 and 1971. From 1971 to 1972, it generally declined, primarily in the 0 to 10 cm depth, (figure 33), which was surprising in view of the aboveground growth in 1972. Perhaps there was more root mortality in the 1971 drought and increased decomposition of belowground organic matter in 1972 when soil water was relatively high.

The greatest concentration of biomass was in the 0 to 10 cm depth for all sampling dates and treatments, and the difference was smaller between the 11 to 20 and 21 to 30 cm depths. There was no evidence of root assimilation on top of the caliche layer. About 50% of the root biomass was in the 0 to 10 cm depth, 30% in the 11 to 20, and 20% in the 21 to 30 cm depth (figure 33).

Belowground:Aboveground relations. Belowground:aboveground ratios

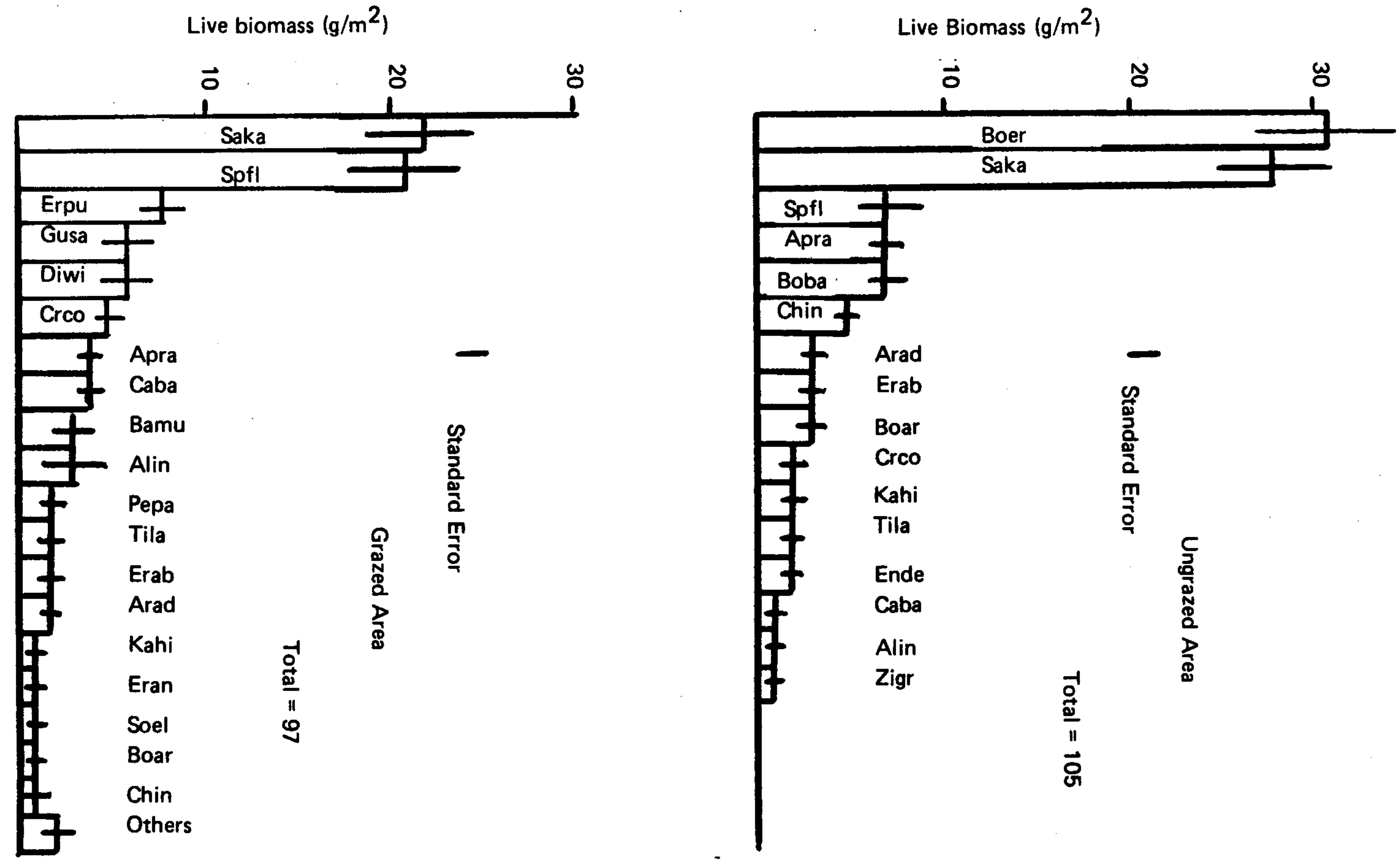

Fig. 31. Standing crop by species of current live biomass for period near peak (September 12, 1972). Species are as follows: Boer - *Bouteloua eriopoda,* Saka - *Salsola kali,* Spfl - *Sporobolus flexuosus,* Apra - *Aphanostephus ramossissimus,* Boba - *Bouteloua barbata,* Chin - *Chenopodium incanum,* Arad - *Aristida adscensionis,* Erab - *Eriogonum abertianum,* Boar - *Bouteloua aristidoides,* Crco - *Croton corymbulosus,* Kahi - *Kallstroemia hirsutissima,* Tila - *Tidestromia lanuginosa,* Ende - *Enneapogon desvauxii,* Caba - *Cassia bauhinoides,* Alin - *Allionia incarnata,* Zigr - *Zinnia grandiflora,* Pepa - *pectis papposa,* Soel - *Solanum elaeagnifolium,* Diwi - *Dithyrea wislizeni,* Erpu - *Erioneuron Puchellum,* Gusa - *Gutierrezia sarothrae,* Bamu - *Baileya multiradiata,* Eran - *Eriogonum annuum.*

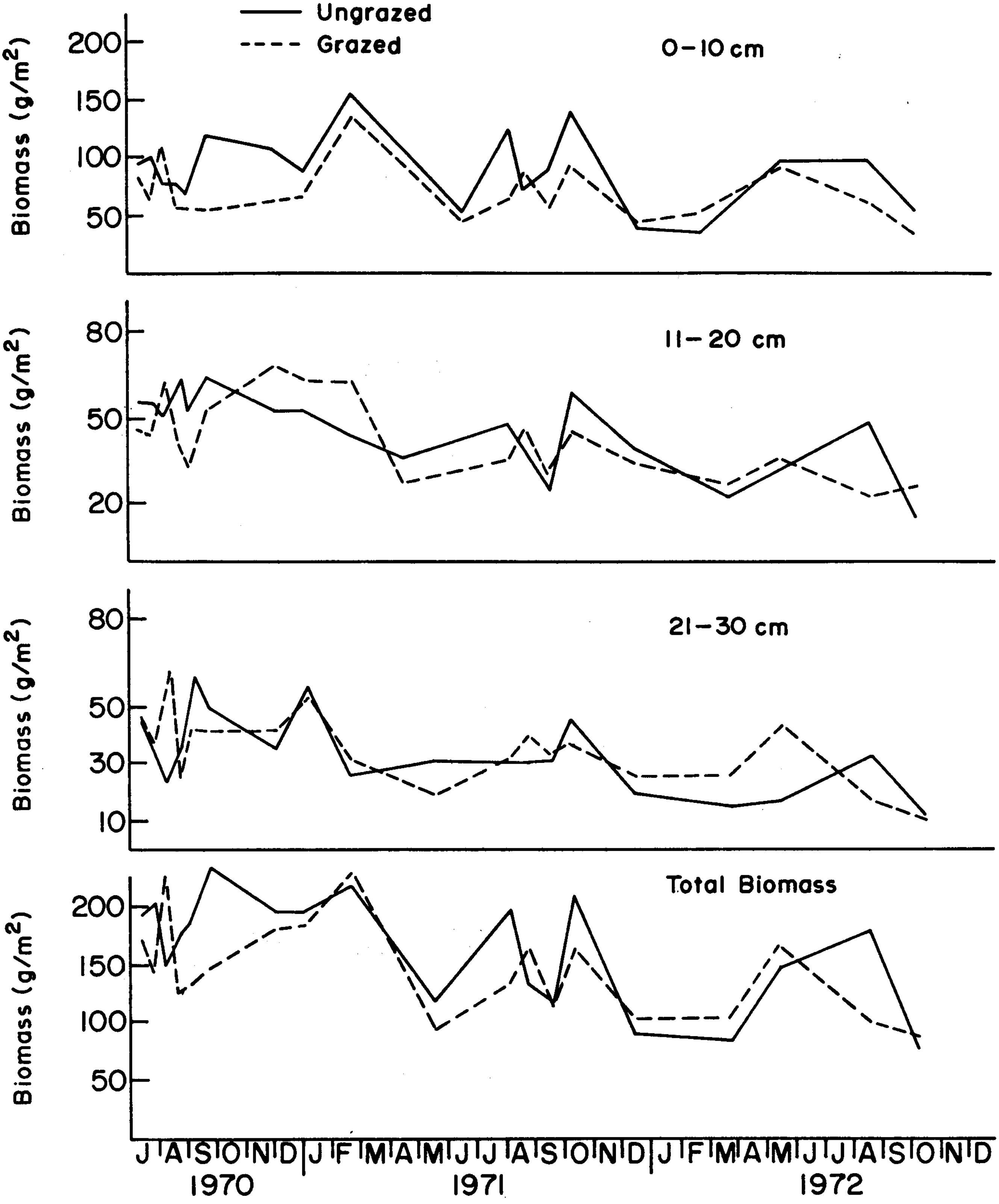

Fig. 32. Belowground standing crop by depth for the ungrazed and grazed treatments.

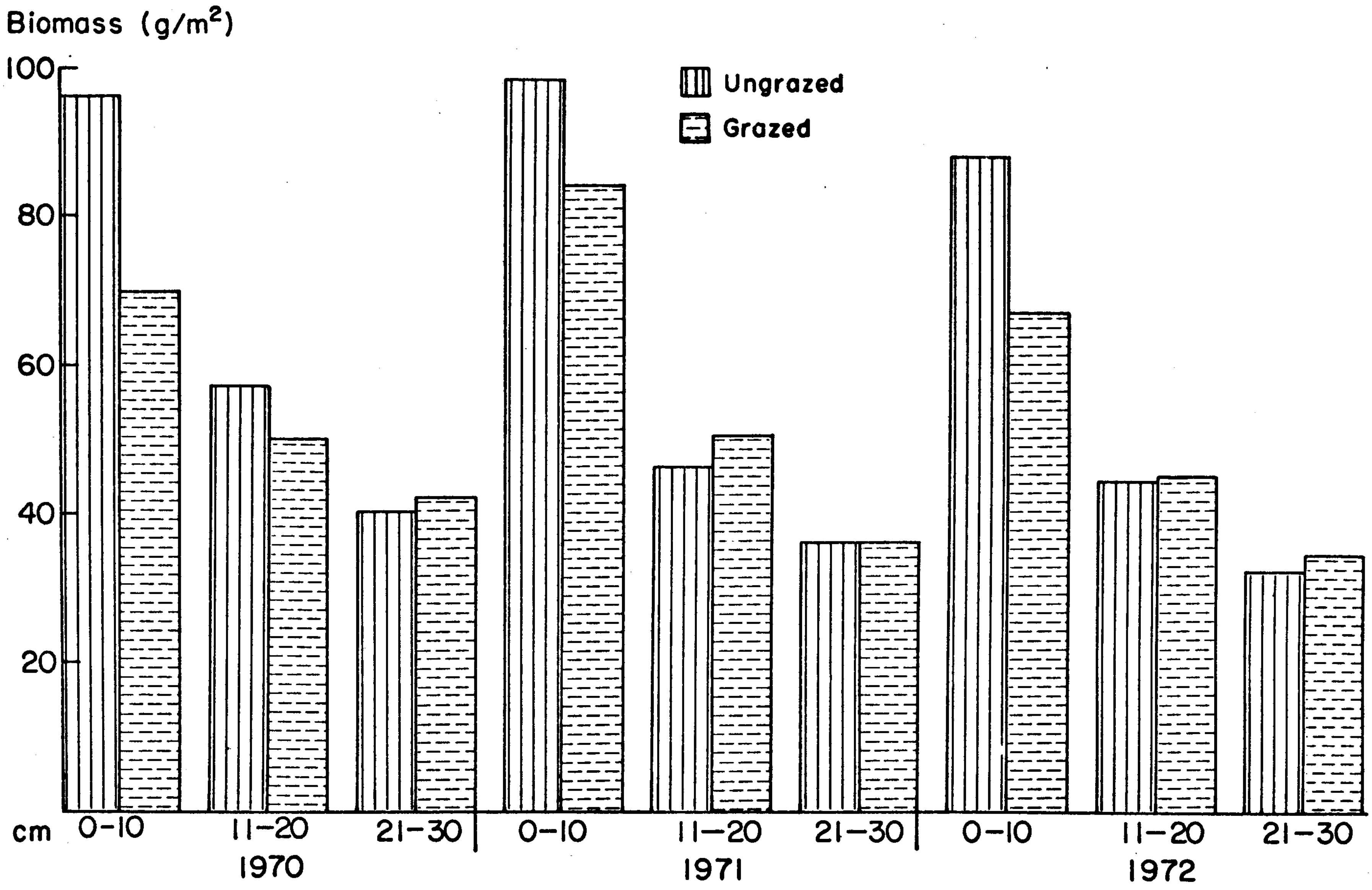

Fig. 33. Belowground biomass averaged over all sample dates withing each of the three years of the study fror all depths and treatments.

were calculated with current live, recent dead, old dead and litter, and with yucca and mesquite included, because these separations could not be made for belowground biomass. All belowground organic matter was sampled, so all aboveground organic matter was included. The data revealed some variable ratios between sampling dates but no consistent seasonal changes. Consequently, only yearly and treatment means are shown in table 24. Belowground:aboveground ratios were consistently higher on the grazed area than on the ungrazed area, because there were only small differences in belowground biomass between treatments and relatively large differences in aboveground biomass. Ratios for 1970 and 1972 were not significantly different ($P<.05$); ratios in 1971 were higher because of the relatively large belowground biomass and the small aboveground biomass.

Consumers

Large mammals. The principal large mammal herbivores on the grazed treatment were cattle and pronghorn antelope. The year-long cattle stocking rates on the Jornada were as follows: in 1970, 531 cows on 42,809 ha; in 1971, 326.2 cows on 57,583 ha; and in 1972, 516.9 animal units on 57,583 ha.

In pasture 9, where the IBP site is located, the following stocking rates in animal units year-long were grazing:

1970	16.0
1971	12.8
1972	14.5

Pasture 9 is 1322 surface hectares in size and by multiplying cattle wet weight by .3 (N. R. French, personal communication), the following dry weight biomass figures were calculated in kg per ha:

1970	1.65
1971	1.31
1972	1.51

The following estimates of pronghorn antelope populations on the Jornada were reported by Howard, Engelking, Glidewell, and Wood (1973):

1965	20
1966	25
1967	31
1968	50
1969	67
1970	69
Average	44

There are 12,800 ha of suitable antelope range relatively free of high brush on the Jornada. If each antelope weighed 54 kg live weight and .3 is used to convert to dry weight, then the average dry weight biomass of pronghorn antelope is .055 kg/ha. This figure may be somewhat conservative, because pronghorn densities were nearly 70 in both 1969 and 1970 and may have been higher than 44 during the years of this study. However, during the dry years of 1970-1971, the population may have declined slightly.

Small mammals. Small mammal densities and biomass vary greatly in both time and space within the desert grassland, although no regular cyclic pattern is discernible. Wood (1965, 1969) studied rodent populations on desert grasslands and shrub areas on the New Mexico State

University College Ranch, adjacent to the Jornada Experimental Range. On deteriorated desert grassland, Ord's kangaroo rat (*Dipodomys ordii*) contributed nearly 70% of the liveweight biomass in the winter of 1960, but only 12% in the winter of 1961 (table 25). During the winter of 1961 and 1962, the spotted ground squirrel (*Spermophilus spilosoma*) and white-throated wood rat (*Neotoma albigula*) were most important.

During the period, from 1960 to 1963 both rodent densities and biomass were higher on vegetational types other than "climax" black grama (Wood 1969, figure 34). The biomass data in this figure have been converted to dry weight by multiplying wet or live weight by .3 (French 1971). Although densities were generally higher in 1960 for all species, biomass fluctuated considerably and was not particularly high in 1960. This lack of correlation between density and biomass probably resulted from a change in species composition and different sizes of rodents.

The densities reported in figure 34 compare fairly well with values taken from the literature for a variety of species (table 26). These data indicate that most desert grassland rodents are present in densities, about 10 to 15 per ha, but higher densities such as 20 Merriam's kangaroo rats per ha in the San Simon Valley (Monson and Kessler 1940) occur at times.

On the IBP grassland site, rodent densities and biomass decreased sharply from the first sampling in April 1970 to late 1972 (figure 35). The same general trends were apparent in both density and biomass, although shifts in species composition resulted in slight inconsistencies between the two parameters. There was a slight indication of

Table 25. Annual change in species composition of a rodent population on a poor-condition desert grassland range (from Wood 1969).

Species	Winter 1960		Winter 1961			Winter 1962		
	Percent Compo-sition	ES	Percent Compo-sition	SE	Different from 1960	Percent Compo-sition	SE	Different from 1960
Dipodomys ordii	57.9	1.8	11.6	3.4	-46.3[a]	24.3	2.9	+12.7[b]
Dipodomys merriami	23.0	1.5	1.2	1.2	-21.8[a]	0.0	--	-1.2
Dipodomys spectabilis	7.7	.9	8.1	2.9	+ .4	5.9	1.1	-2.2
Spermophilus spilosoma	1.3	.3	59.3	5.3	+58.0[a]	49.4	2.5	-9.9
Neotoma albigula	1.7	6.4	16.3	4.0	+14.6[a]	13.5	1.7	-2.7
Neotoma micropus	1.3	.3	0.0	--	-1.3	2.8	.8	+2.8
Onychomys leucogaster	6.0	.8	1.2	1.2	-4.8[a]	3.3	.9	+2.1
Other[c]	.9	.3	2.3	1.6	+1.4	.5	.3	-1.8
Number in sample	779		86			426		

[a] Difference significant at the 99 percent level.

[b] Difference significant at the 95 percent level.

[c] Others include *Perognathus flavus*, *P. penicillatus*, *Peromyscus maniculatus*, *Sigmodon hispidus*, *Reithrodontomys megalotis*.

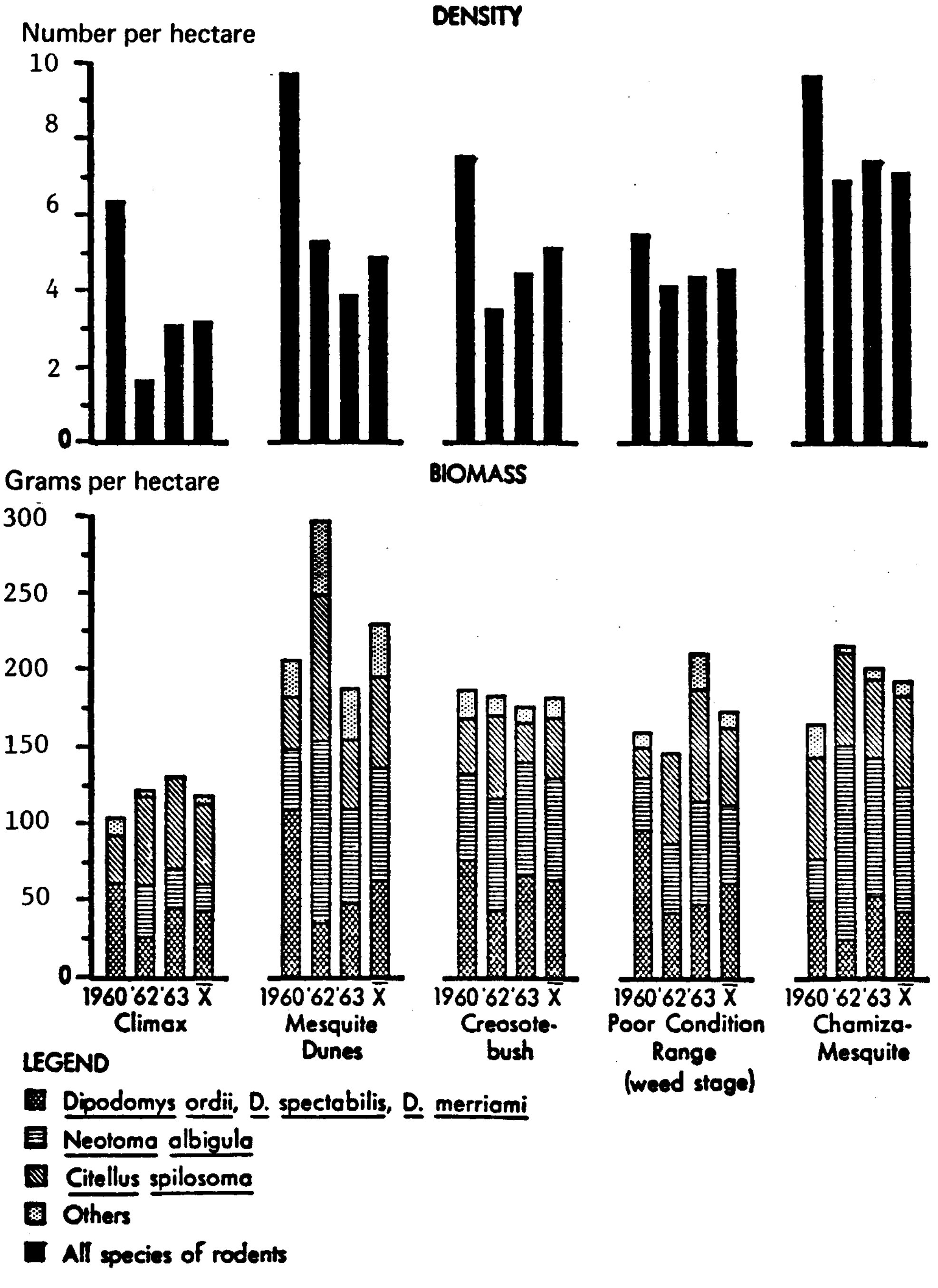

Fig. 34. Density and biomass in grams dry weight per hectare of rodent populations in the major cover types on the College Ranch, Dona Ana County, New Mexico, 1960-63 (from Wood 1969).

Table 26. Density (number per ha) of desert grassland rodent species from several different locations.

Species	Location	Density (no./ha)	Author
Ord's kangaroo rat	Southern New Mexico	2.6-2.9	Blair 1943
	Southern New Mexico	1.2-3.0	Wood 1969
	Texas Panhandle	7.2-21.6	McCulloch and Inglis 1961
Merriam's kangaroo rat	Santa Rita, Arizona	$\bar{x}$ = 9.5 Range 1.4-2.6	Reynolds 1958
	Southwestern New Mexico	$\bar{x}$ = 2.0 Range 1.4-2.6	Monson and Kessler 1940
	Southern New Mexico	$\bar{x}$ = 1.2 Range 0-1.8	Wood 1969
Banner-tailed kangaroo rat	Santa Rita, Arizona	5.0	Vorhies and Taylor 1922
	Northern New Mexico	.7-1.4	Holdenreid 1957
	Southern New Mexico	1.8	Wood 1969
Grasshopper mouse	Southern New Mexico	.2	Blair 1943
	Southern New Mexico	2.4	Wood 1969
Desert pocket mouse	Southern New Mexico	4.4	Blair 1943
	Santa Rita, Arizona	.3	Reynolds and Haskell 1949
Spotted ground squirrel	Southern New Mexico	1.8	Wood 1969

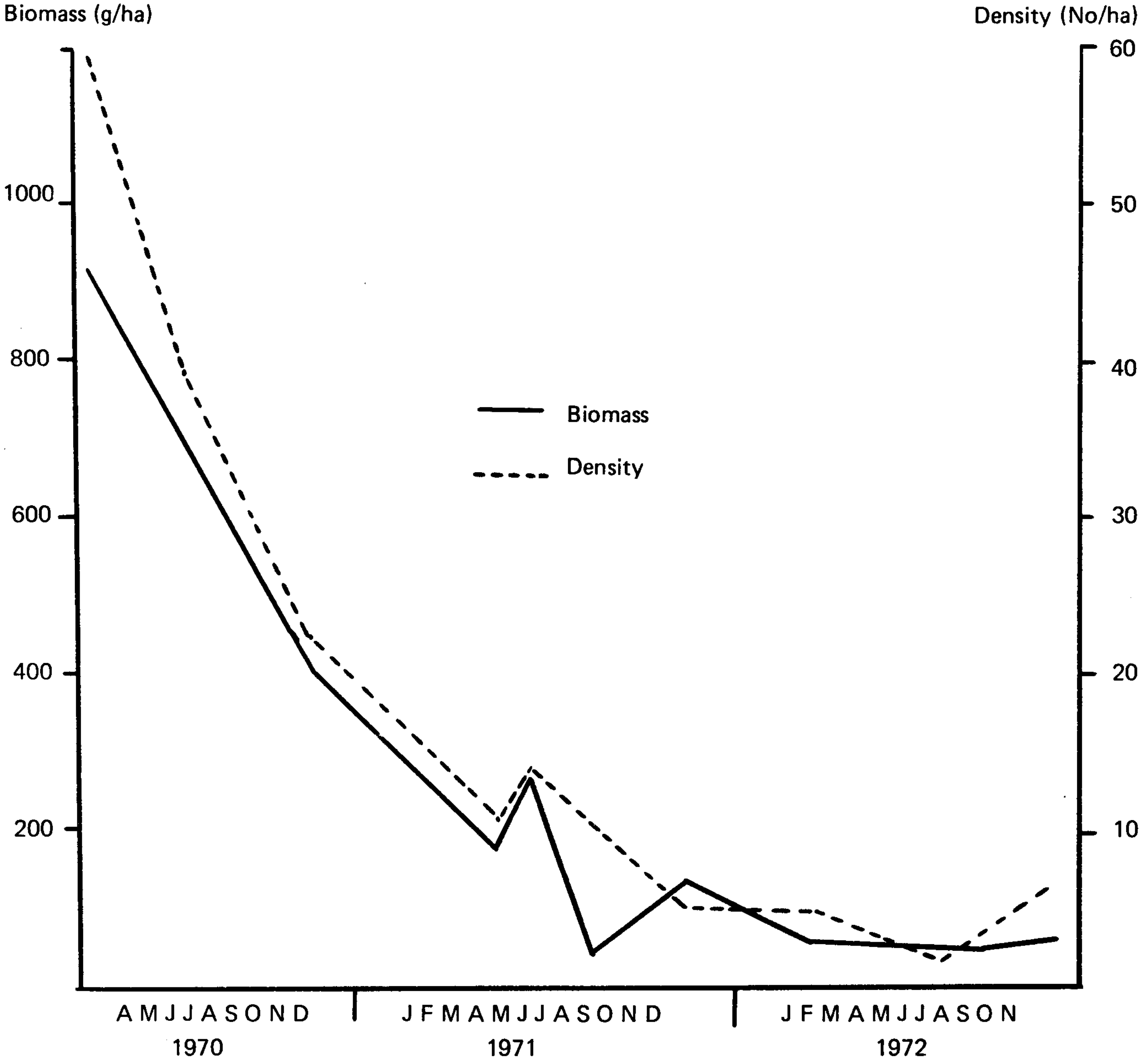

Fig. 35. Small rodent biomass and density for the three years of the study.

increase in rodent density in late 1972, probably because of the abundant vegetational development at that time.

The population of Ord's and the banner-tailed kangaroo rat were over 35 and 5 per ha at the study, but both declined throughout 1970 and early 1971. Population levels of the banner-tailed kangaroo rat remained low throughout 1971 and 1972 (figure 36). Within each of these species, density and biomass followed the same trends very closely. In both 1971 and 1972, there was a slight increase in biomass and density during the summer, possibly resulting from recruitment of young into the population following a brief breeding period.

The spotted ground squirrel population also declined in both biomass and density during 1970 and early 1971, but it rebounded late in 1971, only to decline again in 1972 (figure 37). Both the grasshopper mouse and southern plains woodrat reached low points in their population and were not sampled in late 1971 or 1972 (figure 37).

For the entire period of the study Ord's kangaroo rat contributed the greatest biomass and density; the banner-tailed kangaroo rat was also important throughout the study. Other species, such as the spotted ground squirrel and the wood rats, were important mainly during 1970. Because spotted ground squirrels were trapped at night, the population may have been underestimated, because this species is also diurnal (Packard 1971). Several species of pocket mice were also sampled during 1971 and made modest contributions to the biomass and especially density (figures 38 and 39).

Lagomorph densities fluctuate considerably on desert grasslands. Vorhies and Taylor (1933) stated that jackrabbit densities varied from

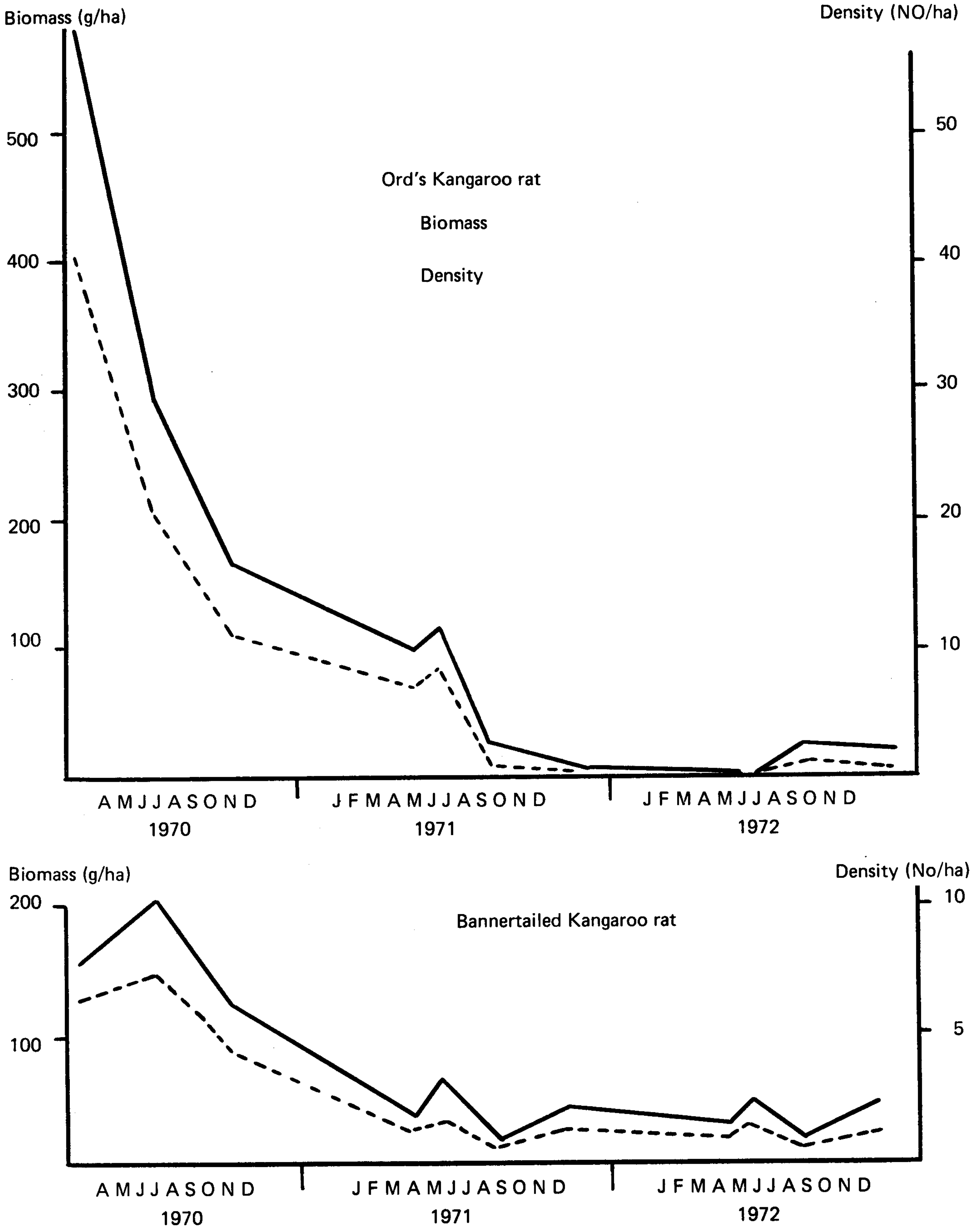

Fig. 36. Biomass and density of Ord's and the bannertailed kangaroo rats.

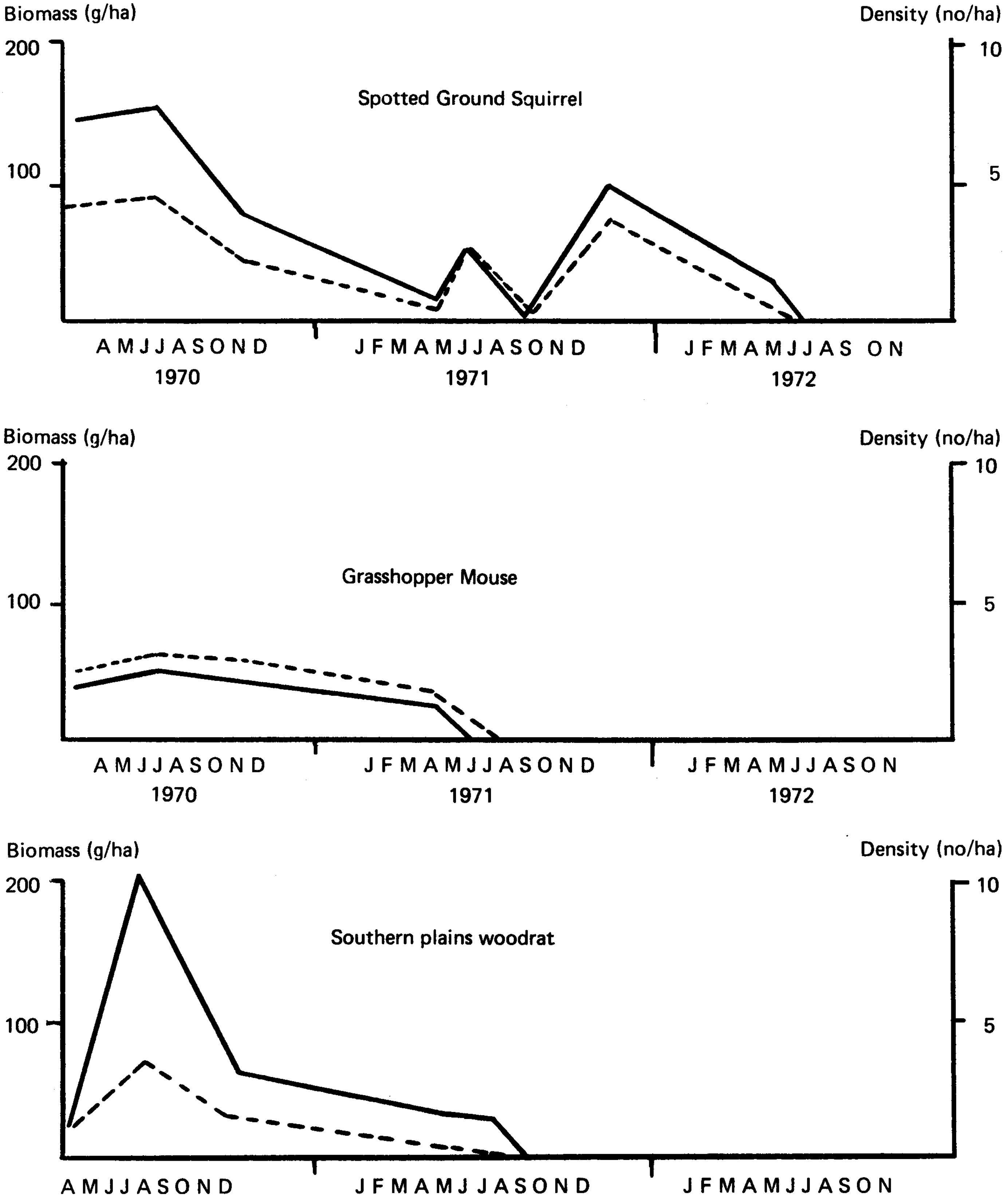

Fig. 37. Biomass and denstiy of the spotted ground squirrel, grasshopper mouse and southern plains wood rat.

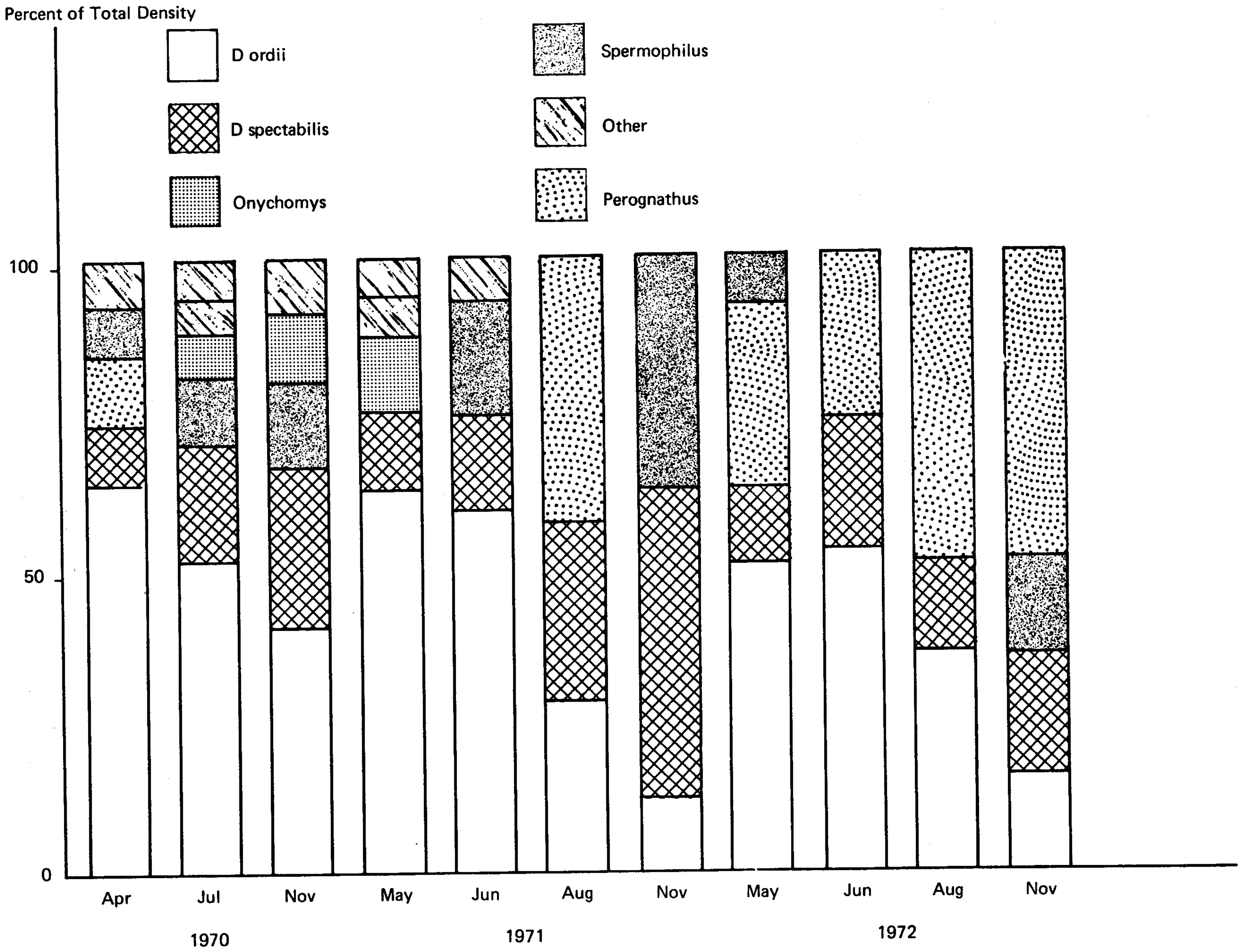

Fig. 38. Species composition of rodents populations based on density.

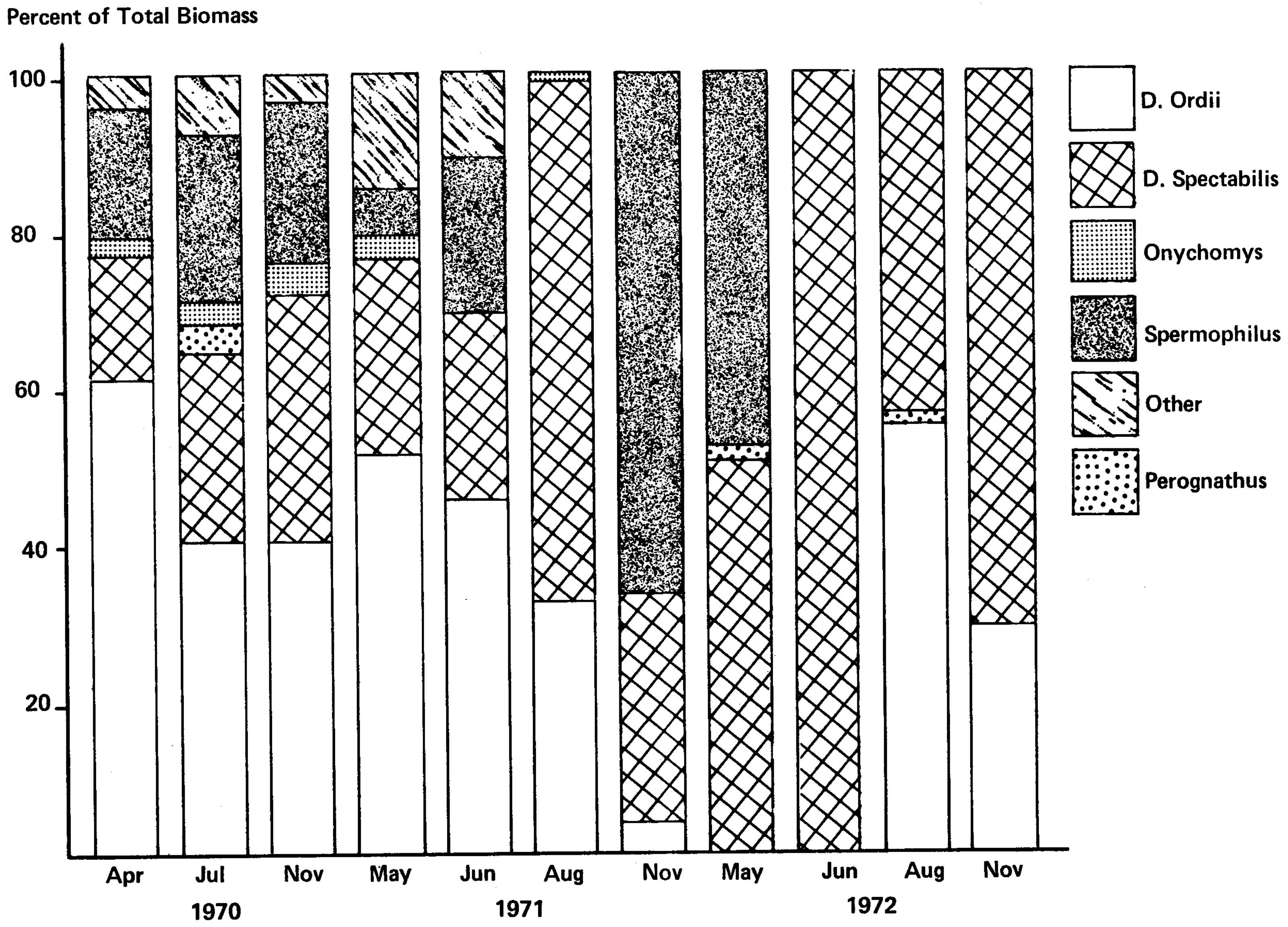

Fig. 39. Species composition of rodents based on biomass.

5000 to 10,000 on the 20,000 ha Santa Rita Experimental Range. During their study *Lepus alleni* averaged .015 individual rabbits per ha while *L. californicus* averaged .05 individual rabbits per ha on the grassland portion of the area only. Densities were slightly higher on shrubby portions of the range.

On the Jornada, both desert cottontail and black-tailed jackrabbit populations were high during the early 1940's and again about 1960 (figure 40). From 1961 to 1968, densities remained at a low and relatively stable level. During the IBP studies, population biomass of the desert cottontail has been low (figure 41). Black-tailed jackrabbit biomass has fluctuated somewhat reaching a peak in August 1971 of about 70 g/ha. There was also an increase in the late summer, early fall, 1972.

Small mammals in desert grasslands vary considerably in live weight (table 27), as they vary in size, from the relatively large black-tailed jackrabbit to the harvest mouse. Many environmental as well as genetic factors influence the weight of an animal. These undoubtedly account for some of the differences shown for different areas in table 27.

Vegetational structure also greatly influences the density and species of small mammals on an area. An unbroken expanse of uniform grassland favors only a few species of small mammals (Wood 1969). On the New Mexico State University College Ranch only one major species of small rodent, silky pocket mouse, was found in climax black grama grassland (Wood 1969). Greatest density and biomass were found in grassland where some shrubby species, such as creosotebush or mesquite, had invaded. Table 28 also shows that, throughout the Southwest, shrubs

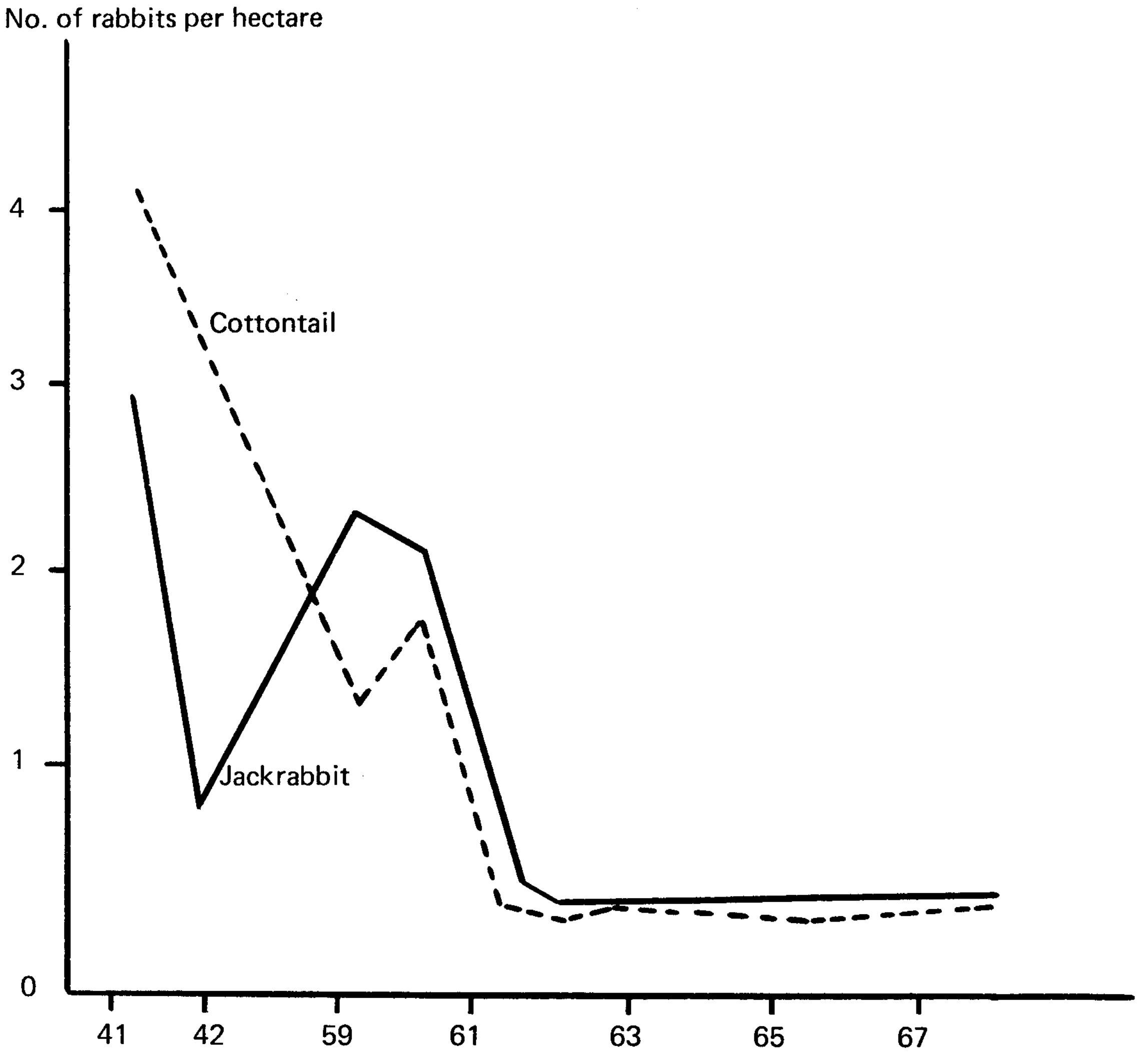

Fig. 40. Rabbit population on the Jornada Range and College Ranch (from Herbel, Dittberner and Bickle 1970).

