Herbage Dynamics and Primary Productivity of a Desert Grassland Ecosystem

CONTENTS

SUMMARY

Primary production was determined for a desert grassland in southern New Mexico with and without grazing. The ungrazed treatment was represented by *Bouteloua eriopoda* grassland, and the grazed treatment was represented by a grassland deteriorated because of drought and grazing pressure. Sampling was conducted approximately biweekly during the growing season and monthly during the dormant season.

Environmental conditions varied considerably during the 3 years of the study and were reflected in variations in herbage standing crop and primary productivity. Weather in 1970 and 1971 was dry, and standing crop of vegetation and primary productivity were lowest on both treatments during 1971. Conditions during 1972 were fairly wet, especially late in the summer, and herbage standing crop and primary productivity were higher on both treatments than for the first 2 years. Herbage biomass was consistently and significantly higher ($P < 0.05$) for the ungrazed than for the grazed treatment for 1970 and 1971, when soil water was limiting.

There was no significant difference in herbage biomass between treatments in 1972, however, which indicated that the potential for primary productivity on the two areas was nearly equal. Annuals apparently serve as the regulating mechanism with ability to fill in the bare spots when soil water is available.

Bouteloua eriopoda contributed more biomass than any other species on the ungrazed treatment; *Xanthocephalum sarothrae* and *Salsola kali* were the principal contributors to

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biomass on the grazed area. A cool-season forb, *Cryptantha crassisepala*, was important in 1972. Average net primary productivity for the 3 years was 148 g/m² on the ungrazed treatment and 109 on the grazed treatment. Maximum net productivity rates for the ungrazed treatment was 2.4 g/m²/day for all species and 2.2 g/m²/day for the grazed area for short periods. Peak productivity of *Bouteloua eriopoda* was 1.3 g/m²/day on the ungrazed treatment. Maximum net productivity on the grazed treatment by one species was 1.1 g/m²day for *Xanthocephalum sarothrae*.

Efficiency of aboveground net primary productivity averaged 0.08% of the useable solar radiation reaching the surface during the thermal growing season for the ungrazed treatment and 0.05% for the grazed treatment. Calculations of compartmental transfer rates indicate that these systems are relatively stable with regard to standing live, recent and old dead, aboveground mulch and belowground biomass.

ACKNOWLEDGMENTS

Herbage Dynamics and Primary Productivity of a Desert Grassland Ecosystem[1]

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Lindeman's (1942) paper on trophic-dynamic aspects of ecology ignited interest in ecological relationships at the ecosystem level. The development of high-speed computers enabled ecologists to analyze complete ecosystems and to model them (Van Dyne 1966). These interests and activities have culminated in the International Biological Program (IBP) Analysis of Ecosystems.

The primary objective of the Analysis of Ecosystems portion of the IBP is to understand the basis of productivity worldwide. This bulletin deals with herbage dynamics and primary production of a desert grassland ecosystem. Primary production is important in any ecosystem; it fuels consumer and decomposer groups. Products from primary production also influence abiotic parameters. Litter on the soil surface influences infiltration rates and, as it is incorporated into the soil, changes physical and chemical soil properties. Many studies have been concerned with desert grassland vegetation and have analyzed end-of-season standing crop of certain groups of plant species, but few have analyzed the details of herbage dynamics, primary production, and energy dynamics of primary producers under desert grassland conditions.

The studies reported here were conducted on the Jornada Experimental Range in southern New Mexico. The site is one of the "comprehensive network" within the Grassland Biome of the Analysis of Ecosystem Studies of the IBP. The comprehensive sites were selected to represent different grassland types for comparison with the "Intensive" site at the Central Plains Experimental Range and Pawnee Natural Grassland in northern Colorado. Detailed measurements of biomass and processes were to be made on all important ecosystem components at the intensive site and a minimum set of measurements were to be made at each comprehensive site. Consequently, the objective of this research was to analyze both seasonal and yearly changes in herbage biomass on a desert grassland and their relation to abiotic variables.

DESCRIPTION OF AREA

The study was conducted on the Jornada Experimental Range in Dona Ana County, New Mexico. The specific location on the Jornada was on the western portion of the range just south of West Well (Herbel and Pieper 1970). The elevation of the site is about 1,350 m, and the topography is nearly level. The site represents the upland conditions as opposed to some of the low-lying areas, which receive some additional moisture as overland flow from areas of higher elevation.

The climate is hot and dry. The mean annual precipitation recorded for a 52-year period at the Jornada headquarters, about 10 km east of the study site, is 228 mm. Variation is wide, however, with about 64% of the years with below-average precipitation and 36% with above-average precipitation. The late 1940's and particularly the early 1950's were marked by severe drought (Herbel, Ares, and Wright 1972). Excluding 1950, the average annual precipitation from 1949 through 1956 was only 168 mm. On several rain gauges, mean annual precipitation from 1951 to 1956 was only 54% of the average (Herbel, Dittberner, and Bickle 1970). The drought was broken in 1957 and 1958, when precipitation was above average.

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Seasonal pattern of precipitation is characterized by small amounts in the spring and peak in late summer, with gradually reduced amounts during fall and early winter. Only in July and August does precipitation average more than 40 mm. Smith (1973) reported that average precipitation during the thermal potential growing season was 146 mm, with a coefficient of variation of 42%. The total for the growing season was the lowest and the coefficient of variation the highest for any site in the Grassland Biome-IBP. The severity of the 1951-56 drought is shown dramatically by comparison of the July, August, and September averages of 64 mm for the drought period to the 52-year average of 122 for the same months.

Summer precipitation originates from intense, local convectional thunderstorms of short duration (Herbel, Dittberner, and Bickle 1970). Consequently, these showers are spotty, and spatial variation is high. Winter moisture originates from the Pacific Ocean, and winter storms are usually relatively general and fairly gentle. However, Pacific air masses lose most of their moisture before reaching southern New Mexico.

Temperatures are high in the summer and low in the winter. The average highest air temperatures are 40 °C or higher during May, June, July, and August. June is the hottest month, with a mean maximum temperature of 36 °C; January is the coldest, with mean maximum temperatures of 13° (Herbel and Pieper 1970). Temperatures during the summer months (June, July, and August) were lower in 1972 than in 1970 and 1971. Air temperatures are high during the summer, but soil temperatures are often much higher (Herbel, Dittberner, and Bickle 1970; Herbel 1971). From July 18 to August 15, 1974, average minimum air temperatures were 19 °C and average maximum were 33 °C, whereas the average maximum soil temperature at the 1.25 cm depth was 57 °C.

Solar radiation reaches a peak in June and declines until December, as cloud cover increases in the summer and the angle of the sun becomes more oblique in the fall and winter. Wind speeds reach a maximum during the spring months of March, April, May, and June. These spring winds cause

much wind erosion and increase water stress on plants. Bryson et al. (1970) calculated the relative evaporative stress for plants growing on the Jornada. Stress is highest during June, when precipitation and relative humidity are low, winds are high, temperatures are high, and there is little cloud cover. Weather Bureau records from El Paso, Texas, about 100 km southeast of the site, show that average cloud cover for June is only 32%, compared with 44% for July and August. Relative humidity for June was 26%, compared with about 42% for July and August. Many events in the Desert Grassland site are linked to precipitation.

Soils on the study area are fairly coarse, with an indurated caliche layer occurring at different depths. Reuss (1971) gave the following classification for the IBP study site: loamy mixed thermic mollic petrocalcic calciorthid. The parent materials of these soils are sandy sediments deposited by the ancestral Rio Grande (Herbel and Gile 1973). The indurated caliche at depths of 25 to 60 cm acts as a restrictive layer and prevents percolation of soil water to underlying layers (Herbel and Pieper 1970).