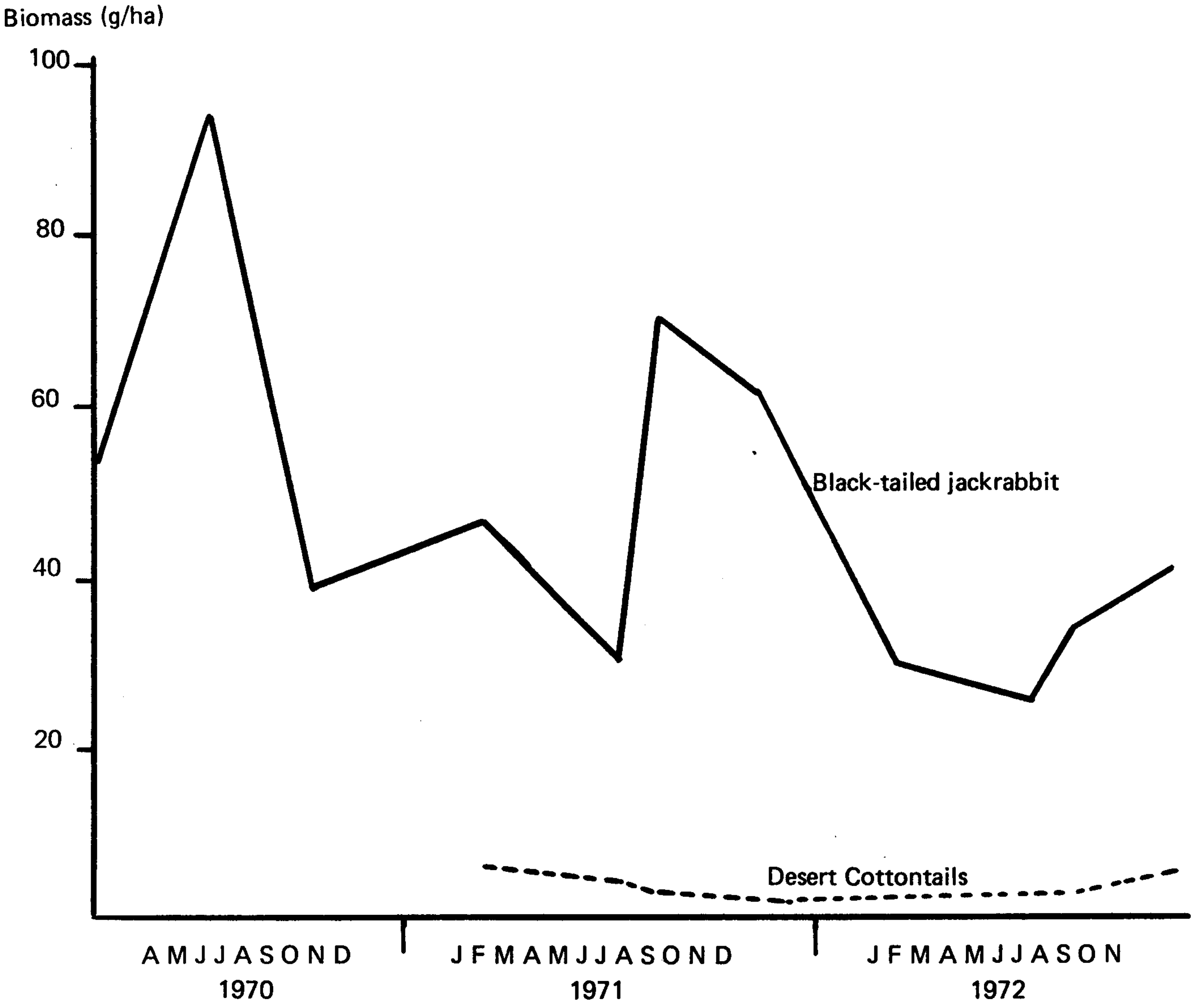

Fig. 41. Biomass of black tailed jackrabbit and desert cottontails on Jornada IBP site.

Table 27. Mean body weight (in grams) of desert rodents and rabbit on desert grassland area (from Laycock 1970).

Species	University Ranch (Wood 1965)	Wood (1969)	Other areas of desert grassland
Spermophilus spilosoma (Spotted ground squirrel	109.0	104.7	136-154 (Hill 1942) 107 (Bailey 1931)
Dipodomys merriami (Merriam's kangaroo rat)	42.0	42.2	40-50 (Bailey 1931) 36-42 in winter, 43-46 in summer (Reynolds 1960)
D. ordii (Ord's kangaroo rat)	51.8	51.0	51-74 (Hill 1942) 40-50 (Bailey 1931)
D. spectabilis (Banner-tailed kangaroo rat)	124.8	124.9	Heaviest weight = 177-178 (Holdenreid 1957) 98-132, $\bar{x}$ = 114.5 (Vorhies and Taylor 1922) 123 (Bailey 1931)
Lepus californicus (Black-tailed jackrabbit)	--	--	2300 (Haskel and Reynolds 1947)
Neotoma albigula (White-throated wood rat)	159.3	159.2	184-224 (Hill 1942) 188 (Bailey 1931) 103 at 66 days of age (weaning) (Richardson 1943)
N. micropus (Southern plains wood rat)	206.6	205.3	No data
Onychomys leucogaster (Grasshopper mouse)	33.9	33.5	41-52 (Hill 1942)
Perognathus flavus (Silky pocket mouse)	6.6	6.3	7-8.5 (Hill 1942) 9-10 (Forbes 1964) 6.5-7.3 (Bailey 1931)
P. penicillatus (Desert pocket mouse)	12.9	13.2	13-20 (Reynolds and Haskell 1949)
Reithrodonotomys megalotis (Harvest mouse)	10.7	10.7	No data
Sylvilagus auduboni (Desert cottontail)	--	--	880 (Hill 1942) 560-956 (Sowls 1957)

Table 28. Habitat "preferences" of desert rodents and rabbits in New Mexico and other areas in the southwest (from Laycock 1970).

	North-central New Mexico (Ivey 1957)	N.M. State Univ. College Range (Wood 1969)	Others
Spermophilus spilosoma (Spotted ground Squirrel)	Overgrazed sheep ranges	Creosote bush and annual weed	Southwest Texas--preference for desert scrub (blackbrush and creosote bush) (Davis and Robertson 1944); Utah--light textured soils (Moore 1930)
Dipodomys ordii (Ord's kangaroo rat)	Wide range from good black grama	Annual weed and mesquite-lowest	Southern Arizona--softer soils and denser vegetation along rivers (Burt 1933)
D. merriami (Merriam's kangaroo rat)	Mesquite areas in lower Sonoran Zone	Creosote bush, annual weed, mesquite, absent	Arizona and New Mexico--creosote bush, shrub areas with good production of annuals (Monson and Kessler 1940); mesquite, *Acacia* (Vorhies and Taylor 1922)
D. spectabilis (Banner-tailed kangaroo rat)	Overgrazed areas Upper and lower Sonoran Zone	Annual weed	Arizona and New Mexico--mixed grass-shrub type with good production of annuals (Monson and Kessler 1940); mesquite, *Acacia* (Vorhies and Taylor 1922)
Lepus californicus (Black-tailed jackrabbit)	--	--	Highest in weed and mesquite sandhills types; lowest in black grama grassland (Norris 1950).
Neotoma albigula (White-throated wood rat)	Pinyon-juniper areas in Upper Sonoran Zone	Mesquite	Utah--creosote bush or cacus (Burt 1933); New Mexico and Arizona--mesquite and other shrubs (Monson and Kessler 1940)
N. micropus (Southern plains wood rat)	Prickly pear areas	Annual weed absent in climax grassland	Southern Texas--highest number of dens in mesquite-cactus community (Johnson 1952)
Onychomys leucogaster (Grasshopper mouse)	--	Creosote bush	
Perognathus flavus (silky pocket mouse)	Overgrazed range sanddrift-shrub areas	Annual weed and tobosa grassland	College Ranch, New Mexico--greatest number of mice of these four species in mesquite sandhills and snakeweed-grass types; low population in grassland (Norris 1950)
P. penicillatus (Desert pocket mouse)	--	Creosote bush absent in climax grass	
Reithrodontomys megalotis (Harvest mouse)	Disturbed areas, sand and shrub areas--Upper Sonoran Zone	Tobosa grassland--absent or low in all other types	
Sylvilagus auduboni (Desert cottontail)	--	--	Highest in weed, mesquite sandhills, and snakeweed, grass types; lowest in black grama and tobosa grasslands (Norris 1950)

and forbs are important components of rodent habitat.

Invertebrates. At the outset of the IBP Grassland Biome program, sampling strategies that would be comparable across sites were given a high priority. Consequently, a biome-wide standardized sampling scheme was adopted, which promised an effective means of across-site sampling of invertebrate populations. In practice, however, specialized sampling problems peculiar to the Jornada site resulted in substantial sampling deficiencies. Superimposed upon the normally low populations associated with dry seasons and dry years were clumped, nonrandom distribution of plants. Large shrubs, such as mesquite and yucca, grew in relatively few samples per replicate. This caused large sampling errors for invertebrate populations. Furthermore, bare ground on the study site comprised approximately 70% of the surface area; the probability of sampling this bare ground and missing reservoir areas of insect populations (in and around vegetation) was great.

Had a large enough sample been taken per sampling date, some of these problems would have been alleviated. The sampling problem, however, had no easy solution. For example, when sample size was doubled in the latter part of 1971, no discernible reduction in sampling error was noted. In addition, observations made while sampling indicated that techniques and procedures highly effective with grass and some forbs permitted the escape of many taxa when sampling *Salsola kali*, *Yucca elata*, or *Xanthocephalum sarothrae*.

In a desert grassland, and specifically on the Jornada, the invertebrate population does not remain at a low and relatively static level. Under the constraints of a standardized, across-site sampling technique and substantially less-than-adequate replicates, the invertebrate picture presented in tables 29, 30, and 31 probably is a reasonable qualitative reflection of the diurnal, terrestrial population for two quite dry years followed by one fairly wet year.

However, during the three years of the study, there was no outbreak of any of a number of likely insect species. Within the experience of the investigators and in the immediate vicinity of the IBP plots, there have been outbreaks of grasshoppers, more than one species of mesquite defoliator, a *Xanthocephalum sarothrae* stem borer, at least two species of thrips, a grass mealy bug, and the desert termite. Had any one of these occurred during the course of this study, the invertebrate biomass picture would have been substantially altered. In other parts of New Mexico's desert grassland, at least three other highly destructive grass-feeding insect species or groups (e.g., range caterpillar, *Phyllophaga* spp., *Labops* spp., and *Irbisia* spp.) periodically totally destroy vegetation on dozens to thousands of hectares of rangelands, while other regions of the desert grassland experience periodic outbreaks of a different group of species. Furthermore, the carrion feeders, the nocturnal species, and the soil inhabiting invertebrate fauna are unaccounted for in these samples.

Also contributing to a biased invertebrate picture was the random distribution of sample sites over a terrain characterized by nonrandom distribution of both total ground cover and the protective habitat provided by yucca and mesquite. This bias might have been overcome with many more random samples or with a ground cover-vegetation species stratification, which in itself would call for a larger sample size.

Table 29. Inter-quadrat comparison of plant species and invertebrates for three sampling dates in 1972. Chi-square values are included only for significant associations ($P<.05$). Larger chi-square values are indicative of stronger species associations.

Invertebrate Taxa	Plant Species[a]							
	YUEL	SPFL	SAKA	TRPU	GUSA	CRCR	BOER	CRCO
Lygaeidae	28.9	--	8.5	--	--	--	--	--
Aphididae	28.9	--	--	--	--	--	--	--
Blattidae	28.9	--	--	--	--	--	--	--
Termitidae	28.9	--	--	--	--	--	--	--
Cicadellidae	--	13.5	10.5	9.3	4.3	--	7.7	--
Tingidae	--	4.3	13.2	6.2	12.6	6.3	--	--
Phloeothripidae	--	5.4	9.7	4.2	5.2	--	5.4	--
Sminthuridae	--	7.6	6.4	6.4	--	--	--	8.3
Coccinellidae	--	5.2	--	--	--	6.3	--	--
Curculionidae	--	5.4	--	--	--	--	--	--
Thripidae	--	--	--	--	9.3	--	--	--
Formicidae	--	--	--	6.3	--	--	--	--
Myrmeleontidae	--	--	--	--	--	4.8	--	--

[a] YUEL = *Yucca elata*
SPFL = *Sporobolus flexuosus*
SAKA = *Salsola kali*
TRPU = *Tridens puchellus*
GUSA = *Gutierrezia (Xanthocephalum) sarothrae*
CRCR = *Cryptantha crassisepala*
BOER = *Bouteloua eriopoda*
CRCO = *Croton corymbulosus*

Table 30. List of families collected on mesquite, July 16 and August 16, 1971.

Order	Family
Orthoptera	Mantidae Phasmidae
Homoptera	Psyllidae Membracidae Fulgoridae Cicadellidae Cercopidae
Hemiptera	Tingidae
Neuroptera	Chrysopidae Myrmeleontidae
Diptera[a]	Asilidae Phoridae Tachinidae
Lepidoptera[a]	Geometridae Tortricidae
Coleoptera	Bruchidae Cerambycidae Curculionidae Nitidulidae Tenebrionidae
Thysanoptera	Phlaeothripidae Thripidae
Collembola	Sminthuridae
Hymenoptera[a]	Formicidae Pompilidae Cynipidae
Acarina[a]	Caeculidae
Araneida	Lycosidae Salticidae Thomisidae Argiopidae

[a] Not all species were identified to family.

Table 31. Summary of invertebrates captured on yucca flowers on May 24 and June 21, 1972.

Order	Family	Life Stage[a]	Total Catch May 24	Total Catch June 21
Thysanoptera	Thripidae	A N	228	187
Hemoptera	Aphididae	N	3000+	3500+
Hemiptera	Miridae	A	6	14
		N	2	3
	Pentatomidae	A	0	6
Diptera		A	1	5
Lepidoptera[b]		A	7	10
Hymenoptera	Formicidae	A	33	65
Coleoptera	Coccinellidae	A	5	12
		N	0	15
	Nitidulidae	A	2	0
	Mordellidae	A	0	1
Araneida	Salticidae	A	1	1
	Thomisidae	A	0	1

[a] A = adult; N = larva or nymph.

[b] At least two families of Microlepidoptera were collected.

It is with these reservations that the invertebrate data for the Jornada are presented. They should be considered minimal estimates at most and many probably do not accurately reflect actual between-treatment differences in numbers or biomass. For example, an analysis of variance of invertebrate data (Appendix table 3) reflected a significant difference among trophic levels and dates for 1970, 1971, and 1972 ($P<.01$) but only between treatments at $P<.10$ in 1970 and not in 1971 or 1972.

A general decrease in invertebrate density on the Jornada IBP site was observed from late summer of 1970 until the summer of 1971, followed by a general increase to the summer of 1972 (figure 42). Biomass was extremely low, but followed the density trends in general. Most often biomass was less than .1 g/m^2 on both the grazed and ungrazed treatments until July-August 1972 when peak biomass on the ungrazed treatment reached .782 g/m^2. Similarly, in October 1972 peak biomass on the grazed treatment reached .42 g/m^2. The increase in both numbers and biomass in 1972 corresponded to increased precipitation and primary productivity, but the large biomass increase for August can only be explained by sampling anomaly. The increase from July to August on the ungrazed treatment is a reflection of only one quadrat sampled in which a large yucca plant and considerable numbers of invertebrates were found. Elimination of adult tenebrionids in the yucca quadrat would reduce biomass for the treatment from .78 to .25 g/m^2. The similarly high biomass peak on the grazed treatment, October 1972, was also a result of one quadrat with yucca.

The apparent lack of close correlation between numbers and biomass

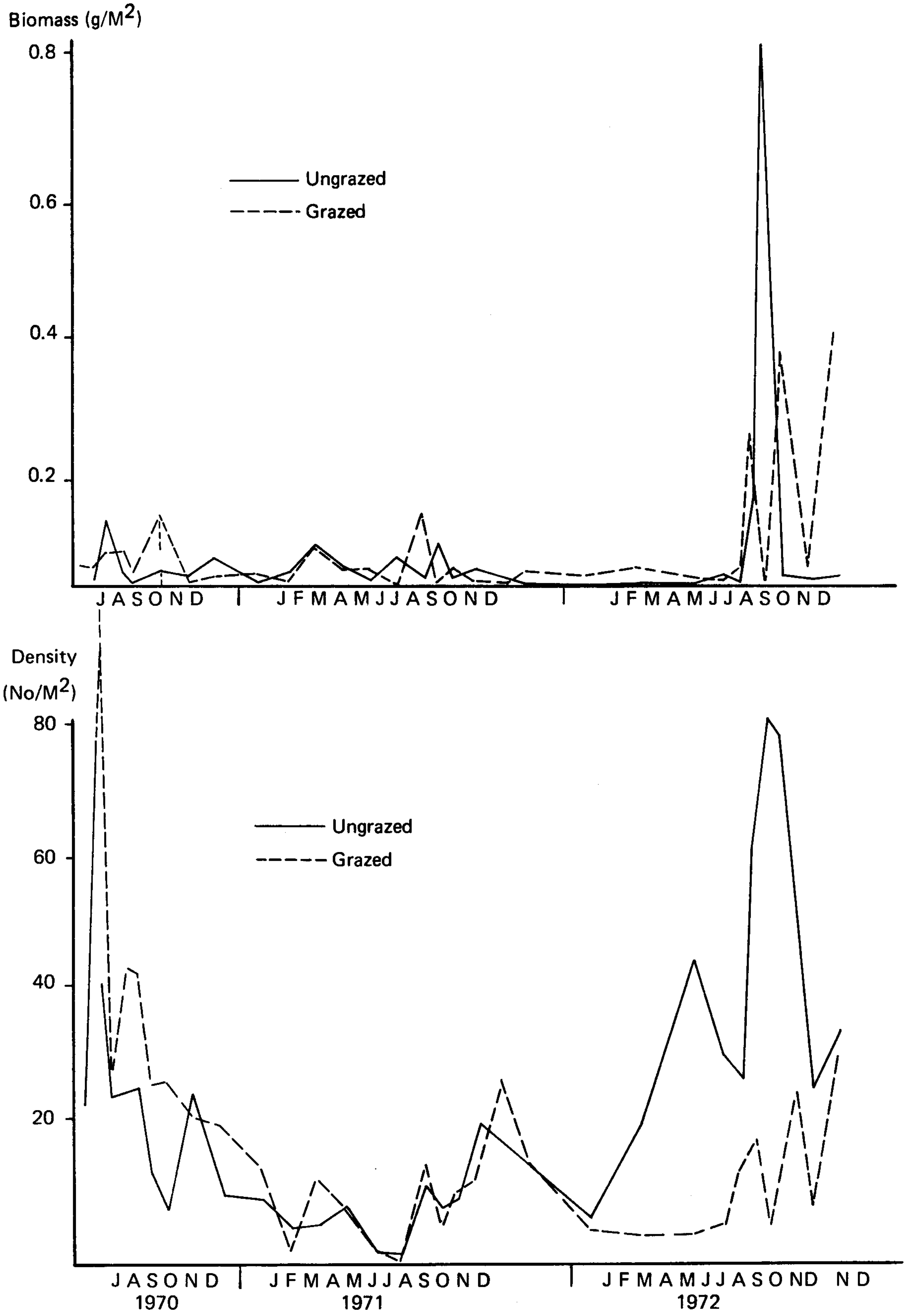

Fig. 42. Invertebrate density and biomass for both treatments and all three years.

(figure 42) resulted primarily from a few large invertebrates such as grasshoppers or beetles (*Eleodes* spp.) in some of the samples (Ellstrom 1973). Body weight of some of these might exceed that of a leafhopper by as much as 1000.

All samples taken over yucca reflected a much higher invertebrate density and biomass than samples from other plant species. In addition, diversity, as might be expected because of the relatively extensive shelter, was much greater in yucca samples than in any other. Therefore, yucca samples have been included in the population analysis despite the increased sampling error incurred by including them. Had more of these plants been encountered earlier in the study, they would have been separated and analyzed separately.

The importance of various invertebrate orders, reflected by the number caught, changed during the study. In 1970, orders with the highest densities on both treatments were (in descending order): Acarina, Homoptera, Hemiptera, and Hymenoptera; in 1971, the Hymenoptera, Coleoptera, Acarina, and Hemiptera were present in the greatest densities. In 1972, the groups with the highest densities were different on the two treatment areas (Ellstrom 1973). On the ungrazed treatment, the orders were ranked as follows: Homoptera, Collembola, Hymenoptera, Hemiptera, and Acarina; on the grazed treatment, the orders were Hemiptera, Hymenoptera, Homoptera, Collembola, and Acarina.

The shift in dominance (density) of the Acarina from 1970 to 1972 is attributable to the gradual decline of populations of *Caeculus* sp., the most frequently collected mite species. The caeculid population reached peak density on July 14, 1970, of $30.8/m^2$ on the ungrazed treatment and $35.0/m^2$ on the grazed treatment. Their density later reached a low point of $0.4/m^2$ in June 1971. The extremely dry growing seasons of 1970 and 1971 and the consequent low secondary productivity may have resulted in the failure of these predaceous mites to regain their former abundance.

Invertebrate data for this study have been classified according to trophic function only for 1972. Herbivores were the most abundant group on both the grazed and ungrazed treatments throughtout the study (figure 43). Populations on both treatments were generally similar, although during the latter part of 1972, herbivores were more abundant on the ungrazed than the grazed treatment. The difference may have been due to the increased precipitation and the fast plant recovery on the ungrazed treatment. Among the important herbivores during 1972, the Cocoidea were dominant during the early part of the growing season, and later the Tingidae, Cicadellidae, Lygaeidae, and Thysanoptera were the most abundant.

While herbivore densities were generally higher than other trophic categories, biomass estimates of herbivores were actually quite low in comparison to that of scavengers (figures 43 and 44). The large oscillations in scavenger biomass are considered to be due to the random capture of large beetles of the genus *Eleodes*. Thus, these data probably do not reflect the true composition of the scavenger compartment. Occasional captures of cockroaches (Blattidae) also contributed in part to these variable peaks. Both the Blattidae and *Eleodes* spp. are closely associated with *Yucca elata* and the scattered distribution

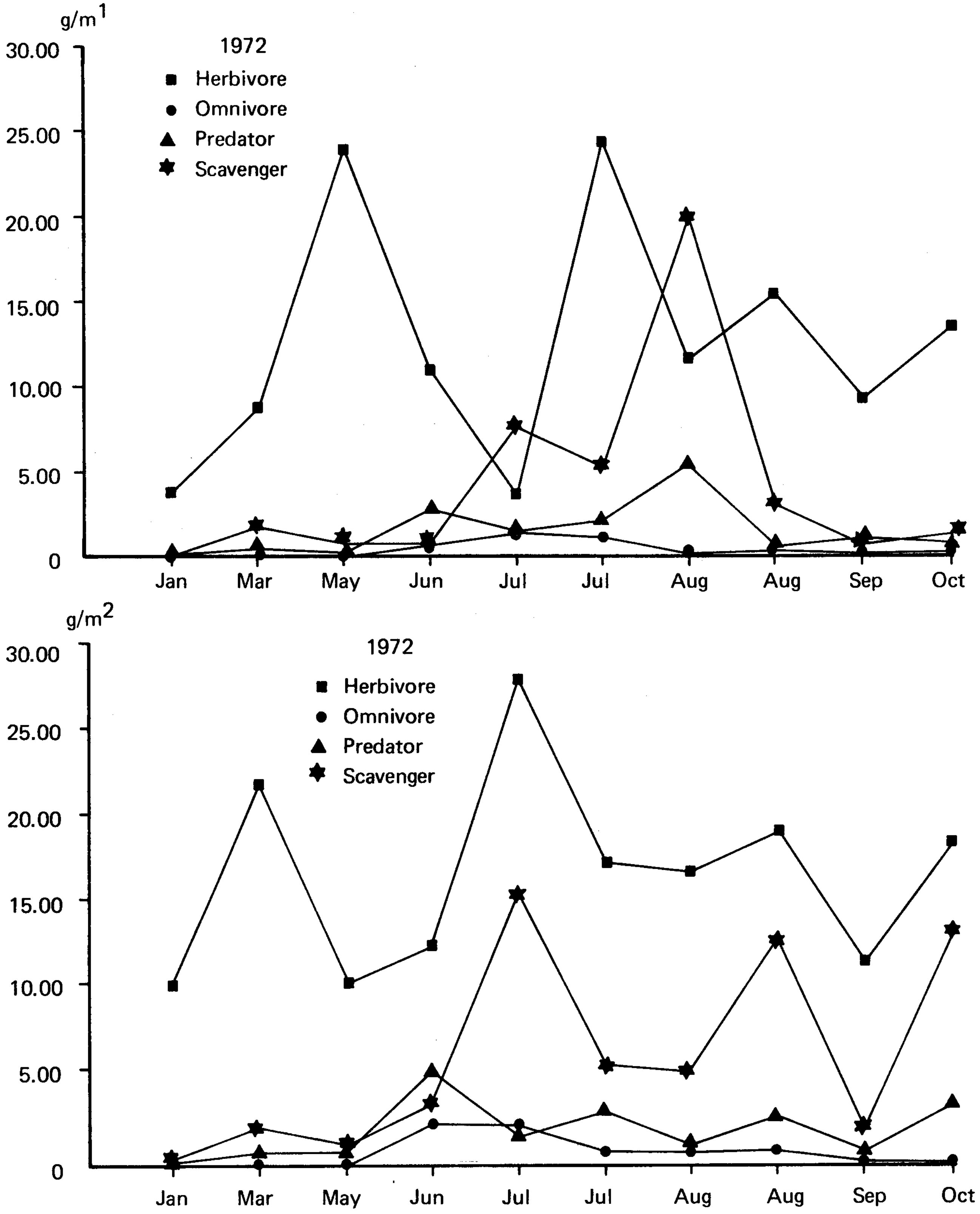

Fig. 43. Mean invertebrate density (nos./m^2) by trophic level for the grazed treatment, 1972 (below) and ungrazed treatment (above).

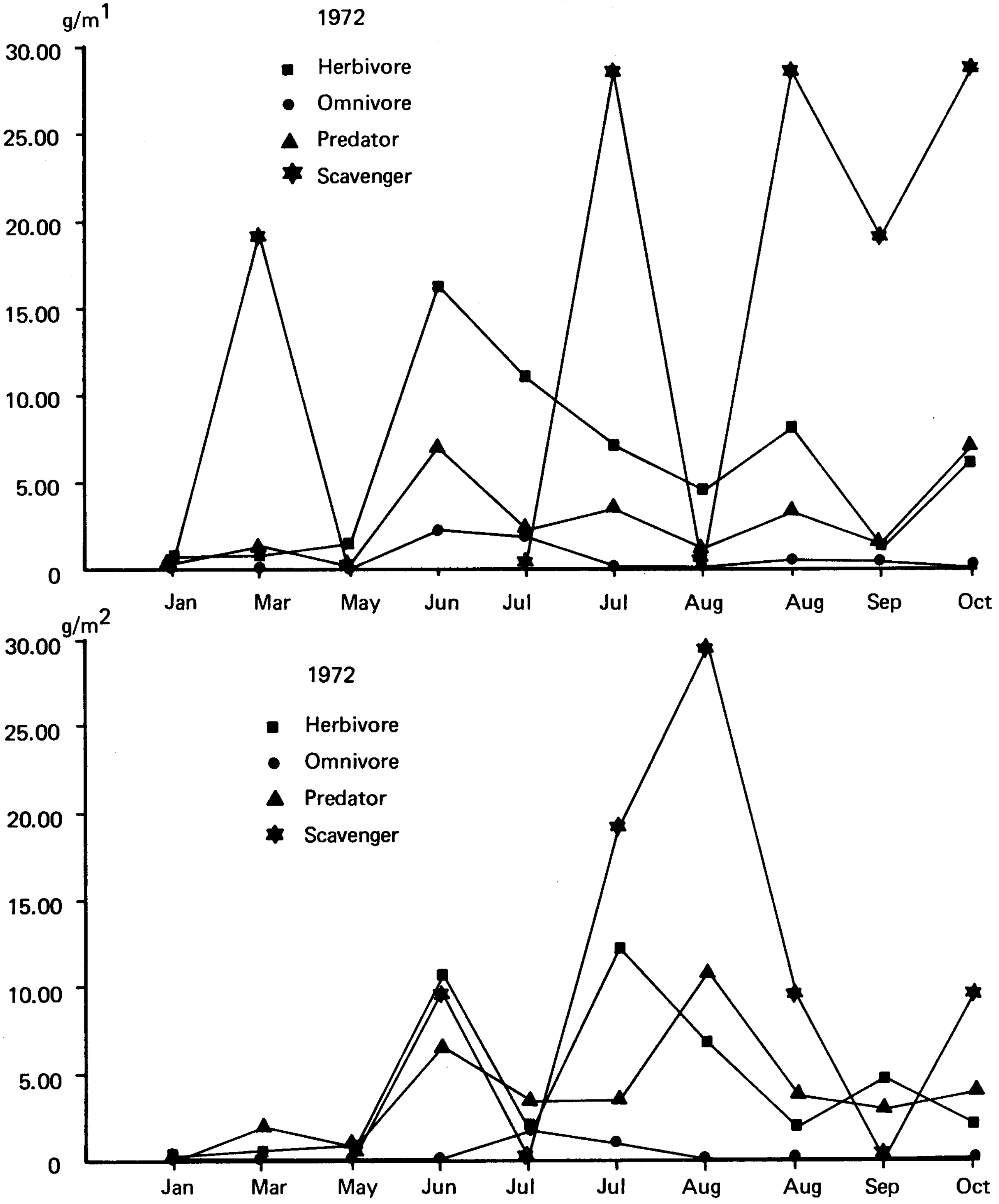

Fig. 44. Mean invertebrate biomass (g/m^2) by trophic level for grazed treatment, 1972 (below) and ungrazed treatment (above).

of these shrubs may account for the wide variation in biomass of these organisms from one sampling period to the next (Ellstrom 1973).

Population densities of omnivores and predator-parasites were very low throughout the study, while biomass was much more variable. Variations in biomass resulting from the occasional capture of crickets and ants from one sampling date to the next are again probably due to sampling error and do not reflect actual changes in the biomass of the field population.

Vegetational structure and species composition of the desert grassland influences invertebrate populations greatly. Both qualitative and quantitative differences in invertebrate populations are found when a specific plant species is sampled. For example, an association analysis of invertebrate taxa and plant species occurring in the same plot revealed some rather specific preferences by some invertebrates for certain plant species, such as Blattidae and Termitidae on *Yucca elata*. Other insects such as the tingids were strongly associated with *Salsola kali* and *Xanthclephalum sarothrae*, but weakly associated with *Sporobolus flexuosus* and *Tridens pulchellum*. In certain earlier years, the cerambycid, *Crossidius pulchellus* LeConte, a host specific stem and root borer on *Xanthocephalom sarothrae*, was abundant in the IBP plot area. Adults commonly fed on the blossoms in September. The larvae in some years infested the roots of a high percentage of the plants. This insect was collected only once, by hand, in the 1970-1972 treatment plots. In other years, the adults, and the larvae if appropriately sampled, would have added substantially to the density and especially to the biomass of the invertebrate samples.

The phenological development of the plant may also drastically influence invertebrate populations. For example, the grass thrips (*Chirothrips simplex* Hood) is completely dependent upon the immature caryopsis of various grasses for oviposition and larval and pupal development. The immature stages are so completely imprisoned on the developing caryopsis by the lemma and palea that they are never sampled or even seen except on dissection from the florets. Thus, its reproduction is limited by the amount of rainfall needed to produce grass seed heads. In the current study, especially in 1971 and 1972, this species contributed very little to the invertebrate density or biomass. In contrast, on the adjoining College Ranch in 1959, 1960, and 1961, its peak population on black grama was measured at 3130, 353, and 3983 adults, respectively, per 100 sweeps with a sweep net (Watts 1965).

Density and biomass estimates in this study were based on field samples taken by the quick trap method (French 1970, 1971, Swift and French 1972, and Blocker 1973). The quick trap procedure does not sample all invertebrates equally well and the total area sampled on each treatment for each sampling date totaled only $5/m^2$ so, additional sampling strategies were necessary. Observations indicated, for example, that invertebrates were primarily situated in close proximity to lush foliage, while the randomized method of assigning sampling locations rarely allowed these sparsely located areas to be sampled. Therefore, it was reasonable to expect that quick trap population estimates would be minimal at best and would probably not reflect the true diversity of the invertebrate fauna present.

For a better understanding of the role of the larger shrubs in respect to invertebrates, selective sampling of both mesquite and yucca plants was undertaken in 1971 and 1972. Table 30 shows a list of families collected from mesquite on two sampling dates in 1971. Several taxa were abundant on mesquite while relatively uncommon in quick trap samples of other plant species. Psyllids and Membracids were taken in large numbers, and the Mantids, Phasmids, and Cercopids were common in mesquite samples, but rare in quick trap samples. Although smaller cerambycids and pompilids were taken in quick traps, the larger *Ergates* spp. and *Pepsis* spp. were taken only on mesquite.

Sampling yucca blooms in the spring of 1972 also yielded some surprising data regarding populations of aphids and thrips (table 31). From a single flower stalk, more than 3000 aphids were captured on each of two sampling dates. Thrips numbers, primarily *Franklinella occidentalis* (Pergarde), were lower than expected, but some may have escaped because of the sampling technique (J. G. Watts, personal communication). Yucca plants in a blooming stage had never been sampled by the quick trap method despite the presence of more than 300 plants on the 10 ha ungrazed plot. Consequently, a substantial aphid population was unaccounted for in population estimates.

Although pitfall and light trap data are not strictly quantitative, evidence from these trapping methods indicates that a number of taxa had been missed entirely or were underestimated by the quick trap. Of the 118 invertebrate families caught at the Jornada site, a total of 29 unique taxa (at the family level) were taken exclusively by methods other than the quick trap. The Gryllacrididae, while taken only once in the quick trap, were abundant (as many as 200 per week) in the 25 pitfall traps used in the spring of 1971 and 1972. The Solpugida, Chrysididae, and Scorpionida were also common in pitfalls, while rare or absent in quick trap samples. Three dung-feeding species of Scarabaeidae (*Canthon puncticollis*, *Canthon imitator*, and *Canthon ebenus*), one silphid (*Nicrophorus* sp.), a trogid (*Trox nodosus*), and a histerid (*Saprinus discoidalis*) were numerous in pitfalls, but were never captured by means of the quick trap. It is likely that some of these were attracted to decomposing invertebrates in the traps, yet their complete absence from quick trap samples is indicative of the need for a broader spectrum sampling technique in assessing population densities.

Light trapping also revealed several taxa that were either completely missed or underestimated by the quick trap. Some of the poorly represented Coleoptera were the Cicindelidae, Cebrionidae, and Scarabaeidae (*Phyllophaga* sp.); yet, all of these were commonly taken by light trapping. Among the lepidopterous representatives at night were the Sphingids, Noctuids, and Pyralids. None of these groups were frequent representatives in quick trap samples.

Watts (1963), sampling *Bouteloua eriopoda* on the College Ranch near the Jornada site, captured 9 orders and 55 families of insects, of which 109 genera and 120 species were identified. Thrips made up more than 50% of the total insect population, a phenomenon not observed at the Jornada site in the 1970 to 1972 study. The diversity of fauna observed by Watts on black grama alone, coupled with observations made at the Jornada site, suggests that a significantly improved means of quantitatively sampling invertebrate populations must be developed before more precise statements regarding the behavior of invertebrate populations can be made.

Little work has been done in New Mexico with grassland soil nematodes, probably because of the difficulty in counting and identifying these organisms. Preliminary data indicates, however, that nematode populations are relatively low at the Jornada site. A list of taxa identified from an August 1973 sample is shown in table 32. Although diversity was quite high, numbers of nematodes were on the order of 0.1 to 0.01 of the populations occurring in some agricultural (monoculture) cropping systems. Some root samples, for example, have revealed as many as 200,000 nematodes per 10 g of roots (Sasser and Jenkins 1960), while 100 cc of soil revealed a population of 3,375 nematodes (Sasser and Jenkins 1960).

An average of eight replications on both the grazed and ungrazed treatments in 1973 yielded a population of 899,500 nematodes per m^2 on the grazed and 1,010,000 per m^2 on the ungrazed treatment. Biomass was 0.0529 g/m^2 on the grazed and 0.0645 g/m^2 on the ungrazed treatment (table 33).

By trophic category, 26% of the nematode biomass on the grazed treatment was attributable to plant feeders, 15% to predators, and 59% to saprophytes. On the ungrazed treatment, the percentages were similar, with 25% plant feeders, 16% predaceous, and 59% saprophitic nematodes. Samples were stratified at 5 and 10 cm intervals to 30 cm. The biomass of the 0 to 10 cm level was three to four times greater than that from 10 to 30 cm.

Birds. Density of birds on the Jornada desert grassland site was

Table 32. Nematode taxa identified[a] from samples obtained from Jornada IBP site, August 27, 1973.

Grazed	Ungrazed
Acrobeles complexus	*Acrobeles* sp.
Acrobeles sp.	*Acrobeles ?*
Acrobeles ?	*Acrobeloides minor*
Acrobeloides buetschli	*Acrobeloides* sp.
Acrobeloides minor	*Acrobeloides tricornis*
Acrobeloides sp.	*Alaimus* sp.
Acrobeloides tricornis	*Aphelenchus* sp.
Alaimus sp.	*Aporcelaimellus* 1J
Aphelenchus avenae	*Aporcelaimellus* 2J
Aphelenchus sp.	*Aporcelaimellus obscurus*
Aporcelaimellus obscurus	*Aporcelaimellus* sp.
Aporcelaimellus sp.	*Boleodorus* sp.
Aporcelaimellus ?	*Boleodorus thylactus*
Axonchium sp.	*Cephalobus persegnis*
Carcharolaimus sp.	*Cephalobus* sp.
Cephalobus persegnis	*Cervidellus serricephalus*
Cephalobus sp.	*Cervidellus* sp.
Cervidellus sp.	*Chiloplacus contractus*
Chiloplacus sp.	*Chiloplacus* sp.
Discolaimum sp.	*Discolaimium* sp.
Discolaimus sp.	*Discolaimus* sp.
Ditylenchus clarus	*Ditylenchus* sp.
Ditylenchus sp.	*Dorylaim* (pred.)
Dorylaim (pred.)	*Dorylaimellus* sp.
Dorylaimoides sp.	*Eudorylaimus* sp.
Eucephalobus oxyuroides	*Hoplolaimus galeatus*
Eucephalobus sp.	*Leptonchus* sp.
Eudorylaimus ettersbergensis	*Nothotylenchus* sp.
Eudorylaimus miser	*Paratylenchus elachistus*
Eudorylaimus sp.	*Pungentus monhystera*
Eudorylaimus ?	*Rhabditis* sp.
Helicotylenchus sp.	*Solidens* sp.
Nothotylenchus sp.	*Thonus* sp.
Stegellata sp.	*Tylencholaimus proximus*
Thonus sp.	*Tylenchorhynchus cylindricus*
Tylenchorhynchus cylindricus	*Tylenchorhynchus grandis*
Tylenchorhynchus grandis	*Tylenchorhynchus* sp.
Tylenchus plattensis	*Tylenchus* sp.
Tylenchus sp.	*Tylenchus ?*
Tylenchus ?	*Xiphinema americanum*
	Xiphinema sp.

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[a] Identified by Dr. Jim Smolik, South Dakota State University.

Table 33. Number and biomass of nematodes/m^2 at Jornada IBP site, August 27, 1973 on two grazing treatments.[a]

Depth (cm)	Plant Feeding		Preacious		Saprophyte	
	Number[b]	Biomass[c]	Number	Biomass	Number	Biomass
			Grazed			
0-5	108,300	0.0038	7,200	0.0011	228,50	0.0136
5-10	113,500	0.0049	18,000	0.0027	178,000	0.0106
10-20	59,600	0.0031	18,400	0.0028	75,000	0.0045
20-30	41,400	0.0018	9,600	0.0015	42,000	0.0025
Total	322,800	0.0136	53,200	0.0081	523,500	0.0312
			Grand Total:		899,500	0.0529
			Ungrazed			
0-5	88,900	0.0037	13,600	0.0021	266,500	0.0159
5-10	81,700	0.0042	20,800	0.0032	184,500	0.0110
10-20	86,200	0.0052	20,800	0.0032	123,000	0.0073
20-30	42,400	0.0026	13,600	0.0021	68,000	0.0040
Total	299,200	0.0157	68,800	0.0106	642,000	0.0382
			Grand Total:		1,010,000	0.0645

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[a] Data produced and analyzed by Dr. Jim Smolik, South Dakota State Univ.

[b] Average of eight replications.

[c] Dry weight in g·m^{-2}.

relatively low in 1970 (except for September) and 1971, but birds were more abundant in 1972 and 1973 (figure 45). Avian biomass dynamics followed closely that of density (figure 46). Raitt and Pimm (1975) have shown that it is possible to discuss the dynamics of the birds on the Jornada grassland in three trophic groups (insectivores, granivores, and raptors) without major loss of resolution. Census data on the Jornada bird plots (close to and almost identical with the plots used by other workers) are presented for insectivores and granivores in tables 34 and 35. Raptor numbers were obtained from censuses over a much wider area of grassland.

Insectivore numbers and biomass in the area were low, increasing slightly throughout the period of censusing, apparently because of the response of insects to the increasing rainfall. All of the breeding species are insectivorous and more than half are migratory, leaving the area in the winter. Their numbers reached only 19.5 birds /km^2 in July 1972, (a year characterized by above-average rainfall during the summer), representing a biomass of only 8.7 g wet weight/ha. Transient migrants, such as warblers, added very little to these totals. The peak biomass in September of 1971 was largely nonbreeding seed-eaters (figure 47).

The granivores were by far the numerically dominant group on the Jornada. The principal species were lark buntings, mourning doves, and horned larks, with sage sparrows, Brewer's sparrows, and in favorable years, Vesper sparrows less common but still important components of the fauna. All but the horned larks tended to arrive early--perhaps in small numbers by the end of July--and to stay until as late as May. The

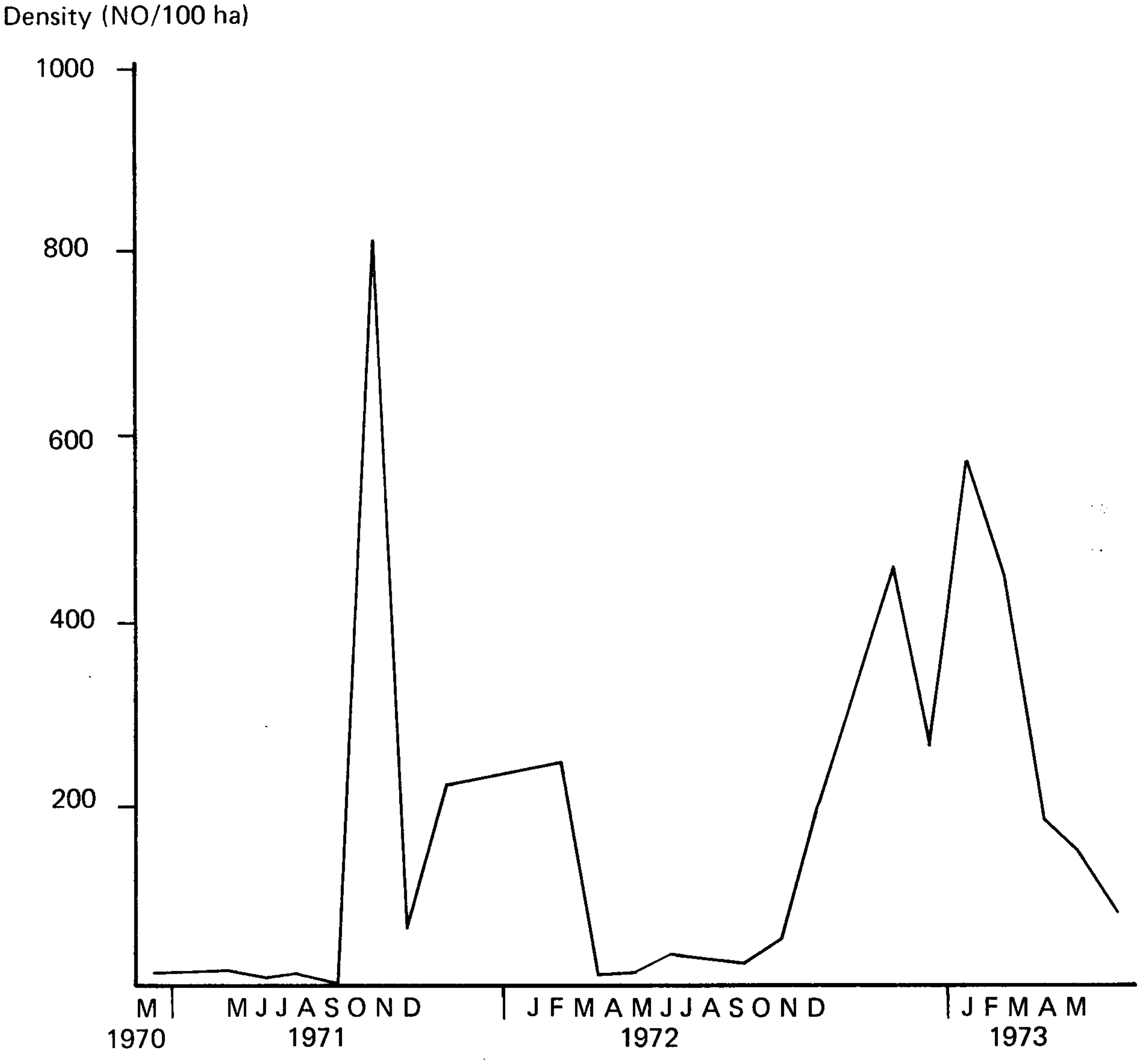

Fig. 45. Density of birds on IBP Jornada site for 3 years.