The vegetation consists mostly of herbaceous species, with a few shrubs scattered throughout the area. Some authors concluded that the desert grasslands were stable climaxes (Clements 1920; Campbell 1929; Gardner 1951; and Shelford 1963); others considered the area transtition between true grasslands and shrub deserts (Shreve 1917). Regardless of questions of classification, there is little doubt that the grassland areas have been invaded by brushy species during the last 100 years (Brown 1950; Buffington and Herbel 1965; and Dick-Peddie 1966). Land survey records in 1858 indicated that the entire Jornada Experimental Range was open grassland, with only scattered shrubs. In 1963, all areas had some shrub populations (Buffington and Herbel 1965).

The drought of the 1950's reduced perennial grass cover on the Jornada. On deep sands, basal cover of perennial grasses was reduced from an average of 0.86% during 1941 to 1950 to 0.01% in 1957, and yield was reduced from 40 g/m² to 3 g/m² (Herbel, Ares, and Wright 1972). The IBP ungrazed treatment was not greatly influenced by the drought and still supports a high cover of perennial grasses.

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However, on the grazed treatment east of the permanent exclosure, the effects of grazing and drought have reduced perennial grass cover.

The principal grasses on the study area are *Bouteloua eriopoda* Torr. with *Sporobolus flexuosus* (Thurb.) Rybd. in lesser amounts. The principal halfshrub is *Xanthocephalum sarothrae* (Gray) Rothr. Annual forbs include *Sasola kali* and *Cryptantha crassisepala* (T. & G.) Greene. The annual plant populations fluctuate drastically, depending on available soil water.

METHODS AND PROCEDURES

Most of the methods used in this study followed closely those outlined for the Grassland Biome of the IBP (French 1970; French 1971; and Swift and French 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*, which had been lightly grazed in previous years. A "grazed" treatment was located about 200 m east of the permanent exclosure on a deteriorated *B. eriopoda* rangeland with less of this species and more bare ground than in the permanent exclosure. This reduction in cover was due primarily to drought, but perhaps also to 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 3 years of the study.

Following methods of Dyksterhuis (1949), Lewis (1971) calculated that the vegetational composition in 1970 was

86% of climax on the ungrazed treatment and 50% on the grazed treatment. The similarity index calculated by Grant (1971) for the comparison of the grazed and ungrazed treatment was 0.61, indicating considerable vegetational differences between the two treatments.

Although the dry-weight rank method was used for sampling in 1970 and the weight-estimate method in 1971 and 1972, only clipped plot data are reported in this paper. In 1970, the plot was a long rectangle, 762 x 6.6 cm, for the sparse vegetation, but still meeting the area requirement of 0.5 m² area. In 1971, circular quadrats were used to conform with the rest of the network sites and to reduce perimeter-to-area ratios. A 0.5 m² quadrat was used for herbaceous species and a concentric 2 m² quadrat for the shrubby species. Results from the 1971 sampling indicated that the 2 m² quadrat was not effective in sampling shrubs, and only a 0.5 m² circular quadrat was used in 1972.

Sampling

Since the dry-weight rank method was being used in 1970 for evaluation of species composition, only 10 quadrats per replication and 20 per treatment were clipped. Sample sizes were doubled in 1971 and 1972, and 20 quadrats per replication or 40 per treatment were clipped, based on analysis of 1970 data.

All vegetational material was collected for each quadrat. Standing material rooted in the quadrat was clipped at ground level. The herbage of each species was visually separated in the field into standing current live, standing recent dead, and standing old dead. Standing live was green material produced and senescing during the year of sampling; recent dead was light brown, dead material produced during the year of sampling; and old dead material was that produced during previous years. Litter was collected by hand from each quadrat, but no attempt at species separations was made. Herbage was dried at 70 °C before being weighed.

All species were listed in ecological categories based on growth form, growth period, and life span. The ecological categories used were perennial warm-season grasses, annual warm-season grasses, perennial warm-season forbs, annual

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warm-season forbs, perennial cool-season forbs, annual cool-season forbs and shrubs.

Belowground material was sampled with a soil corer 7.62 cm in diameter. The corer was driven by hand into the soil to the caliche layer. One core was taken in each of the quadrats clipped for aboveground standing crop. The soil core was divided into three segments, starting from the soil surface: 0-10 cm, 11-20 cm, and 21-30 cm. The belowground samples were dried at 65 °C for 24 hours, after which they were gently agitated on a 500 micron screen. The portion which remained on the screen was placed in a seed separation blower which was operated at two speeds to separate the fine root hairs and then the large ones. Any large roots remaining in the residue were easily visible and removed by hand. All belowground material was again dried at 65 °C, and then weighed and ashed at 550 °C for 40 hours. Root crowns were included in belowground samples.

Sampling of aboveground biomass was conducted at approximately two-week intervals during the growing season and at monthly intervals during the dormant season. Belowground biomass was sampled five or six times each year, which was less often then aboveground biomass was sampled. Voucher specimens of all plant species collected are on deposit in the herbarium at the Jornada Headquarters. Plant nomenclature follows that of Correll and Johnston (1970).

RESULTS

Driving Abiotic Variables

The first two years of the study, 1970 and 1971, were very dry. Most of the growing season precipitation fell in July 1970 and July and August in 1971 (figure 1). Little precipitation fell from July 1970 to July 1971. No precipitation was recorded in February, March, and May of 1971 and only a little over 17 mm for January, April, and June. Soil water followed these precipitation trends rather closely, although the readings were taken about 2 km from the IBP site. Soil water was recorded at tensions of less than -16 atm for only a short period in August 1970 and in August and September,

Fig. 1. Monthly precipitation at International Biological Program Site for the 3 years of the study. Totals for the period January though June 1970 were taken from records for the Jornada Headquarters, since the rain gauge was established in June.

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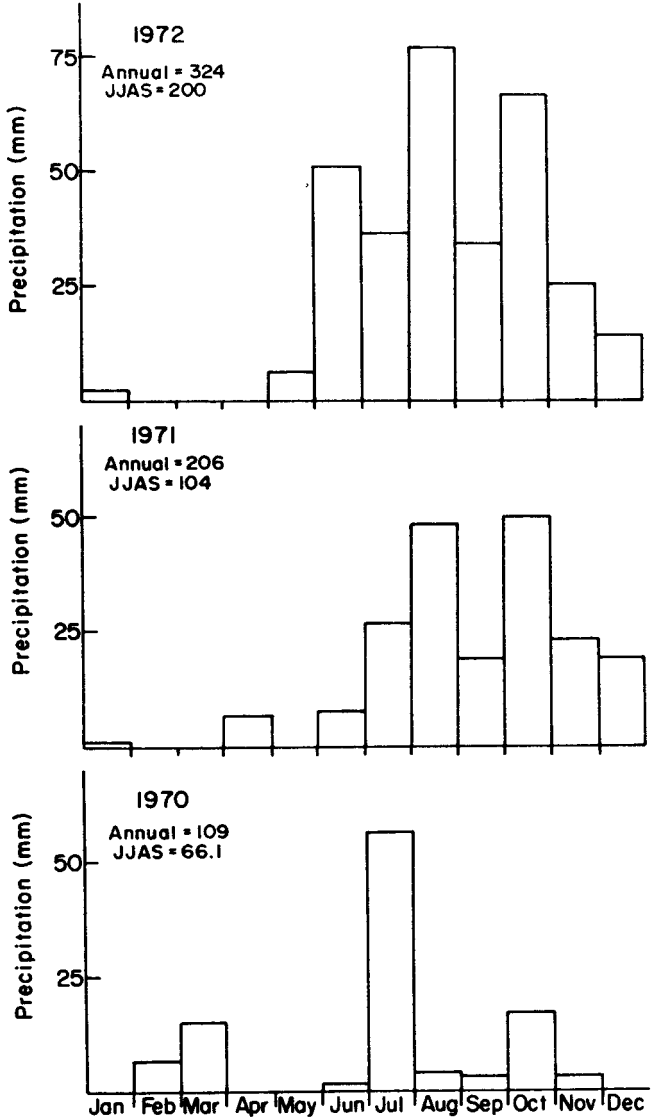
1971. Soil water in 1972, in contrast, was held at tensions of less than -1 atm from the first of January to April at all depths. This soil water probably resulted from rains in the last 3 months of 1971, since spring precipitation was very low in 1972 (figure 1). Summer rainfall was heavy in 1972, and soil water was available for plant growth throughout the summer, June through September.