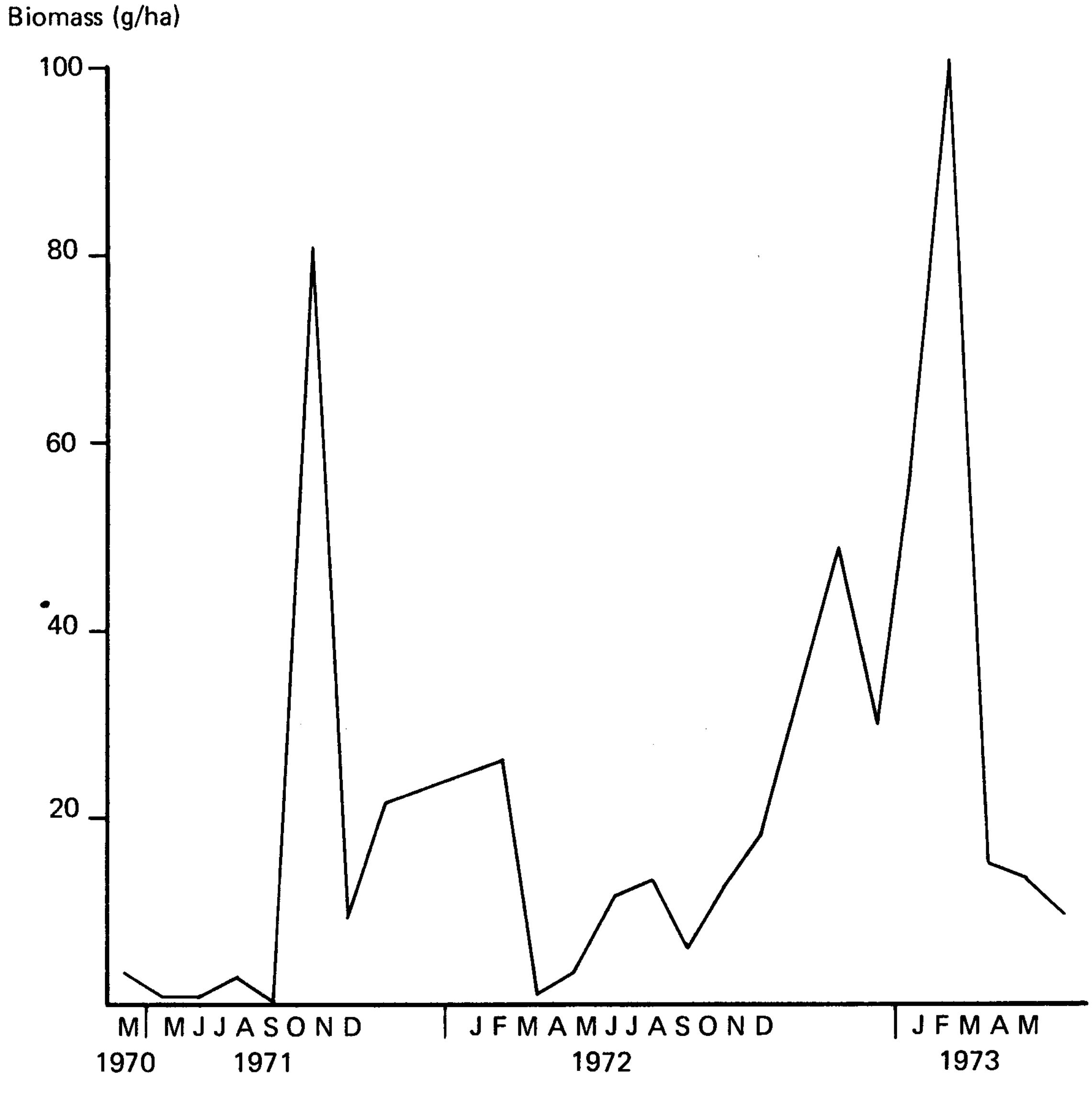

Fig. 46. Biomass of total bird population at IBP grassland site on the Jornada.

Table 34. Monthly mean numbers (per km^2), Jornada grassland plots (from Raitt and Pimm, 1978).

Species[a] Group	1971							1972			
	May	Jun	Jul	Aug	Sep	Oct	Nov	Feb	Mar	Apr	May
RA	0.0	0.0	0.7	0.0	1.4	2.5	2.2	0.7	0.0	1.4	0.3
BS	14.9	5.0	8.9	0.0	11.8	4.5	10.3	4.3	3.3	5.2	12.1
01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	4.8	2.4	0.7
WS	0.0	0.0	0.0	0.0	796.3	46.0	207.5	234.4	4.8	0.0	0.0
DQ	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	25.8
MS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.0
Total	15.4	5.0	9.6	0.0	809.5	52.0	220.0	240.6	12.9	13.3	38.9

Species[a]	1972						1973				
	Jun	Jul	Aug	Sep	Nov	Dec	Jan	Feb	Mar	Apr	May
RA	1.5	0.0	2.8	5.6	1.0	0.4	1.4	8.4	5.6	2.8	0.0
BS	14.6	19.0	9.7	8.8	7.3	3.3	2.7	3.4	0.0	3.9	8.9
01	0.0	0.5	3.5	3.5	0.0	0.0	0.0	11.2	0.0	5.6	0.0
WS	0.0	0.0	37.5	155.7	459.5	254.8	550.3	427.0	182.0	132.2	65.5
DQ	20.5	8.9	0.0	2.4	0.0	8.5	15.8	0.0	2.8	4.8	6.1
MS	1.2	0.0	3.5	21.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	37.8	28.4	57.0	197.0	467.8	267.0	570.2	450.0	190.4	149.3	80.5

[a] RA = raptors, BS = breeding species, 01 = nonbreeding insectivores, WS = nonbreeding seed-eaters, DQ = doves and quail, MS = miscellaneous species.

Table 35. Monthly mean standing crop biomass (g live weight/ha), Jornada grassland plots (from Raitt and Pimm, 1978).

Species[a] Group	1971							1972			
	May	Jun	Jul	Aug	Sep	Oct	Nov	Feb	Mar	Apr	May
RA	0.0	0.0	7.2	0.0	2.2	11.0	2.4	3.7	0.0	1.6	2.9
BS	4.4	2.2	3.7	0.0	5.8	2.2	6.3	2.3	1.3	2.6	5.2
01	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.7	0.5	0.2
WS	0.0	0.0	0.0	0.0	264.7	14.3	58.5	71.8	0.6	0.0	0.0
DQ	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3	28.9
MS	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5	0.0
Total	5.0	2.2	10.9	0.0	272.7	27.5	67.4	78.3	3.6	12.5	37.2

Species[a]	1972						1973				
	Jun	Jul	Aug	Sep	Nov	Dec	Jan	Feb	Mar	Apr	May
RA	14.4	0.0	28.2	6.5	3.1	3.5	9.0	163.1	31.9	14.6	0.0
BS	6.6	8.4	4.2	4.3	1.9	0.6	1.4	0.0	0.0	3.9	4.0
01	0.0	0.3	0.7	0.7	0.0	0.0	0.0	3.2	0.0	1.0	0.0
WS	0.0	0.0	7.5	31.2	160.1	90.4	166.3	168.9	21.9	24.0	23.1
DQ	23.0	10.0	0.0	2.7	0.0	9.5	17.6	0.0	3.1	5.4	6.8
MS	0.1	0.0	0.2	16.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	44.1	18.7	40.8	62.2	165.1	104.0	194.3	335.2	56.9	49.0	33.9

[a] RA = raptors, BS = breeding species, 01 = nonbreeding insectivores, WS = nonbreeding seed-eaters, DQ = doves and quail, MS = miscellaneous species.

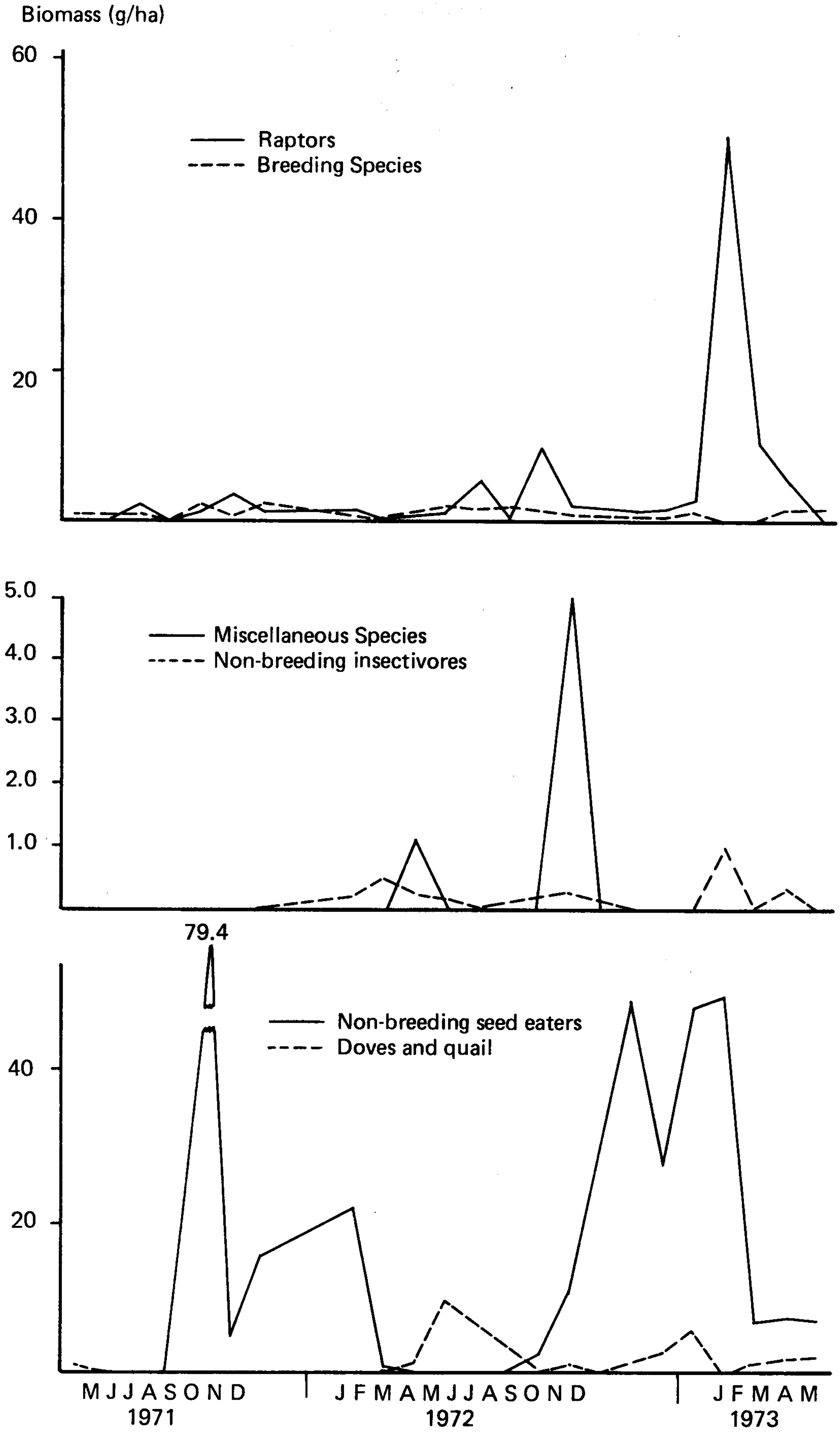

Fig. 47. Biomass of birds by ecological categories on IBP Jornada site.

horned larks, when present, were very abundant, but their presence (along with the longspurs which accompany them) was limited to late December, January, and February. The temporal pattern is seen more clearly in the roadside counts in table 36. These data were obtained over a wider area than the plot census data and are less subject to errors in sampling large mobile flocks of birds. The numbers of seed-eaters varied considerably from year to year, which tends to be a reflection of the production of seeds on the area. The differences between years were less in the peak numbers recorded than in the duration of residence of the flocks in the area. In the winter of 1971-1972, roadside totals exceeded or approached 1000 birds only in December; the following year totals exceeded 1000 from September until January. In 1973-1974, the usual flocks of lark buntings had totally disappeared by October and did not return.

Raptors are particularly difficult to census. In summer the Swainson's hawk was the only common nester on the Jornada grassland. Pilz (1977) estimated that there was one pair per ha in grassland areas where yuccas are sufficiently tall for this species' nests. Prairie falcons and great horned owls also nested, but at densities too low to estimate accurately. They would seem to be no commoner than 1% to 10% of the Swainson's hawk density. Turkey vultures were seen commonly but nest off the area; no density estimate is available.

In winter, the area is utilized by ferruginous and red-tailed hawks and golden eagles. Their numbers depend on the availability of small mammal prey and were reduced in the winter of 1972-1973 from the previous winter, following the reduction in numbers of small mammals early

Table 36. Monthly total members counted on 2-day roadside censuses (from Raitt and Pimm, 1978).

Species[a] Group	1971								1972		
	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
RA	3	6	3	5	8	12	17	10	5	9	5
BS	52	46	14	64	16	28	32	13	9	12	6
01	0	0	2	0	2	0	1	0	2	18	2
WS	0	0	4	88	59	566	411	1841	587	535	26
DQ	4	3	23	5	0	21	0	0	4	0	0
MS	0	0	1	2	0	33	0	0			
Total	59	55	47	164	85	660	461	1864	607	574	39

Species[a] Group	1972								1973				
	Apr	May	Jun	Jul	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
RA	3	1	2	9	29	11	6	4	6	3	11	4	3
BS	12	43	66	61	34	23	7	14	15	15	20	54	74
01	14	9	0	0	4	0	1	8	0	8	34	0	0
WS	46	1	0	20	1029	1328	1392	828	1113	371	353	609	0
DQ	2	17	20	45	84	27	16	112	49	10	2	26	99
MS	3	0	0	4	12	2	1	0	0	1	0	0	2
Total	80	71	88	139	1192	1391	1423	966	1183	408	420	693	178

[a] RA = raptors, BS = breeding species, 01 = nonbreeding insectivores, WS = nonbreeding seed-eaters, DQ = doves and quail, MS = miscellaneous species.

in 1972. Perhaps the commonest winter hawk is the marsh hawk, which often follows flocks of seed-eating passerines; its numbers increased on the Jornada in the winter of 1972-1973, probably due to the increase in the numbers of seed-eaters. The numbers of these raptors and their prey are shown in table 37.

Reptiles. Lizards are important insectivores in desert grasslands and possibly the most important insectivores in southern desert grassland ecosystems. The high densities and biomass, when compared with birds, tends to support this contention. Although birds have a higher metabolic rate, active lizards have metabolic rates higher than those of mammals (Asplund 1970), and it has been estimated that *Cnemidophorus tigris* assimilates 71 cal/g/day (Johnson 1966). When the biomass of adult active lizards (table 38) is compared with the avian biomass (table 35), it is apparent that lizards consume five to seven times more insects.

The most important feature of the population dynamics of lizards on the Jornada is the dependence of reproductive success on adequate soil moisture and recruitment of juveniles, which depends on arthropod abundance and availability. Population densities of lizards on the Jornada fluctuated from 1970 to 1973, with population changes keyed to seasonal pattern and quantity of rainfall (Figure 48). Drought conditions in 1971 resulted in virtual absence of successful reproduction in most lizard species. Reproductive success and recruitment was probably above average in 1972 and 1973, due to favorable soil water conditions in spring and summer and large numbers of active insects (figure 42).

Except in 1971, most adult lizards disappeared from the active

Table 37. Annual differences in raptor populations (mean number seen per roadside census ± SE of mean) and their food supply (from Raitt and Pimm).

Species or Group	May-October 1971	October-March 1971-1972	May-October 1972	October-March 1972-1973
Raptors				
Swainson's Hawk	3.0 ± 0.20		7.6 ± 1.88	
Prairie Falcon Hen Harrier		1.0 ± 0.20		1.4 ± 0.23
Buteo spp. Golden Eagle		5.7 ± 0.97		3.2 ± 0.36
Prey animals				
Lizards (Playa)	317 g/ha		431 g · ha^{-1}	
Birds		131/100 ha		389/100 ha

Table 38. Changes in peak density (numbers/ha) and biomass (g/ha) of adult lizards in a Chihuahuan desert grassland community (playa fringe of the Desert Biome Jornada Validation Site) from 1970-1973. Data from Whitford et al. (in preparation). Densities are in column D and biomass in column B.

Genus/Species	1970		1971		1972		1973	
	D	B	D	B	D	B	D	B
Cnemidophorus tigris	7.2	39.6	22.5	122.8	35.0	178.0	57.0	227.0
Cnemidophorus tesselatus	18.0	95.8	1.3	6.4	1.3	6.4	0.9	3.4
Phrynosoma cornutum	2.0	18.0	2.3	24.8	4.0	50.2	24.0	269.8
Other species	2.0	6.0	1.5	4.0	4.0	12.0	7.2	13.3
TOTALS	29.2	159.4	27.6	158.0	44.3	246.6	89.1	513.5

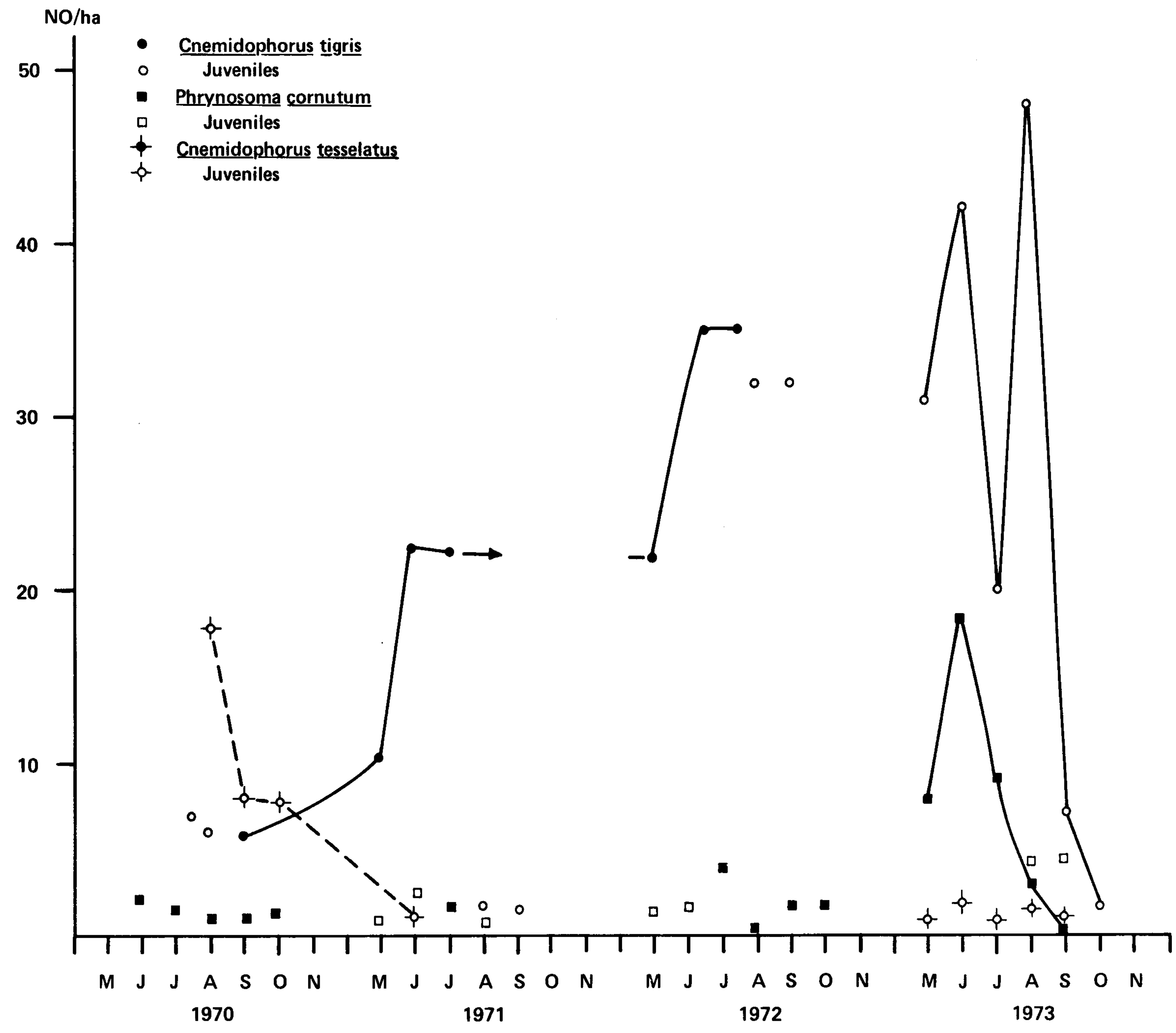

Fig. 48. Lizard densities on IBP Chihuahuan desert site, approximately 4 miles from desert grassland site.

population in late July to mid-August. The disappearance of adult lizards was nearly coincident with hatching and recruitment (figure 48). In 1971 drought conditions extended into late August. High temperatures and dry soils curtailed surface activity of most species of ants, and there was a virtual absence of surface activity of subterranean termites. From May through August recaptured *Cnemidophorus tigris* and *Phrynosoma cornutum* exhibited weight losses or stable weight indicative of inadequate or marginal food supply. In other years, emergent lizards exhibited marked weight gains through mid-June, then weight loss particularly in females, probably coincident with egg laying. From July to early August, adult lizards again exhibited weight gain then disappeared from the population.

The overwinter survivorship of juvenile lizards is a function of post-hatching growth rates, which are dependent on food availability and climate. Although drought conditions in summer 1971 reduced reproductive success, the juveniles recruited into the population exhibited high survivorship, probably as a result of high insect productivity and activity in the late summer and fall (figure 48).

The marked decrease in population density of *Cnemidophorus tesselatus* from 1970 to 1971 may be due to drought conditions and the attendant limited insect diet in late summer of 1970 through August 1971. *C. tesselatus* is more abundant in more mesic habitats in other areas in southern New Mexico. A combination of mid-summer mortality and overwinter mortality of juveniles and adults could result in low densities the following year. Subsequently, competition with *C. tigris* could make population recovery difficult.

There are no studies of grassland lizard communities apart from those undertaken as part of IBP. In addition, there are few studies where densities of lizard species are reported from desert grassland sites. Tinkle (1967) reported an average density of approximately 19 adult and 60 juvenile *Uta stansburiana* per ha, with an average biomass of 108 g/m^2 in a desert grassland near Kermit, Texas. *Uta stansburiana* is the only lizard species that may approach *C. tigris* in numbers in southern desert grasslands. Even in grassland communities where *U. stansburiana* is relatively abundant, it is probably less important than *Cnemidophorus* species because of its lower weight and because it is essentially an annual-turnover species.

Because of their secretive nature, snakes are not as readily sampled as lizards, so population estimates are always tenuous at best. Records of snakes captured on the 36-ha IBP desert playa study area have been kept since 1970. By combining these data, it is possible to arrive at a conservative estimate of snake densities in a desert grassland community (table 39). Mark-recapture techniques are of little use because, as Fitch and Shirer (1971) have demonstrated, snakes move erratically and at random over considerable distances.

The most abundant snake species in southern New Mexico desert grasslands are the prairie snake (*Crotalus viridus*) and gopher snake (*Pituophis melanoleucus*), respectively. These snakes are predators on small mammals and probably represent the most important small mammal predators. The third most abundant species is the coachwhip snake (*Masticophis flagellum*), which is a lizard predator. The remaining species feed on small rodents, insects, frogs, young birds, and lizards

Table 39. Estimated densities of snakes in a desert grassland in southern New Mexico based on data from the Desert Biome Jornada Playa Validation Site. Densities are expressed as numbers per 100 hectares. Densities were computed by averaging the number of individuals captured from 1970-1973 on the 36-ha study site.

Species	Estimated Density (Numbers/100 ha)
Crotalus viridis	38.1
Pituophis melanoleucus	12.0
Masticophis flagellum	6.4
Sistrurus catenatus	3.7
Crotalus atrox	2.8
Hypsiglena torquata	2.8
Salvadora hexalepis	1.7
Arizona elegans	1.7
Rhinocheilus lecontei	0.8
Lampropeltis getulus	0.8

in varying amounts, depending on the species and size of the snake.

Trophic Structure: Biomass Pyramids

Most of the biomass on the ungrazed treatment was concentrated in the primary producer compartment. For the three years of the study, biomass of aboveground plant material was 1.5 million kg ha^{2} compared with only 426 kg/ha for all consumer groups (table 40 and figure 49). Over half the plant biomass was living material with about one-third in standing dead categories and about 17% in the mulch compartment.

Primary producer biomass was lowest in 1971 because of the drought and highest in 1972. Mulch biomass declined throughout the study with the greatest decline coming from 1971 to 1972 because of the low primary productivity during 1971 (table 40). Standing dead biomass varied considerably within a year and from year to year.

Among the primary consumer groups, the small mammals dominated in 1970, but declined sharply from 229 kg/ha to 23 kg/ha in 1971. Antelope biomass, as calculated following the assumptions outlined earlier in this section, remained constant at 55 kg/ha and was second highest among primary consumers in 1970 (table 40). The black-tailed jackrabbit and desert cottontail averaged 17 kg/ha in 1970 and reached a peak in October 1972 of 44 kg/ha. Averaged over the three years of the study, the lagomorphs contributed about 7% of primary consumer biomass, which was nearly the same as the birds (figure 49).

Biomass of small mammals was highest among secondary consumer groups for the three years (figure 49), but was second to invertebrates in 1972 (table 40). Birds and coyotes contributed very small amounts to

Table 40. Dry weight biomass (g/ha) of various primary producer and primary and secondary consumer groups on the ungrazed treatment of a desert grassland ecosystem.

Date	Primary Producers				Primary Consumers						Secondary Consumers				
	Live	Dead	Mulch	Total	Invertebrates	Small mammals	Birds	Antelope	Lagomorphs	Total	Invertebrates	Small mammals	Birds	Coyotes	Total
7-14-70	770,000	150,000	810,000	1,730,000	10.6	337.7	0.3	55.0	28.3	431.9	19.3	292.3	1.0	0.9	313.5
9-1-70	1,340,000	270,000	1,000,000	2,610,000	19.7	242.4	0.3	55.0	11.4	328.8	30.4	222.0	1.0	0.9	254.3
12-1-70	1,390,000	0	310,000	1,700,000	5.2	106.7	0.3	55.0	11.4	178.6	39.2	113.0	1.0	0.9	154.1
Avg	1,166,667	140,000	706,667	2,013,333	11.8	228.9	0.3	55.0	17.0	313.0	29.6	209.1	1.0	0.9	240.6
8-14-71	330,000	650,000	530,000	1,510,000	1.5	34.3	0.0	55.0	22.0	112.8	1.2	35.4	0.0	0.9	37.5
9-14-71	480,000	160,000	810,000	1,450,000	55.7	16.8	81.1	55.0	22.0	230.6	53.6	31.8	0.7	0.9	87.0
11-8-71	130,000	140,000	430,000	700,000	8.4	16.5	19.7	55.0	22.0	121.6	10.3	44.7	0.7	0.9	56.6
Avg	313,333	316,667	590,000	1,220,000	21.9	22.5	33.6	55.0	22.0	155.0	21.7	37.3	0.5	0.9	60.4
5-18-72	220,000	370,000	220,000	810,000	43.0	46.5	10.2	55.0	1.6	156.3	37.7	38.4	1.0	0.9	78.0
7-31-72	520,000	170,000	240,000	930,000	470.2	50.0	3.0	55.0	7.8	586.0	115.4	46.5	1.3	0.9	164.1
10-7-72	1,340,000	640,000	220,000	2,200,000	154.0	54.2	6.0	55.0	44.0	313.2	113.3	48.6	4.3	0.9	167.0
Avg	694,000	393,333	226,667	1,313,333	222.4	50.2	6.4	55.0	17.8	351.8	88.8	44.5	2.2	0.9	136.4

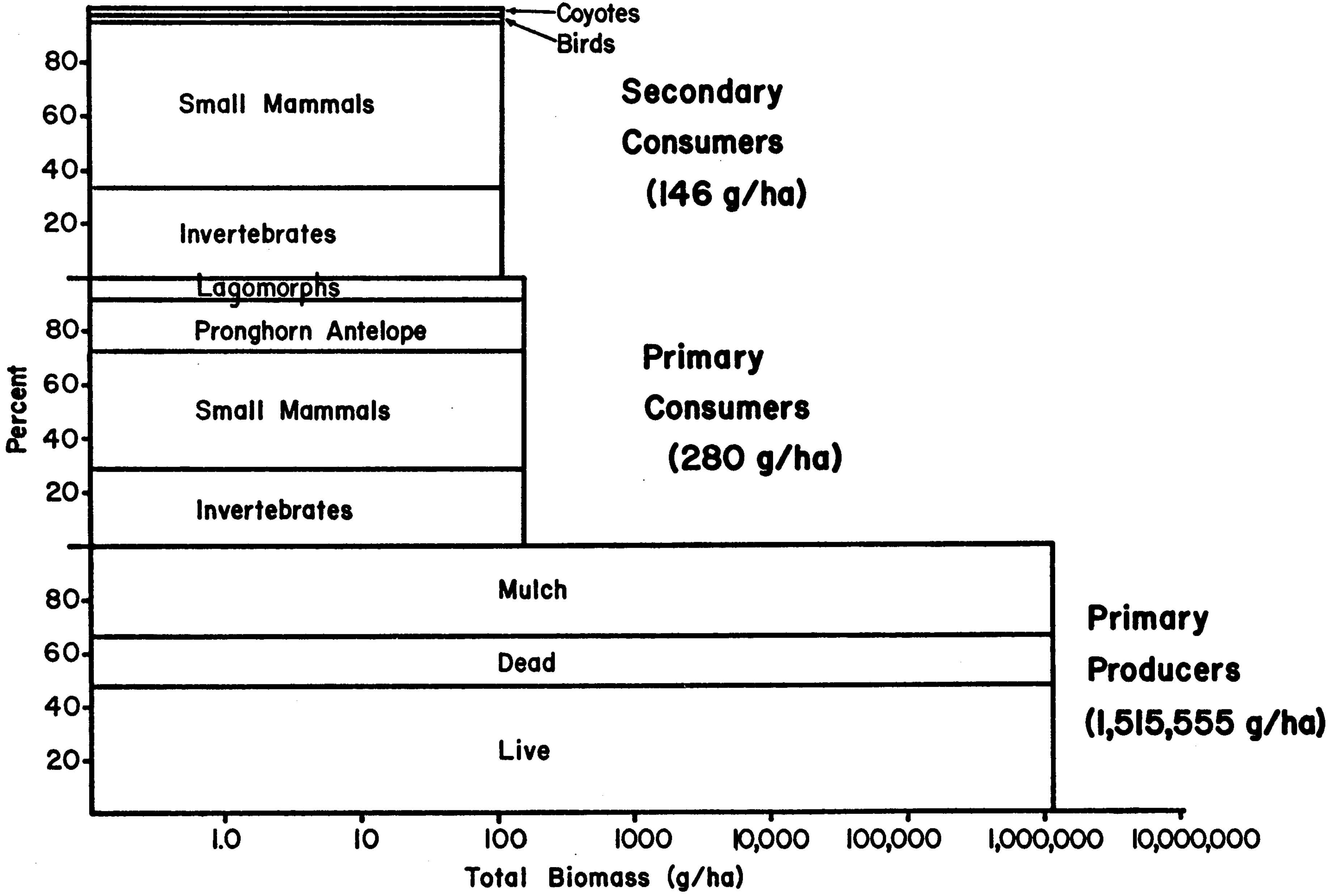

Fig. 49. Biomass pyramids for aboveground primary producers and various consumer groups averaged over 3 years and 3 dates per year.

secondary consumer biomass. In some instances, biomass of invertebrate secondary consumers exceeded that of the invertebrate primary consumers. Possible lag effects and storage may account for some of these apparent anomalies.

Ratios of live biomass of primary producers to primary consumers varied from a high of 4075 in September 1970 to a low of 784 in December 1970 (table 41). Ratios between primary and secondary consumers varied from 3.35 in September 1971 to 1.16 in December 1970 and August 1971. Primary producer biomass exceeded that of primary consumers by over 1100 times while primary consumer biomass exceeded that of secondary consumers by only two times (table 41). These ratios again illustrate the dominance of the primary producer groups over the consumers. It appears that the primary consumers more nearly utilize their food supply than the secondary consumers. Decomposers must utilize most of the primary production under desert grassland conditions.

Table 41. Biomass ratios between various trophic levels on a desert grassland ecosystem.

Date	Live Primary Producers / Primary Consumers	Primary Consumers / Secondary Consumers
July 1970	1783	1.38
September 1970	4075	1.29
December 1970	784	1.16
August 1971	1694	1.16
September 1971	1536	3.35
November 1971	797	2.88
May 1972	1288	2.18
July 1972	887	3.33
October 1972	1380	1.61
Average	1128	2.04

FUNCTION OF DESERT GRASSLAND ECOSYSTEMS

Abiotic Functions: Water Movement

Precipitation

Most of the summer rain storms in the desert grassland region are intense convectional types with substantial amounts falling in relatively short periods. Spatial and temporal variations in precipitation within the desert grassland were covered in earlier sections.

Infiltration and Percolation

Infiltration rates have not been measured on many areas within the desert grassland. On grassland sites in the foothills of the Sacramento Mountains in south-central New Mexico, Pieper, Montoya, and Groce (1971) reported that infiltration rates varied from about 3.2 to 1.2 cm/ha. These variations are probably related to soil characteristics as well as initial water content of the soil.

Bailey (1967) reported on depth of soil water penetration following the application of 1.2, 2.5, and 3.7 cm of simulated rainfall on various soils on the Jornada Experimental Range (table 42). Soil water penetration did not differ greatly among the different soil types, but the deepest penetration from the 1.2 cm rainfall was 2.4 cm on the Sonoita loamy sand and the least penetration was on the Cacique loamy sand. Deepest penetration from the 3.7 cm rainfall was 5.1 cm on the deep phase of the Simona loamy sand. The Simona loamy sands are most similar to soils of the IBP grassland site.

A larger portion of the 1.2 cm rain was retained in the profile of

Table 42. Depth of visual water penetration (cm) 24 hours after simulated rainfall at 1.2, 2.5, and 3.7 cm respectively (from Bailey 1967).

Soil Type	Simulated Rainfall (cm)		
	1.2	2.5	3.7
Sonoita loamy sand	1.8	3.2	4.7
Palma loamy sand	2.4	3.5	4.3
Cacique loamy sand	1.6	3.0	4.7
Simona loamy sand	1.9	3.5	5.1
Simona loamy sand, shallow	1.9	3.0	3.5

the shallow phase of the Simona loamy sand than for the other soils (table 43). However, evaporation was probably greater for this soil type than for the others, since the soil water was held above the petrocalcic layer (Bailey 1967). In addition, some of the moisture may have percolated downward in cracks in the caliche. Bailey (1967) reported that very little soil water from a 1.2 cm storm would be available for plant growth.

Soil water regimes were studied for seven soil types on the Jornada (Herbel and Gile 1973). The characteristics of the soils are given in table 44. Two of the soils were on slopes of the San Andres Mountains, one was a playa bottom, and the others were on the basin floor.

Precipitation was similar over all sites from 1960 to 1970, while soil water regimes varied considerably. On the Onite and Hueco soils, soil water was above -15 bars for almost 200 days per year while on the Stellar and Reakor soils, soil water in the 0 to 10 cm layer was above -15 bars less than 100 days per year (table 45). On the Algerita soil, soil water was always held at tensions more than -15 bars at the 90 and 120 cm depth. Soil water was held at tensions between 0 and -15 bars for over 150 days throughout the profile on the Stellar soil. Intake on the Reakor and Stellar soils was restricted with soil water between 0 and -15 bars less than 100 days per year throughout the profile.

Even though the upper horizons of the wedgy Stellar site are high in clay, subsoil wetting results from depressions, tubes and cracks in the soil. The regular Stellar soil lacks these avenues for water to reach the subsoil horizons (Herbel and Gile 1973). The relatively long period with soil water between 0 and -15 bars for the Hueco soils can

Table 43. Approximate soil water and maximum potential yield of black grama, *Bouteloua eriopoda* (from Bailey 1967).

	Simulated Rainfall									
	1.2 cm			2.5 cm			3.7 cm			
Soils	Total water applied[a/] $(g\cdot m^{-2})$	Increase in soil water $(g\cdot m^{-2})$	Availability of water in soil[b/] (%)	Total water applied $(g\cdot m^{-2})$	Increase in soil water $(g\cdot m^{-2})$	Availability of water in soil (%)	Total water applied $(g\cdot m^{-2})$	Increase in soil water $(g\cdot m^{-2})$	Availability of water in soil (%)	Dry matter black grama $(g\cdot m^{-2})$
Sonoita loamy sand	12,644	8,065	47.4	25,288	17,058	46.2	37,931	27,410	53.7	
Palma loamy sand	12,644	4,499	15.2	25,288	15,518	49.4	37,931	17,362	57.8	
Cacique loamy sand	12,644	5,464		25,288	17,621	52.5	37,931	19,976	59.9	
Simona loamy sand	12,644	6,537	28.7	25,288	16,238	60.7	37,931	27,601	64.9	
Simona loamy sand, shallow	12,644	10,342	28.1	25,288	13,533	46.1	37,931	21,126	58.2	

[a/] Total water applied was calculated on the basis that 1 cubic foot of water weighed 62.28 pounds, assuming the temperature of the water was approximately 90°F.

[b/] Percent of increase in soil water held at tensions less than 15 atmospheres.

Table 44. Some characteristics of soils and landscapes of various sites on the Jornada (from Herbel and Gile 1972).

Site	Soil series, Variant or phase	Classification	Landscape position and slope	Gemorphic surface and age
A	Canutio, coarse-loamy variant	Typic Torriothent, coarse-loamy, mixed, thermic	fan-piedmont slope 2%	Organ (Holocene)
B	Stellar, wedgy subsoil variant	Ustollic Haplargid, fine, mixed, thermic	Fan-piedmont toeslopes	Jornada II (Late-Pleistocene)
C	Stellar	Ustollic Haplargid, fine, mixed, thermic	Basin floor nearly level	Jornada I (Late-mid-Pleistocene)
D	Reakor[a]	Ustollic Calciorthid, fine-silty, mixed, thermic	Basin floor nearly level	Petts Tank (Late-Pleistocene)
E	Lagerita[a], deep gypsum phase	Typic Calciorthid, fine-loamy, mixed, thermic	Playa, level	Alluvium in floor of playa (Latest Pleistocene-Holocene?)[b]
F	Onite, buried soil variant	Typic Haplargid, coarse-loamy, mixed, thermic	Basin floor nearly level	Apparent eolian accumulation (Holocene?) on La Mesa surface (Mid-Pleistocene)[b]
G	Hueco[a]	Petrocalcic Paleargid, coarse-loamy, mixed, thermic	Basin floor nearly level	La Mesa (Mid-Pleistocene)

[a] Tentative series.

[b] Details of the stratigraphy and chronology are not known in this part of the Experimental Range, and assigned chronology must be considered tentative.

Table 45. Soil water expressed as the number of days during which soil water was between 0 and -15 bars for various sites on the Jornada from 1960 to 1970 (from Herbel and Gile 1973).

Soil Series	Precipitation (cm)		Soil Depth					
	Mean	Range	10 cm	25 cm	40 cm	60 cm	90 cm	120 cm
Canutio	20.8	10.5-32.5	130	108	61	59	6.6	--[a/]
Stellar (wedgy subsoil variant)	19.8	8.0-32.0	172	167	191	204	176.0	188
Stellar	19.6	11.8-32.0	92	40	33	31	33.0	38
Reakor	19.6	11.8-32.0	78	45	28	29	27.0	27
Algerita	18.8	8.9-31.1	113	72	38	2	0.0	0
Onite	19.3	10.8-29.8	192	174	122	90	19.0	--
Hueco	18.9	11.5-34.9	194	212	159	117	97.0	--

[a/] Soil profile not 120 cm deep.

be attributed to the coarse texture of the upper horizons and the rapid infiltration rates (Herbel and Gile 1973). The Hueco soil is similar to that at the IBP grassland site.

Net Primary Productivity

Aboveground

Aboveground net primary productivity (ANPP) has been calculated by many approaches using harvest data for herbaceous species such as collected in this study. Many studies have shown that using peak community standing crop as a measure of ANPP may produce a serious underestimate, because the contribution of individual species or groups of species that grow at approximately the same time may not be taken into account (Odum 1960; Malone 1968; Kelley, Van Dyne, and Harris 1974; Pieper, Dwyer, and Banner 1975; Sims and Singh 1971). Adding the peak standing crop by species may underestimate ANPP if there are periods of growth cessation, with reduction of aboveground live material followed by a period of renewed growth. Adding the sum of all positive increments by species would take these declines and growth spurts into account, but could result in some overestimates of ANPP, especially if sampling variation was high and positive increments were added which were merely random sampling fluctuations from one period to the next.

Table 46 shows that a wide variation in ANPP can be obtained from the data for the IBP Desert Grassland site by use of different methods of calculation. In general, use of peak community live standing crop gave the lowest values, especially for 1972 when growing-season precipitation was above average. However, there were some lower values for

Table 46. Net aboveground primary productivity (g/m/yr) calculated by different methods for the ungrazed (U) and grazed (G) treatments.

Method	1970		1971		1972		Average	
	U	G	U	G	U	G	U	G
Peak live standing crop	134	74	207	34	108	99	150	69
Peak standing live + recent dead	134	74	231	34	120	119	162	76
Sum of species peaks standing live + recent dead	172	124	318	73	186	180	225	126
Sum of species peaks of standing live	134	97	125	51	186	180	148	109
Sum of positive increments of standing live of all species	61	56	205	30	160	112	142	66
Sum of positive increments by species	140	90	315	78	264	163	240	110

other methods and treatments. There was considerable variation among the methods by year and treatment. When biomass for soaptree yucca and mesquite were included in the data, results were rather surprising. For example, with the peak standing crop, yucca included, ANPP was 207 g/m on the ungrazed treatment in 1971, when conditions were very dry, and only 108 g/m in 1972, when conditions were much wetter. In addition, the peak of 207 g/m occurred during the dormant season in December. Most of the relatively high values for the 1971 ungrazed treatment could be attributed to high yucca biomass. Therefore, the best estimates of ANPP were those with yucca and mesquite deleted. The sum of species peaks was used, with yucca and mesquite deleted, for all the calculations that follow. This is probably justified because rather large sampling errors were involved. Most of the peaks used were fairly realistic.

ANPP was considerably higher for the ungrazed treatment than for the grazed treatment in 1970 and 1971. In 1971, ANPP was nearly 140% higher on the ungrazed treatment than on the grazed treatment (table 46). However, in 1972 there was little difference in ANPP between the two treatments, because of the contribution by annual forbs and mesa dropseed.

Ecological groups making the largest contribution to ANPP were warm-season species (table 47), with grasses most important on the ungrazed treatment and shrubs on the grazed treatment. Cool-season forbs were important only in 1972, when *Cryptantha crassisepala* was abundant on all areas.

The highest community productivity for any period actually occurred

Table 47. Percentage contribution to net primary production by various ecological categories, based on time-weighted seasonal biomass means (U = grazed).

Ecological Category	1970		1971		1972	
	U	G	U	G	U	G
Warm season grasses	53.0	14.6	37.1	21.0	41.5	18.6
Cool season grasses	0.0	0.0	0.0	0.0	0.0	0.0
Warm season forbs	8.0	24.8	12.2	18.4	22.7	35.0
Cool season forbs	1.0	0.2	0.0	0.0	10.0	15.0
Warm season shrub	18.5	40.4	11.8	41.4	11.2	23.7
Cool season shrub	0.0	0.0	0.0	0.0	0.0	0.0
Warm season succulent	0.0	1.8	0.2	1.4	0.1	2.9
Cool season succulent	0.0	0.0	38.8	17.8	17.4	5.7

in August 1970, when productivity on the ungrazed treatment was 2.4 g/m^2/day table 48), which corresponds to the period following precipitation. Soil water availability in 1972 brought only modest productivity on the ungrazed treatment. This is probably a result of lack of photosynthetic tissue following the drought of 1971. Productivity was sustained over a longer period in 1972 than in the other years resulting in the high biomass and ANPP on the ungrazed treatment in 1972.

Highest productivity on the grazed treatment occurred between August 23 and September 12, 1972, when over 2.15 g/m^2/day were produced (table 49). Much of this was contributed by warm-season grasses, especially mesa dropseed, and annual forbs. Surprisingly, Russian thistle contributed very little during this period.

On both areas, shrub productivity was highest in 1970 and was reduced thereafter because of the drought (tables 48 and 49). For any single species, productivity was highest for black grama in August 1970 and from May 14 to June 14, 1972 on the ungrazed treatment, when productivity was over 1 g/m^2/day. Mesa dropseed productivity also approached and exceeded 1 g/m^2/day on both treatments. Russian thistle and *Cryptantha crassisepala* had the highest productivity of any forbs. Most of the warm-season species probably follow the C_4 photosynthetic pathway while the main cool season forb, *Cryptantha crassisepala*, is a C_3 plant (Lewis 1972). Primary productivity of this desert grassland is lower than that of all ungrazed grasslands reported by Lewis (1971) for the 1970 season wih the exception of the Pawnee shortgrass site. Productivity of over 6 g/m^2/day were calculated for two tallgrass

Table 48. Aboveground net primary productivity ($g/m^2/day$) for all species, some groups of species, and some individual species for the ungrazed treatment.