The length of the growing season, calculated from thermal characteristics only, was somewhat shorter for 1971 than for 1970 or 1972 (Smith 1973). However, the growing season is probably defined more by available soil water than by temperature. Even though the thermal growing season was shorter in 1971, average growing-season temperatures were more than 2 °C higher in 1970 and 1 °C more than in 1972 (Smith 1973). Thus, total evaporative stress on plants was probably accentuated because of high temperatures and low precipitation.

The 3 years differed little in total incident radiation or in daily radiation during the growing season. Because of the shorter growing season in 1971, both total incident and usable solar radiation were lower than during 1970 and 1972. Usable solar radiation, which is potentially usable for photosynthesis, was calculated as 45% of the total.

Seasonal Herbage Dynamics

Phenology. Phenological observations were made on the major species at each sampling date in 1971 and 1972. Because of the limited precipitation, in 1971, all species developed in a similar pattern. *Sporobolus flexuosus* developed a little earlier than the other species, but there was little difference in phenology among *Bouteloua eriopoda*, *Salsola kali*, and *Xanthocephalum sarothrae*. All species completed most of their life cycle during August, September, and early October. In 1972, when soil water was available for a much longer time, phenological development differed markedly among the species. *Cryptantha crassisepala*, a cool-season annual forb, began growth in February, was in midbloom in May and had ripe seed in June. *Xanthocephalum sarothrae*, which is classified as a warm-season shrub, started growth early in the spring but was still in the prebud

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stage in July. Most of its phenological development past the flowering stage actually occurred at the same time as that of *Sporobolus flexuosus* and *Bouteloua eriopoda*, both warm-season grasses. Although *Xanthocephalum sarothrae* can grow in the spring at relatively low temperatures if soil water is available, most of its growth occurs during the summer. *Salsola kali* completed its life cycle somewhat earlier than the perennial grasses. Annual plants often complete their life 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 elata* (Engelm.) and *Prosopis juliflora* (Swartz) DC. because of sampling problems discussed later.

The analysis of variance for all 3 years showed a significant difference between the grazed and ungrazed treatments in amounts of current-live and recent-dead categories ($P < 0.01$ or 0.05). However, there was no difference 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 ($P < 0.05$) among sampling dates for all years and ecological categories except the old-dead and current-live compartments in 1972. 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. Biomass differences were not so great between treatments early in the growing season as later in the season.

The pattern of seasonal changes in current-live biomass of all species was a build-up phase, a short period of maximum biomass, and a rapid decline (figures 2, and 3). The rapid decline in standing live material does not represent a transfer to litter, but rather a transfer to recent-dead. The decline in current-live was usually accompanied by rapid and corresponding increases in recent-dead. For example, current-live material declined from 100 g/m^2 on September 1, 1970 to 56 g/m^2 on September 26, 1970, while the recent-dead in-

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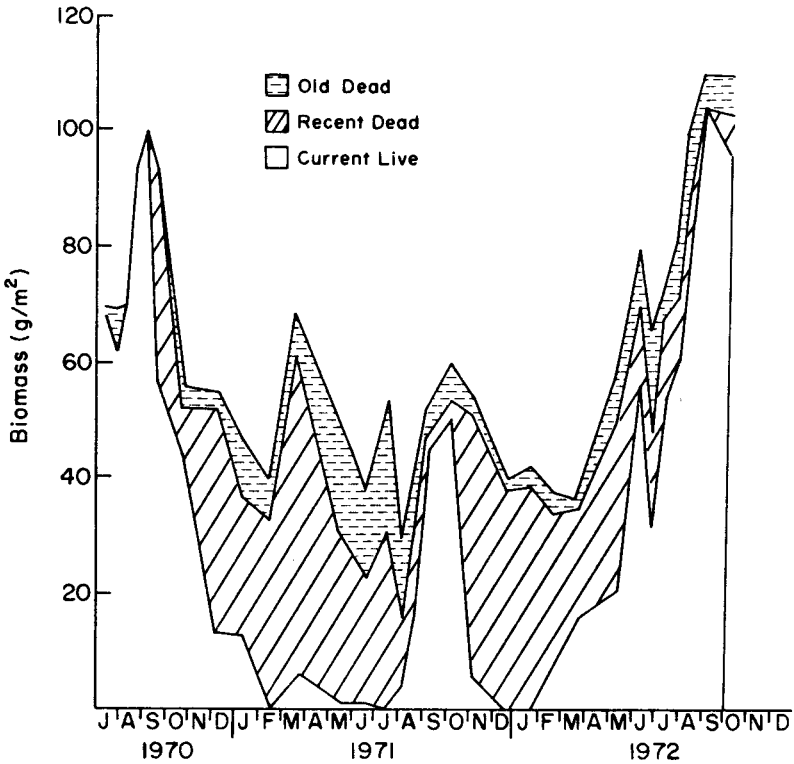
creased from 0 to 34 g/m² (figure 3) on the ungrazed treatment. The general pattern for recent-dead on both treatments was a gradual decline during the dormant season as the material turned grey or black until it was reclassified as old-dead material (figures 2 and 3). The old-dead standing crop was more uniform throughout the year with higher values on the ungrazed treatment 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, the old-dead was detached and became part of the mulch at about the same rate as the recent-dead was added to old-dead.
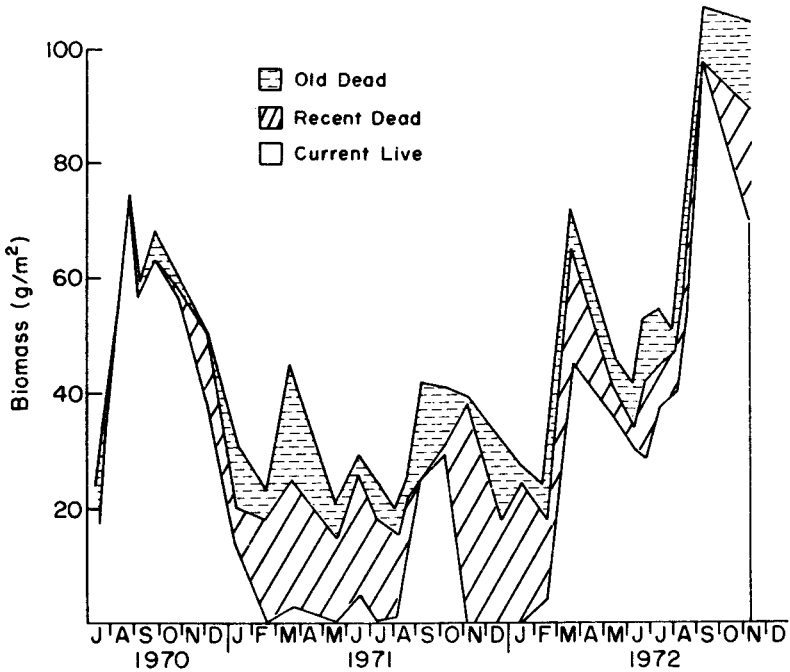
Although precipitation was much lower in 1970 than in 1972, peak standing crop was only slightly higher in 1972 than in 1970 on the ungrazed treatment (figure 3). However, on the grazed treatment, the peak standing crop was about 25 g/m² greater in 1972 than in 1970. These differences can probably be explained by a decrease in basal area of *B. eriopoda* plants during the dry years of 1970 and 1971. Such reductions in *B. eriopoda* cover during droughts are typical in the southwest (Lohmiller 1963; and Valentine 1970; and Herbel, Ares and Wright 1972). Therefore, there probably were not enough *B. eriopoda* plants to take advantage of the added soil moisture in 1972, and the annual forbs and grasses added some biomass, but not so much as *B. eriopoda*. Parker (1963) showed that *B. eriopoda* cover was a major factor in