Period	All Species	PWSG[a]	AWSF	ACSF	Shrubs	BOER	SPFL	SAKA	CRCR	GUSA
1970										
7/14- 7/30	--[b]	0.50	0.27	0.19	--	0.63	--	0.18	0.36	--
7/31- 8/10	0.73	0.10	0.50	--	0.09	--	0.18	0.20	--	--
8/11- 8/20	2.40	2.60	0.09	--	--	1.30	1.20	0.17	--	--
8/21- 9/1	0.50	--	--	--	1.17	--	--	--	--	0.41
9/2 - 9/26	--	--	--	--	--	--	--	0.03	--	--
9/27-10/31	--	--	--	--	--	--	0.03	--	--	0.06
1971										
7/14- 8/3	0.21	0.21	--	--	--	0.16	--	--	--	--
8/4 - 8/20	0.71	0.35	0.18	--	1.12	0.35	0.06	--	--	--
8/21- 9/11	1.38	0.52	0.52	--	--	0.24	0.19	--	--	--
9/12-10/7	0.23	--	0.35	--	0.04	--	--	0.11	--	0.04
1972										
1/8 - 2/24	0.18	--	--	0.08	0.12	--	--	--	0.08	0.08
2/25- 3/28	0.28	0.13	--	0.22	--	--	--	--	0.22	--
3/29- 5/13	0.11	--	0.02	0.09	0.02	--	--	0.02	0.09	--
5/14- 6/14	1.17	1.23	0.10	--	0.05	1.03	0.13	--	--	0.23
6/15- 6/30	--	--	0.18	--	--	--	--	0.24	--	--
6/31- 7/19	0.90	0.55	0,55	--	0.25	0.05	--	0.15	--	0.05
7/20- 8/2	0.61	--	0.46	--	--	0.92	0.28	0.61	--	--
8/3 - 8/22	1.22	0.22	0.33	--	0.33	0.25	--	0.70	--	--
8/23- 9/12	1.10	0.35	0.70	--	--	0.25	--	0.70	--	--
9/13-10/7	--	--	--	--	0.19	0.15	--	--	--	0.19

[a] Symbols are as follows: PWSG = perennial warm season grass; AWSF - annual warm season forb; ACSF = annual cool season forb; BOER = *Bouteloua eriopoda;* SPFL = *Sporobolus flexuosus*; SAKA = *Salsola kali*; CRCR = *Cryptantha crassisepala*; GUSA = *Gutierrezia sarothrae.*

[b] Indicates a decrease or no change in biomass for period.

Table 49. Aboveground net primary productivity (g/m^2/day) for all species, some groups of species, and some individual species for the unungrazed treatment.

Period	All Species	PWSG[a]	AWSF	ACSF	Shrubs	SPFL	SAKA	CRCR	GUSA
1970									
7/14- 7/30	1.19	0.06	0.06	--[b]	1.06	0.06	0.13	0.06	1.13
7/31- 8/10	1.64	0.64	0.91	--	--	0.45	0.82	--	--
8/11- 8/20	1.90	--	0.90	--	1.40	--	0.40	--	1.40
8/21- 9/1	--	--	0.42	--	--	--	0.58	--	--
9/2 - 9/26	0.24	--	--	--	0.64	--	--	--	0.76
9/27-10/31	--	0.12	--	--	--	--	--	--	--
1971									
7/14- 8/3	0.05	0.05	--	--	--	0.05	--	--	--
8/4 - 8/20	0.64	--	0.23	--	0.29	--	--	--	--
8/21- 9/11	0.62	0.05	0.43	--	--	0.05	0.09	--	0.18
9/12-10/7	0.15	0.15	0.08	--	0.04	0.08	0.04	--	--
1972									
1/8 - 2/24	0.10	--	--	0.03	--	--	--	0.10	--
2/25- 3/28	1.22	0.06	0.09	0.63	--	0.06	--	0.63	0.03
3/29- 5/13	--	--	0.04	--	0.09	--	0.02	--	0.02
5/14- 6/14	--	0.07	0.27	--	0.10	0.03	0.07	--	0.13
6/15- 6/30	--	0.06	--	--	--	--	--	--	0.06
6/31- 7/19	0.50	--	0.70	--	--	0.05	0.30	--	--
7/20- 8/2	0.80	--	--	--	--	--	0.23	--	0.08
8/3 - 8/22	0.78	0.28	0.50	--	0.17	0.90	0.50	--	--
8/23- 9/12	2.15	0.95	0.45	--	0.25	--	0.05	--	0.15
9/13-10/7	--	--	--	--	--	--	0.38	--	--

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[a] Symbols are as follows: PWSG = perennial warm season grass; AWSF = annual warm season forb; ACSF = annual cool season forb; SPFL = *Sporobolus flexuosus*; SAKA = *Salsola kali*; CRCR = *Cryptantha crassisepala*; GUSA = *Gutierrezia sarothrae*.

[b] Indicates a decrease or no change in biomass for period.

sites and over 5 $g/m^2/day$ for two mixed-grass sites. Productivity for the Pawnee site was about 2 $g/m^2/day$. The reason for the low productivity at the Jornada is probably related as much to lack of leaf area and photosynthetic tissue as to lack of moisture. In late summer of 1972, soil water was probably not restricting photosynthesis, and yet productivity was only just over 2 $g/m^2/day$. Even on good condition desert grassland, however, basal area of perennial grasses is often less than 2%. Most of the herbaceous species present are relatively short and lack large leaves. Consequently, even when soil water is available and annual forbs become established, productivity is relatively low.

Belowground

Four methods were compared for calculation of belowground net primary productivity (BNPP). The four methods yielded variable results; 1972 data were particularly troublesome (table 50). Lowest BNPP values were those representing the difference between the peak and the preceding minimum value. For this method and the one summing the positive increments in total belowground biomass, BNPP on the grazed treatment was 0, indicating no increase. This seems unrealistic in view of the favorable growing conditions during 1972. The methods that took into account changes in biomass by depth did show some belowground biomass productivity for 1972 on the ungrazed treatment while there was considerable variation among methods for 1970 and 1971.

Sampling belowground biomass and productivity is fraught with many problems. The samples collected for this study represented total belowground organic matter. It was not possible to make any separations

Table 50. Estimates of annual belowground productivity calculated by four methods for the Jornada (g/m^2). (U = ungrazed, G = grazed).

Method[a]	1970		1971		1972	
	U	G	U	G	U	G
1	84	69	87	72	83	0
2	90	129	176	184	83	0
3	112	113	195	194	83	0
4	112	95	97	81	83	51
Average	100	101	138	132	83	32

[a] Methods were as follows: 1 = Maximum total biomass minus preceding total minimum biomass; 2 = Summation of significant positive increases in total biomass; 3 = Summation of significant positive increases in biomass by depth; 4 = Maximum--preceding biomass by depth.

even between living and dead portions. If a substantial portion of the belowground biomass is dead, this would tend to mask changes in the living portion. Separation by species was also not possible and if roots of one species were decreasing while another was increasing, the net change may be zero. Some of these species shifts may have been occurring in 1972. No direct measure of belowground decomposition was made and this was certainly a complicating factor.

Method 3 in table 50, the sum of positive increments by depth, was the method used in all the following discussion and calculations. In general, BNPP was similar for both treatments. Therefore, it appears that root biomass was greater on a plant or basal area basis on the grazed treatment than on the ungrazed treatment, although no measure of basal cover or plant density was made. BNPP appears to be inversely related to precipitation since values were highest for 1971, the driest year, and lowest for 1972, the wettest year. A satisfactory explanation for these relationships is not possible with the present data, but they are probably related to differences and changes in species competition, belowground decomposition, and carbohydrate storage.

Efficiency of Net Primary Productivity

Relative efficiency of converting solar radiation to plant biomass was calculated with the usable growing-season solar radiation (table 51). Plant biomass was converted to caloric values by multiplying aboveground biomass by 4 and belowground biomass by 4.7 (Sims and Singh 1971). Thus, net primary productivity values presented in table 51 are in direct relation to those presented in g/m^2 in tables 48 and 49.

Efficiency of energy capture by desert grassland plants on the

Table 51. Net primary productivity and percent efficiency (in parentheses) of utilization of solar energy on grazed and ungrazed treatments.

Treatment	1970	1971	1972	Average
	Aboveground net primary productivity (kcal m^2)			
Ungrazed	536 (0.07)	500 (0.07)	744 (0.10)	593 (0.08)
Grazed	388 (0.05)	204 (0.03)	720 (0.09)	437 (0.05)
	Belowground net primary productivity (kcal m^2)			
Ungrazed	526 (0.07)	917 (0.13)	390 (0.05)	611 (0.08)
Grazed	531 (0.07)	912 (0.13)	362 (0.05)	602 (0.08)
	Total net primary productivity (kcal m^2)			
Ungrazed	1062 (0.13)	1417 (0.21)	1134 (0.15)	1204 (0.16)
Grazed	912 (0.11)	1116 (0.16)	1082 (0.14)	1039 (0.14)

Jornada was very low; less than 0.2% of the total usable solar energy reaching the plant canopy actually was converted to stored energy (table 51).

Efficiencies were slightly higher for belowground productivity than aboveground for 1970 and 1972 and higher for above ground in 1972. Aboveground efficiency was higher on the ungrazed treatment than on the grazed treatment, but there were no differenes between treatments for belowground efficiency. Efficiency for total net primary productivity varied from a low of 0.11% on the grazed treatment in 1970 to a high of 0.21% on the ungrazed treatment in 1971 (table 51). The high efficiencies for total net primary productivity were a result of the high biomass and efficiency for BNPP in 1971.

Compartmental Transfers

Rates of transfer from ANPP to standing dead and standing dead to litter and litter disappearance were calculated with the biomass data (table 52, figure 50). These data indicate some of the lag effects in these transfers. For example, the transfer from ANPP to standing dead in 1970 exceeded ANPP that year by over 40 g/m^2 and was probably a result of aboveground biomass produced the previous year. Transfers from ANPP to standing dead in 1972 were considerably less than ANPP, probably reflecting relatively low ANPP the previous two years. Although no studies have been made to measure these transfers directly, it is likely that standing material may remain several years since there is seldom snow cover to accelerate transfer to litter. Wind is a factor for some species, such as Russian thistle and mesa dropseed, which are

Table 52. Compartmental transfers for growing season (g/m^2) for ungrazed and grazed treatments.

Year	Treatment	ANPP	SD[a]	L[b]	LD[c]	BNPP[d]	RD[e]
1970	Ungrazed	134	178	140	188	112	92
	Grazed	97	92	79	111	113	67
1971	Ungrazed	125	132	123	131	195	147
	Grazed	51	67	53	62	194	161
1972	Ungrazed	186	100	131	120	83	106
	Grazed	180	81	73	67	77	185
Average	Ungrazed	148	137	131	146	130	115
	Grazed	109	80	68	80	128	138

[a] Transfer to standing dead

$$\left(\text{ANPP} + \begin{array}{c}\text{Initial live}\\ \text{biomass}\end{array}\right) - \begin{array}{c}\text{Final live}\\ \text{biomass}\end{array} = \text{SD}$$

[b] Transfer from SD to litter compartment

$$\left(\text{SD} + \begin{array}{c}\text{Initial biomass}\\ \text{of standing dead}\end{array}\right) - \begin{array}{c}\text{Final biomass}\\ \text{of litter}\end{array} = \text{L}$$

[c] Litter disappearance

$$\left(\text{L} + \begin{array}{c}\text{Initial biomass}\\ \text{of litter}\end{array}\right) - \begin{array}{c}\text{Final biomass}\\ \text{of litter}\end{array} = \text{LD}$$

[d] Summation of significant positive increases in biomass by depth.

[e] $$\left(\text{BNPP} + \begin{array}{c}\text{Initial belowground}\\ \text{biomass}\end{array}\right) - \begin{array}{c}\text{Final belowground}\\ \text{biomass}\end{array} = \text{RD}$$

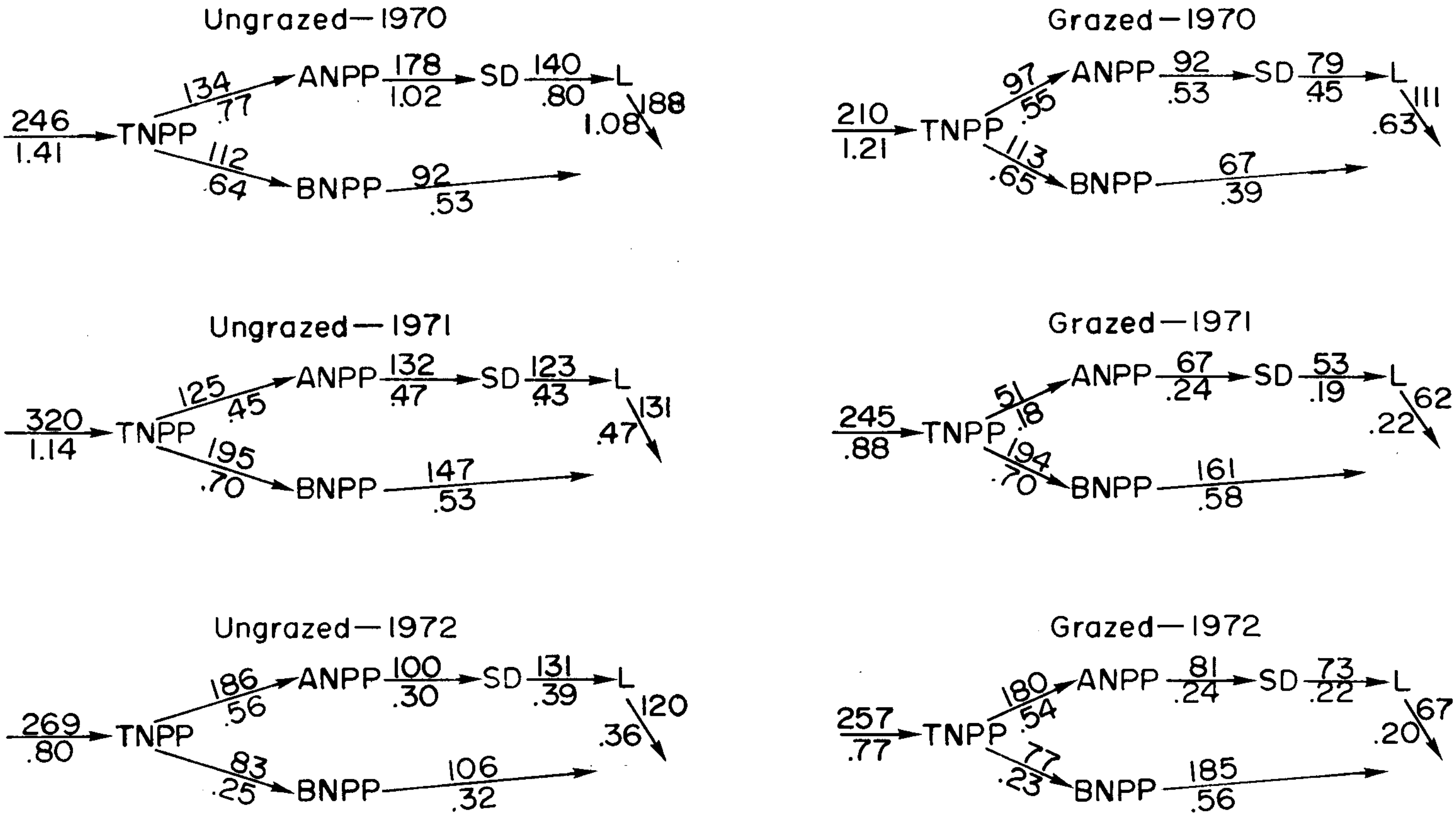

Fig. 50. Rates of transfer from one compartment to another. Figures above the line are annual rates in g·m^{-2} while those below the line are daily rates in g/m^2/day. Rates per day were calculated on a sampling season of 174 days in 1970 and a growing season of 280 days for 1971 and 333 days for 1972 taken from table 17.

easily broken off and added to the litter.

Root disappearance was calculated by two methods as shown in table 53. Differences between the two methods were small in some cases and rather large in others. The data from the second method were used for calculations in table 52. In 1970 and 1971, root death or disappearance was less than BNPP while in 1972 the reverse was true. Root disappearance was greater on the ungrazed treatment in 1970, but greater on the grazed treatment for 1971 and 1972.

Although climatic variations in desert grasslands are great as are yearly variations in primary productivity, the data indicated that over the three-year period equilibria in compartmental transfers were present. On the ungrazed treatment, there was little difference between the biomass transferred from ANPP to standing dead and that added from standing dead to litter (table 52). ANPP and litter disappearance were nearly equal for the three years. On the grazed area, transfer to standing dead and litter disappearance were equal for the three years. There were some differences in BNPP and root disappearance, but these were not great. Apparently the two dry years followed by a wet year resulted in balances for these productive characteristics.

Table 54 shows the compartmental transfer functions as percentages of transfer from one box to another. For example, in 1970 on the ungrazed treatment, 54% of total net primary production was accounted for by aboveground net primary productivity and 46% by belowground net primary productivity. Values close to unity indicate that the input in a particular box equals output. For example, the transfer of ANPP to SD in 1970 and 1971 was about 1 for both treatments, indicating nearly

Table 53. Annual rate of belowground biomass disappearance calculated by two methods for the Jornada.

Year	Method	Ungrazed	Grazed
1970	1[a]	50	86
	2[b]	92	67
1971	1	139	203
	2	147	161
1972	1	101	119
	2	106	185

[a] Method 1: Peak biomass - Succeeding biomass minimum = RD.

[b] Method 2: (BNPP + Initial root biomass) - Final root biomass = RD.

Table 54. Compartmental transfer functions for all three years on ungrazed (U) and grazed (G) treatments. Values are ratios between compartment values and that transferred to the next compartment. See text for full explanation.

Transfer	1970		1971		1972	
	U	G	U	G	U	G
TNPP to ANPP[a]	0.54	0.46	0.39	0.21	0.69	0.70
TNPP to BNPP	0.46	0.54	0.61	0.79	0.31	0.30
ANPP to SD	1.33	0.95	1.06	1.31	0.54	0.45
SD to L	0.79	0.86	0.93	0.79	1.30	0.90
ANPP to L	0.95	0.81	1.05	1.21	0.64	0.37
L to LD	1.34	1.41	1.07	1.17	0.90	0.91
BNPP to RD	0.82	0.59	0.75	0.82	1.28	2.40

[a] TNPP is total net primary productivity; ANPP is aboveground net primary productivity; BNPP is belowground net primary productivity; SD is standing dead; L is litter; LD is litter disappearance; RD is root disappearance.

complete transfer of live material to standing dead. In 1972 only about half the material was transferred, indicating that since sampling was discontinued in October, not all the transfers were complete. The transfers of litter to litter disappearance exceeded 1 in 1970 and 1971 indicating a net loss of litter, probably because of low ANPP for those two years and higher rates of litter disappearance.

Turnover rates of belowground biomass are shown in table 55. During 1970 and 1971 turnover rates were about 50% or less for both treatments. During 1972, however, turnover rates were accelerated, probably reflecting the favorable soil water conditions. Except for 1972, there was little difference in turnover rates between treatments. Since belowground biomass was lower in 1972 than in the previous two years, it appears that turnover rates were inversely related to biomass.

The values shown in table 55 are comparable with those for other grassland ecosystems reported by Sims and Singh (1971), Kucera (1973), and Dahlman and Kucera (1965).

Transfers from Plants to Herbivores: Herbivory

Large Mammals

Where species of sagebrush (*Artemisia*) are not present, forbs contribute most to the pronghorn antelope diet (Pieper 1969; Howard, Engelking, Glidewell, and Wood 1973; Buechner 1950a,b). Apparently, pronghorn select their diet from a wide range of plant species and can adapt to the species present in a particular location. Russell (1964) reported that pronghorn herds near Roswell, New Mexico consumed more

Table 55. Turnover of belowground biomass on both treatments for three years.

Treatment	1970	1971	1972
Ungrazed	0.44	0.44	0.80
Grazed	0.52	0.42	0.59

than 90% of their diet in forbs. Near Datil, browse made up from 50% to 75% of pronghorn diet, but two species of sagebrush, *Artemisia caruthii* and *A. frigida*, comprised the bulk of the diet (Russell 1964). Near Mosquero, forbs contributed from 22% to 90% of the diet depending on site and season of the year. Howard et al. (1973) reported 54 species of food plants present on the Jornada Experimental Range. Buechner (1950a, b) found many species were grazed by pronghorn on desert grassland areas in the Trans-Pecos region of Texas near Marfa and Alpine. Pronghorn exhibited changes in species preference with season, but utilized many species at every season.

Since information on pronghorn densities and food habits were not a part of this study, estimates of pronghorn consumption were based upon values obtained from the literature. Howard et al. (1973) reported that the average density of pronghorn on the desert grassland portions of the Jornada from 1965 to 1970 averaged one pronghorn per 294 ha. The density of pronghorns may have been increasing slightly from 1968 to 1970, but the drought years of 1970 and 1971 may have decreased the population. Wesley, Knox, and Nagy (1973) reported that tame 40-kg pronghorn consumed 900 g/day during the fall and winter and 805 g/day during the spring and summer. Consumption of wild pronghorn may not be the same as that of tame animals, but those consumption figures give some measure of the impact and role of pronghorn on the Jornada. Percentage composition of pronghorn diets by categories of forbs, grass, and shrubs was taken from Buechner (1950) for the trans-Pecos region of Texas.

Forbs made up the largest portion of pronghorn diets; a total of

0.065 g/m^2 were consumed by pronghorn annually, while only 0.03 g/m^2 of grass and 0.032 g/m^2 of shrubs were consumed (table 56). There was very little seasonal differences in amounts of the different categories consumed. Toal annual consumption was 0.1 g/m^2. Obviously, such calculations do not take into account many of the variables encountered under field conditions and are included here only for general comparisons.

Several studies have been conducted on food habits of domestic livestock on desert grasslands. Most of these studies have shown that cattle prefer grass during the growing season although other groups may be important at other seasons of the year. At Fort Stanton, New Mexico, grass comprised almost 60% of cattle diets annually (Thetford, Pieper, and Nelson 1971) while on the Santa Rita in southern Arizona the grass content of the diet comprised from 72% to 95% of steer diets (Galt et al. 1969) (tables 57 and 58). In the Fort Stanton study, forbs were important in the spring when vervain (*Verbena* spp.), scarlet globemallow (*Sphaeralcea coccinea*), and carruth sagewort (*Artemisia caruthii*) were green, but grass species were not. In the Santa Rita study, forbs were not important. Plains bristlegrass (*Setaria macrostachya*) and Arizona cottontop (*Trichachne californica*) were important constituents of the diet in September and October while Lehman lovegrass (*Eragrostis lehmanniana*) became important during November and December (table 58).

On the Jornada Experimental Range, Herbel and Nelson (1966b) found that forbs were more important in the fall and spring than they were in the winter and summer. On the adjacent Collage Ranch, however, Rosiere (1973) found that forbs comprised almost 60% of the cattle diet (table 59 and figure 51). Herbel and Nelson (1966b) listed 49 species

Table 56. Estimated pronghorn antelope consumption based on a density of one pronghorn per 294 ha on the Jornada Experimental Range.[a]

	Plant Category[b]						
Season	Forbs		Grass		Shrubs		Total
	%	g/m^2[c]	%	g/m^2	%	g/m^2	g/m^2
Summer	67.5	0.017	5.6	0.001	26.9	0.007	0.0246
Fall	55.5	0.015	6.9	0.002	37.6	0.010	0.0275
Winter	65.8	0.016	1.1	>0.001	33.1	0.009	0.0275
Spring	70.7	0.017	3.8	0.001	25.5	0.006	0.0246
Total		0.067		0.005		0.032	0.1042

[a] Density of antelope was taken as the average from 1965 to 1970 on the Jornada Range (Howard et al. 1973).

[b] Proportion of grasses, forbs, and shrubs by season was taken from Buechner (1950b) for Trans-Pecos, Texas.

[c] Intake of 900 g/individual antelope during the fall and winter and 805 during the spring and summer were taken from Wesley, Knox, and Nagy (1973).

Table 57. Average botanical composition (percent dry weight) of sheep and cattle diets at Fort Stanton 1969-1970 (from Therford, Pieper, and Nelson 1971).

Species	April		June		July		August		October		January	
	Sheep	Cattle	Sheep	Cattle	Sheep	Cattle	Sheep	Cattle	Sheep	Cattle	Sheep	Cattle
Grasses												
Bouteloua gracilis	15.5	21.7	9.8	35.5	34.5	35.4	27.4	50.1	20.3	28.6	22.1	34.0
Bouteloua curtipendula	1.7	2.4	2.6	7.7	4.0	7.4	2.2	10.0	3.8	5.0	4.9	5.1
Lycurus phleoides	3.4	2.3	2.5	7.3	8.2	9.6	4.5	19.2	1.3	6.6	0.7	5.9
Aristida spp.	5.9	5.1	6.5	8.3	8.3	4.4	16.9	0.0	1.9	15.9	3.5	16.5
Panicum hallii	3.2	1.3	0.5	1.1	3.0	5.7	4.5	4.4	1.9	2.4	0.0	0.2
Sitanion hystrix	0.4	0.0	0.3	1.5	0.0	1.1	0.0	5.2	1.2	0.3	0.0	0.2
Sporobolus cryptandrus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Muhlenbergia torreyi	0.0	0.3	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.2
Total	32.5	33.1	22.2	61.4	58.0	64.9	55.5	88.9	30.4	58.8	31.2	62.1
Forbs												
Artemisia Carothii	42.3	42.0	31.2	10.9	10.3	0.0	8.7	1.1	25.6	14.1	18.5	9.4
Sphaeralcea coccinea	3.6	0.5	16.0	14.2	7.7	29.3	2.8	2.2	16.1	3.8	3.5	0.2
Verbena spp.	8.8	2.0	20.8	4.2	19.1	0.0	13.3	0.0	16.9	8.7	23.1	4.9
Astragalus spp.	4.6	0.3	8.3	0.4	0.0	1.4	15.4	0.0	7.2	1.9	21.2	14.0
Xanthocephalum sarothae	1.7	1.4	1.2	4.2	3.4	0.2	2.2	5.6	1.9	7.3	0.7	3.2
Lesquerella gordoni	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
Pectis papposa	0.0	0.8	0.0	1.4	0.6	0.4	1.6	0.0	0.0	0.9	2.0	0.2
Total	61.0	47.0	77.8	35.3	41.1	31.3	44.0	8.9	67.7	36.7	69.0	32.1
Browse												
Quercus undulata	5.0	19.0	0.0	1.7	0.0	3.7	0.0	2.2	1.9	4.0	0.0	0.7
Atriplex canescens	0.0	0.6	0.0	1.0	0.6	0.0	0.0	0.0	0.0	0.3	0.0	0.5
Berberis haematocarpa	0.9	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.3	0.0	1.5
Total	5.9	19.6	0.0	2.7	0.6	3.7	0.5	2.2	1.9	4.6	0.0	2.7

Table 58. Botanical composition (percent by weight) of rumen samples collected from fistulated steers on the Santa Rita Experimental Range (from Galt et al. 1969).

Collection Date	September 21		October 2		October 23		November 6		November 20		December 4[a]	January 5	
	Steer 1	Steer 2	Steer 1	Steer 2	Steer 1	Steer 2	Steer 1	Steer 2	Steer 1	Steer 2	Steer 2	Steer 1	Steer 2
Grasses													
Setaria macrostachya Plains bristlegrass	66	48	69	76	47	56	60	33	7	5	5	T[b]	T
Digitaria californica Arizona cottontop	26	24	15	8	43	35	11	22	9	9	17	6	T
Eragrostis lehmanniana Lehmann lovegrass	T	6	T	8	5	T	8	16	60	54	44	40	54
Bouteloua eriopoda Black grama	--	--	--	T	T	T	T	5	T	5	6	38	24
Total Grasses	92	78	84	92	95	91	79	76	76	73	72	84	78
Shrubs													
Calliandra eriophylla False-mesquite	T	19	T	T	T	--	T	15	--	T	--	--	--
Opuntia englemonnia Englemann prickly-pear	--	--	--	T	--	--	--	--	--	--	15	3	8
Other plant species[c]	8	3	16	8	5	9	21	9	24	27	13	13	14

[a] Sample from steer number 1 for December 4 was lost in storage.

[b] T refers to trace amount less than 5% weight and not considered in the total.

[c] Values were determined by difference, since weight was not determined for individual species. This group includes 5 forb species and 5 shrub species.

Table 59. Average seasonal herbage preference (%) by Hereford and Santa Gertrudis cows for the 1961-1964 study period (from Herbel and Nelson 1966b).

Species	Fall		Winter		Spring		Summer	
	H[a/]	SG[a/]	H	SG	H	SG	H	SG
Aristida longiseta	5.1	2.9	0.4	1.2	7.3	4.7	4.6	4.7
Bouteloua eriopoda	6.5	5.2	19.3	26.8	2.2	4.2	4.5	6.4
B. curtipendula	--	--	--	0.1	--	--	--	--
Hilaria mutica	0.6	4.2	--	1.7	1.0	0.7	8.8	14.5
Muhlenbergia arenacea	0.8	2.0	--	2.6	--	--	2.9	0.5
M. porteri	--	0.6	--	--	--	--	--	--
Panicum hallii	6.1	0.6	0.4	0.3	--	--	--	--
P. obtusum	0.8	0.5	--	0.4	--	--	3.1	1.3
Scleropogon brevifolius	6.9	11.5	3.7	14.1	0.1	7.5	11.4	15.5
Sporobolus airoides	4.9	3.9	2.6	4.0	12.7	25.8	8.0	11.4
S. flexuosus	15.7	11.0	14.2	11.4	11.7	13.6	21.8	12.8
Tridens pulchellus	1.1	3.1	1.9	0.5	--	1.9	--	4.9
Total perenial grasses	48.5	45.5	42.5	63.1	35.0	58.4	71.4	72.0
Bouteloua aristidoides	--	--	--	--	--	--	--	0.1
B. barbata	1.7	3.3	7.1	1.9	--	--	--	9.4
Munroa squarrosa	--	0.5	--	--	--	--	--	--
Total annual grasses	1.7	3.8	7.1	1.9	--	--	--	9.5
Allionia incarnata	--	0.6	--	--	--	--	2.2	--
Bahia absinthifolia	1.2	--	--	0.1	0.9	--	--	--
Baileya multiradiata	1.0	1.6	--	--	--	--	0.4	2.4
Chamaesaracha conoides	--	--	--	--	1.8	--	--	--
Cirsium ochrocentrum	1.4	0.3	--	--	--	--	--	--
Croton corymbulosus	5.9	12.3	2.8	2.9	7.3	12.0	11.4	10.5
Erysimum capitatum	--	1.0	--	--	--	--	--	--
Lesquerella fendleri	0.4	--	3.7	0.3	0.8	1.0	--	--
Melampodium leucanthum	1.6	--	--	--	0.7	0.8	0.3	--
Perezia nana	2.9	2.7	--	0.2	--	--	--	--
Psilostrophe tagetinae	4.5	7.3	2.5	5.2	16.4	10.7	0.6	1.4
Solanum elaeagnifolium	1.8	0.2	--	--	--	--	--	--
Sphaeralcea subhastata	6.8	1.0	0.2	--	0.5	0.3	--	0.1
Zinnia grandiflora	2.4	1.4	0.5	--	--	--	0.5	1.2
Total perennial forbs	29.9	28.4	9.7	8.7	28.4	24.8	15.4	15.6
Aphanostephus ramosissimus	--	--	--	--	--	0.4	--	--
Corispermon nitidum	0.1	--	8.8	6.0	--	--	--	--
Cryptantha crassisepala	--	--	--	--	6.1	--	--	--
Descurainia menziesi	--	--	--	0.8	--	--	--	--
Dithyrea wislizeni	--	3.0	5.9	2.2	0.3	--	--	--
Gutierrezia sphaerocephala	1.2	--	--	--	--	--	--	--
Hoffmanseggia densiflora	0.4	--	--	--	--	--	--	--
Iva dealbata	3.2	7.2	--	1.3	--	0.5	--	--
Kallstroemia hirsutissima	--	--	--	--	--	--	--	0.1
Montzelia albicaulis	--	--	1.9	--	1.4	--	--	--
Nama hispidum	--	--	--	--	0.3	0.6	--	--
Phacelia intermedia	--	--	--	--	--	0.2	--	--
Salsola kali	6.1	4.2	1.0	0.7	3.7	3.1	7.1	1.1
Tribulus terrestris	0.4	--	--	--	--	--	--	--
Total annual forbs	11.4	14.4	17.6	11.0	11.8	4.8	7.1	1.2
Atriplex canescens	0.5	0.1	--	--	0.1	--	--	0.2
Ephedra trifurca	4.5	4.8	2.0	0.6	2.3	--	0.8	0.2
Flourensia cernua	--	2.0	0.9	--	--	--	0.6	--
Gutierrezia sarothrae	1.0	--	0.6	0.2	3.1	0.1	--	--
Prosopis juliflora	--	--	0.2	--	--	--	0.8	1.2
Yucca elata	2.4	0.9	19.3	14.4	19.3	11.7	3.7	0.3
Total shrubs	8.4	7.8	23.0	15.2	24.8	11.8	5.9	1.9

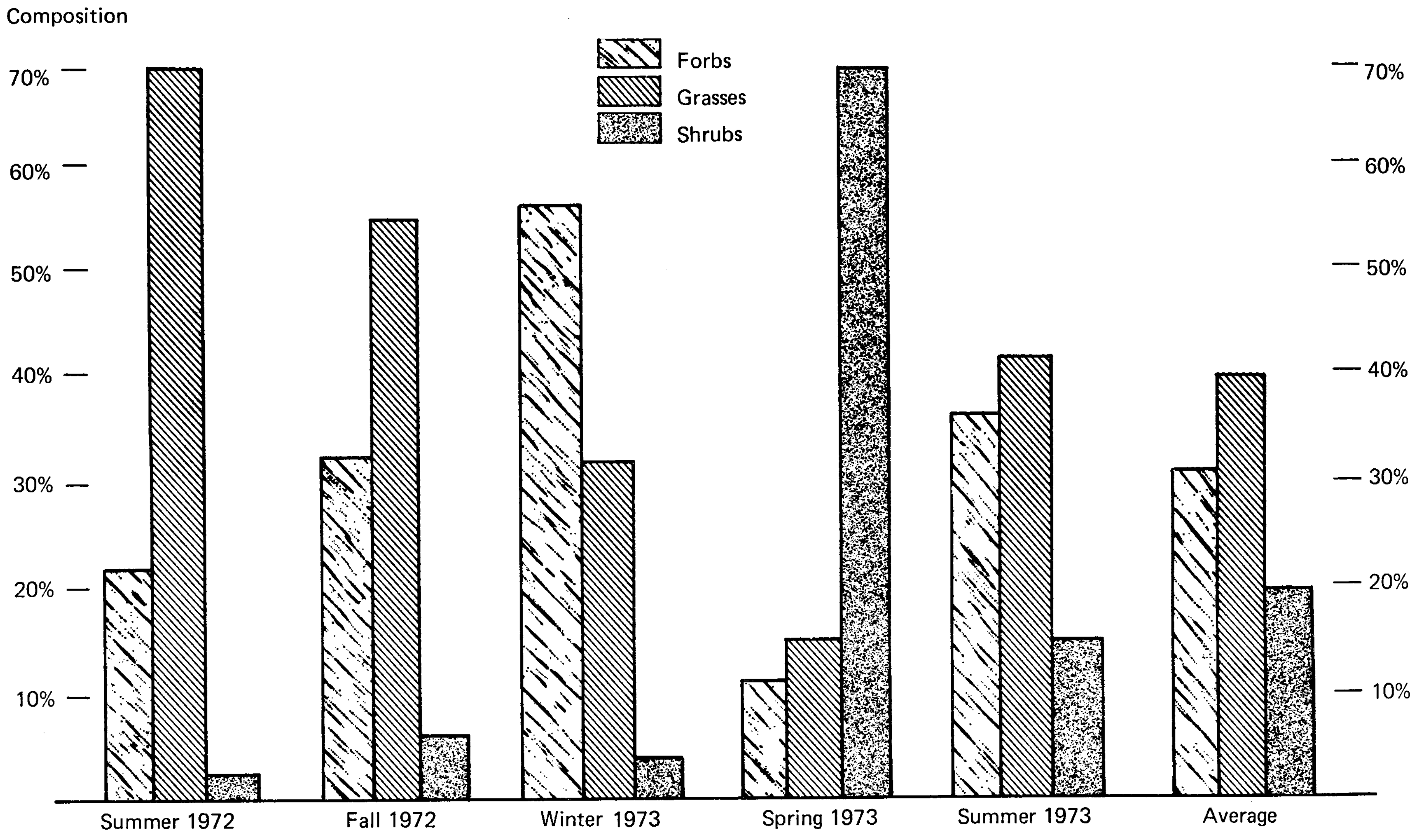

Fig. 51. Seasonal precentages of forbs, grasses, and shrubs in Hereford steer diets on the New Mexico State University College Ranch (from Rosiere 1973).

consumed by cattle at all seasons while Rosiere (1973) listed 28 species. Data reported by Nelson and Herbel were collected by use of feeding minutes; those reported by Rosiere were collected with microscopic analysis of esophageal samples as described by Sparks and Malechek (1968).

Both Rosiere (1973) and Herbel and Nelson (1966) reported fairly high consumption of soaptree yucca during certain seasons. For example, almost 25% of Hereford diets was yucca during the springs of 1961 and 1964 on the Jornada and almost 70% of the spring 1973 diets was yucca on the College Ranch.

Black grama comprised less than 30% of cattle diets in both studies (tables 59 and 60). During the summer, fall, and winter of 1973 the annual grass *Aristida adscenscionis* contributed from 15% to 20% of the steer diets with the exception of one pasture in the winter of 1973 (table 60). Mesa dropseed was the most important species on a yearlong basis in both studies. Tansy mustard (*Descurainia menziesi*) and *Sisymbrium linearifolium* were important components of steer diets on the College Ranch during the winter of 1973.

Rosiere (1973) also calculated preference indices for the species occurring in the steer diets by the following relationship (table 61).

$$\text{Preference index} = \frac{\text{\% dry wt of species in diet}}{\text{\% dry wt of species in herbage}}$$

An index of less than 1 indicates that a species was consumed in a smaller percentage than it was available in the herbage; an index exceeding 1 indicates that the species was eaten in a greater proportion than present in the herbage.

Table 60. Botanical composition of cattle diets for year-long use pasture (15) and seasonal suitability pastures (3N, 3W, and 3S) (from Rosiere 1973).

Species	Summer 1972		Fall 1972		Winter 1973		Spring 1973		Summer 1973	
	15	3N	15	3W	15	3W	15	3N	15	3S
	Percent of Diet[a]									
Grasses										
Aristida adscensionis	17.1	30.5	18.9	28.1	6.8	15.3		0.8	1.9	0.9
Aristida sp. (perennial)	5.7	2.7	1.8	4.6	1.9	1.0			2.9	3.8
Bouteloua eriopoda	5.7	15.5	20.0		10.0		5.4	3.8	12.1	7.8
Erioneuron pulchellus	0.9								1.0	0.9
Sporobolus flexuosus	32.8	29.3	10.4	26.9	16.3	11.0	8.6	12.1	25.9	26.7
Subtotal	62.2	78.0	51.1	59.6	35.9	27.3	14.0	16.8	43.8	40.1
Forbs										
Allionia incarnata									2.9	
Aphanostephus ramosissimus	2.8	3.6						0.8	2.9	1.9
Boerhaavia torreyana	0.9									
Cassia bauhinoides								0.2	1.9	1.9
Chenopodium sp.	5.7	0.9		0.9					1.0	
Croton corymbulosus	2.8	0.9	1.8	5.5	0.9	1.0	0.7	0.8	2.9	1.9
Cryptantha crassisepala					8.8	4.8				
Descurainia menziesi					10.9	22.2				
Dithyraea wislizeni	0.9			0.9	4.8	5.8	3.8	0.6	4.9	
Eriogonum abertianum	1.9									
Hoffmannseggia sp.	1.0		0.9	0.9					1.9	0.5
Hymenopappus robustus							2.3	3.1	5.7	7.3
Lepidium sp.							0.7		4.8	0.1
Lesquerella fendleri		1.8					2.3	6.2	1.2	9.8
Noma hispidum									1.0	
Perezia wrightii			5.5	2.7	0.9					
Portulaca sp.	8.7	2.7								
Psilostrophe tagetinae									8.4	7.8
Salsola kali tenuifolia	3.7	4.6	30.6	15.6	12.1	14.2			1.9	
Sisymbrium linearifolium					14.1	13.1				
Subtotal	28.4	14.5	38.8	26.5	42.5	61.1	9.8	11.7	41.5	31.2
Shrubs										
Ephedra torreyana	2.8	0.9	1.8	7.5	1.9	3.8				
Prosopis juliflora									1.0	9.9
Yucca elata			1.8	0.9	1.9		71.6	66.9	7.9	11.0
Subtotal	2.8	0.9	3.6	8.4	3.8	3.8	71.6	66.9	8.9	20.9
Unidentified	6.6	6.6	6.5	5.5	7.8	7.8	4.6	4.6	5.8	7.8
Total	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

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[a] Percentage basis including unidentified particles.

Table 61. Preference indices for cattle-selected forage plants (from Rosiere 1973).

Species	Summer 1972		Fall 1972		Winter 1973		Spring 1973		Summer 1973	
	15	3N	15	3W	15	3W	15	3N	15	3S
Grasses										
Aristida adscensionis	0.6	0.8	0.5	0.6	0.3	0.3	0.0	0.5	1.5	0.6
Aristida sp. (perennial)	1.0	4.5	0.4	3.8	0.4	2.5	0.0	0.0	5.8	5.4
Bouteloua eriopoda	0.9	1.2	1.3	--	1.7	--	0.7	0.7	1.3	1.7
Erioneuron pulchellus	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.5
Sporobolus flexuosus	3.6	2.4	1.3	3.5	1.8	1.9	2.0	1.5	1.4	1.5
Subtotal	1.2	1.1	0.7	1.0	0.7	0.4	0.8	0.9	1.3	1.5
Forbs										
Allionia incarnata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.0
Aphanostephus ramosissimus	1.9	0.8	0.0	0.0	0.0	0.0	0.0	0.1	0.5	0.6
Boerhaavia torreyana	3.0	--	0.0	0.0	0.0	0.0	0.0	--	0.0	--
Cassia bauhinoides	--	--	--	--	--	--	--	1.0	--	0.2
Chenopodium sp.	3.8	1.8	0.0	0.8	0.0	--	0.0	--	2.0	0.0
Croton corymbulosus	0.6	0.9	1.2	1.5	0.8	1.7	0.1	0.5	0.3	0.3
Cryptantha crassisepala	--	--	--	--	0.9	0.9	0.0	0.0	0.0	0.0
Descurainia menziesi	--	--	--	--	54.5	20.2	0.0	0.0	0.0	0.0
Dithyraea wislizeni	4.5	0.0	--	3.0	2.2	1.3	1.6	0.9	1.8	0.0
Eriogonum abertianum	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hoffmannseggia sp.	25.0[a]	0.0	9.0	4.5	--	--	0.0	0.0	9.5	5.0
Hymenopappus robustus	--	--	--	--	--	--	11.5	2.2	8.1	3.3
Lepidium sp.	--	--	--	--	--	--	0.1	0.0	1.9	1.0
Lesquerella fendleri	--	--	--	--	0.0	--	3.8	0.4	6.0	1.8
Noma hispidum	--	--	--	--	--	--	0.0	0.0	1.3	0.0
Perezia wrightii	0.0	--	18.0	67.5[a]	22.5[a]	--	0.0	0.0	--	--
Portulaca sp.	217.5[a]	9.0	--	--	--	--	--	--	--	--
Psilostrophe tagetinae	--	--	--	--	--	--	0.0	0.0	7.6	7.8
Salsola kali tenuifolia	6.2	1.0	3.4	3.5	4.2	5.1	0.0	0.0	3.2	0.0
Sisymbrium linearifolium	--	--	--	--	141.0	65.5	--	--	--	--
Subtotal	0.6	0.5	1.6	0.9	1.4	2.2	0.1	0.2	0.7	0.4
Shrubs										
Ephedra torreyana	70.0[a]	22.5[a]	45.0[a]	1.6	1.4	0.8	--	0.0	0.0	--
Prosopis juliflora	--	--	--	0.0	0.0	--	0.0	0.0	0.4	9.9
Yucca elata	--	--	1.0	22.5[a]	0.3	0.0	21.7	14.2	2.9	11.1
Subtotal	*[b]	*[b]	2.0	0.9	0.3	0.6	6.2	6.7	1.3	10.5

[a] Based on 0.04% in standing crop.

[b] Omitted due to insufficient sampling of shrubs.

The preference index for mesa dropseed exceeded 1 throughout the study; that for black grama was below 1 during the spring (table 61). *Aristida adscensionis* was not preferred and was probably eaten mainly because it was present in large amounts. Certain species such as tansy mustard, *Sisymbrium linearifolium*, and *Hoffmanseggia* sp. were highly preferred at certain seasons.

Seasonal transfer rates to cattle were calculated for the IBP Grassland site for the major species by use of literature values and actual stocking rates for the three years of the study on Pasture 9 of the Jornada Experimental Range. A daily intake rate of 8.6 kg per animal unit (a 394 kg cow plus calf or equivalent) was used, as reported by Hill (1965) for Herefords on the Jornada Experimental Range. Since the plant species on the area studied by Rosiere (1973) differed somewhat from those on the IBP Grassland site, the formula for preference index was used to calculate the percentage of each of eight species in the diet. The preference index given by Rosiere was used, and the average biomass (current live, recent and old dead for the season) was used to represent total herbage available. An example shows the calculation for *Sporobolus cryptandrus* (Spfl) for the summer of 1970 on the ungrazed treatment

$$\text{Preference index} = \frac{\text{\% of Spfl in diet}}{\text{\% of Spfl in herbage}}$$

% in diet = (Preference index) (% Spfl in herbage) = (2.2) (11.3) = 24.9. The summer period was considered to be 90 days (July, August, and September). In 1970 the stocking rate was 80.25 ha per animal unit or 0.01246 AU/ha. However, for good condition range as represented by the ungrazed treatment, the stocking rate was considered 25% higher than the actual rate. Hence, the stocking rate was calculated as 0.0167 AU/ha. Total herbage consumption during the summer was calculated as follows:

$$(0.0167)\ (8.6)\ (90) = 12.93 \text{ kg ha or } 1.293 \text{ g/m}^2$$

If 24.9% of this was mesa dropseed, consumption of mesa dropseed was $(0.249)\ (1.293) = 0.32 \text{ g/m}^2$.

This value is reported in table 62 for the ungrazed treatment for 1970. Other values in the table were calculated in a similar manner. For these calculations, the following months were included in the season for 1970 and 1971:

Summer:	July, August, and September, 90 days
Fall:	October and November, 60 days
Winter:	December, January, and February, 90 days
Spring:	March, April, May, June, 120 days

Because of the growth in June 1972 that month was considered to be a summer month instead of a spring month for that year.

Chemical composition data for major species were available from the IBP Grassland site for each season. However, in vitro digestibility coefficients for these whole-plant samples were much lower than those reported by Rosiere (1973) for esophageally collected samples. Consequently, digestibility coefficients were calculated using data for individual species and the formula calculated by Rosiere (1973).

$$\begin{aligned}\text{In vitro organic matter digestibility} &= 52.3 + (2.15)\ (\%\text{ protein}) - (1.16)\ (\%\text{ lignin}) \\ &\quad + (1.00)\ (\%\text{ ash}) + (0.52)\ (\%\text{ Fiber})\end{aligned}$$

Table 62. Dynamics of transfer from herbage standing crop to cattle for ungrazed treatment at different seasons.