Fig. 4. Aboveground current-live standing crop for perennial and annual warm-season grasses on ungrazed and grazed treatments.

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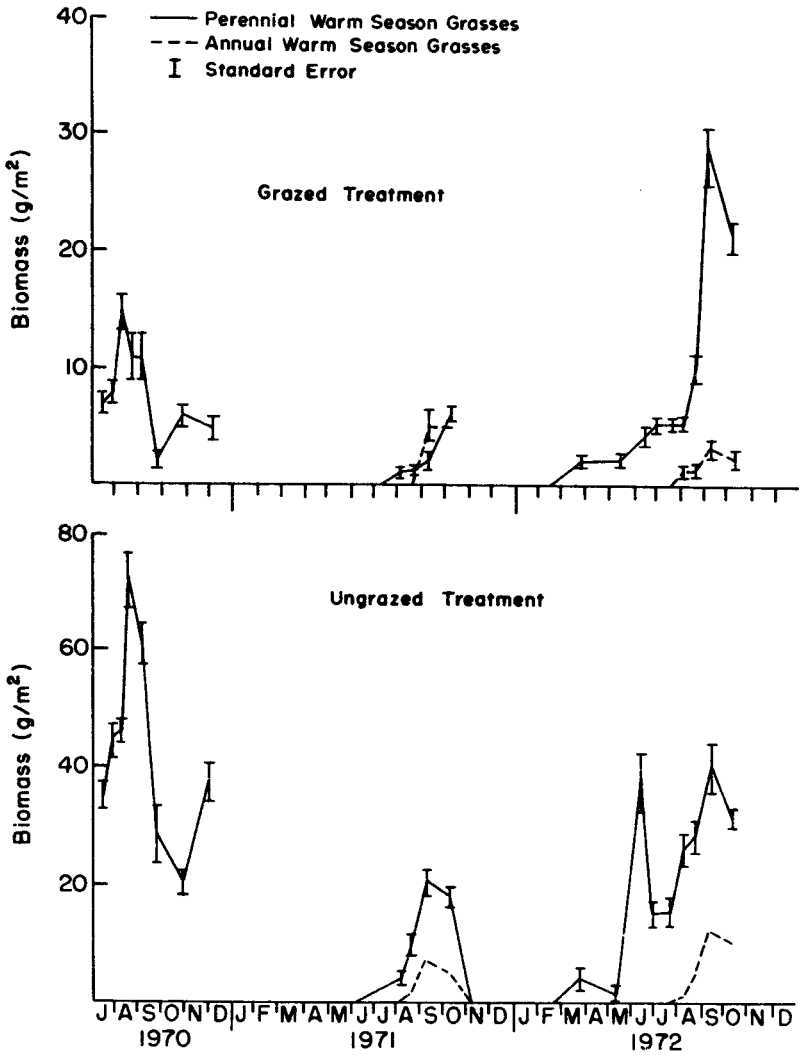
effective utilization of soil water. *B. eriopoda* responds to wet years very slowly since its main method of reproduction is vegetative.

In both 1970 and 1971, the current-live standing crop in the ungrazed treatment greatly exceeded that of the grazed treatment (figures 3 and 4). These differences reflect the greater vegetational cover and higher range condition in the ungrazed treatment than in the grazed treatment. However, in 1972, peak live biomass was nearly as great in the grazed as in the ungrazed treatment. Species compositional differences probably account for these differences.