Species	Season	Average Total Standing Crop (g/m^2)	Cattle Diet (%)	Consumed by Cattle (g/m^2)	Digestibility (%)	Retained (g/m^2)
Black grama	Summer 1970	43.8	35.5	0.46	42.8	0.20
	Fall 1970	26.0	25.4	0.22	37.4	0.08
	Winter 1970-71	25.0	50.5	0.63	34.9	0.22
	Spring 1971	20.0	17.0	0.27	35.4	0.10
	Summer 1971	21.0	30.4	0.36	42.8	0.15
	Fall 1971	20.5	21.7	0.17	37.4	0.06
	Winter 1971-72	16.7	40.6	0.44	34.9	0.15
	Spring 1972	17.5	15.4	0.21	35.4	0.07
	Summer 1972	28.2	24.6	0.25	42.8	0.11
	Fall 1972	31.0	17.0	0.12	37.4	0.05
Mesa dropseed	Summer 1970	9.2	24.9	0.32	49.3	0.16
	Fall 1970	5.0	27.0	0.23	37.9	0.09
	Winter 1970-71	4.7	19.4	0.24	30.6	0.07
	Spring 1971	4.7	15.6	0.24	37.5	0.09
	Summer 1971	4.8	24.2	0.28	49.3	0.14
	Fall 1971	3.5	18.0	0.14	37.9	0.05
	Winter 1971-72	2.7	13.3	0.14	30.6	0.04
	Spring 1972	2.5	9.0	0.12	37.5	0.05
	Summer 1972	5.2	13.6	0.14	49.3	0.07
	Fall 1972	3.0	7.8	0.05	37.9	0.02
Leatherweed croton	Summer 1970	1.5	0.9	0.01	52.5	0.01
	Fall 1970	1.0	2.7	0.02	56.2	0.01
	Winter 1970-71	0.3	0.4	0.005	37.6	0.00
	Spring 1971	1.0	1.0	0.016	57.6	0.01
	Summer 1971	1.3	11.5	0.02	52.5	0.01
	Fall 1971	1.0	2.5	0.02	56.2	0.01
	Winter 1971-72	1.3	4.1	0.04	37.6	0.02
	Spring 1972	1.5	1.0	0.01	57.6	0.01
	Summer 1972	2.5	1.5	0.02	52.5	0.01
	Fall 1972	3.0	5.6	0.04	56.2	0.02
Spectacle pod	Summer 1970	0.5	1.2	0.02	73.9	0.01
	Fall 1970	0.3	1.5	0.01	59.5	0.01
	Winter 1970-71	0.0	0.0	0.00	52.1	0.00
	Spring 1971	0.0	0.0	0.00	73.6	0.00
	Summer 1971	0.0	0.0	0.00	73.9	0.00
	Fall 1971	0.0	0.0	0.00	59.5	0.00
	Winter 1971-72	0.0	0.0	0.00	52.1	0.00
	Spring 1972	0.0	0.0	0.00	73.6	0.00
	Summer 1972	2.5	6.0	0.06	73.9	0.04
	Fall 1972	1.0	1.8	0.01	59.5	0.01
Russian thistle	Summer 1970	4.0	5.0	0.06	48.1	0.03
	Fall 1970	7.0	12.7	0.11	51.0	0.06
	Winter 1970-71	2.7	6.0	0.08	46.9	0.04
	Spring 1971	1.0	1.5	0.02	84.5	0.02
	Summer 1971	0.5	2.9	0.03	48.1	0.01
	Fall 1971	2.5	15.4	0.12	51.0	0.06
	Winter 1971-72	0.7	8.5	0.09	46.9	0.04
	Spring 1972	0.0	0.0	0.00	84.5	0.00
	Summer 1972	11.8	4.2	0.04	48.1	0.02
	Fall 1972	37.0	10.7	0.07	51.0	0.04

Table 62. (Continued)

Species	Season	Average Total Standing Crop (g/m^2)	Cattle Diet (%)	Consumed by Cattle (g/m^2)	Digestibility (%)	Retained (g/m^2)
Broom snakeweed	Summer 1970	14.5	3.6	0.05	49.1	0.02
	Fall 1970	3.0	1.7	0.01	56.0	0.01
	Winter 1970-71	9.7	2.1	0.03	21.4	0.01
	Spring 1971	21.3	8.5	0.13	36.1	0.05
	Summer 1971	8.5	3.9	0.05	49.1	0.02
	Fall 1971	6.0	3.2	0.03	56.0	0.02
	Winter 1971-72	6.7	1.8	0.02	21.4	0.00
	Spring 1972	6.0	6.4	0.09	36.1	0.03
	Summer 1972	7.5	1.8	0.02	49.1	0.01
	Fall 1972	11.0	3.0	0.02	56.0	0.01
Cryptantha	Summer 1970	1.7	0.0	0.00	55.0	0.00
	Fall 1970	0.0	0.0	0.00	46.5	0.00
	Winter 1970-71	0.0	0.0	0.00	41.2	0.00
	Spring 1971	0.3	0.3	0.01	58.0	0.01
	Summer 1971	0.0	0.0	0.00	55.0	0.00
	Fall 1971	0.0	0.0	0.00	46.5	0.00
	Winter 1971-72	1.0	2.3	0.02	41.2	0.01
	Spring 1972	12.5	23.9	0.33	58.0	0.19
	Summer 1972	8.8	0.0	0.00	55.0	0.00
	Fall 1972	1.0	0.0	0.00	46.5	0.00
Three awns	Summer 1970	0.0	0.0	0.00	55.1	0.00
	Fall 1970	0.0	0.0	0.00	46.5	0.00
	Winter 1970-71	1.7	6.7	0.08	37.6	0.03
	Spring 1971	0.7	7.0	0.11	51.1	0.06
	Summer 1971	0.3	1.2	0.01	55.1	0.01
	Fall 1971	0.5	2.3	0.02	46.5	0.01
	Winter 1971-72	0.3	1.4	0.02	37.6	0.01
	Spring 1972	1.5	16.0	0.22	51.1	11.20
	Summer 1972	0.0	0.0	0.00	55.1	0.00
	Fall 1972	0.0	0.0	0.00	46.5	0.00
Other Species	Summer 1970	7.6	47.9	0.46	59.5	0.27
	Fall 1970	1.0	33.9	0.22	39.2	0.09
	Winter 1970-71	5.7	46.4	0.45	48.1	0.22
	Spring 1971	20.3	70.9	0.71	63.7	0.45
	Summer 1971	7.8	46.8	0.29	59.5	0.17
	Fall 1971	17.0	23.4	0.14	39.2	0.05
	Winter 1971-72	5.4	20.3	0.18	48.1	0.09
	Spring 1972	11.5	64.7	0.67	63.7	0.43
	Summer 1972	19.6	51.8	0.40	59.5	0.24
	Fall 1972	31.0	55.9	0.29	39.2	0.11

For species with unknown chemical compositions, data from Nelson, Herbel, and Jackson (1970) were used.

Based on the conservative stocking rates used, small amounts of plant material were consumed by the cattle. On the ungrazed area 0.63 g/m^2 of black grama were consumed (hypothetically) while an average of 25 g/m^2 were available (table 62) during the winter of 1970-1971. On the grazed area, 0.26 g/m^2 of mesa dropseed were consumed from an average standing crop of 6.5 g/m^2 in the summer of 1970 (table 63). Black grama and mesa dropseed were the major species consumed on the ungrazed area while mesa dropseed and Russian thistle were the most consistent species. Forbs such as *Croton corymbulosus*, *Dithyrea* spectacle pod, and *Cryptantha crassisepala* were important mainly during the period when they were present in largest amounts in the herbage standing crop.

Annual total consumption for the ungrazed treatment was about 4.7 g/m^2 while that for the grazed treatment was about 3.5 (table 64). The difference is mainly a reflection of differences in stocking rate. Since digestibility was a little higher than 50%, fecal output was somewhat less than half the amount consumed for both treatments (table 64).

These data are based on many assumptions that may vary somewhat under actual conditions. They are presented to show the magnitude of herbivory by cattle. Under heavier stocking rates this influence would be much greater. Lewis (1971) reported cattle consumption of 14 and 8 g/m^2 from the ungrazed and grazed treatments, respectively. He used stocking rates of 24 and 40 ha/AU for the ungrazed treatments and

Table 63. Dynamics of transfers from herbage standing crop to cattle for grazed treatment at different seasons.

Species	Season	Average Total Standing Crop (g/m^2)	Cattle Diet (%)	Consumed by Cattle (g/m^2)	Digestibility (%)	Retained (g/m^2)
Black grama	Summer 1970	2.3	5.7	0.06	42.8	0.03
	Fall 1970	3.0	6.6	0.04	37.4	0.01
	Winter 1970-71	0.7	3.4	0.01	34.9	0.00
	Spring 1971	0.7	1.4	0.01	35.4	0.00
	Summer 1971	0.5	2.3	0.02	42.8	0.01
	Fall 1971	0.5	1.7	0.01	37.4	0.00
	Winter 1971-72	1.0	6.5	0.06	34.9	0.02
	Spring 1972	1.5	1.8	0.02	35.4	0.01
	Summer 1972	0.2	2.2	0.02	42.8	0.01
	Fall 1972	0.0	2.9	0.01	37.4	0.00
Mesa dropseed	Summer 1970	6.5	27.1	0.26	49.3	0.13
	Fall 1970	3.0	14.8	0.10	37.9	0.04
	Winter 1970-71	5.0	27.2	0.26	30.6	0.08
	Spring 1971	3.3	16.5	0.17	37.5	0.06
	Summer 1971	3.5	27.9	0.24	49.3	0.12
	Fall 1971	4.5	33.1	0.19	37.9	0.07
	Winter 1971-72	2.7	19.6	0.17	30.6	0.05
	Spring 1972	5.5	16.3	0.17	37.5	0.06
	Summer 1972	6.3	22.7	0.18	49.3	0.03
	Fall 1972	11.0	19.1	0.10	37.9	0.04
Leather weed Croton	Summer 1970	1.8	1.7	0.02	52.5	0.01
	Fall 1970	3.0	7.1	0.04	56.2	0.02
	Winter 1970-71	1.0	3.5	0.03	37.6	0.01
	Spring 1971	0.4	0.4	0.04	57.6	0.02
	Summer 1971	0.8	1.5	0.01	52.5	0.01
	Fall 1971	1.5	5.3	0.03	56.2	0.02
	Winter 1971-72	0.3	1.3	0.01	37.6	0.00
	Spring 1972	2.0	1.1	0.01	57.6	0.01
	Summer 1972	2.8	2.3	0.02	52.5	0.01
	Fall 1972	2.0	1.7	0.01	56.2	0.01
Spectacle pod	Summer 1970	0.0	0.0	0.00	73.9	0.00
	Fall 1970	0.0	0.0	0.00	59.5	0.00
	Winter 1970-71	0.0	0.0	0.00	73.1	0.00
	Spring 1971	0.0	0.0	0.00	73.6	0.00
	Summer 1971	0.0	0.0	0.00	73.9	0.00
	Fall 1971	0.0	0.0	0.00	59.5	0.00
	Winter 1971-72	0.0	0.0	0.00	73.1	0.00
	Spring 1972	1.5	3.1	0.03	73.6	0.02
	Summer 1972	3.5	11.4	0.09	73.9	0.07
	Fall 1972	1.0	1.8	0.01	59.5	0.01
Russian thistle	Summer 1970	14.2	10.0	0.09	48.1	0.04
	Fall 1970	20.0	23.1	0.15	51.0	0.08
	Winter 1970-71	7.3	13.6	0.13	46.9	0.06
	Spring 1971	2.0	0.0	0.00	84.5	0.00
	Summer 1971	0.8	7.5	0.07	48.1	0.03
	Fall 1971	3.0	26.6	0.15	51.0	0.08
	Winter 1971-72	2.3	41.0	0.36	46.9	0.17
	Spring 1972	0.5	0.0	0.00	84.5	0.00
	Summer 1972	11.7	3.7	0.03	48.1	0.01
	Fall 1972	40.0	15.0	0.08	51.0	0.04

Table 63. Continued.

Species	Season	Average Total Standing Crop (g/m^2)	Cattle Diet (%)	Consumed by Cattle (g/m^2)	Digestibility (%)	Retained (g/m^2)
Broom snakeweed	Summer 1970	20.0	7.6	0.07	49.1	0.03
	Fall 1970	28.0	14.5	0.09	56.0	0.05
	Winter 1970-71	15.0	4.3	0.04	21.4	0.01
	Spring 1971	7.3	10.8	0.11	36.1	0.04
	Summer 1971	13.8	10.0	0.09	49.1	0.04
	Fall 1971	13.0	9.9	0.06	56.0	0.03
	Winter 1971-72	13.0	4.9	0.04	21.4	0.01
	Spring 1972	10.5	9.2	0.10	36.1	0.04
	Summer 1972	11.8	3.9	0.03	49.1	0.01
	Fall 1972	20.0	3.6	0.02	56.0	0.01
Cryptantha	Summer 1970	0.3	0.0	0.00	55.0	0.00
	Fall 1970	0.0	0.0	0.00	46.5	0.00
	Winter 1970-71	0.0	0.0	0.00	41.2	0.00
	Spring 1971	0.0	0.0	0.00	58.0	0.00
	Summer 1971	0.0	0.0	0.00	55.0	0.00
	Fall 1971	0.0	0.0	0.00	46.5	0.00
	Winter 1971-72	1.3	4.4	0.04	41.2	0.02
	Spring 1972	24.0	3.8	0.04	58.0	0.02
	Summer 1972	5.0	0.0	0.00	55.0	0.00
	Fall 1972	0.0	0.0	0.00	46.5	0.00
Three awns	Summer 1970	0.0	0.0	0.00	55.1	0.00
	Fall 1970	0.0	0.0	0.00	46.5	0.00
	Winter 1970-71	0.3	1.6	0.02	37.6	0.01
	Spring 1971	0.0	0.0	0.00	51.1	0.00
	Summer 1971	0.3	4.0	0.04	55.1	0.00
	Fall 1971	0.0	0.0	0.00	46.5	0.00
	Winter 1971-72	0.3	2.0	0.02	37.6	0.00
	Spring 1972	0.0	0.0	0.00	51.1	0.00
	Summer 1972	0.3	2.0	0.02	55.1	0.01
	Fall 1972	0.0	0.0	0.00	46.5	0.00
Other species	Summer 1970	1.8	28.9	0.37	59.5	0.22
	Fall 1970	11.7	7.3	0.06	39.2	0.02
	Winter 1970-71	2.2	14.9	0.19	48.1	0.09
	Spring 1971	--	64.4	1.01	63.7	0.64
	Summer 1971	1.7	35.9	0.42	59.5	0.25
	Fall 1971	22.5	36.9	0.29	39.2	0.11
	Winter 1971-72	8.9	28.0	0.30	48.1	0.14
	Spring 1972	5.5	28.3	0.39	63.7	0.25
	Summer 1972	17.7	48.3	0.50	59.5	0.30
	Fall 1972	24.0	54.1	0.37	39.2	0.12

Table 64. Herbage consumption by cattle, forage digestibility, and amount retained and deposited as feces by season for both treatments.

Season	Average Total Herbage Standing Crop (g/m^2)	Consumed by Cattle (g/m^2)	Digestibility (%)	Amount	
				Retained (g/m^2)	Fecal Output (g/m^2)
		Ungrazed			
Summer 1970	81.5	1.29	54.2	0.70	0.59
Fall 1970	54.0	0.86	39.2	0.34	0.52
Winter 1970-71	46.3	1.25	48.1	0.60	0.65
Spring 1971	50.7	1.57	63.7	1.00	0.57
Total		4.97		2.64	2.33
Summer 1971	43.5	1.18	54.2	0.64	0.54
Fall 1971	56.5	0.78	39.2	0.31	0.47
Winter 1971-72	38.3	1.08	48.1	0.52	0.56
Spring 1972	47.0	1.37	63.7	0.87	0.50
Total		4.41		2.34	2.07
Summer 1972	84.2	1.03	54.2	0.56	0.47
Fall 1972	111.0	0.69	39.2	0.27	0.42
		Grazed			
Summer 1970	52.7	0.96	54.2	0.52	0.44
Fall 1970	58.0	0.64	39.2	0.25	0.39
Winter 1970-71	35.0	0.96	48.1	0.46	0.50
Spring 1971	34.0	1.00	63.7	0.64	0.36
Total		3.56		1.87	1.69
Summer 1971	27.5	0.88	54.2	0.48	0.40
Fall 1971	39.5	0.58	39.2	0.23	0.35
Winter 1971-72	26.3	0.88	48.1	0.42	0.46
Spring 1972	57.0	1.06	63.7	0.68	0.38
Total		3.40		1.81	1.59
Summer 1972	61.2	0.77	54.2	0.42	0.35
Fall 1972	105.0	0.52	39.2	0.20	0.32

daily consumption of 10 kg per head.

The average stocking rate of Pasture 9 has been 24 ha/AU since 1915. At this stocking rate, annual livestock consumption is about 12 to 14 g/m^2 (table 65). However, stocking rates have been reduced over the years, and from 1955 to 1967 stocking was 41 ha/AUY (Wright 1972). Annual consumption then was about 8 g/m^2 (table 65). Under any non-destructive stocking rate for desert grasslands, only a relatively low proportion of the available herbage standing crop is consumed by livestock. If consumption is compared to aboveground net primary productivity, the percentage consumed by livestock is even lower.

Small Mammals

Many desert grassland rodents are granivores and require a fairly consistent supply of seeds or alternative food sources. One hypothesis to explain the greater abundance of rodents on rangelands of low successional stage is the presence of forbs and annual plants, which supply seeds in greater quantity than perennial grass such as black grama and tobosa. The heteromyid rodents, notably the kangaroo rats, depend largely on seeds as their main food source (table 66). These rodents appear very adaptable and take seeds from whichever plants are present on the area. On the College Ranch, Wood (1969) found that 66% of the stomach contents of Ord's kangaroo rats was seeds, while only 37% of the stomach contents of the banner-tailed kangaroo rat was seed (table 67). However, Monson and Kessler (1940) found that the diet of banner-tailed kangaroo rats in southern Arizona was composed of 60% seeds, mostly annual grasses (table 66). Many of these kangaroo rats

Table 65. Calculated annual intake (g/m^2) by cattle under different stocking rates for desert grassland.

Stocking Rate		Annual Intake
AUY/ha	ha/AUY	(g/m^2)
0.200	5	62.8
0.100	10	31.4
0.050	20	15.7
0.025	40	7.9
0.017	60	5.4
0.013	80	3.9
0.010	100	3.1

Table 66. Food habits of desert rodents and rabbits on southwestern desert ranges (from Laycock 1970).

Species	Food Habits
Spermophillus spilosoma (Spotted ground squirrel)	Seeds of annuals, grasses, and shrubs including mesquite; green vegetation; cactus (Bailey 1931). Insects and animal material--58%, cactus--18%, green vegetation--10%, consumes 21 g/day (17 lb/year) per animal (16 pounds of plants) (Wood 1969). Similar species in California consumed 91.0 lb (dry wt) of herbage per year per individual (Fitch and Bentley 1949).
Dipodomys ordii (Ord's kangaroo rat)	Seeds: *Amaranthus* in Texas (Allan 1946). Grasses in Idaho (Johnson 1961). Desert plants including mesquite but also some green material (Bailey 1931). Seeds--66%, green vegetation--15%, insects and larvae--10%; consumes 8 g/day or 6 lb/year per animal (Wood 1969).
Dipodomys merriami (Merriam's kangaroo rat)	Seeds of desert plants including mesquite and creosote bush (Bailey 1931). Seeds--*Aristida*, annual gramas, creosote bush, snake weed (Monson and Kessler 1940). Seeds of grasses, forbs, mesquite, cactus in cheek pouches; stomachs also contain green material; large seeds preferred (Reynolds 1950). Mesquite beans a preferred food (Reynolds and Glendening 1949). Seeds: grasses--49%, forbs--33%, shrubs--12%. Also green material--5%; annual *Aristida* and gramas preferred; each animal ate 4.9 g/day; this equals 4 lb/year (Reynolds 1958).
Dipodomys spectabilis (Banner-tailed kangaroo rat)	Seeds: annual grasses (mainly *Bouteloua aristidoides*)--60%, also *B. rothrockii, Aristida adscencionis* (Monson and Kessler 1940). Seeds of these same species plus crowns of *B. rochrockii* and mesquite beans (Vorhies and Taylor 1922). Green vegetation--42%, seeds--37%, succulents--11%; consumes 8 g/day (6 lb/year) per individual (Wood 1969).
Lepus californicus (Black-tailed jackrabbit)	Grass, cactus, bark of mesquite, and other shrubs (Bailey 1931). Grass--24%, mesquite--56%; 30 jackrabbits = 1 sheep; 148 jackrabbits - 1 cow (Vorhies and Taylor 1933). One rabbit eats 0.27 lb (122 g) of food per day; this is equivalent to 98 lb/year (Haskell and Reynolds 1947).

Table 66. Continued.

Species	Food Habits
Neotoma albigula (White-throated wood rat)	Mesquite beans (Feldman 1935). Bark of *Rhus trilobata* (Hanson 1957). Cactus fruits and joints (Spencer and Spencer 1941). Cactus--44%, mesquite--30%, grasses--5% (Vorhies and Taylor 1940). Mesquite, cactus, cholla, *Acacia* (Monson and Kessler 1950). Green vegetation--38%, yucca--33%, composite heads --18%; consumes 21 g/day (17 lb/year) per individual (Wood 1969).
Neotoma micropus (Southern plains wood rat)	Mesquite beans (Feldman 1935). Flesh and fruit of cactus, green vegetation, fruit, seeds, mesquite beans (Bailey 1931). Green vegetation--43%, succulents--20%, composite heads--16%, yucca--16%; consumes 23 g/day (19 lb/year) per individual (Wood 1969).
Perognathus flavus (Silky pocket mouse)	Seeds of *Salsola, Chenopodium, Festuca, Cryptantha, Amaranthus, Opuntia, Oryzopsis, Sphaeralcea* (Forbes 1962). Shelled seeds, green vegetation, cactus (Bailey 1931).
Perognathus penicillatus (Desert pocket mouse)	90% seeds, mainly annual grasses and forbs but also perennial grasses and shrubs including mesquite (Reynolds and Haskell 1949).
Reithrodontomys megalotis (Harvest mouse)	Seeds of annual grasses, especially *Avena* in California (Cook 1959). Seeds and green foliage (Bailey 1931).
Sylvilagus auduboni (Desert cottontail)	Green grass and other vegetation in summer; twigs, bark, and cactus in winter (Bailey 1931). Ingested 171-209 g of food in 15 hours (this is equivalent to 138 to 168 lb/year, if this is assumed to be the daily ingestion rate) (Ingles 1941).

Table 67. Percentage of food volume eaten by rodents (number in sample in parentheses) on the College Ranch, Dona Ana County, New Mexico (from Wood 1969).

Kinds of Food	*Neotoma albigula* (147)	*Neotoma micropopus* (22)	*Dipodomys ordii* (72)	*Dipodomys spectabilis* (18)	*Spermophillus spilosoma* (291)
Plant Foods					
Green vegetation	38	43	15	42	10
Succulent vegetable[a]	7	20	9	11	18[b]
Seeds	Tr	Tr	66	37	5
Composite heads	18	16	--	--	4
Yucca leaves	33	16	--	--	--
Ephedra	Tr	3	--	--	5
Total Plant Material	97	98	90	90	42
Animal Foods					
Insects[c]	2	Tr	1	--	23
Lepidoptera larvae	1	2	9	4	18
Ants	--	--	--	--	2
Termites	--	--	--	--	9
Rodents	Tr	Tr	--	6	6[d]
Total Animal Material	3	2	10	10	58

[a] Largely *Opuntia* pods and yucca flowers and culms.

[b] Largely the succulent blooms of flowering plants.

[c] Largely Coleoptera and Homoptera.

[d] One percent lizard remains.

also eat mesquite beans when they are available (table 67).

The white throated and southern plains wood rats appear to be mixed feeders. Wood (1969) reported that the stomach contents of both species included green vegetation, succulent vegetation, composite heads, and yucca leaves, but few seeds (table 67). Other authors reported mesquite beans and the bark of some of the shrubs as important constituents of wood rat diets (table 66). Most of the plant food of the spotted ground squirrel consisted of green vegetation and succulents on the College Ranch (Wood 1969, table 67), but Bailey (1931) reported seeds of annual grasses and forbs as well as shrubs as components of squirrel diets (table 66).

The black-tailed jackrabbit and the desert cottontail are both grazers. Vorhies and Taylor (1933) reported that black-tailed jackrabbits consumed 24% grass, 56% mesquite in southern Arizona (table 66).

Several studies have also been conducted on quantity of food ingested by various small mammals. Many of these have been determined in feeding trials. Wood (1969) determined consumption rates for the most important rodent species on the College Ranch by using weight of full stomachs. He found that spotted ground squirrel populations consumed the most plant material annually (0.605 g/m^2), followed by the white throated wood rat and Ord's kangaroo rat. The total rodent community consumed 1.36 g/m^2 (dry weight) annually. Ord's kangaroo rat, the bannertailed kangaroo rat, white throated, and southern plains wood rats were mostly herbivores, while the spotted ground squirrel consumed both insects and plant material. The grasshopper mouse was mostly insectivorous (table 68). The percentages of dietary plant material reported in Wood's (1969) study differed somewhat from those determined from IBP studies (French 1974, table 69), but they are similar (table 69).

Rodents also alter patterns of mulch deposition by moving and storing plant material. Wood (1969) reported that 77% of wood rat dens had stored material ranging from 0.04 to 4.2 kg. Stored material included mesquite beans and seeds of cactus and forbs. Kangaroo rat dens contained 1.0 kg of stored material containing 18% perennial grass, 23% annual grass, 43% snakeweed, and 7% peppergrass (*Lepidium* sp.). About 10.6% of the area was denuded around the kangaroo rat dens.

Rodent consumption for the three years of IBP studies were calculated by a program developed at the Natural Resource Ecology Laboratory at Colorado State University by French and Swift (1974). The procedure is to utilize biomass by age classes with age class boundaries and weight by age class from trapping data collected by Packard (1972, 1973). A linear interpolation is made between sampling periods so that a smooth annual curve can be derived for biomass for each species. The average daily metabolic rate (ADMR) equation is developed with adjustments made for activity, temperature, thermal conductivity, reproduction, hibernation or torpor and the growing season. From these modified ADMR equations, a daily energy budget is developed with the energy consumed partitioned into production and respiration. Consumption of the plant material was calculated by multiplying the herbivory percentage shown in table 69 by total consumption.

Greatest consumption of plant material was in 1970, when the rodent

Table 68. Food habits of rodents on the New Mexico State University College Ranch (from Wood 1969).

Species	Plant Material Consumed ($g/m^2/year^1$)	Insects Consumed (g/m^2)	Total Food Consumed (g/m^2)
Ord's kangaroo rat	0.228	0.025	0.253
Banner-tailed kangaroo rat	0.059	0.003	0.062
White-throated wood rat	0.385	0.008	0.393
Southern plains wood rat	0.082	0.002	0.084
Spotted ground squirrel	0.605	0.749	1.354
Grasshopper mouse	0.003	0.034	0.037
Total	1.362	0.821	2.183

Table 69. Percent herbivory by various small mammal species on the IBP Jornada Site.

Species	Percent Herbivory
Ord's kangaroo rat	74.85
Banner-tailed kangaroo rat	15.99
Spotted ground squirrel	26.28
White-throated wood rat	100.00
Southern plains wood rat	98.00
Pocket mouse	97.81

population consumed 2.56 g/m^2 (table 70). About 82% of this was by Ord's kangaroo rat, which exhibited very high densities early in the summer of 1970. Rodent consumption declined in 1971 and 1972, following the large-scale decline in rodent densities during these two years. Even in 1971 and 1972, greatest consumption was by Ord's kangaroo rat. Pocket mouse consumption was nearly as great as that of Ord's kangaroo rat in 1972. However, because of population decline in 1971 and 1972, there was no wood rat consumption in these two years (table 70). Over the three years, rodent consumption averaged 1.26 g/m^2, which is slightly more than was reported by Wood (1965). For example, Wood (1969) reported 1.3 g/m^2 rodent consumption, while the lowest calculated for the IBP Grassland site was 0.56 g/m^2 in 1972 (tables 68 and 70). Part of the reason for the differences may be related to the method of calculating consumption and differences in density of rodents on the two areas and different years.

Consumption of material of animal origin (mainly invertebrates) by small mammals was less than that for plant material (table 71). Consumption was greatest in 1970 when 1.52 g/m^2 were consumed. Since this is greater invertebrate biomass than that sampled on the area either there were errors in sampling, assumptions underlying some of these calculations, or small mammals consumed invertebrates not sampled by the quick trap technique.

Consumption of animal material was greatest by the banner-tailed kangaroo rat and Ord's kangaroo rat with only a small contribution by the spotted ground squirrel. This contrasts with data from Wood (1969, table 68) who reported that consumption of invertebrates by spotted

Table 70. Average annual consumption of plant material (g/m^2) by small mammals on the Jornada IBP Site.

Species	1970	1971	1972	Average
Ord's kangaroo rat	2.10	0.48	0.27	0.95
Banner-tailed kangaroo rat	0.15	0.06	0.04	0.08
Spotted ground squirrel	0.01	0.02	0.02	0.05
White throated wood rat	0.04	0.00	0.00	0.01
Southern plains wood rat	0.03	0.09	0.00	0.04
Pocket mouse	0.14	0.02	0.23	0.13
Total	2.56	0.69	0.56	1.26

Table 71. Consumption rates (g/m^2) of animal material by small mammals on IBP site for three years.

Species	1970	1971	1972	Average
Ord's kangaroo rat	0.70	0.16	0.09	0.32
Banner-tailed kangaroo rat	0.79	0.32	0.21	0.44
Spotted ground squirrel	0.03	0.06	0.06	0.05
Total	1.52	0.54	0.36	0.81

Table 72. Annual consumption (g/m^2) for lagomorph populations on Jornada IBP grassland site for three years.

Species	1970	1971	1972	Average
Black-tailed jackrabbit	0.012	0.010	0.006	0.009
Desert cottontail	*[a/]	0.004	0.004	0.004
Total	0.012	0.014	0.010	0.012

ground squirrels was 0.75 g/m^2 annually. Differences in population densities of spotted ground squirrels between the two studies undoubtedly accounts for these differences.

Annual lagomorph consumption was estimated with daily consumption rates from the literature and average density values from the census conducted by Packard (1972). For the black-tailed jackrabbit, a daily consumption of 122 g/day was used (Haskell and Reynolds 1947) while 190 g/day were used for the desert cottontail (Ingles 1941).

Consumption by the black-tailed jackrabbit was consistently higher than that for the desert cottontail (table 72) because of much higher population densities. For the three years of the study black-tailed jackrabbit consumption averaged only 0.009 g/m^2 compared to 0.004 g/m^2 for the desert cottontail.

Secondary productivity of small mammals. Secondary productivity of small mammals was calculated by two methods. One of these used an adjusted metabolic rate as described earlier in the section (French and Swift 1974); the other method involved simply adding any positive increments in biomass by species from one sampling period to the next regardless of statistical differences.

Secondary productivity of small mammals was consistently larger by the metabolic rates method than that using biomass estimates (table 73). Because of relatively few sample dates in the year and lack of precision of biomass estimates, the method using metabolic rate was used.

Over the three-year period, Ord's kangaroo rat contributed almost 62% of the rodent productivity (table 73), followed by the banner-tailed kangaroo rat, spotted ground squirrel, and pocket mouse. Secondary

Table 73. Annual net secondary productivity (g/ha) of small mammals on Jornada IBP site by two methods.

Species	1970		1971		1972		Average	
	Method 1[a]	Method 2[a]	Method 1	Method 2	Method 1	Method 2	Method 1	Method 2
Ord's kangaroo rat	483	0	91	21	48	26	207	16
Banner-tailed kangaroo rat	143	400	47	46	33	52	74	166
Spotted ground squirrel	42	10	7	38	7	0	19	16
White-throated wood rat	36	61	0	0	0	0	9	20
Southern plains wood rat	27	2	7	26	0	0	11	9
Pocket mice	17	6	2	4	30	2	16	4
Total	748	479	154	135	118	80	336	231

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[a] Method 1 is based on an adjusted average daily metabolic rate and interpolation procedure for density of each species. See text for full explanation.

[b] Method 2 involved adding positive increments of biomass by species with no restrictions on significant differences between sampling dates.

productivity was much greater for all species during 1970 and declined considerably the following two years as one might expect from the density data. Over the three-year period total rodent productivity was 336 g/ha (or 0.034 g/m^2).

Mammalian Predation

Although many mammalian predators are present in desert grasslands, information on food habits and consumption are available only for coyotes, and this information is limited. Coyotes are often classified as predators; in actuality they appear to be omnivores. Studies by Rogers (1965) on College Ranch and by Meinzer, Ueckert, and Flinders (1975) in western Texas show that plant material such as mesquite pods contribute substantially to coyote diets (tables 74 and 75). In western Texas, rodents, rabbits, and carion contributed over 50% of the volume of coyote stomachs and plant material contributed over 20%. In New Mexico, rabbits and rodents also contributed the bulk of material in stomachs of coyotes collected during the winter an early spring (table 74). Of the rodents, kangaroo rats made up 20% of the volume of coyote stomachs, with 38% frequency.

Annual coyote consumption was calculated on the assumption of an average live weight of 10.3 kg, a biomass of 0.00213 g dry weight/m^2 for coyotes and a daily intake of 2.5% of body weight. The average weight of coyotes and daily intake rates were obtained from Dr. Jim Ellis, (personal communication NREL Colo. St. Univ.), while coyote biomass was calculated from literature values from similar areas. These data show no seasonal variations nor fluctuations in coyote density.

Table 74. Stomach contents of coyotes collected during winter and early spring of 1964-65, Dona Ana County, New Mexico (from Rogers 1965).

Food Item	Percent Volume	Percent Occurrence
Mammal	85.7	
Rabbit	49.0	63.5
Desert cottontail	26.1	28.8
Black-tailed jackrabbit	18.5	25.0
Unidentified rabbit	4.3	9.6
Rodent	24.8	46.2
Kangaroo rat	20.3	38.4
Wood rat	4.5	13.5
Pocket mouse	Trace	5.8
Cattle	6.7	7.7
Coyote	4.0	7.7
Pronghorn Antelope	1.2	1.9
Birds	6.7	
Quail	2.7	5.8
Meadowlark	Trace	3.8
Cactus Wren	Trace	1.9
Roadrunner	Trace	1.9
Sparrow Hawk	Trace	1.9
Mountain Bluebird	Trace	1.9
Unidentified birds	1.0	7.7
Plants	4.9	11.5
Mesquite	4.9	9.6
Screwbean	Trace	1.9
Reptile	1.7	17.3
Insects	1.0	3.8

Table 75. Mean percent volume of food items in coyote diets from July 1971 through June 1973 as determined by examination of stomach contents (from Meinzer, Ueckert, and Flinders 1975).

Food Items	July 1971- Apr. 1972[a]	July 1972- June 1973[b]	Mean Diet	Rank
Plants				
Mesquite pods	11.3	3.2	7.2	5
Juniper berries	0.9	4.6	2.8	8
Opuntia fruit	5.5	6.4	6.0	6
Lotebush berries	0.0	1.0	0.5	13
Ironwood berries	0.6	0.0	0.3	15
Plums	0.0	1.9	1.0	10
Elbowbush berries	0.0	1.5	0.8	11
Unknown berry	0.0	0.2	0.1	15
Wheat	0.0	0.2	0.1	15
Grass and leaves	1.4	2.0	1.7	9
Rodents	11.4	28.9	20.2	2
Leporids	11.5	10.1	10.8	4
Moles	0.0	0.8	0.4	14
Deer	0.6	0.0	0.3	15
Carrion	21.0	21.3	21.1	1
Insects	12.7	10.8	11.7	3
Turtle	0.1	0.0	Trace	16
Salamander	0.1	0.0	Trace	16
Unknown bones	1.2	0.0	0.6	12
Quail and quail eggs	1.1	0.4	0.8	11
Dove and dove eggs	0.0	0.6	0.3	15
Other birds and eggs	2.7	4.1	3.4	7
Unidentifiable material	1.6	0.0	0.8	11
Calf manure	9.9	2.1	6.0	6
Cottonseed cake	5.0	0.0	2.5	9
Miscellaneous	1.2	0.0	0.6	12

[a] No samples were taken during May or June 1972. A total of 71 coyotes were killed of which 32 had empty stomachs.

[b] A total of 66 coyotes were killed of which 11 had empty stomachs.

Total annual consumption by coyotes was calculated as 0.19 g/m^2 (table 76). Contribution by rabbits and rodents was highest followed by cattle and birds, and plants.

Energy Flow Through Bird Populations

The energy flow through bird populations depends on a variety of factors in addition to the numbers of birds present. The energy requirements of an individual bird vary with its weight, the ambient temperature, the photoperiod, and whether the bird is engaged in breeding or molting. Only a portion of the material eaten is used in maintaining energy balance. The rest is waste in the form of feces. Estimating all the parameters involved in energy flow for a particular species is therefore a complex task. It can be divided into two parts, by estimating separately: (i) the normal daily energy budget and (ii) the energy expended in breeding and reproduction. Normal daily energy budgets were calculated using estimates of metabolic rates and estimates of density described earlier. Reproductive effort was determined by direct censusing of eggs and young on the site; additional data on the duration of fledging and incubation were obtained for localities close to the site. The results are presented in figure 52; granivores are shown on a scale 10x, that of insectivores and insectivore reproductive effort is shown separately. Molting activities of the granivores are not shown, and the insectivores found on the site generally involve species whose molt occurs in regions outside the desert grassland. The data presented are for the energy assimilated by the community; the energy consumed would be greater since assimilation efficiences are of

Table 76. Annual consumption (g/m^2) of various food items by coyotes on the Jornada Experimental Range.

Food Item	Consumption (g/m^2)[a]
Desert cottontail	0.0055
Black-tailed jackrabbit	0.0040
Total rabbits	0.0095
Rodents	0.0048
Cattle	0.0013
Coyote	0.0008
Pronghorn antelope	0.0002
Birds	0.0013
Plants	0.0009
Reptiles	0.0003
Insects	0.0002
Total	0.0193

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[a] Annual consumption based on 10.3 kg live weight for coyotes, 3.09 kg dry weight, a biomass of 0.00213 g dry weight of coyotes per m^2 and consumption of 2.5% of body weight daily. Data on food items are from Rogers (1965).

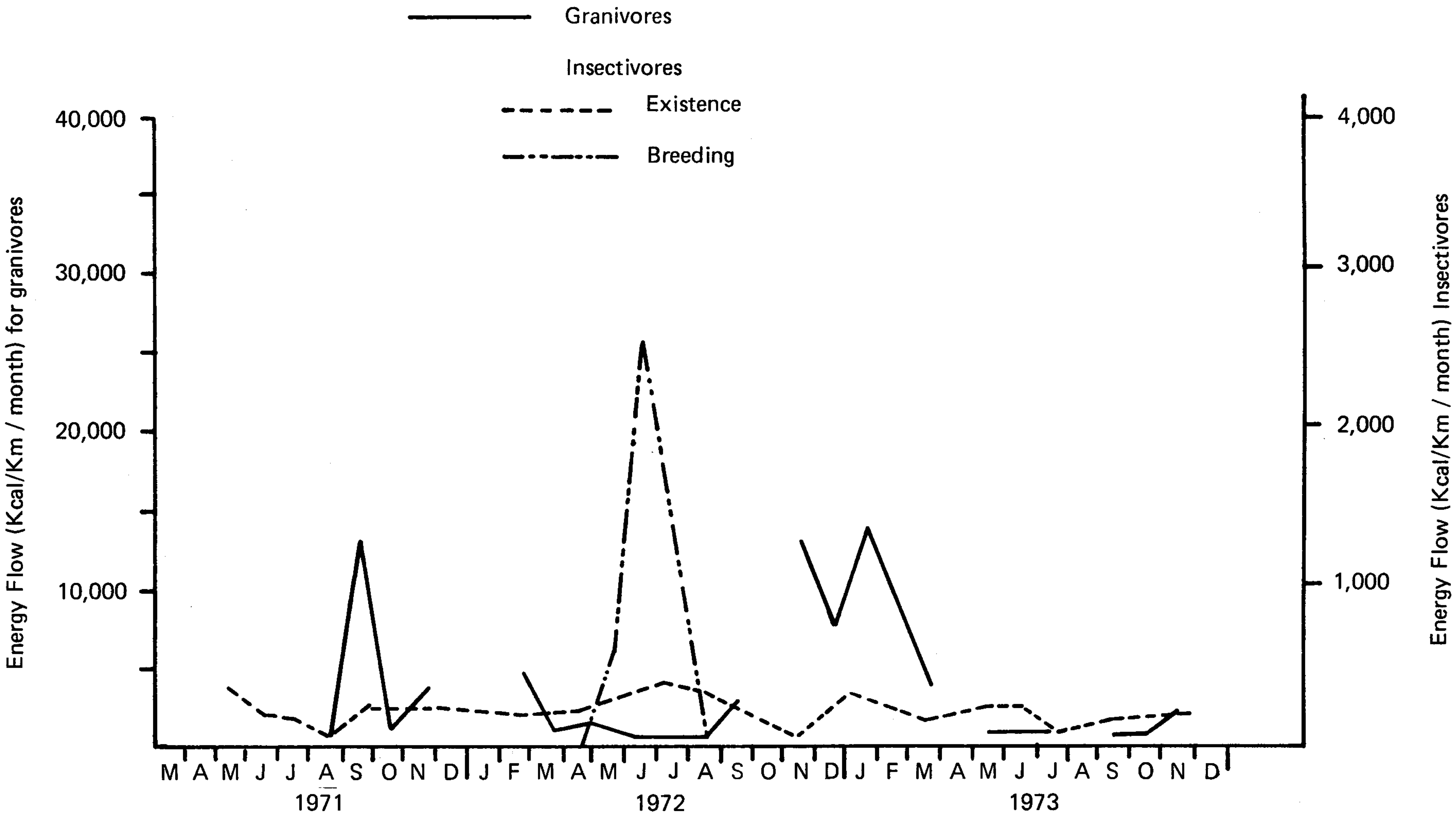

Fig. 52. Energy flow through bird populations on desert grassland plots.

the order of 70%.

With granivores, energy requirements closely follow density trends, peaking in the winter. Insectivore energy requirements are more complex. Non-breeding energy requirements follow the changes in numbers with slight peaks in the summer. However, the amount of energy required for these processes is dwarfed by the energy required for breeding. Only in the most productive year--1972-- was breeding observed on the site and the energy required to rear and produce the new birds was almost equal to the total energy required in the other two years. The data show a pattern repeated more clearly in nearby desert areas of breeding activity occurring only when there is a threshold level of energy flowing through the community. In 1971 and 1973, energy flow through the grassland community seemed insufficient to permit breeding.

Annual consumption by granivores generally follows the same trend from year to year as that of the energy flow (table 77). Both granivore and insectivore consumption were much higher in 1972 than either 1971 or 1973, reflecting high densities of avian populations on the study area in 1972. Averages for the three years showed that granivore consumption was 0.051 g/m^2 compared to 0.0054 for insectivores. Raptor populations were so low (on an area basis) that consumption rates and energy flow were not calculated. It would be much smaller than that for insectivores. Raptor populations apparently are not involved in large transfers of energy or matter in desert grassland ecosystems.

Invertebrates

The invertebrates of the desert grassland represents a diverse

Table 77. Annual consumption (g/m^2) by bird populations on the Jornada.

	1971	1972	1973	Average
Granivores	0.0336	0.0650	0.0550	0.0510
Insectivores	0.0021	0.0104	0.0036	0.0054

community with a wide range of food sources. Trophic level assignments based on known food habits of closely related taxa were made for more than 90% of the invertebrate fauna collected, enabling some basic calculations of invertebrate energy flow and consumption to be made.

Based on population densities and biomass data, calculations of energy flow during the 1970, 1971, and 1972 growing seasons (May 1 to October 31) were made for the following arthropods: Orthoptera, Hymenoptera (Formicidae), Homoptera, Hemiptera (herbivores and predators separately), Coleoptera (phytophagous in general and specifically for Curculionidae, Chrysomelidae, Scarabaeidae, Carabidae, Tenebrionidae), and Araneida. Calculations were made using a computer program adapted from Dr. Robin Andrews (Virginia Polytechnic Institute).

Respiration--A determination of respiration in cal/m^2 was based on the data of Reichle (1971) and Van Hook (1971). First, individual dry weights of adults, $CD(I)_A$, and of larvae, $CD(I)_L$, were converted to wet weights:

$$CD(I)_A \text{ Wet} = CD(I)_{A/.3} \text{ (Van Hook 1971)}$$

$$CD(I)_L \text{ Wet} = CD(I)_{L/.2} \text{ (Shroeder 1973)}$$

Next, respiration, RO_2 in microliters O_2/hour/individual given CD(I) wet weight in milligrams was calculated:

$$RO_2 = 0.339 \times CD(I)^{.808}_{Wet} \text{ (Reichle 1971)}$$

Then, respiration was converted to calories/m^2/60-day period;

$$R = RO^2 \times 1440 \times .0048 \times (CWT/CD(O)) \times CATEX \times 2.0$$

where 1440 converts hourly respiration to days, 0.0048 converts respiration in microliters O_2 to calories, and CWT/CD(I) converts respiration from a per individual basis to a per m^2 basis (CD = mean dry wt per individual and CWT = total wt of individuals). CATEX revises respiration calculations on the basis of a Q_{10} of 2 (Reichle 1971). Mean metabolic temperatures for each month (0.65/max-min) + min) are used in this calculation based on the method of Menhinick (1967) as in Van Hook's (1971) activity factor of 2.

Production--Production was calculated from mean standing crop for each 60-day period,

$$P = CWT \times Kp,$$

where Kp = 5.777, the number of calories available per milligram of arthropod tissue (Reichle 1971).

Energy flow--Energy flow is calculated as the sum of respiration and production,

$$EF = R + P$$

Consumption--Consumption, in calories, was calculated as follows:

$$C_{cal} = (R + P)/CNAEF$$

where C_{cal} is consumption in calories and CNAEF is the assimilation efficiency. Various figures for assimilation efficiencies were either drawn from the literature or estimated as follows: Predators = 0.9 (Van Hook 1971), herbivores = 0.35 (Van Hook 1971, Shroeder 1973, Mitchell and Pfadt 1974), Homoptera = 0.7 (Weigert 1964), ants (omnivores) = 0.6, a value between herbivores and predators, scavengers = 0.3, a value lower than herbivores.

Finally, caloric consumption was converted to grams of food consumed by use of various data available in the literature

$$C_g = C_{cal/Neq}$$

where Neq = 4.0 to 4.7 kcal/g for litter (Van Hook 1971), 4.5 kcal/g for plant sap (Weigert 1964), 5.777 kcal/g for arthropods (Reichle 1971), and 4.8 to 5.0 kcal/g for live plants (Van Hook 1971).

Tables 78 and 79 show calculated invertebrate consumption for three growing seasons at the Jornada desert grassland site. Data for only two-thirds of the 1970 growing season were available, but these were extrapolated over the entire season. The total arthropod population consumed an average of 1/33 g/m^2 on the grazed and ungrazed treatments during the 1970 growing season, while an average of 0.835 g/m^2 was consumed in 1971, and 4.03 g/m^2 was consumed during 1972. These figures generally correlate with primary productivity on the desert grassland which was low in 1971 and higher in both 1970 and 1972. Consumption for 1972 on the grazed treatment may be too high due to the large biomass of scavengers captured on that treatment.

Herbivore consumption during the three years of study was 35% of the total arthropod community consumption on the ungrazed treatment in 1970, 6.6% during 1971, and 27% during 1972. Respective figures for the grazed treatment are 69%, 3.2%, and 18.6%. Omnivores during the three-year period consumed generally 1% or less of the total community consumption, while predator consumption ranged from 2.67% on the ungrazed in 1971 to 11% on the ungrazed in 1972. The data indicate that the scavengers were the most important consumers during the study, especially during 1971, when they consumed 89% and 93.5% of the

Table 78. Consumption (g/m^2) of invertebrates for three growing seasons on grazed (G) and ungrazed (U) treatments.

Group	1970		1971		1972	
	U	G	U	G	U	G
Herbivores	0.47	0.92	0.05	0.03	0.79	0.95
Omnivores	0.01	0.01	0.01	0.01	0.03	0.03
Scavengers	0.78	0.28	0.67	0.86	1.80	3.98
Predators	0.08	0.11	0.02	0.02	0.34	0.14
Total Arthropods	1.34	1.32	0.75	0.92	2.96	5.10

Table 79. Respiration, production, and assimilation (energy flow) for various invertebrate groups on grazed (G) and ungrazed (U) treatments 1970-1972. Units are in cal/m^2 for each growing season.

Group	Respiration		Production		Assimilation	
	U	G	U	G	U	G
Herbivores						
1970	437	803	158	395	595	1198
1971	72	56	28	12	100	68
1972	1739	1715	419	525	2158	2240
Predators						
1970	243	315	80	104	323	419
1971	67	65	22	25	89	90
1972	1363	529	416	183	1779	712
Omnivores						
1970	18	26	3	4	21	30
1971	20	19	5	3	25	22
1972	59	71	11	13	70	84
Scavengers						
1970	480	160	224	94	704	254
1971	526	696	275	336	801	1032
1972	1451	2884	714	1906	2165	4790
Total Arthropods						
1970	1178	1304	465	597	1643	1901
1971	685	836	330	376	1015	1212
1972	4612	5199	1560	2627	6172	7826

total community consumption on the ungrazed and grazed treatments, respectively. These data suggest that during the drought of 1971 the scavengers were less influenced by lowered primary productivity than other consumers.

Consumption by invertebrates on the desert grassland was much lower than that measured by investigators in other grassland situations. Energy flow peaked on the desert grassland on the ungrazed treatment during 1972 at 7.8 kcal/m^2 compared to 69.5 kcal/m^2 on a Tennessee grassland (Van Hook 1971) and 59.2 kcal/m^2 on the old field in South Carolina (Weigert and Evans 1967) for herbivores alone. On the other hand, a few studies have shown much lower energy flows. Weigert (1965) reported an energy flow of 2.51 kcal/m^2 for spittlebugs and grasshoppers in a Michigan old field, while Menhinick (1967) calculated a value of 4.8 kcal/m^2/year for herbivore energy flow in a South Carolina lespedeza stand. Spiders, the most prevalent predaceous species in the desert grassland, showed an energy flow of 1.7 kcal/m^2 for 1972 on the ungrazed treatment compared to 0.32 kcal/m^2 for spiders in Menhinick's (1976) study.

Decomposer Functions

Decomposition was studied by use of two methods, mulch bags and CO_2 evolution. Mulch bags containing a standard bluestem hay provided by Dr. John Harris of Kansas State University were buried in 1970 and removed through April of 1971. These bags were buried at 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, and below 30 cm depths. Figure 53 shows that weight loss of bluestem hay followed the same general trend for all burial depths. Weight changes were generally higher for those bags

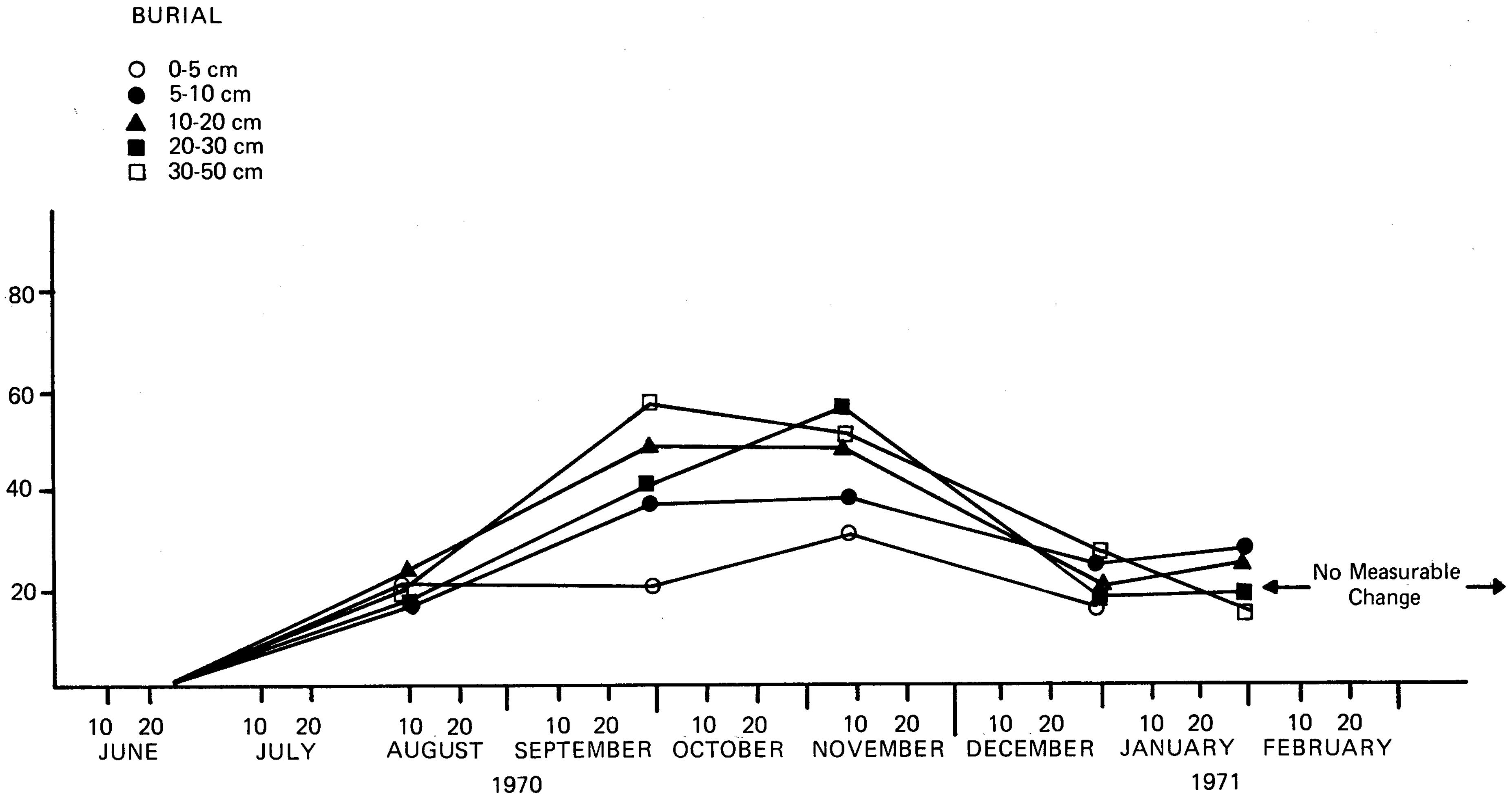

Fig. 53. Weight loss of bluestem hay buried at various depths in 1970 and measured for one year.

buried at the greater depths than for those buried near the surface. For example, hay buried at the 0-5 cm depth had lost only about 20% of the initial weight by October 1, 1971, while those buried at depths below 30 cm lost nearly 60% of the initial weight by the same date. Normally, plant leaves and stems are deposited on the surface and decomposition rates of materials at the 0-5 cm depth would be most representative of aboveground plant mulch.

Weight losses reached the maximum during the period from August through November, and by January measurable changes had ceased. These data indicated that decomposition rates lagged somewhat behind plant growth for the same period and were sustained much later into the fall than was primary productivity. Apparently soil temperatures were high enough to support microbial activity as late as November.

Weight losses of bluestem hay (figure 54) buried in 1971 were also higher in mulch bags buried at depths greater than 20 cm than for those buried at the 5-10 cm depth. Highest weight losses were observed in September for the deeper depths and in late July for the shallow depths.

Other substrates were used including filter paper and native black grama. Weight losses of filter paper were dependent upon the time the filter paper was introduced into the soil. Filter paper buried on June 21, 1970 lost nearly 75% of the original weight within 50 days while that buried shortly after July 1, 1970 lost 70% of the original weight within 70 days (figure 54).

Black grama plant material, buried at 10 and 20 cm depths in 1971, exhibited no reduction in weight during May, June, or July of that year (figure 55). However, following the first rain of the season in late

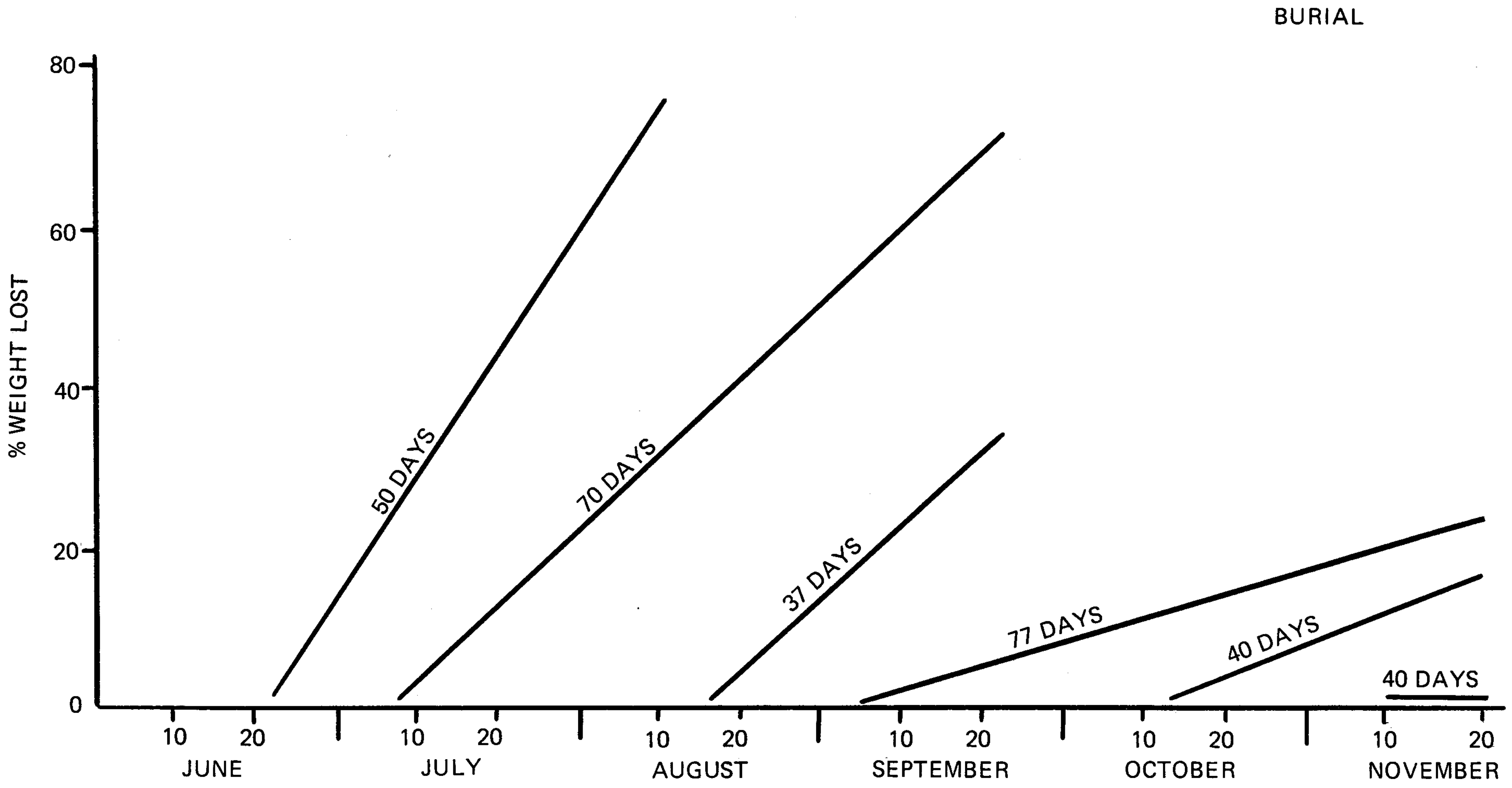

Fig. 54. Rates of filter paper weight loss when buried 5-10 cm in Jornada soil, 1970.

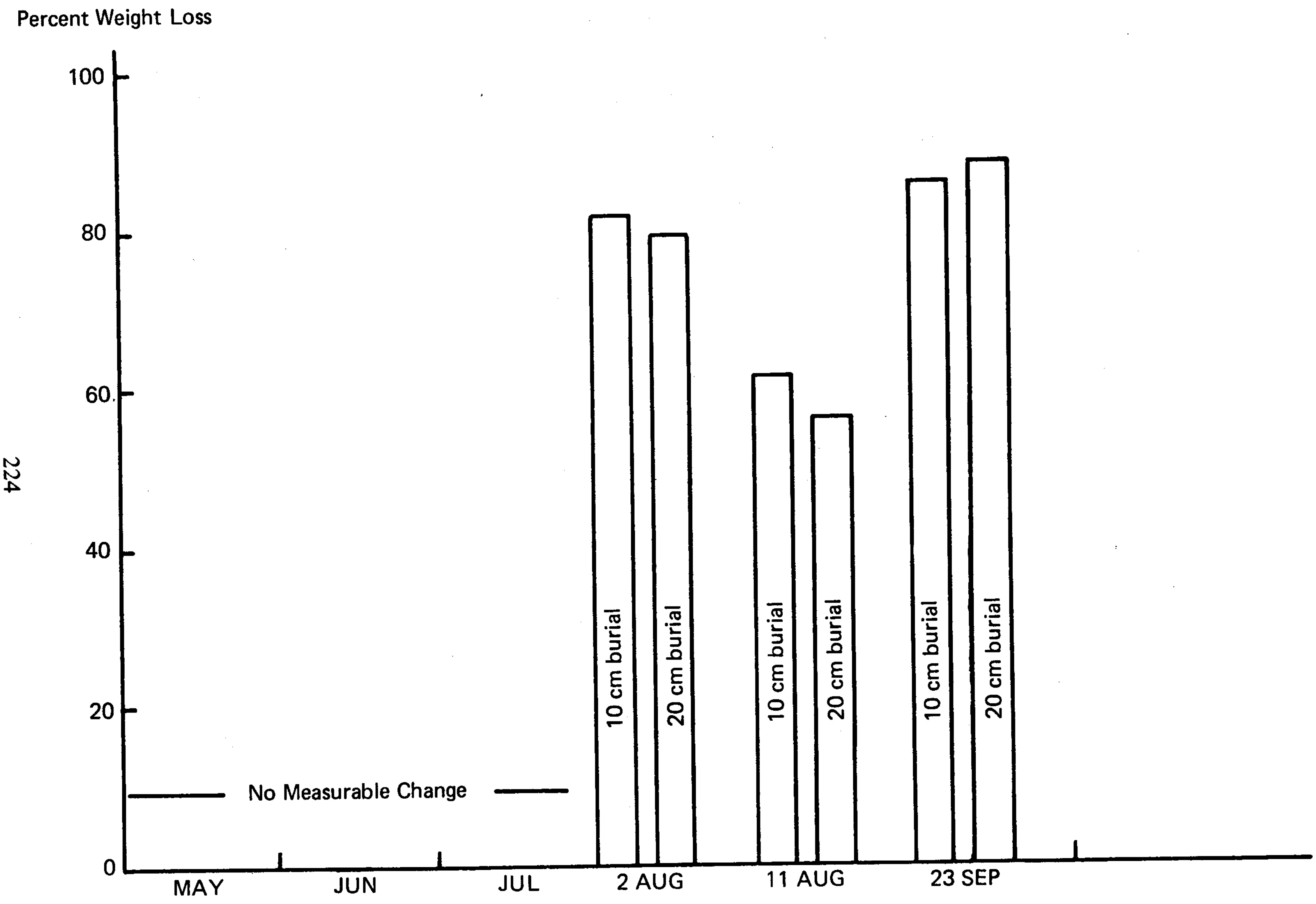

Fig. 55. Weight loss of black grama hay buried in Jornada soil on April 1971.

July, decomposition rates increased very rapidly and continued through September. Apparently, when soil water is available weight loss from organic material is very rapid during the summer months. These data exhibited only slight differences in weight between litter bags buried at different depths. The differences between depths was not consistent for the different dates when the litter bags were removed and weighed.

The mulch-bag technique presented some problems for determining decomposition rates under desert grassland conditions. Observations indicated that some of the mulch bags were influenced by termites. Termite species were not determined, nor were the termite population density or biomass determined in the quick-trapping procedure. Observations indicated that termite consumption of plant mulch might have been as much as actual microbial decomposition.

The technique involving measurement of CO_2 evolution eliminated some of the problems encountered in the mulch-bag technique. CO_2 evolution data for 1972 indicated substantial variation in CO_2 evolution during the growing season (figure 56). Maximum CO_2 evolution of 1.25 g $CO_2/m^2/day$ was measured during the period of June 6 to 14. By the week of July 7 to 11, CO_2 evolution had declined to less than 0.2 g CO_2 m^2/day. Early in August CO_2 evolution was elevated again but declined to early November. CO_2 evolution rates as high as 0.7 $g/m^2/day$ were measured during 1972. This is considerably lower than minimum net primary productivity of 2.4 $g/m^2/day$ reported earlier in the section.

The 1971 season was exceptionally dry during the major portion of the growing season, and decomposition was rapid during short intervals following periods of rainfall. During 1972, greater amounts of

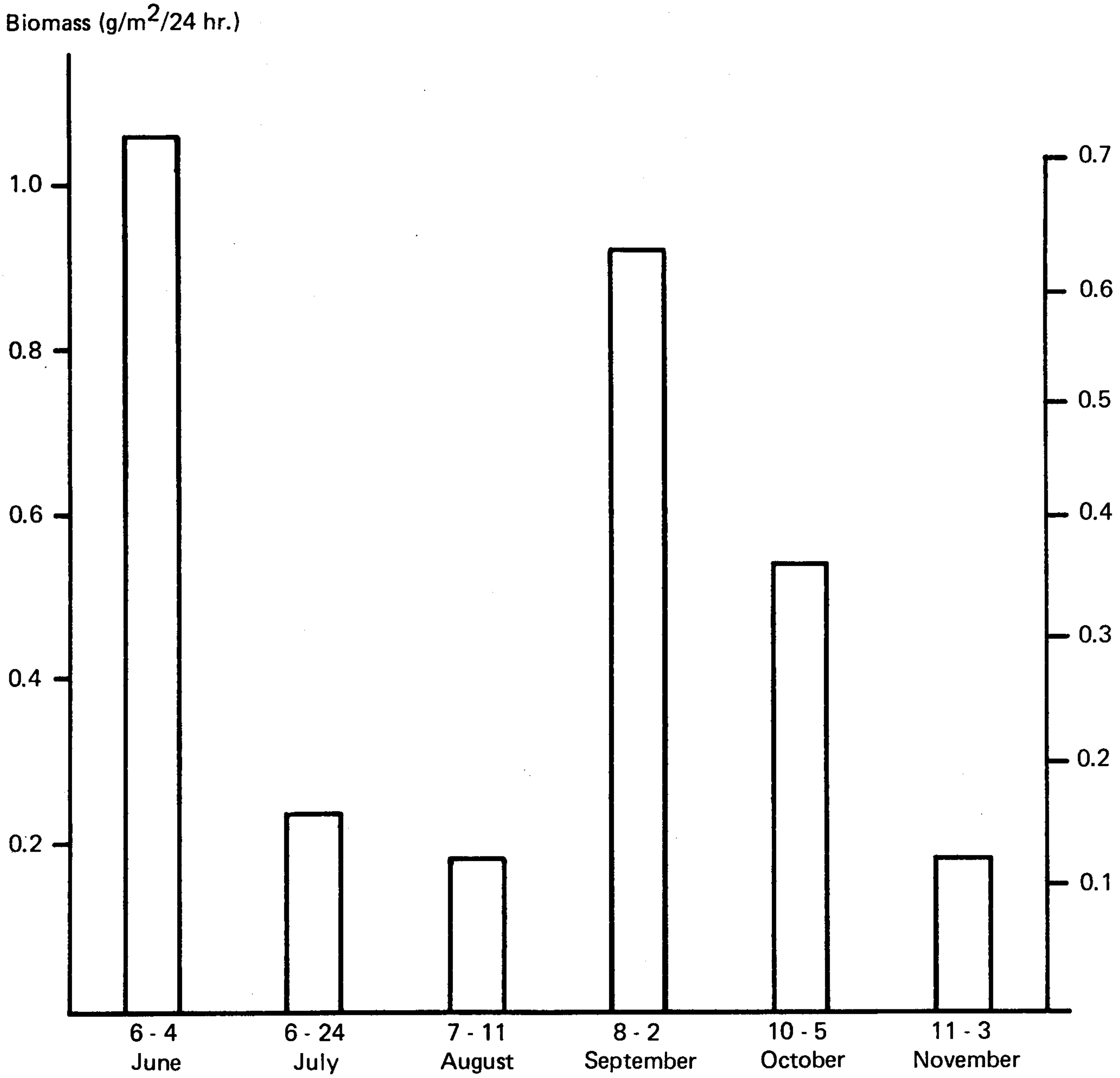

Fig. 56. CO_2 evolution measured during the summer and fall of 1972 at the Jornada IBP site.

precipitation induced much more decomposition than was measured in 1971. Observations on both filter paper and plant material in litter bags exhibited losses followed by gains in weight during dry periods.

Other field and laboratory observations indicated that microorganisms carrying on the decomposition process produced the greatest amounts of CO_2 that were evolved in this study. Substantial losses in mulch bag weight were associated with termite tunnels and encrustments which were found on the bags. It was assumed that substantial amounts of the plant materials were removed by termites and in some instances the bulk of the weight loss in mulch bags was due to this activity.

The factors that were found to be closely related to the decomposition process on the Jornada site in 1973 are summarized in table 80. Grass stems appeared to be primarily decomposed by microbes, and little termite activity was observed, while root losses were primarily induced by termite activity and very little microbial activity was measured. Highest microbial activity was measured in the plant materials taken to the field in May followed by July and least in February. Termite acitivity was highest in materials placed in the field in July and was followed by the May and finally the February placed material. The mean loss of the July placed material was 27.7% due to termite removal, and this value could be higher if the leaching values used were overestimated.

Conducting CO_2 evolution studies concurrently with and on the same materials as the weight loss determinations was essential in this experimentation. Where weight determinations or CO_2 evolution measurements

Table 80. Factors influencing the decomposition process of plant materials on the Jornada Grassland Site, 1973.

Plant Material	A CO_2 Evolved (%)	B Weight Loss (%)	C = B - A Difference	Precipitation Throughfall	D Soak Loss (%)	E = C - D Termite Removal (%)
Leaf						
February	5.4	3.0	-2.4	2.9	7.7	--
May	22.5	56.0	33.5	2.9	7.7	25.8
July	15.3	61.0	45.7	2.9	7.7	38.0
Stem						
February	6.0	16.0	10.0	2.9	8.5	1.5
May	22.8	27.0	4.2	2.9	8.5	--
July	9.6	23.9	13.4	2.9	8.5	4.9
Crown						
February	2.4	15.0	12.6	4.3	10.2	2.4
May	10.5	30.0	19.5	4.3	10.2	9.3
July	5.4	46.5	41.1	4.3	10.2	30.9
Root						
February	1.8	34.0	32.2	4.0	8.5	23.7
May	4.2	45.0	40.8	4.0	8.5	32.3
July	1.5	45.0	43.5	4.0	8.5	35.0

were made in 1970, 1971, and 1972, this information could be an over or under evaluation of what actually occurred. Until more multiple measurements are utilized, vague and incomplete conclusions will be drawn.

COMPARTMENT MODEL: SYSTEM-LEVEL COMPARISONS

Transfer from Plants to Animals: Herbivory

Desert grassland herbivores actually consumed a very small proportion of the total aboveground net primary productivity (table 81). Cattle consumed the greatest amount of plant biomass followed by rodents. These two groups of herbivores were the only groups consuming more than 1 g/m^2 of plant biomass. Consumption by invertebrates sampled averaged only 0.4 g/m^2 annually for the three years. These estimates of invertebrate consumption underestimated actual consumption considerably. However, even if invertebrate consumption exceeded these calculated rates by several orders of magnitude, their consumption would still not be large in relation to aboveground net primary productivity. Consumption by rabbits, pronghorn antelope, and birds was small, less than 0.1 g/m^2 annually. Data for pronghorn and rabbits were estimates but probably reflect general trends.

For the three years of the study, consumption by all herbivores was only 6.1 g/m^2 compared with aboveground net primary productivity of 148 g/m^2 (table 81). In addition, many of the consumer groups are somewhat selective feeders. For example, many birds and rodents are seed eaters. Unfortunately, the net primary production represented by reproductive structures was not measured.

In much of the range science literature herbage utilization figures as high as 60% to 80% are common (Stoddart, Smith, and Box 1975; Heady 1975). These figures are considerably higher than those calculated for the IBP desert grassland site. However, most utilization figures are

Table 81. Aboveground net primary production and consumption (g/m^2) by various herbivore groups.

Item	1970	1971	1972	AVG
Anpp	134.0	125.0	186.0	148.0
Pronghorn antelope	0.1	0.1	0.1	0.1
Cattle	5.0	4.4	3.4	4.3
Rodent	2.6	0.7	0.6	1.3
Rabbit	0.01	0.01	0.01	0.01
Invertebrates	0.5	0.05	0.8	0.4
Birds	0.5	0.03	0.07	0.05
Total all herbivores	8.3	5.3	4.9	6.1

Table 82. Annual consumption by carnivore groups (g/m^2).

Carnivore Group	3-year Average Consumption ($g\ m^2$)
Predaceous invertebrates	0.147
Small mammals	0.810
Coyotes	0.0193
Insectivorous birds	0.005
Total	0.981

reported on "Key" perennial grass species which reflect only a portion of net primary productivity. In addition, most range studies have underestimated net aboveground primary productivity since only end-of-season standing crop is reported (Pieper et al. 1974).

The relatively low herbivore consumption reported here agrees with the summary of Lewis (1971) from all the IBP grassland sites. Apparently, aboveground herbivory accounts for only a small percentage of total plant material across the grasslands, even those grazed by domestic livestock.

Transfer from Animals to Animals: Carnivory

Data in table 82 indicated that consumption by small rodents was highest among the carnivore groups for which consumption was measured, followed by invertebrates, coyotes, and birds in descending order. This listing is not complete since many groups present on the site were not included. Calculations were not included for raptors, mammalia, carnivores other than coyotes and rodents, reptiles, etc. It is difficult to estimate how much the total of less than 1 g/m^2 annual consumption by carivores in table 82 underestimates actual consumption by all carnivores on the site.

Energy Flow Through Desert Grassland Ecosystem

A compartmental model for energy transfers is shown in figure 57 for the three years of data for the IBP desert grassland ecosystem. Values shown by the arrows represent energy flows from one compartment to another in $kcal/m^2$. Values in the boxes represent annual

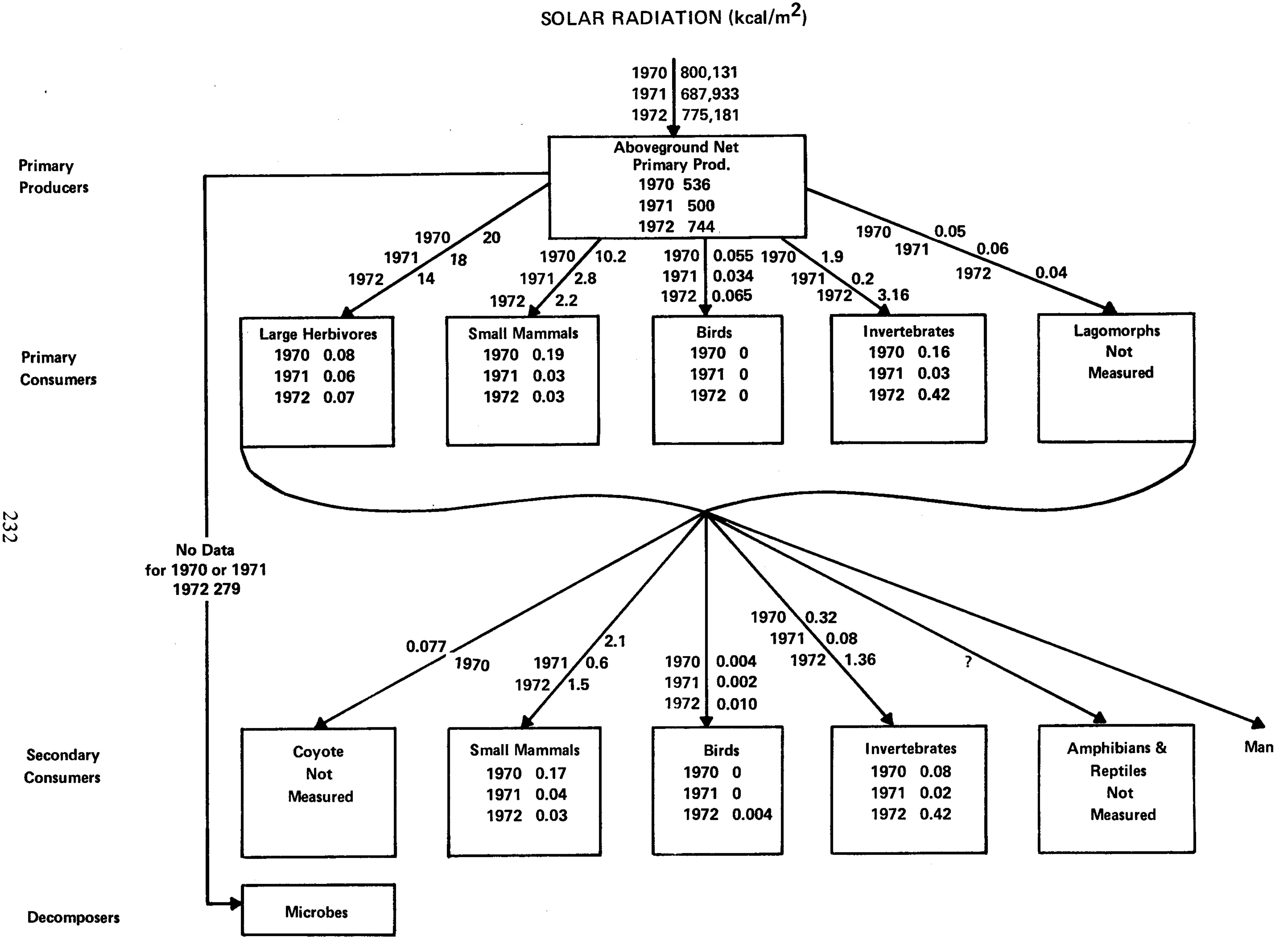

Fig. 57. Compartmental model showing energy flow among trophic levels for the desert grassland ecosystem. All values are kcal m^{-2}. Figures on arrows represent transfer rates while those in boxes represent productivity.

productivity for that particular compartment.

Only a small portion of the energy captured by plants is transferred to the herbivores shown in figure 57. During the three-year period, ANPP averaged 593 kcal/m^2 while only 24 kcal were transferred to herbivores. Cattle were the major herbivores with an average consumption of 17 kcal/m^2 followed by small mammals and invertebrates. Transfer to birds and rabbits represented less than 1 kcal/m^2.

The fact that herbivores are responsible for only a relatively small turnover of primary production in desert grassland is not surprising considering data from other studies. For example, Soholt (1973) estimated that Mojave Desert Merriam kangaroo rat populations consumed only 96 megacalories per hectare annually from an annual aboveground net primary production of over 1200 megacalories per hectare (table 83). However, the rat population consumed 98% of the net primary production of *Erodium cicutarium* fruits. Therefore, in terms of its food resources, the rat populations were exploiting them very efficiently (Soholt 1973).

Unfortunately, data for seed production on the desert grassland IBP site are not available. Studies on grassland playa of the Desert Biome about 4 miles from the desert grassland site indicated that production of reproductive parts of herbaceous species was less than 5 g/m^2 annually. Consumption rates of 2.6 g/m^2/yr in 1970 (table 81) by small mammals would mean utilization of over 50% of the available food resources.

Other studies with grassland invertebrates also show that these groups consume only a small percentage of net primary production. Van

Table 83. Total net primary production, net seed production, and consumption by Meriam's kangaroo rat in southern California (from Soholt 1973).

Species	Biomass Produced (kg/ha^{1} yr)	NPP Total (Mcal/ha yr)	NPP Fruit (Mcal/ha/yr)	Seed Consumption by Kangaroo (Mcal/ha^{1}/yr)
Bouteloua barbata	63.0	259.1	77.9	4.9
Erodium cicutarium	40.8	168.1	74.4	72.8
Eriophyllum spp.	38.6	169.4	22.5	0.0
Chaenactis fremonti	20.5	80.5	17.8	3.9
Eriogonum spp.	7.4	30.3	6.6	0.0
Other annuals	54.0	174.6	Not determined	14.8
Total annuals	224.3	882.2	--	96.4
Shrubs	69.9	338.8	3.2	0.0
Total, all species	294.2	1221.0	--	96.4

Hook (1971) reported that orthopteran herbivores consumed 112 kcal/m^2 yearly and omnivores only 9.6 kcal/m^2 yearly in eastern Tennessee grasslands where annual net aboveground primary production was 1274 kcal/m^2. Again, there was no measure of food resources available for each invertebrate group.

Wiens (1973) calculated consumption rates for avian populations from several IBP grassland sites. Consumption on these sites was greater than on the desert grassland, but still represented only a small fraction of net aboveground primary production (table 81 and figures 57, 58). Many grassland birds are granivorous and put additional pressures on plant reproductive parts.

Data on plant decomposition are available for 1972 only. As determined by CO_2 evolution, 279 kcal/m^2 of plant energy were released by decomposer organisms. Total intake by herbivores was only 19.5 kcal/m^2 for the year, leaving 465 kcal/m^2 not accounted for by consumption or decomposition. Undoubtedly there is some lag effect between net primary production and decomposition. Probably some of the 1972 accumulation of mulch was decomposed in 1973 as well as 1972. Much more detailed analysis is necessary to complete an annual budget and to account for all the energy. According to standing crop data (figure 50, table 52) about 480 kcal/m^2 of litter disappeared during 1972. This amount is greater than that calculated from the CO_2 data and nearly equals ANPP for the previous year.

Among the secondary consumers or carnivores, energy flow was greatest to small mammals followed by invertebrates and birds (figure 57). However, no measurement was made for reptiles and amphibians.

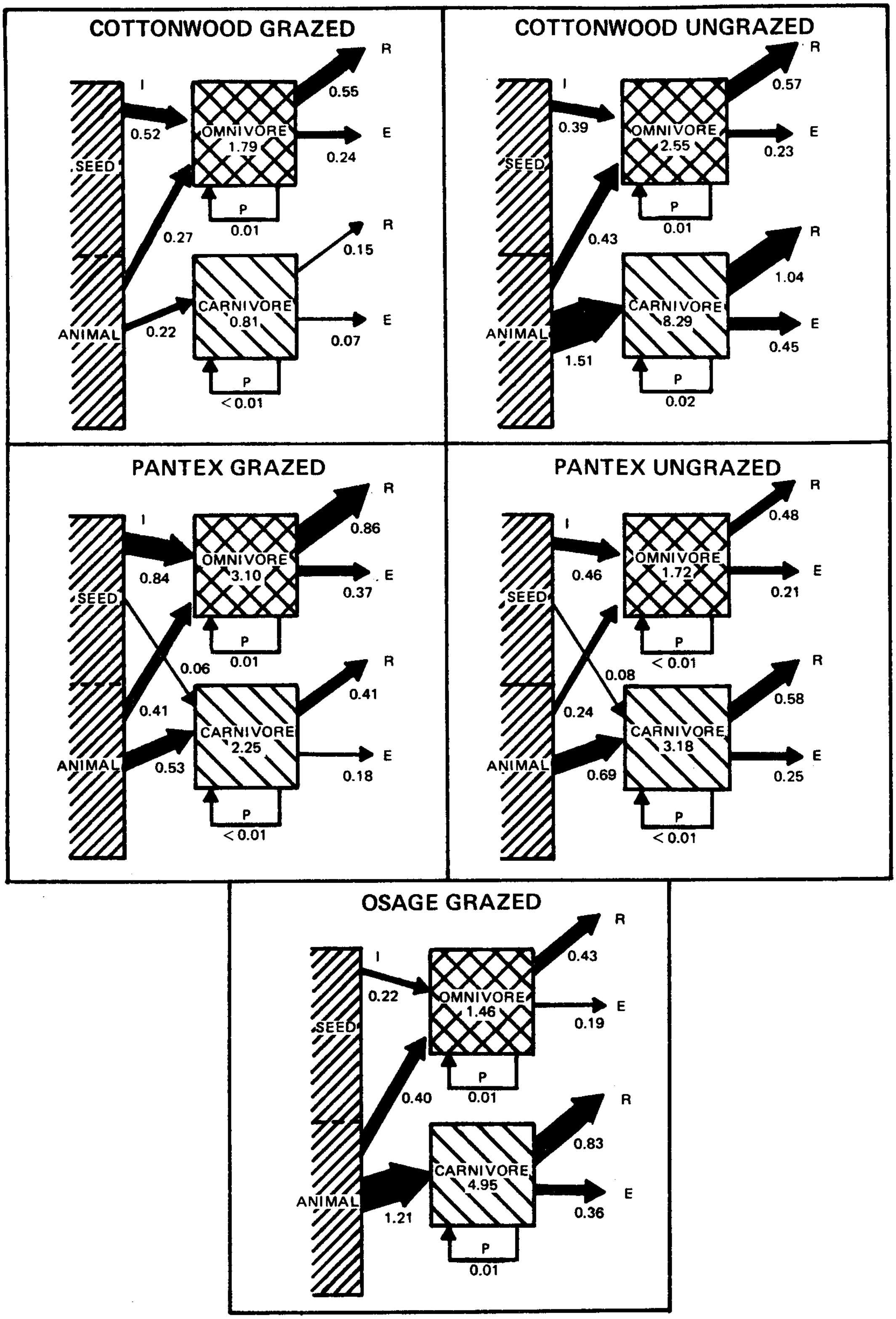

Fig. 58. Compartmental diagrams of patterns and magnitudes of estimated energy flow through breeding bird populations at five grassland plots from April 1 to August 31, 1970. Values are kilocalories per suqare meter per season. I = intake, P = production, R = respiration, E = excretion or egestion. Values in omnivore and carnivore compartments are standing crops X days, calculated from wet weight values, assuming a caloric value of 2.8 kcal/g wet weight. (From Wiens 1973).

Observations on the site indicated that reptiles and amphibians may have been quite important, especially during 1972. Lack of such data is a serious deficiency in the present studies (table 84). Most of the efficiencies reported by Soholt (1973) show efficiencies below 1 for small mammal populations. Exceptionally high efficiencies were reported by Soholt (1973) for Merriam kangaroo rat populations in the Mojave Desert. Chew and Chew (1970) also reported efficiencies of 1.2 for Sonoran Desert populations of Merriam's kangaroo rats. All the efficiencies shown in table 84 were not calculated in the same manner. For example, Golley (1960) used above- and belowground plant biomass to calculate net primary productivity while Soholt used only aboveground biomass.

In 1970, small mammal efficiency at the desert grassland site was higher than that reported by Chew and Chew (1970) for small populations in Southern Arizona. Soholt (1973) offered no explanation for the relatively high efficiencies of desert small mammal populations.

Interpretations based on consumption of total net primary productivity may be misleading for drawing conclusions on exploitation of food resources by herbivores. Several studies have shown that small mammal populations utilize more than 10% of the available production (table 84). Such data have led some workers to conclude that most small mammal populations are not food limited (Slobodkin, Smith, and Hairston 1967 and Wiegert and Owen 1971). However, Soholt (1973) reported that Merriam kangaroo rat populations utilized over 95% of the available food resources in his study.

Productivity by the various carnivorous groups was also very low.

Table 84. Consumption (I_p) of net primary production (NPP) and available production (AP) by several different small mammal populations (from Soholt 1973).

Species	I_p	NPP (Mcal/ha/yr)	AP	I_p/NPP (%)	I_p/AP (%)	Source
Dipodomys merriami	96.4	1.400	900	6.9	10.7	Soholt 1973
Dipodomys merriami	69.8	5,700	710	1.2	9.8	Chew and Chew 1970
Lepus californicus and *Sylvilagus audobonii*	28.1	5,700	2,260	0.1	2.0	Chew and Chew 1970
Omychomys torridus	0.8	5,700	710	--	0.1	Chew and Chew 1970
Peromyscus eremicus and *P. maniculatus*	6.5	5,700	965	--	0.7	Chew and Chew 1970
Ammospermophilus harrisii and *Spermophilus spilosoma*	1.1	5,700	1,201	--	0.1	Chew and Chew 1970
Perognathus spp. and *Reithrodontomys megalotis*	2.7	5,700	710	--	0.4	Chew and Chew 1970
Neotoma lepida	1.8	5,700	2,302	--	0.1	Chew and Chew 1970
Peromyscus polionotus	74.4	10,000	750	0.7	10.0	Odum et al. 1962
Microtus pennsylvanicus	250.0	59,500	15,800	0.5	1.6	Golley 1960
Citellus tridecemlineatus	56.0	13,600	--	0.4	--	Wiegert and Evans 1967
Peromyscus spp.	10.5	13,600	--	0.1	--	Wiegert and Evans 1967
Pitymys subterraneus and *Microtus agrestis*	76.0	7,400	7,400	1.0	1.0	Grodzinski et al. 1966
Clethrionomys rutilus	47.6	10,232	480	0.6	9.9	Grodzinski et al. 1966
Tamiasciurus hudsonicus	59.9	10,232	455	0.6	13.2	Grodzinski et al. 1966
Microtus oeconomus	24.6	10,232	660	0.2	3.7	Grodzinski et al. 1966
Glaucomys sabrinus	10.2	10,232	455	0.1	2.2	Grodzinski et al. 1966

However, in 1972 invertebrate productivity was 0.42 kcal/m^2. Data for birds do not include raptors, but this group would probably not add much because of their low density.

Ecological Efficiencies

Although efficiencies have been calculated by several approaches (Kozlovsky 1968) and have different meanings, they are useful for comparative purposes. The efficiencies in table 85 were calculated as the ecological efficiency EE4-0 (Kozlovsky 1968) and denoted by $\frac{NPn}{In}$ where I = ingestion (consumption) and NP = net productivity. The large herbivore group was the only one with efficiencies greater than 3% for the study period (table 85). Efficiency of small mammals in 1970 was equal to that of the large herbivores in 1972, but less than 1 for the three years. Average efficiency for all herbivores was only 4.3 for the study period (table 85).

Efficiencies for the small mammal population on the desert IBP site were well within the range of those reported from a number of studies. In desert and desert grassland situations, herbivores need a broad selection of food types to meet fluctuating availability of food sources. Such detailed studies of the food habits and availability of different food resources have not been made for the desert grassland IBP site.

Efficiencies for individual secondary consumers have not been calculated because of lack of information on specific food sources for these groups.

Table 85. Efficiency (consumption/NPP x 100) of transfer from primary producers to herbivores on desert grassland.

Herbivore Group	1970	1971	1972	Average
Large herbivores	3.7	3.6	1.9	3.1
Small mammals	1.9	0.6	0.3	0.9
Lagomorphs	>0.1	>0.1	>0.1	>0.1
Birds	>0.1	>0.1	>0.1	>0.1
Invertebrates	0.4	<0.1	0.4	0.3
All herbivores	6.0	4.2	2.6	4.3

DESERT GRASSLAND ADAPTATION OF ELM MODEL

The widespread use of computers in science has allowed the implementation of a large variety of models in which a number of basic approaches can be used. These approaches may be structural or dynamic. Both are used in this volume to demonstrate the structure, function and utilization of a desert grassland ecosystem. Structural models are more traditional; they may include word models, graphic models, and statistical models.

A written or verbal organization (word model) of thoughts and concepts often aids the organization of information available. Most scientific papers in biology consist of word models that describe a theory, process, relationship, or condition. The word model may also serve as a first step toward the implementation of graphic or other models.

Graphic models may take many forms, but the principal objective of all is to illustrate relationship(s) in various degrees of complexity. Histograms and frequency distributions illustrate simple relationships, while polygonal graphs, multidimentional graphs, and others illustrate more complex relationships. Flow diagrams are used in this volume to represent the flow of some element (carbon, nitrogen, energy, etc.) throughout the component of the system (figure 59). With this representation, the boxes represent the system components (state variables) considered, and the arrows represent material flows from one component to another. Later diagrams will also utilize dotted lines for information flows, bowties ($\underline{\bar{X}}$) to symbolize control points on flows, and arcs (⌢) for sources of external information. These symbols follow

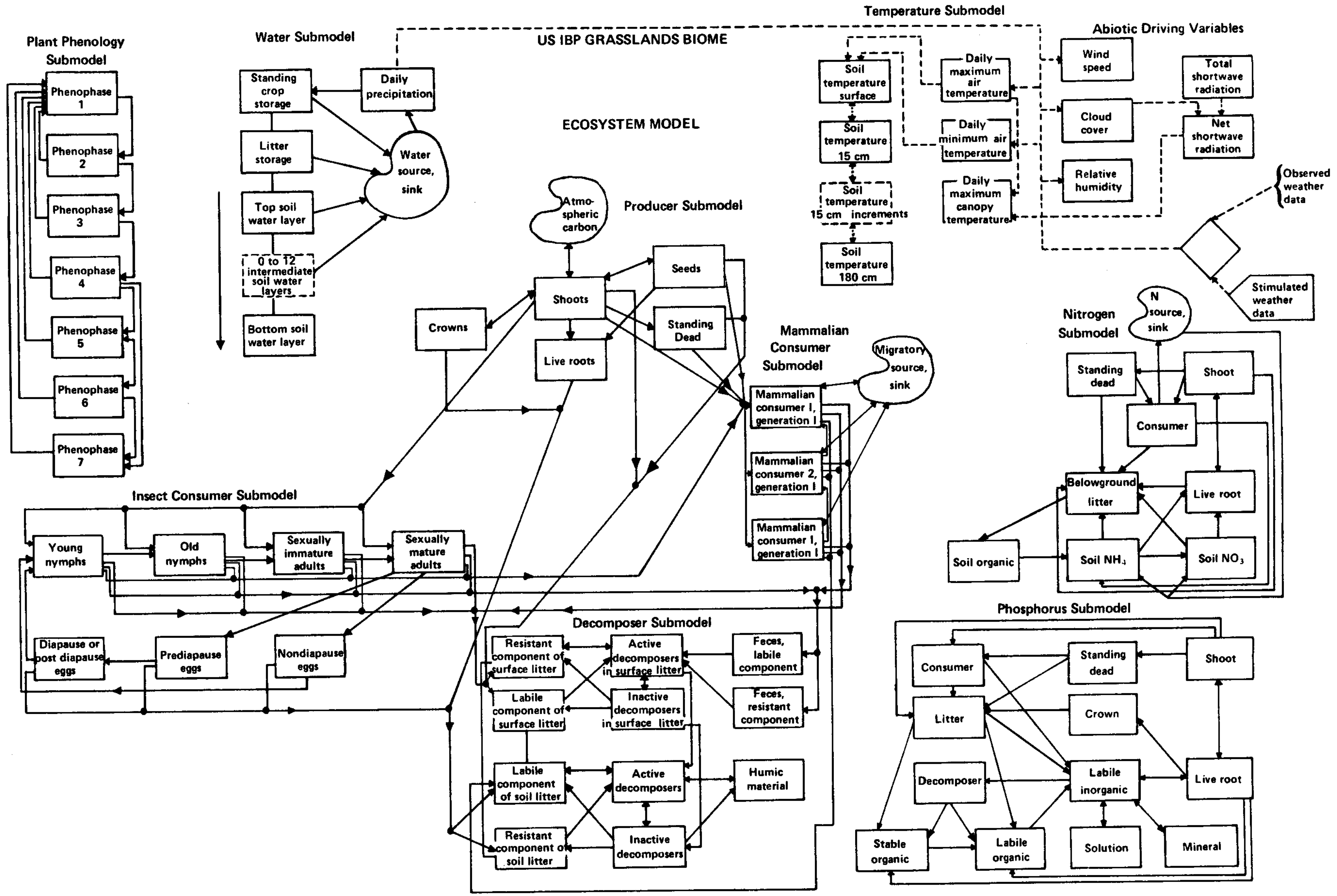

Fig. 59. Carbon flow sections of the ELM model.

those of Forrester (1961).

Statistical models generally are concerned with experimental design (i.e., analysis of variance) or prediction (i.e., multiple nonlinear regression analysis). They may serve as an end in themselves or may be used to derive parameters and equations and to structure simulation models.

Dynamic Simulation Models

Models may be deterministic or stochastic; their design may be mechanistic or empirical. Empirical implies the model outputs are based on observed, experimental data and involve the mathematical derivation of outputs via regression function, for example, whether they represent the biological process or not. Mechanical models presuppose that natural processes can be mechanistically defined at some level of resolution and are capable of explanation by the laws of biology through mathematical representation. A stochastic model involves variables that may take on any one of a specified set of values with a specified probability of occurrence at each point in time. A deterministic model yields one and only one set of unique outputs for any one set of input values.

In general, empirical models are more typical of the biological sciences; mechanistic models are more characteristic of the engineering and physical sciences.

Models may be developed for predictive or descriptive purposes. A predictive model must only produce accurate predictions of the output variables in the system. In this case the modeler is not concerned that the relationships employed in the model to generate the predicted output conform with the mechanisms in the real system which lead to the same outputs. In contrast, descriptive models must not only generate predictions in agreement with real system output, but the intermediate relationships employed in the model must also be realistic representations of the real processes influencing the observed results.

The dynamic simulation model (ELM) utilized in this study is deterministic and predictive. The principal objective in developing it was to reflect and predict, as a total system, the biomass dynamics for a grassland in a model that is representative of the sites in the US/IBP Grassland Biome network and with which there can be relatively easy interaction.

The term total system is used in the sense that each of the abiotic, producer, consumer, and decomposer sections of the system is represented. (A total system model is all-encompassing without being all-inclusive.) The term biomass dynamics identifies the principal concern as carbon flow (or energy flow) within the system. Flows of nutrients and water are important but are not the principal concern. Representative indicates that the model is valid, provided that it can predict the direction and order of magnitude of the response of the system to certain perturbations, as well as predict the "normal" dynamics. Finally, the relatively easy interaction is to assure that teams of modelers and biologists can decide which major changes in the system they wish to study, implement the changes in the model, and get results from the computer run in a few hours. We have interpreted this to mean that once the biological input has been decided upon, we should be able to run the model and get input within 30 minutes.

The objective serves to specify the direction of the effort, but it is still too general to provide a basis for a number of the decisions that have to be made in the development of a model. For a basis for these decisions, the following six specific questions were chosen as points to be addressed in the ELM model:

1. What is the effect on net or gross primary production as a result of the perturbations: (i) variations in the level and type of herbivory, (ii) variations in the precipitation or applied moisture and temperatures, and (iii) variations in added nitrogen or phosphorus?
2. How is the carrying capacity of a grassland affected by these perturbations?
3. Are the results of an appropriately driven model run consistent with field data taken in the Grassland Biome program? If not, why not?
4. What are the changes in the composition of the producers as a result of these changes in driving variables.
5. What are the qualitative differences in primary production between grassland sites and how are they affected by these changes in driving variables?

This model addresses perturbations of a "reasonable" sort, that is, those common to grasslands. It also addresses perturbations of an "unreasonable" sort, by which is meant those variations occurring once in decades, such as drought.

Table 86 provides a general overview or major interconnections

Table 86. Some of the major control functions that operate within ELM.

Section	Variable	Control or Process
Consumer	Consumer biomass	Consumption rate (herbiviores, omnivores and carnivores)
		Litter accumulation rate (feces and cripping)
		Nutrient cycling (urine)
		Population dynamics (mortality and natality)
Decomposer	Decomposer biomass	Nutrient availability
		Litter decomposition rate
		Belowground decomposition rate
Nutrient	Soil available nutrients	Nutrient uptake by plants
	Live plant nutrient	Translocation
		Photosynthesis
		Phenology
		Consumption by herbivores
	Litter nutrient	Litter decompositon rate
	Belowground dead matter nutrient	Belowground decomposition rate
Abiotic	Soil water	Photosynthesis rate (Producer section)
		Soil heat flow (Abiotic section)
		Nutrient uptake rate (Nutrient Section)
		Decomposition rate (Decomposer section)
		Phenological progression (Producer section)
		Translocation (Producer section)
		Death rate (Producer section)
	Soil temperature	Photosynthesis rate
		Phenological progression
		Translocation
		Nutrient uptake rate
		Decomposition rate
Producer	Aboveground live	Photosynthesis
		Death rate
		Translocation
		Soil surface temperature
		Soil surface water
		Soil water flow
		Consumption by herbivores
		Nutrient uptake rates
	Belowground live	Translocation
		Nutrient uptake
		Nutrient availability
		Soil heat flow
		Soil water flow
		Root death rate
	Standing dead	Litter accumulation rate
		Soil surface water
		Soil surface temperature
		Consumption by herbivores
		Photosynthesis rate (shading)
	Litter	Soil surface temperature
		Soil surface water
		Consumption by herbivores
		Litter decomposition rate

between compartments. In this table, the first column shows the section of the model in which the variables defined in the second column are modeled as state variables. The third column entitled "Control or Process" lists some of the state variables and flows which are directly affected by the variable of column 2. While this table does not purport to show all of these interactions, it does list some of the more important ones and does provide the reader with some idea of the extent of the interactions and control variable ties among the many compartments that occur within ELM. This model is reported in Technical Report ELM 73 and in a number of other publications (Anway 1978, Cole et al. 1977, Hunt 1977, Parton 1975, Rodell 1977, Sauer 1977, Reuss and Innis 1977).

In its current form ELM consists of approximately 180 state variables. Changes of these state variables with time are described by difference equations rather than differential equations (Innis 1972), and these difference equations are solved using the SIMCOMP compiler (Gustafson and Innis 1972). There are approximately 3000 parameters and other variables within conditions under which a given model run is to operate (e.g., an abiotic regime or grazing treatment) and to communicate between model segments. Because of the numerous feedback mechanisms within and between submodels, the model has a stability that is identifiable with the stability of a real biological system. If parameters are appropriately set, then the stable system of the model is recognizable as the biological system that it purports to represent. If parameters are appropriately chosen or scaled, the system still tends to stabilize, but in a condition that is not recognizable.

The large number of parameters and other variables within ELM is designed to provide it with the capability of being adapted via simple parameter changes to a wide variety of grassland ecosystem types, including the desert grassland version which this volume includes.

Climatic Factors: Word Model and Box and Arrow Diagram

A simplified precipitation model is shown in figure 60. This diagram, taken from the ELM model, depicts three possible pathways for rainfall entering a desert grassland ecosystem: It may be intercepted by standing vegetation or litter, or it may fall on bare soil (Anway et al. 1972). Most of the rainfall intercepted by standing vegetation is evaporated back into the atmosphere. Rainfall striking bare ground may be lost as runoff or infiltration into the soil. Since many grassland sites are relatively level, runoff was not considered in the ELM model and this is the case for the Jornada grassland site. Water that infiltrates may also be evaporated from the bare soil, as depicted in figure 56. Some of the water striking bare soil or litter percolates into the soil profile where it may be taken up by plant roots and transpired. The total evapotranspiration potential is great for desert grasslands because there is little moisture in the air, temperatures are high, and wind velocities may be high, especially during the spring. Consequently, many desert grassland plant species have evolved mechanisms, such as thickened epidermis, low density of stomatas, etc., which serve to reduce transpiration stress (McCleary 1968).

The model in figure 60 shows soil depth of only 30 cm, the maximum depth at the jornada IBP grassland site to the restrictive catena layer. Many desert grassland soils have deeper profiles, and these could be

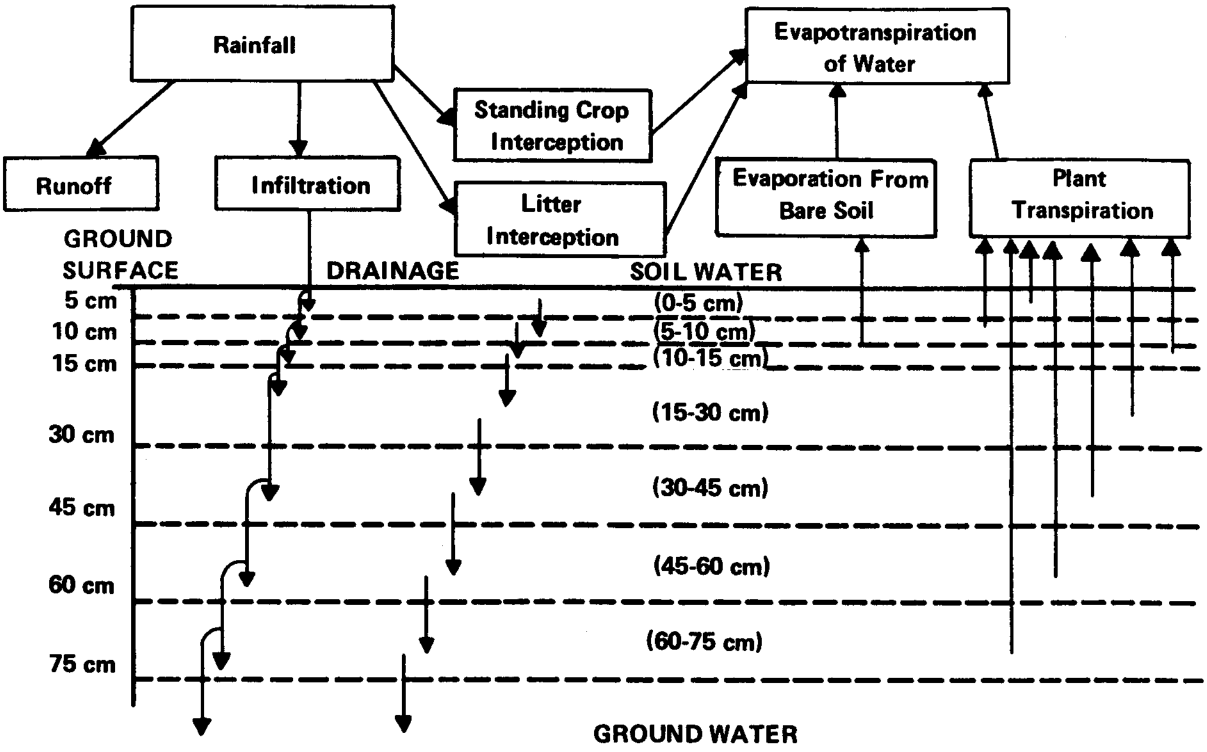

Fig. 60. Diagram depicting water movement in desert grassland ecosystem. Adapted from ELM model. (from Anway et al. 1973)

shown in the diagram by utilizing additional soil layers.

The ELM model also has a heat distribution submodel based primarily on air and soil temperatures and solar radiation (Anway et al. 1972). The heat distribution submodel and the water flow model interact extensively.

Simulation Model: Producer Submodel

This submodel considers carbon and phenological dynamics of the primary producers in the grassland ecosystems. The five ecological categories of primary producers simulated in the Jornada version of ELM were warm-season perennial grass, represented as *Bouteloua eripoda* and *Sporobolous flexuous*; cool-season annual forb, represented as *Dithyrea wislizeni*; warm-season annual forb, represented as *Salsola kali* var. *tenuifolia*; and a shrub category, represented as *Xanthocephalum sarothrae*, these species are the principal contributors to biomass within these categories.

The carbon submodel simulates the dynamics of the following state variables for each species or group: live shoots, standing dead shoots, live roots, seeds, and crowns (figure 61). In addition, litter and dead root variables are simulated for all producer species combined.

The processes simulated are gross photosynthesis, shoot respiration, shoot to crown translocation, shoot death, crown death, root respiration, root death, seed growth, seed germination, and the fall of standing dead to litter.

The phenology submodel simulates qualitative information on the producer species. It is used to regulate seasonal activity of the

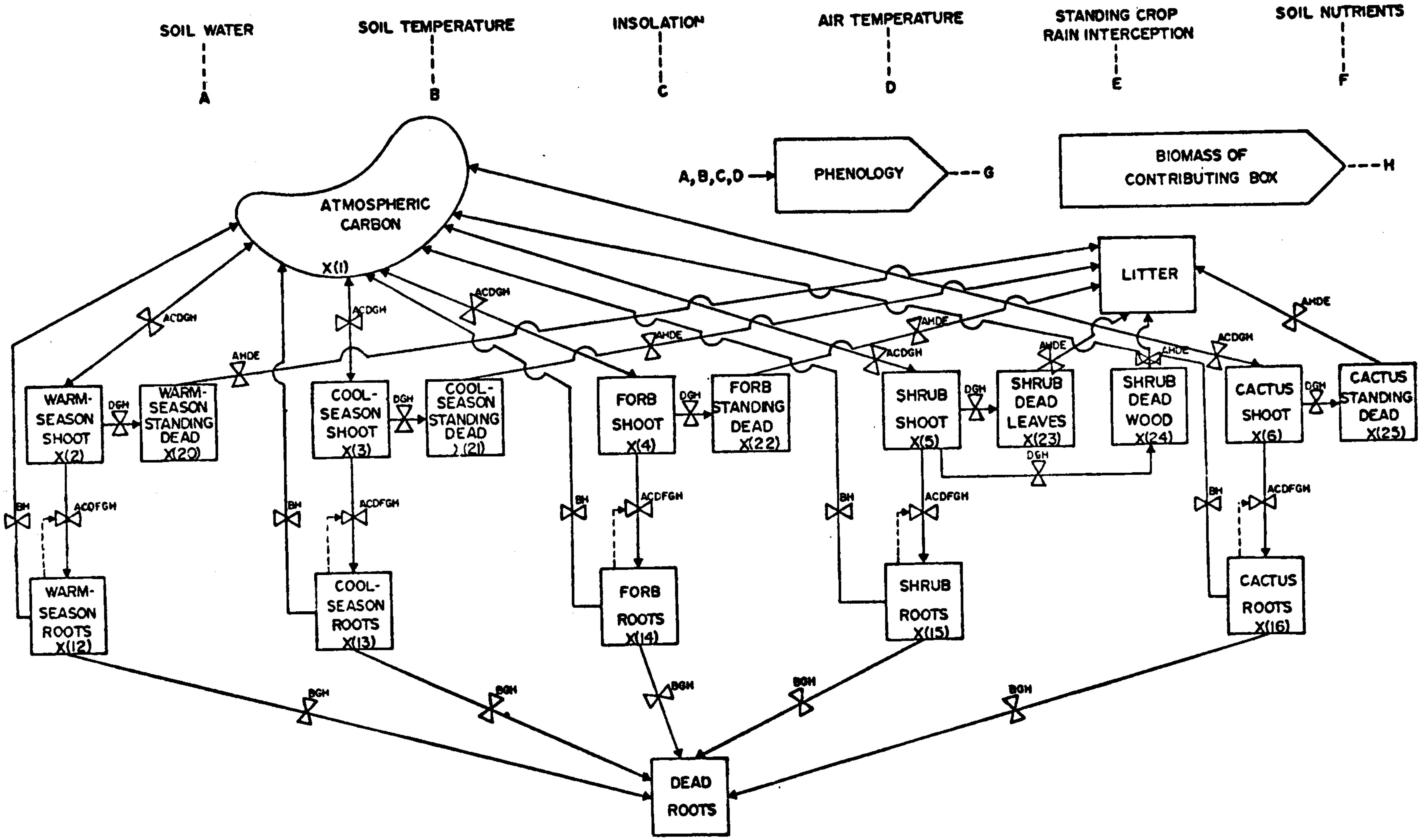

Fig. 61. Box and arrow diagram of the producer section.

producer species. Seven phenological stages are simulated. These include winter dormancy and early vegetative growth through flowering and fruiting and then through senescence.

The progression of phenophases is regulated by maximum air temperature, insolation, soil water potential, soil temperature, and day length. The biomass of the model species may be distributed or proportioned through several phenophases simultaneously. As this distribution changes, so does the mean phenophase of that species.

The processes shown in figure 61, such as photosynthesis, translocation, etc., are under the control of the abiotic driving variables shown. The individual transfers or processes and their controls are shown in figure 61.

The control variables and their alphabetic symbol are shown at the top of figure 61. Their points of impact on flows or transfers are represented by the letters being present at a flow control point symbolized as a $\underline{\bar{X}}$. The control variables include: the driving variables (A-F) = soil water, soil temperature, insolation, air temperature, standing crop, rain interception, and soil nutrients; phenology (G); and biomass of contributing state variable (H).

Simulation Model: Decomposer Submodel

The decomposer submodel (Hunt 1975) is designed to simulate dynamics of litter, dead roots, and decomposer biomass. Substrates are considered to have varying proportions of a rapidly decomposing component and a slowly decomposing component. The decomposition rate of the two components is influenced by temperature, water tension, and the concentration of the inorganic nitrogen. Rate parameters control the influence of these factors at the surface and per each soil stratum as well as between rapid and slow components. The decomposer biomass is simulated in its entirety as one group, rather than consider the great variety of microbial and invertebrate species actually involved. Figure 62 illustrates the flows and state variables for decomposers in feces, surface litter, and the three belowground layers considered.

Simulation Model: Invertebrate Submodel

The invertebrate submodel (Rodell 1977) simulates a primary consumer whose dynamics depend on and/or influence the dynamics of producers, other consumers, and decomposers. In turn, it is also influenced by abiotic driving variables. One major objective is to consider what effect invertebrates have on the functioning of the total system. An additional objective is to use the model as a means for estimating the energy flow via invertebrates through the ecosystem. In the invertebrate submodel daily air temperature and moisture conditions are important factors and have a direct influence on the flows involving forage intake, litter production, and life cycle phenomena (hatching, development, sexual maturation, egg laying, and mortality). The invertebrate submodel also simulates the flow from live shoots to litter because of damage by insects. Figure 63 illustrates the principal flows within the invertebrate submodel.

Simulation Model: Mammal Submodel

The mammalian submodel considers relationships and functions common

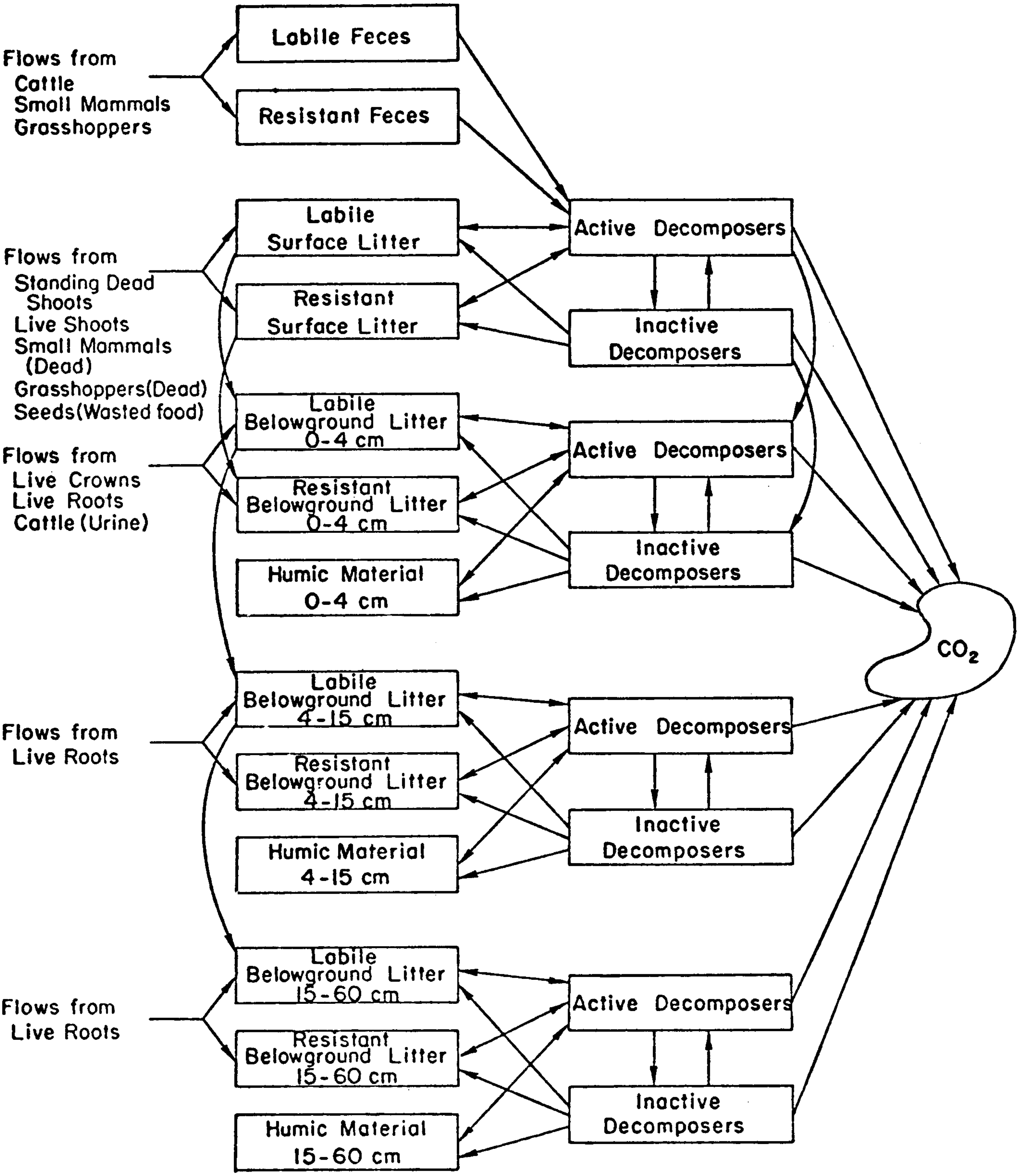

Fig. 62. Decomposer section of ELM model.

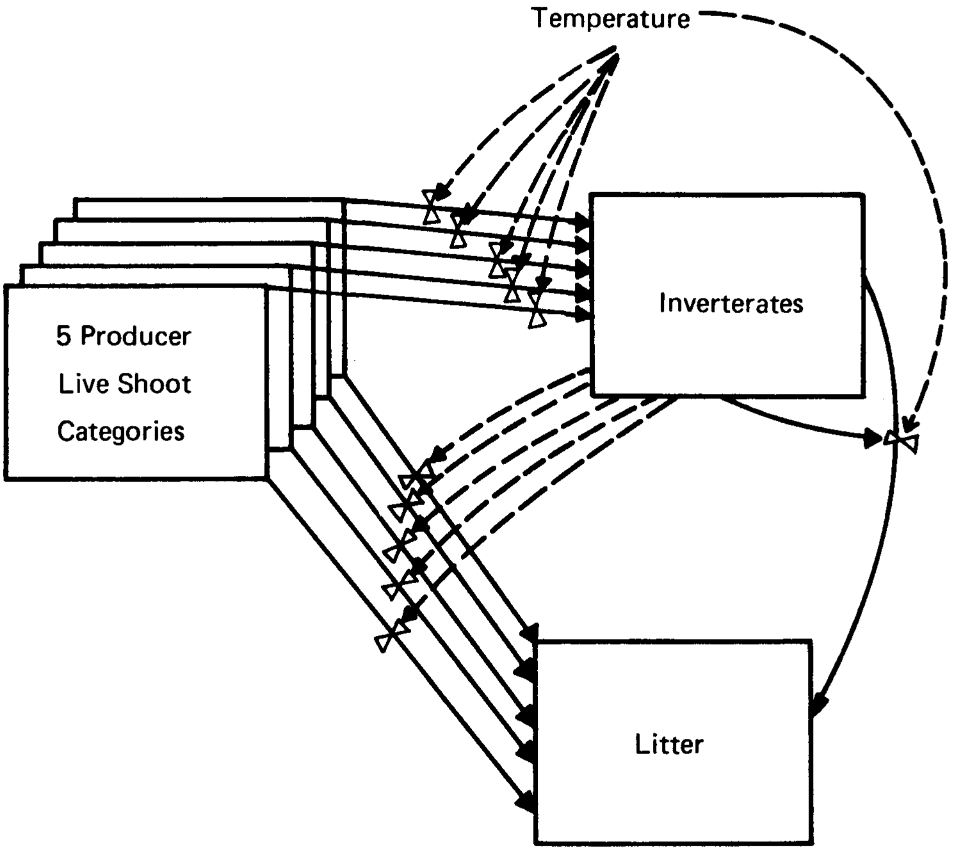

Fig. 63. Principal flows and controls in the invertebrate submodel

to all mammalian consumers as well as the interconnections of that consumer with the other parts of the system (figure 64).

The model incorporates the assumption that two principal processes through which mammal consumers affect grasslands are food intake and animal products. The principal control on these processes is metabolism or energy balance that is influenced in turn by air temperature, animal weight, wastes, activity, reproductive state, population density, animal phenology, hunger, potential intake amount, food availability or accessibility, preference, and digestibility of foods.

The driving variables for this submodel include temperature, plant phenology, external controls on cattle grazing, and food category biomass.

Eight mammals were chosen as representative of the mammalian portion of the system. These eight were *Bos taurus* (cattle), *Antilocapra americana* (antelope), *Canis latrans* (coyote), *Lepus californicus* (jack rabbit, considered as representing all rabbits), *Dipodomys ordii* (Ord's kangaroo rat), *Dipodomys spectatilus* (spectacled kangaroo rat), *Spermaphilis spilosoma* (spotted ground squirrel), and *Perognathus* sp. (all pocket mice). Thus, we have represented large and small herbivores, omnivores, and one carnivore. The food arrays utilized are appropriate for these categories, and each flow is under the controls mentioned above. The calculation block in the upper portion of figure 63 is to indicate that all calculations for each consumer are considered via the same functions, utilizing differing parameters to control simulation response to its appropriate category.

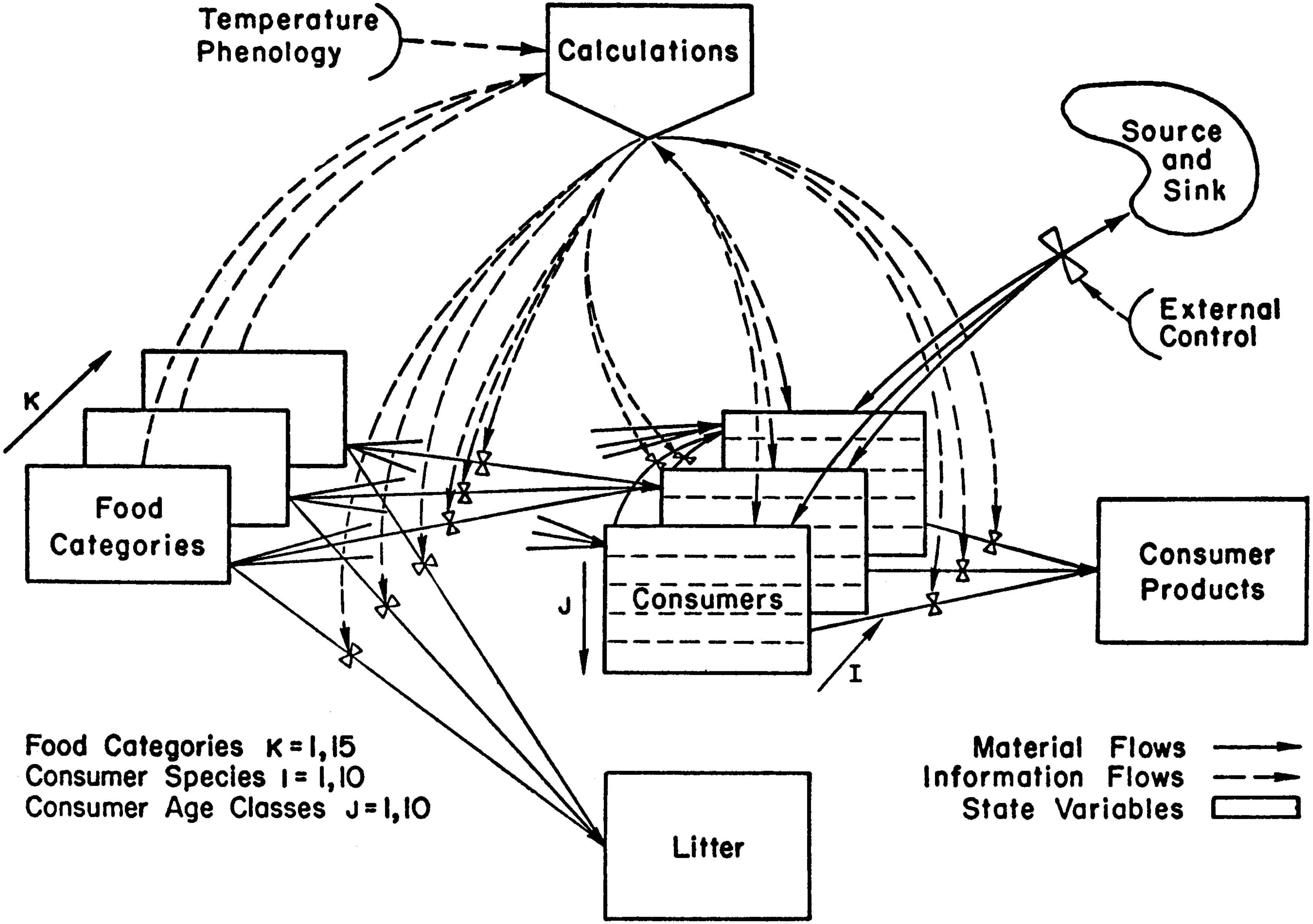

Fig. 64. Flow diagram for mammalian consumers ⟶ = material flows, - - → = information flows, ⋈ = control points ▭ = state variables where food categories may have up to 15, consumers up to 10.

Tuning the Model

Primary Producers

Parameters were adjusted with 1970 and 1971 data to provide the best fit possible. Abiotic data from the study area were used to generate the curves shown in figures 65 through 69 and were compared to actual field data. For black grama the ELM curve showed a lower biomass peak than field data in 1970 and a higher value in 1971 (figure 65). Apparently, soil water characteristics of the desert grassland site were enough different from the Pawnee site where the model was developed that further tuning was not possible. Curves for Leatherweed croton, representing warm season, perennial forbs fit most of field data confidence intervals very well (figure 66). Likewise for spectaclepod, a cool season perennial forb, the ELM model output agreed very closely with field data, except for early in 1970 (figure 67). For broom snakeweed the data agree very well for 1970, but not for 1971 (figure 68). Most of the broom snakeweed plants were seedlings which might not have reached the size of mature plants in 1971. Also, many mature plants died during 1970 and snakeweed density was lower in 1971 than 1970.

Data for Russian thistle agree fairly well except for some data points during both springs (figure 69).

Apparently the ELM model can be adjusted to field data for some groups of primary producers, but not so well for others.

Small Mammals

The model followed the general trend of biomass for most species

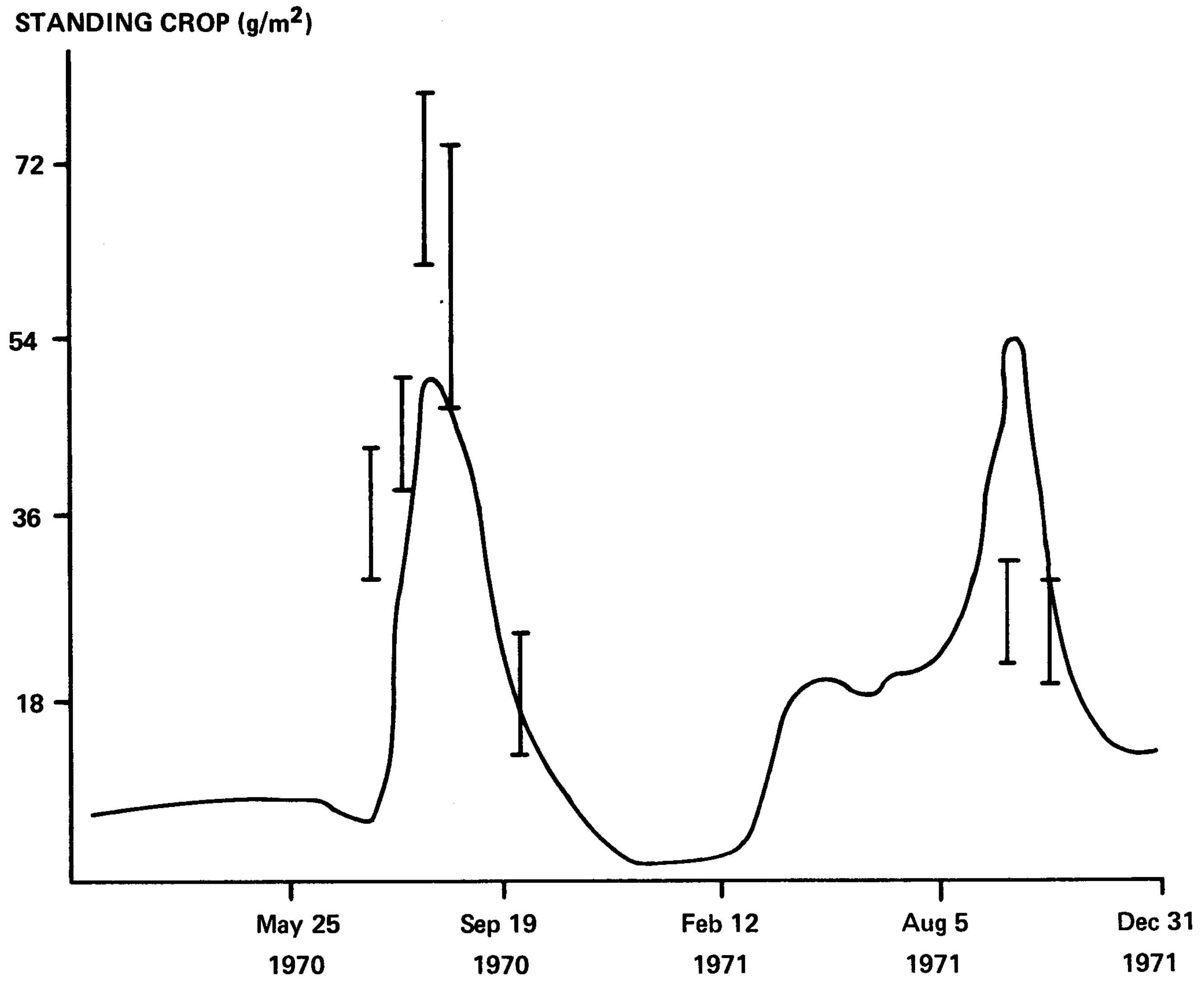

Fig. 65. Seasonal changes in black grama live standing crip derived from the ELM model. Vertical bars represent 95% confidence intervals for field sample means.

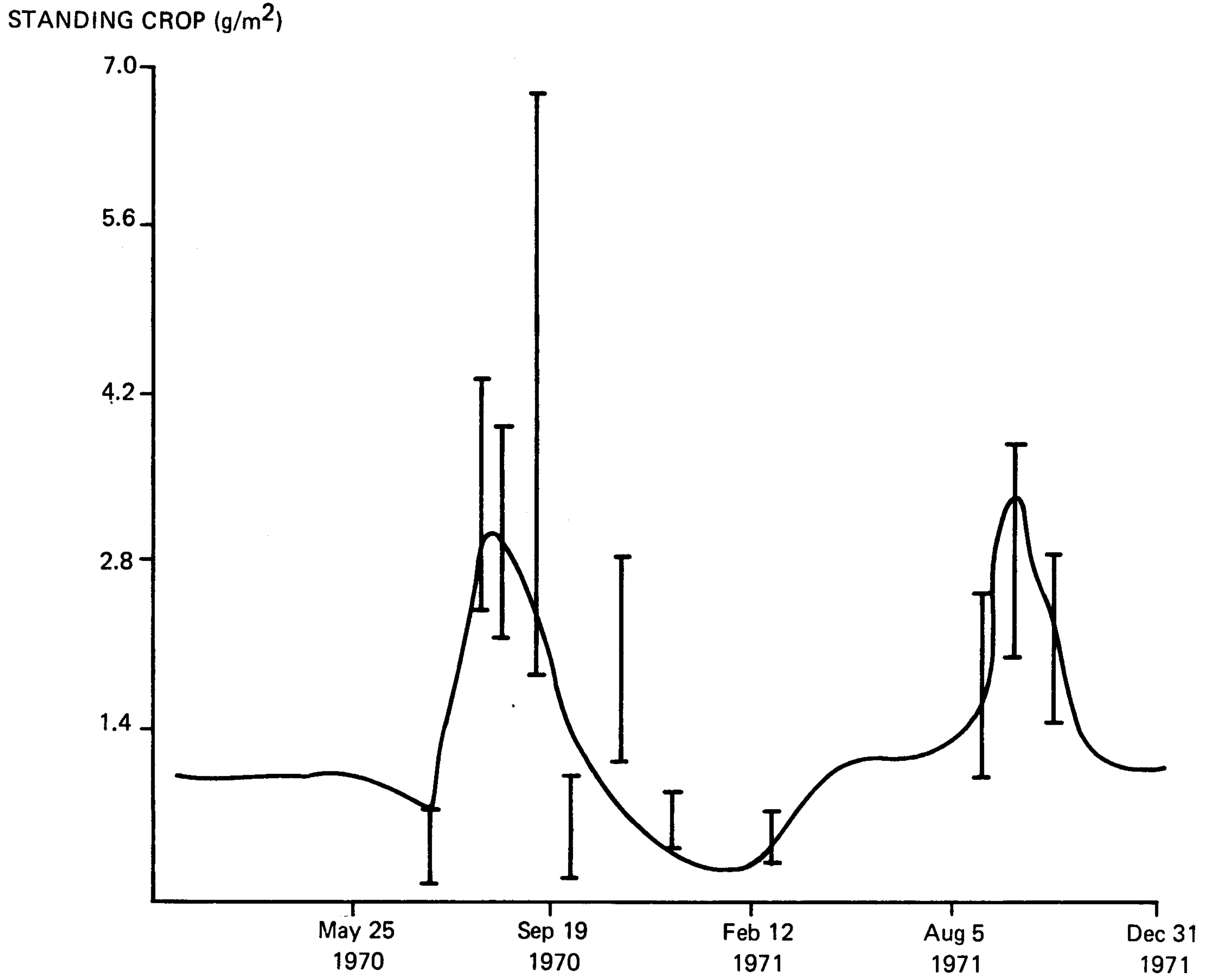

Fig. 66. Seasonal changes in live leatherweed croton standing crop derived from ELM model. Vertical bars represent 95% confidence intervlas intervals for field sample means.

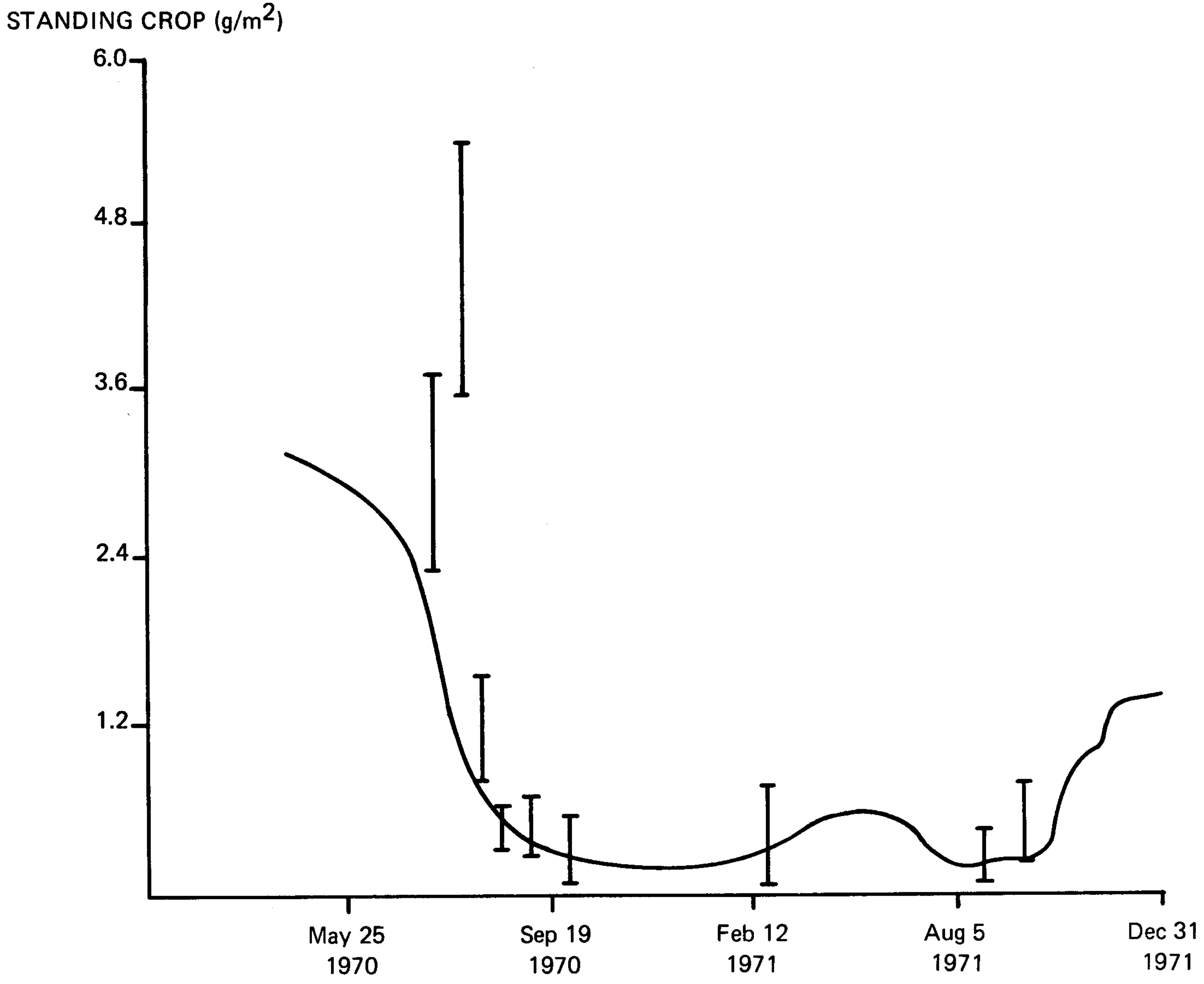

Fig. 67. Seasonal changes in live standing crop spectaclepod biomass for 1970 and 1971 derived from the ELM model. Vertical lines represent 95% confident intervals for means of sample data.

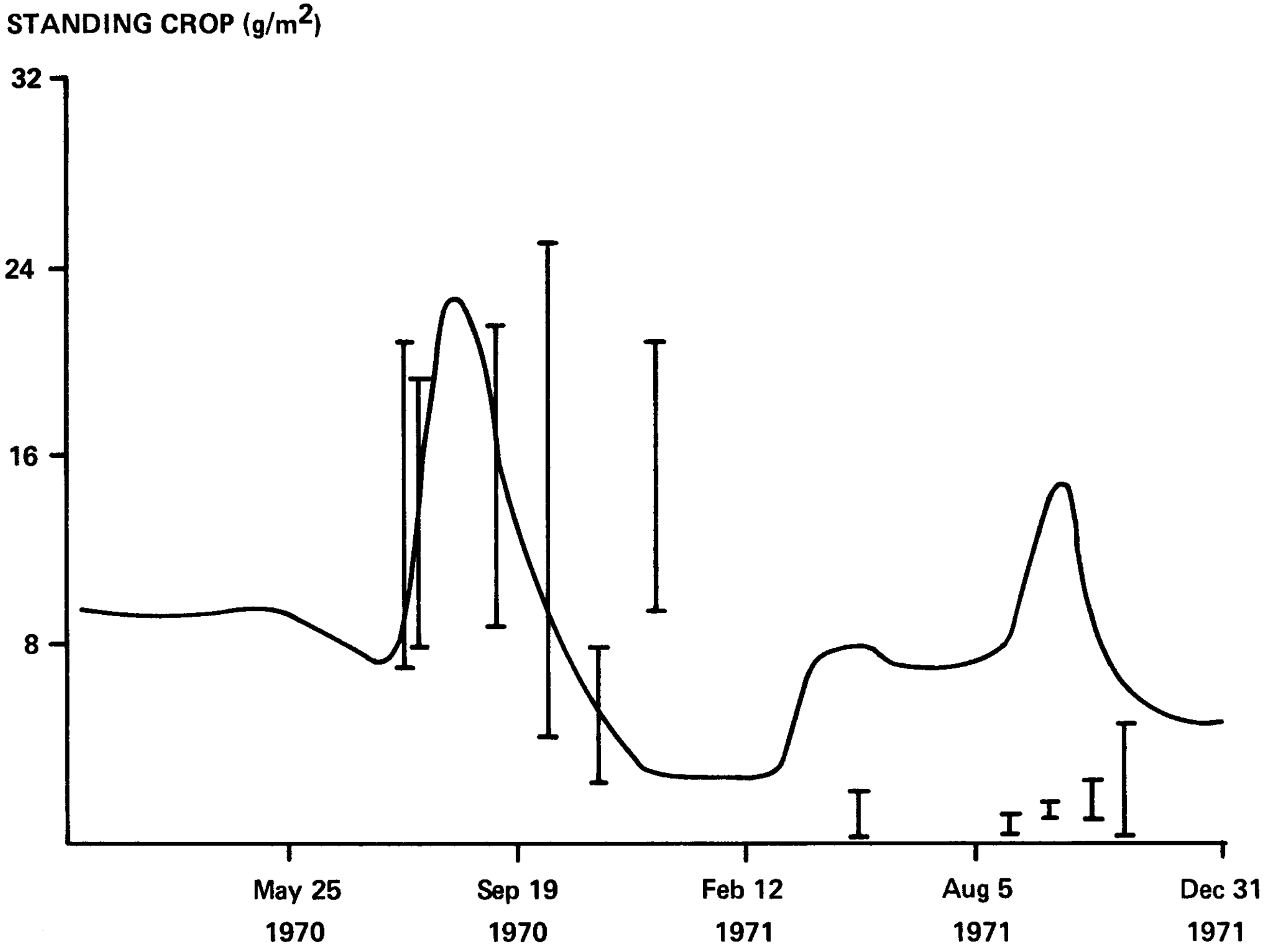

Fig. 68. Seasonal changes in live standing crop of broom snakeweed for 1970 and 1971 derived from ELM model. Vertical bars represent 95% confidence intervals for field sample data.

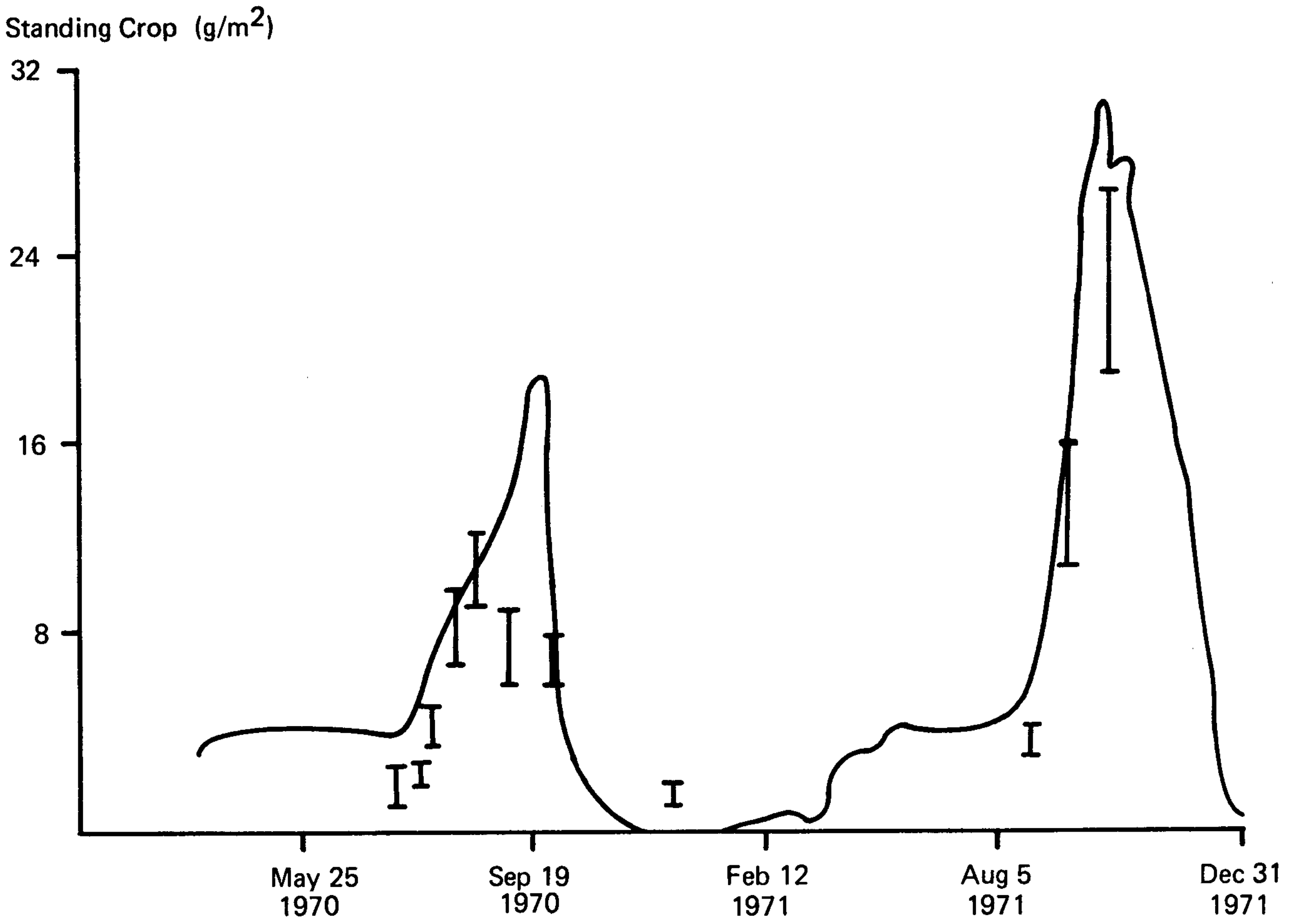

Fig. 69. Seasonal changes in live standing crop of Russian thistle for 1970 and 1971 derived from the ELM model. Vertical bars represent 95% confidence intervals for sample means collected in the field.

of small mammals fairly well in 1971 and 1972 when population levels were low (figures 70-73). However, model output was consistently low for early sampling periods in 1970. The curve for pocket mice populations was the only one with lower actual values than model output (figure 70). Visual inspection indicates that the model fits the data for the banner-tailed kangaroo rat best since the model output curve is within the 95% confidence interval for every date after July 1970 except for June 1972 (figure 71). Model output for Ord's kangaroo rat did not follow some of the minor fluctuations of actual data, but followed general trends pretty well (figure 72). The model generally underestimated carbon biomass of the spotted ground squirrel (figure 73), especially in 1972.

Most of the confidence intervals are very broad, indicating low precision of biomass estimates. Therefore, it is difficult to make stringent comparisons of model output and field data.

Other Models

Russell (1973) used several regression approaches to predict end of season standing crop of vegetation at the Jornada Experimental Range based on long-term records. He reported on R^2 values of 0.95 for the relationship between number of days when soil water was held at tensions less than -15 bars in the top 25 cm of the soil profile during the growing season. Other combinations of soil water content at various tensions and depth resulted in R^2 values varying from 0.29 to 0.91.

Using long-term records from the Jornada, Russell (1973) developed

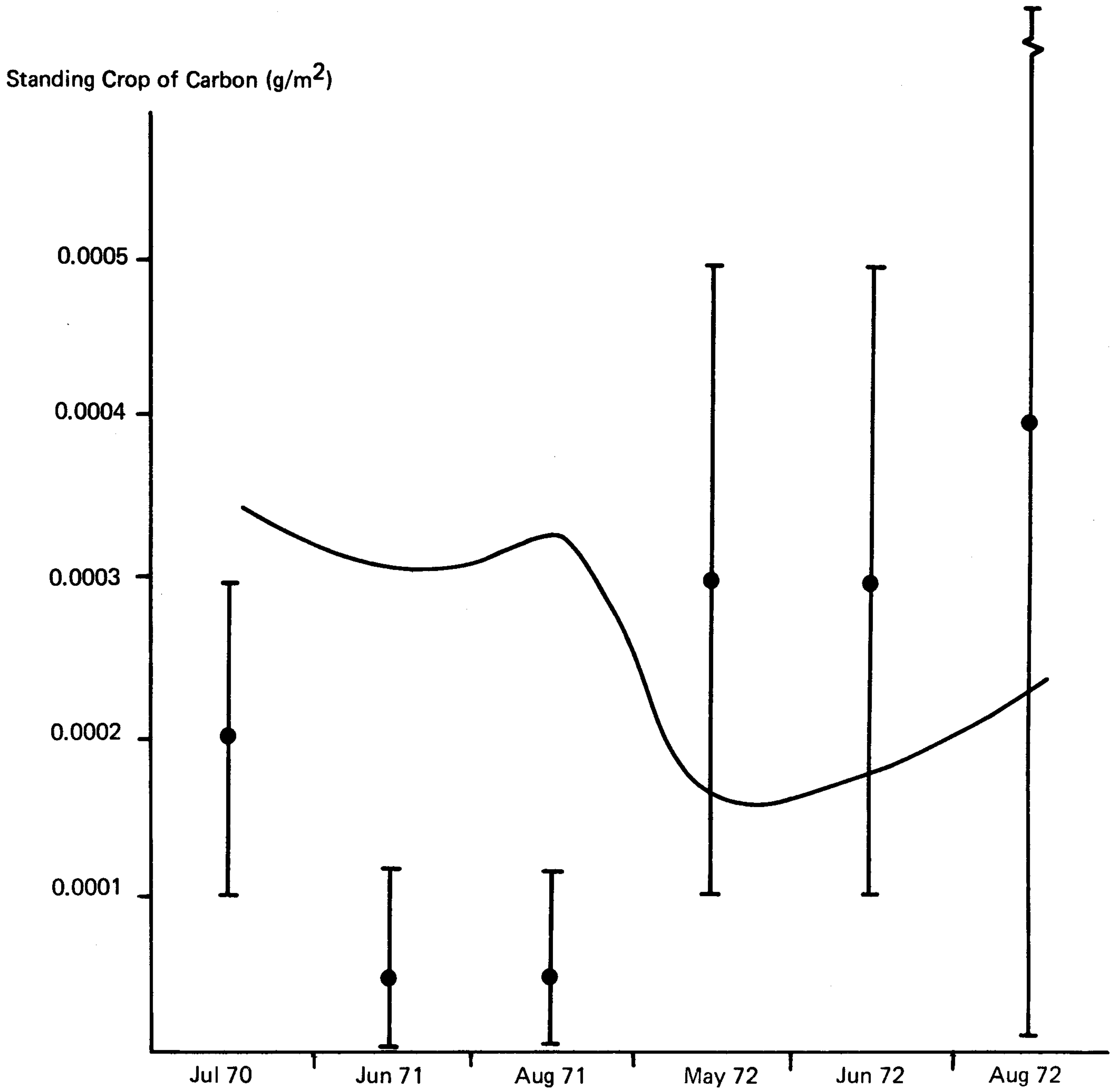

Fig. 70. Standing crop of Carbon in pocket mouse (*Perognathus* spp.) populations. Vertical lines represent 95% confidence intervals of field data while solid line represent ELM model output.

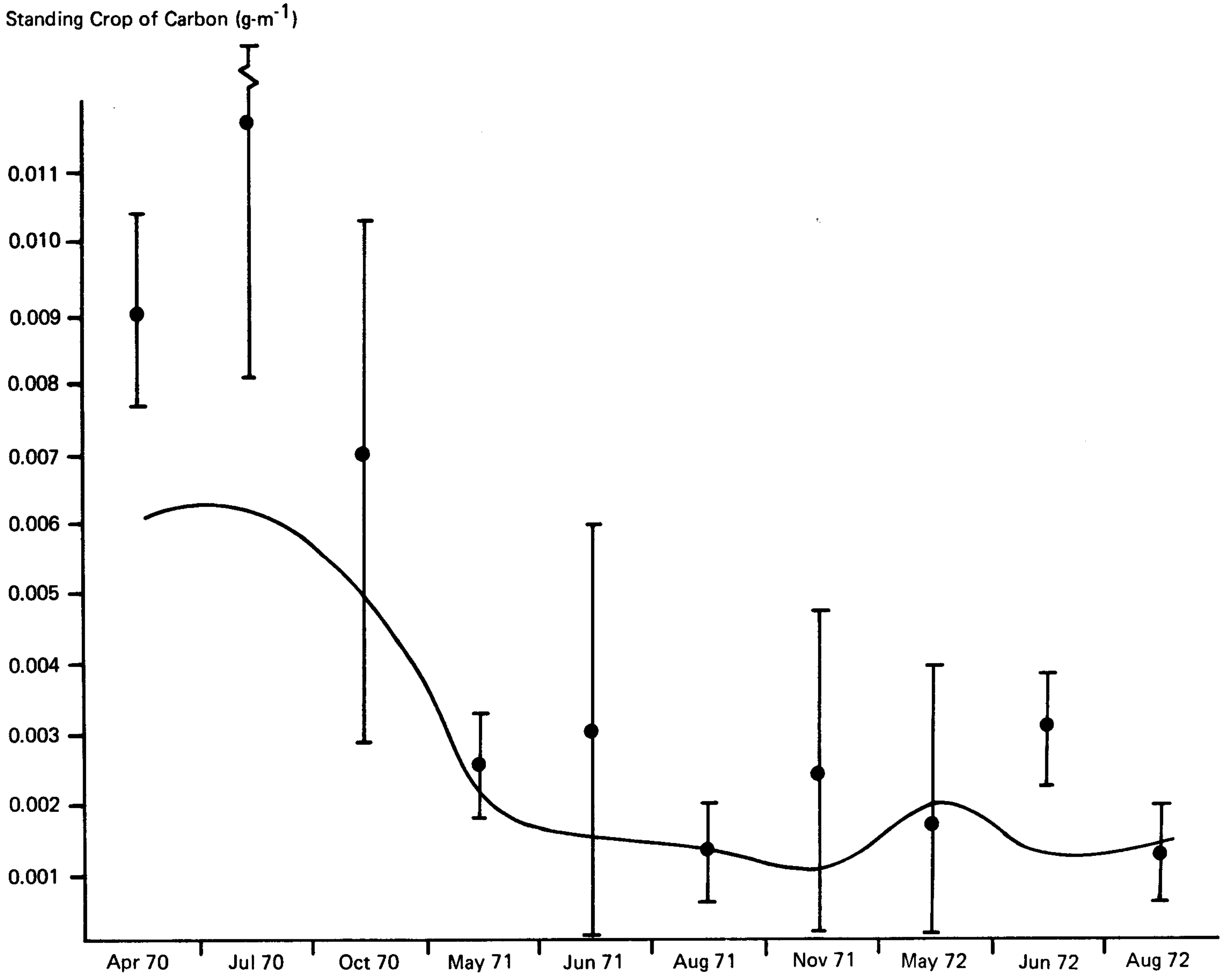

Fig. 71. Standing crop of carbon in bannertailed kangaroo rat populations. Vertical lines represent 95% confidence intervals about the mean for field data. Solid line represents ELM data output.

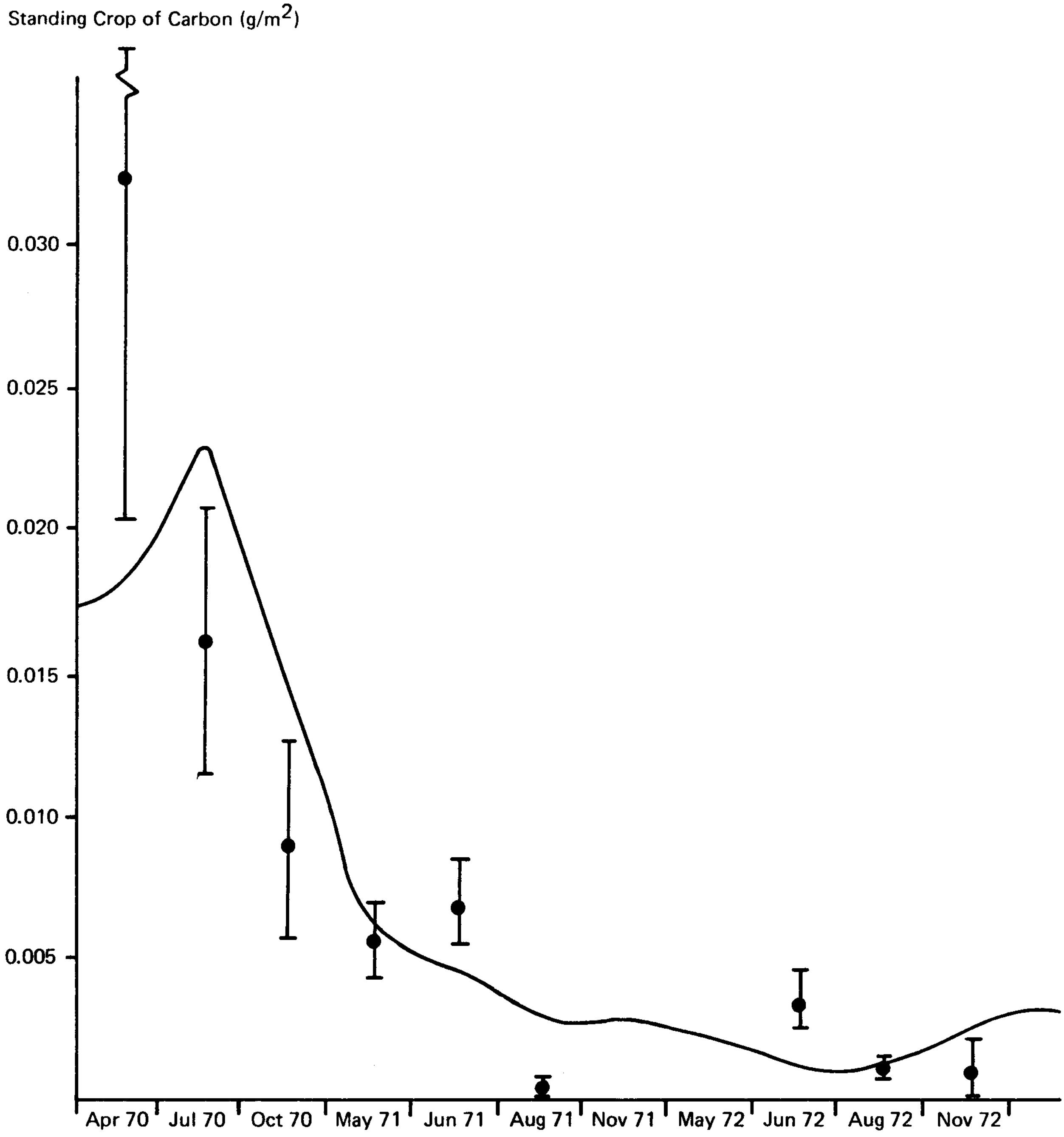

Fig. 72. Seasonal changes in standing crop of carbon in ord's kangaroo rat populations. Vertical lines represent 95% confidence intervals about means from field data while solid lines represent output from ELM model.

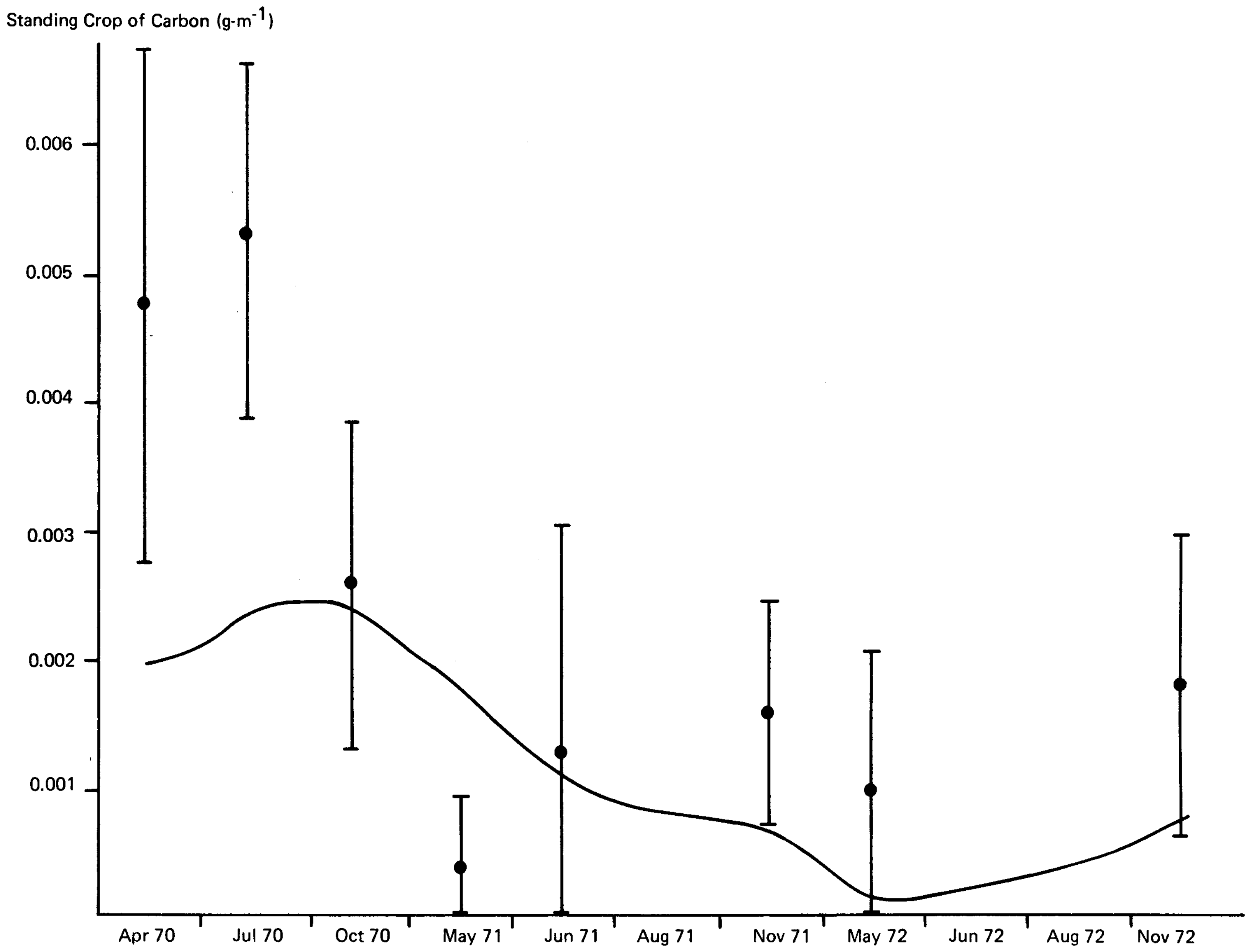

Fig. 73. Standing crop of carbon in spotted ground squirrel population. Vertical lines represent 95% confidence intervals about means from field data and solid line represent ELM model output.

models for predicting weekly herbage productivity under different soil water levels (figure 74). This curve was developed under optimum temperature conditions. Other curves were developed to relate air temperature to primary productivity.

Cable (1975) developed prediction equations for perennial grass production on desert grassland ranges on the Santa Rita Range in southern New Mexico. He found that previous June through September precipitation and current August precipitation were the best predictors of annual production (figure 75). The R^2 values varied from 0.80 to 0.95 on various pastures. Precipitation was utilized more effectively on pastures where mesquite had been controlled than on pastures where it had not.

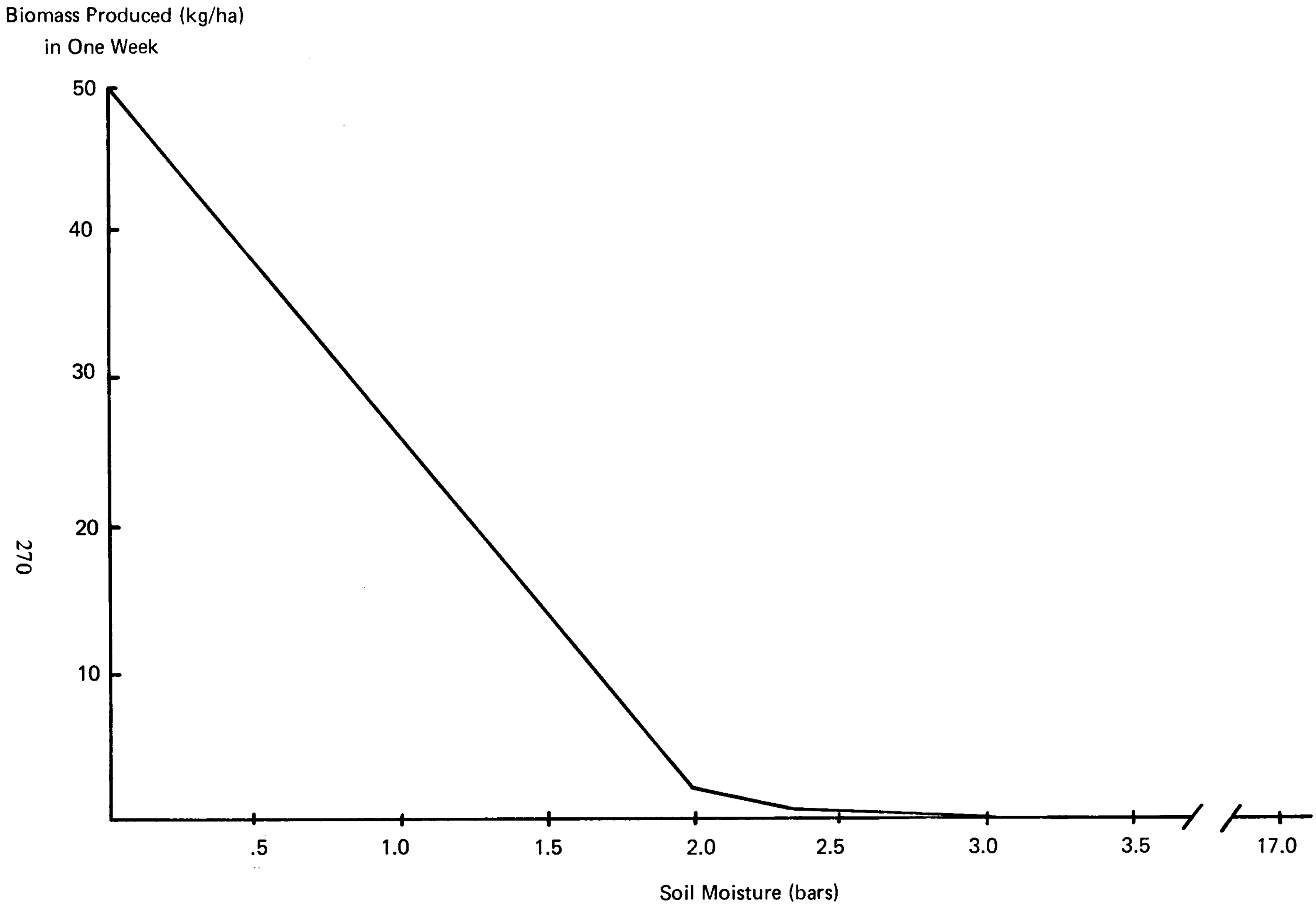

Fig. 74. Initial curve of estimated biomass produced under optimum temperature at levels of soil moisture in one week.

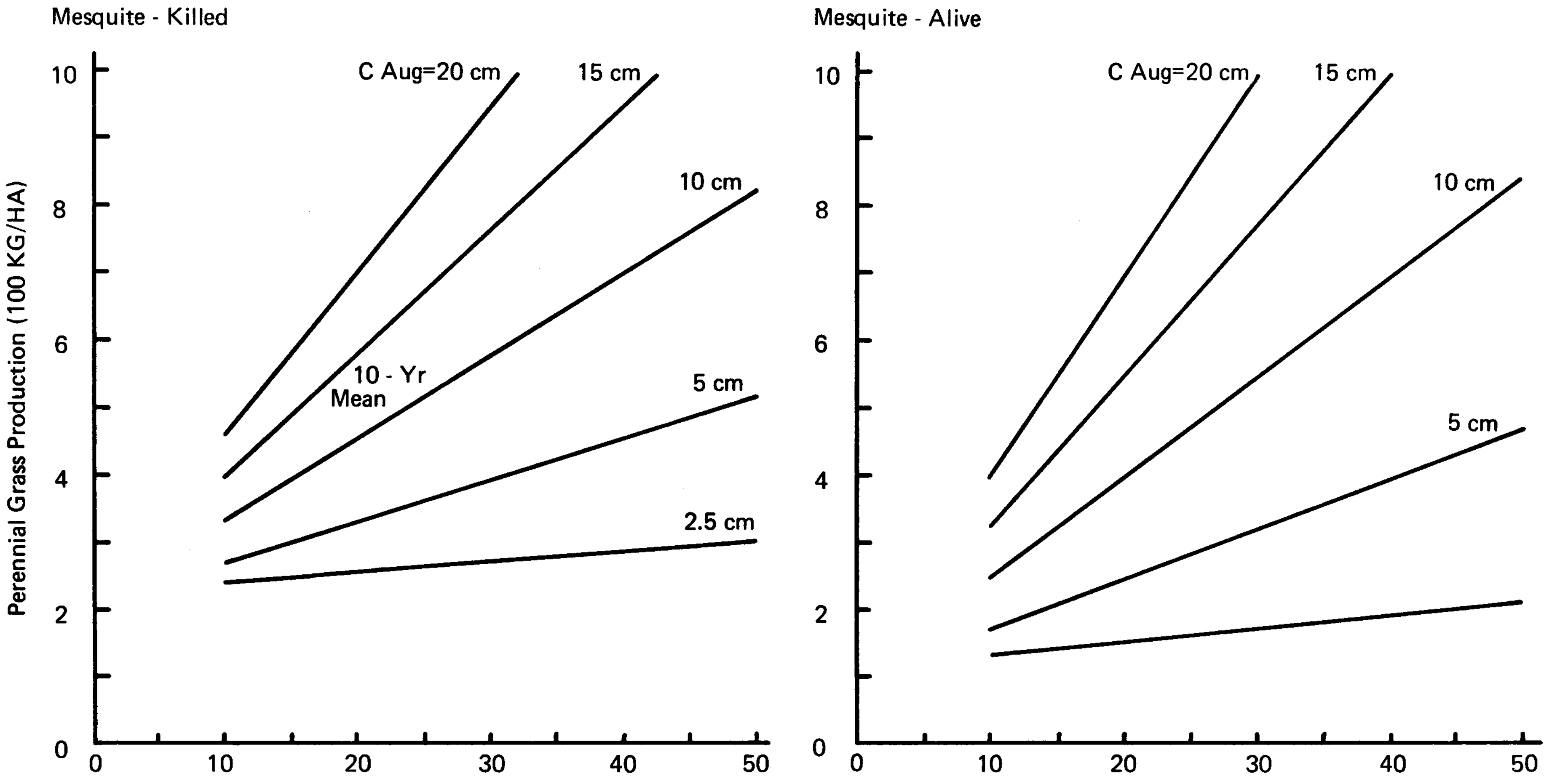

Fig. 75. Predicted perennial grass production for known previous June-September (PJS) rainfall and various levels of expected current August (CAug) rainfall on mesquite-killed pastures (kft) and mesquite-alive pastures (right), (from Cable 1975).

CONCLUSIONS

General Nature of Desert Grassland Ecosystem

The desert grassland may be viewed as a system fluctuating in rhythm to variations in precipitation. Many state factors and processes seem to be almost directly related to precipitation, others are more indirectly related. Plant biomass and net aboveground primary productivity apparently vary almost directly with precipitation, providing there is a certain level of leaf material available for photosynthesis. Areas with few perennial plants and hence less leaf area have lower productivity than areas with more plants. Annual plants apparently act to occupy empty niches in years of plentiful precipitation, such as during 1972 when there was little difference in total plant biomass between the grazed and ungrazed treatments.

Decomposition is another process that is directly dependent on precipitation. When soil water is present decomposition rates are very rapid, but long periods occur when no measurable decomposition takes place. Some buried filter paper appeared unchanged after several months and had not lost any weight.

Population densities of invertebrates and small mammals also varied in response to precipitation but in different ways. Invertebrate density and biomass was moderate in 1970, very low in 1971, and high in 1972. These populations were probably responding to food conditions. On the other hand, small mammal populations were very high at the start of the study in 1970, but declined sharply later in 1970 and remained at a low level throughout the study. There was some indication that the population might be responding to the high rainfall year of 1972, but the trend could not be followed beyond the late summer of 1972. There is undoubtedly a marked lag effect in response to abiotic and biotic variables by species with a fairly long reproductive cycle.

Avian populations were consistently low on the desert grassland site compared to other grassland sites. During periods when avian density and biomass were high, a large porportion of the birds were migrants. Wiens (1973) has suggested that reptiles and rodents, particularly heteromyids, have occupied some of the feeding niches of birds on desert grasslands. Detailed food habits studies for granivorous birds as well as the reptiles and heteromyids are lacking and tests of hypotheses concerning feeding ecology of these groups are not possible until such studies are conducted.

The adaptation of the ELM model to desert grassland conditions was only partially successful. There still remains some doubt how closely the ELM model can be adapted to desert grassland conditions. Insufficient time was available for modelers to complete the work of adjusting the model to desert grassland conditions. Visual inspections indicated that the model generated plant biomass data that mimicked real data reasonably well and compared favorably to that for some treatments on the Pawnee shortgrass site (Van Dyne and Anway 1976, Sauer 1975). However, the ELM may not have better predictive qualities than other, perhaps simpler, models such as regression techniques used by Parker (1963) and Russell (1973).

Little was accomplished in comparing model output with real data for various herbivore groups. Consequently, little can be said about the suitability of the ELM model to simulate herbivore dynamics.

One of the original objectives behind the modeling efforts of the Grassland Biome of the IBP was the identification of gaps and weak points in information about grassland ecosystems. Unfortunately, modeling activities were never ahead of field data collection at any of the comprehensive network sites to allow for this. Collection of field data had been stopped prior to final adjustment of the ELM model for the desert grassland. Even if problems could have been identified with the model, it would not have been possible to collect field data under the IBP program. Ideally, the modeling activities and validation would be an iterative process during the field-sampling phase. Probably the most that can be said for the modeling phase at the Jornada was that it was incomplete.

One of the objectives of the IBP program was to test hypotheses concerning ecosystem functioning. Many hypotheses could not be tested with data from the desert grassland because a period of three years was not sufficient to study phenomena related to successional changes. In other instances, data were not sufficient to draw definitive conclusions on many points.

Ecological Hypotheses

Some of the hypotheses on which data are available for the desert grassland site follow:

1. Long-term grazing causes a shift in botanical composition and increases belowground biomass.

Results from the first field season seemed to indicate larger belowground biomass under grazing for many of the grassland sites (Sims and Singh 1970). On the desert grassland site, however, this did not hold. Belowground biomass, especially in the 0-10 cm depth, was higher on the ungrazed treatment. Over the three years of the study, belowground:aboveground ratios were 2.0 on the ungrazed area and 1.4 on the grazed. Most other grassland sites have much higher ratios (Sims and Singh 1970). Since the grazed area has fewer perennial plants and more annuals than the ungrazed area, it is not surprising that belowground biomass was higher on the ungrazed area.

2. Diversity of producers is a function of climatic stability with grasslands of low climatic variability having high species diversity and greater biotic resiliency if perturbations do occur.

Data from several grassland sites indicate that diversity of plant species may not be directly related to climatic stability. Smith (1973) indicated that the desert grassland site was the most variable in terms of annual precipitation among the Grassland Biome IBP sites, yet the number of species was the greatest (Marshall 1972). The number of species contributing more than .01 g/m^2 was consistently greater on the grazed area on the desert grassland site than on the ungrazed site. Grazing or drought stress apparently opens the area to annuals, which tend to increase species diversity over the perennially dominated areas.

3. Change in biomass in on ecosystem compartment results in comparable changes in another compartment.

This hypothesis appears to be true within some limits for the desert grassland. However, there are some lag effects such as those in invertebrate populations in 1970 and 1971 when peak density and biomass occurred after the period of peak plant growth. The relationship between prey biomass and predator biomass is not clear because of lack of precision on predator biomass data.

4. Little energy fixed by natural grassland ecosystems is channeled through consumers; the major pathway leads directly to decomposers.

This seems to be true in most grasslands as well as the desert grassland (Lewis 1970). Even considering domestic livestock, only a small portion of plant biomass passes through consumers. Apparently several herbivore food niches are not occupied. Many consumer groups (small mammals, invertebrates, birds, ets.) feed on seeds, but few tissue-feeding groups make large demands on vegetative parts of plants, with the exception of cattle. Pronghorn antelope presently use little of available food resources. It is likely that pronghorn were more abundant in the past and occupied some of these food niches. Now lack of suitable habitat may be more limiting than food resources (Howard et al. 1973).

In terms of additional sources of human food, grasslands appear to offer some possibilities for increased utilization of primary production by herbivores. However, we do not yet know how to do this while maintaining continued productivity and ecosystem stability.

Decomposer data were lacking for the first two years of the study and data for 1972 were not adequate to account for all the net primary production.

5. Grassland biomass pyramids change shape seasonally, reflecting changes in rates of transfer of available energy at different

seasons.

Data (table 40) indicate some rather drastic seasonal changes in compartmental biomass. Loss of mulch by decomposition is strongly seasonal and related to precipitation events.

6. Changes in species composition of grassland producers will lead to predictable changes in consumer species composition.

This hypothesis is difficult to evaluate with present desert grassland data. Detailed food habits of major consumers are not available. Some information from the literature indicates that some of the small mammals such as kangaroo rats may have a relatively wide range of food sources. It appears that most consumers would need a wide range of species as potenial food. For example, if some consumers used seeds or other parts of *Crypantha crassisepala*, the supply would have been virtually nonexistent in 1971, but plentiful in 1972. Alternate food sources would have been particularly important with such fluctuation in plant species populations. For the major native ungulate on the desert grassland site, the pronghorn antelope, many species serve as food sources and fluctuations in herbaceous species population would likely have little effect on the pronghorn density. It seems that changes in producer species composition would not have large effects on species composition of consumer groups.

7. Consumer biomass increases directly with increases in biomass of food plants because the amount of consumer biomass accumulated depends largely on the amount of producer biomass available.

Desert grassland data generally supports this hypothesis, although the exact relationships between consumer biomass and food availability are not completely clear. Changes in invertebrate biomass roughly coincided with changes in plant biomass, but small mammal biomass did not respond so directly. Avian biomass of breeding birds was relatively small, but there were large influxes of migrating birds that were probably not related to plant biomass or primary productivity.

8. Energy transfer efficiencies increase with each transfer step away from photosynthesis.

This hypothesis is supported by our data, although they are not complete. In some cases consumption rates for secondary consumers exceed productivity of the suspected food source. Sampling techniques used for intevertebrate populations seriously underestimated density and biomass for some groups. The elucidation of food webs was not possible in this study and calculations of efficiencies above the herbivore level were not possible.

9. Flux rates among grassland ecosystem compartments are equal over time so that there is no net gain or loss in biomass.

A three-year study is inadequate to study these kinds of equilibria under the widely fluctuating climatic regime of the desert grassland. However, in vegetation compartments (standing live, standing dead, and mulch) an equilibrium appeared to be nearly established over the three years. That is, the amount of biomass transferred from standing live compartments to standing dead nearly equaled that transferred from standing dead to mulch and mulch disappearance.

Data for other transfers among trophic levels were not sufficient to test the hypothesis. Small mammal biomass declined in 1970 and never reached its former status. Consequently, equilibria involving small mammal populations would not be established in three years.

Questions concerning stability of the desert grassland ecosystems using such indices as production, respiration ratios, or production: biomass ratios were not answered except as indicated for the previous hypothesis. Over time, decomposition plus consumer respiration would equal primary production in a stable ecosystem. However, decomposition rates were not determined during the first two years of the study. In addition it is unlikely that questions concerning ecosystem stability and equilibria can be answered by short-term studies.

Evaluation of Desert Grassland Studies

Plant reproductive parts and invertebrates seem to be the hubs of the desert grassland ecosystem for many consumer groups. Fruits and seeds serve as important food sources for many species of invertebrates such as ants, for small mammals such as the kangaroo rats, and birds such as the nonbreeding seed eaters. Unfortunately, we have no measure of this important food component. A knowledge of seasonal as well as yearly variations in plant reproductive parts is essential for complete understanding of feeding ecology of these groups. Intensive, detailed food habit studies are also needed for all consumer groups. We have little information concerning dietary overlap among consumers or amplitude of food sources by various consumers.

Invertebrates serve as food sources for small mammals such as ground squirrels, for other invertebrate predators, reptiles, and insect-eating birds. We need more detailed inforamtion on this group--those active aboveground, and especially belowground groups.

SUMMARY

The North American Desert Grassland has been considered a stable grassland by some authors and a transition between grassland to the north and east and deserts to the west. The vegetation is dominated by species of *Bouteloua*, *Hilaria*, *Aristida*, and *Sporobolus*. Small mammal populations have definite similarities to warm desert groups, with kangaroo rats (*Dipodomys* spp.) and pocket mice (*Perognathus* spp.) common. Bird populations vary tremendously, with large numbers of "migrants" during certain seasons. The loggerhead shrike and cactus wren are among the more common breeding birds. Invertebrates are represented by large numbers of families and genera. Grasshoppers, ants and termites are among the most abundant.

Climatically, the desert grassland is characterized by hot temperatures and low precipitation. Much biological activity occurs during the summer, when most effective precipitation falls and temperatures are high. During the period of this study, 1970 and 1971 were considered "dry" and 1972 was considered "wet".

The study was designed to compare two treatments, one in "high" range condition, represented by a 10-ha exclosure with no grazing by domestic livestock. The other treatment was represented by a temporary exclosure, which was moved annually on areas that were in "low" range condition and open to livestock grazing.

During 1970 and 1971, peak standing live plant biomass was higher on the ungrazed area than on the grazed area. In 1972, however, there was no difference in peak standing live biomass between the two treatments. Annuals, which responded to the favorable growing season in 1972, contributed substantially to plant biomass on the grazed treatment. On the ungrazed treatment, perennial warm-season grasses contributed over 50% of the standing peak live plant biomass. *Bouteloua eriopoda* was dominant followed by *Sporobolus flexuosus*. On the grazed treatment, annual warm-season forbs (mainly *Salsola kali*) and shrubs (mainly *Gutierrezia sarothrae*) contributed most of the live plant biomass.

Small mammal biomass was highest during the spring of 1971 and declined sharply after that period. Ord's (*Dipodomys ordii*) and the bannertailed kangaroo rat (*D. spectabilis*) contributed most of the biomass during the early part of the study. During the later stages of the study, the pocket mice (*Perognathus* spp.) dominated small mammal biomass. Black-tailed jackrabbit populations fluctuated considerably during the study, while desert cottontail populations remained low during the whole study.

Invertebrate populations were low during 1970 and 1971, but responded to the high precipitation and plant biomass during 1972. Biomass of invertebrates was generally less than 0.1 g/m^2 on both treatments in 1970 and 1971. In 1972 peak biomass was 0.8 g/m^2 on the ungrazed treatment and 0.4 g/m^2 on the grazed.

Herbivores dominated invertebrate population density measurements on both treatments usually followed by scavengers. However, scavengers had the highest biomass during many sampling periods, although considerable variation occurred among sampling dates. Many invertebrate groups were inadequately sampled with the "quick-trap" technique. Both density and biomass estimates considerably underestimated actual field values.

Densities of bird populations were relatively low in 1970 and 1971. Responding to the favorable year of 1972, the birds maintained relatively high numbers from September 1972 to March 1973. Granivores were by far the numerically dominant group on the desert grassland site.

Aboveground net primary productivity averaged 148 g/m^2 on the ungrazed area and 109 on the grazed treatment during the three years of the study. However, during 1972, aboveground net primary productivity was about 180 g/m^2. Highest daily net aboveground primary productivity of 2.4 g/m^2 occurred between August 11 and 20, 1972. Net aboveground primary productivity utilized less than 0.1% of usable solar energy received by the site. During the three years, compartmental transfers from standing live to standing dead to mulch were nearly equal. Belowground turnover rates were about 0.5 for 1970 and 1971, but considerably higher for 1972.

Consumption by various herbivore groups was low compared with primary production. Cattle, small mammals, and invertebrates were responsible for the largest consumption rates. Consumption by pronghorn antelope, birds, and rabbits was very small. Total consumption averaged only 6 $g/m^2/yr$ by all herbivores over the three years of the study. Almost 80% of this was by domestic livestock.

Energy transfer from plants to herbivores represented less than 25 $kcal/m^2$ over the three years. Total aboveground net primary productivity was about 600 $kcal/m^2$. Therefore, ecological efficiency of energy transfer from plants to herbivores was just over 4%. Secondary productivity of herbivores was highest for invertebrates, large herbivores, and small mammals.

Adaptations of the ELM grassland model to the desert grassland were only partially successful because of a lack of time. The model followed actual plant biomass changes through the season, but often showed spring growth when none occurred. General trends during the growing season were mimicked fairly well. The model did not show as high populations of small mammals early in the season as actual data did. During the rest of the study, when small mammal populations were low, the model output followed actual data fairly well.

The desert grassland ecosystem is viewed as a system, pulsing with rainfall events when temperatures are favorable for biological activity.

Production of seeds is viewed as an important process for several groups of herbivores. Production of invertebrates is considered an important process for carivorous groups.

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APPENDIX

Appendix Table 1. Analysis of variance (mean squares) for total aboveground herbage biomass for current live, recent dead, and old dead on the Jornada IBP Grassland Site for the three years of the study.

Source	1970						1971						1972					
	df[a]	Current Live	df	Recent Dead	df	Old Dead	df	Current Live	df	Recent Dead	df	Old Dead	df	Current Live	df	Recent Dead	df	Old Dead
Ecological category (Ec)	7	7798***[b]	1	506***	4	130***	5	584***	5	1754***	3	862***	7	67	6	600***	3	1347***
Treatment (Tr)	1	486***	1	151***	1	52	1	218***	1	502***	1	16	1	168**	1	216**	1	11
Tr x Ec	7	3061***	1	161***	4	45	5	182***	5	419***	3	589***	7	40	6	343***	3	270***
Rep/TrEc	16	53	4	11	10	21	12	15	12	60**	8	55*	16	36	14	42***	8	25
Error (a)	288	70	72	15	180	4	456	19	456	29	304	30	608	48	532	19	304	62
Date (D)	7	3120***	7	370***	7	83***	7	873***	7	477***	7	109**	10	218***	10	199***	10	64
D x Ec	49	12493***	7	36***	28	85***	35	184***	35	175***	21	199***	70	47	60	225***	30	56
D x Tr	7	1558**	7	88***	7	58*	7	79	7	117**	7	118**	10	103**	10	59**	10	28
D x Tr x Ec	49	10798***	7	89***	28	57***	35	47	35	53	21	56	70	48	60	86***	30	31
D x R/TrEc	112	12016***	28	10	70	28***	77	5	85	46***	56	43***	160	56	140	28***	80	74
Error (b)	2016	67	504	16	1260	4	3192	17	3192	29	2128	30	6080	56	5320	18	3040	69

[a] df is degrees of freedom.

[b] * = significant at P<0.10; ** = significant at P<0.05; *** = significant at P<0.01.