The mulch data were quite variable, and seasonal trends were difficult to discern. The quadrats were not well suited for sampling mulch on desert grasslands. During the windy season, most of the light and moderately light mulch is redistributed and tends to be concentrated at the base of shrubs and within shrub crowns. Consequently, there are many areas nearly bare whereas other areas have concentrations of mulch. Differential size of mulch also contributed to high variability in weight among quadrats. Plants such as *Yucca elata, Prosopis juliflora,* or *Xanthocephalum sarothrae* may contribute much weight in certain quadrats and none in others. The large differences in mulch between two consecutive sampling dates probably reflect sampling variation, rather than mulch dynamics.

Sampling did show that mulch biomass was always significantly greater on the ungrazed than on the grazed treatment and that the amount of mulch decreased during the 3 years of the study (table 1). Since aboveground herbage was generally higher on the ungrazed treatment than on the grazed treatment, it is not surprising that mulch biomass was also greater. The reduction of mulch from 1970 to 1971 probably resulted from the low aboveground production in 1971.

Mulch values fall within the 20 to 2500 g/m², of mulch standing crop reported by Tomanek (1969) for the Northern Great Plains. Few data are available for desert grassland areas.

Seasonal changes in ecological groups and individual species. Two shrubby species, *Yucca elata* and *Prosopis*

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Table 1. Standing crop of mulch (g/m^2) averaged over all dates for each of the three years of the study on ungrazed and grazed treatments.

Treatment	1970	1971	1972	Average
Ungrazed	A[1] 58.2 a	B 46.4 a	C 28.1 a	44.2
Grazed	A 40.1 b	B 24.0 b	C 21.3 b	28.5
Average	A 49.1	B 35.2	C 24.7	

[1] Means with different capital letters are significantly different (P < 0.05) among years within treatments; means with different lower case letters are not significantly different (P < 0.05) within a year between treatments.

juliflora were difficult to sample because of their scattered distribution and large size. These species were found in only a few of the rectangular and circular quadrats used in the study. When a quadrat included one of these shrubs, the biomass was often 100 to 1000 times the average quadrat biomass. Distinctions between current-live and perennial-live material were also difficult to make. Consequently, sampling variation with *Y. elata* and *P. juliflora* from one sampling period to another were a reflection of the number of quadrats containing these plants rather than growth or loss of biomass.

The average biomass *Y. elata* was much higher on the ungrazed treatment than on the grazed treatment. *Y. elata* was often encountered on only 1 to 2 quadrats per replication. In 1971, the highest average biomass recorded for *Y. elata* was 191 g/m² and it occurred on only a few quadrats. The greatest biomass for *P. juliflora* was 46 g/m² in 1971 and 48 g/m² in 1972 on the ungrazed treatment.

The analysis of variance showed a significant difference (P < 0.01) among ecological categories for all compartments. This difference is obvious considering the relatively large biomass of perennial warm-season grasses and annual warm-season forbs compared to some of the cool-season species and

perennial forbs. The treatment x ecological category inter-action was also significant (P < 0.01) for all compartments and years, except the old-dead compartment in 1970, indi-cating differences in biomass of the different ecological categories on the grazed and ungrazed treatments. For example perennial warm-season grasses comprised 63% of the time-weighted seasonal biomass means on the ungrazed treatment in 1970 but 15% on the grazed treatment (table 2). However, annual warm-season forbs and shrubs contributed much more biomass on the grazed treatment.

Biomass of perennial warm-season grasses was higher in 1970 than in 1972 on the ungrazed treatment, but higher in 1972 on the grazed treatment (figure 4, table 2). These differences may have been a result of mortality of *B. eriopoda* and a reduction in vigor on the ungrazed area and establishment of new seedlings of *S. flexuosus* on the grazed area. The standing crop curves for *B. eriopoda* and *S. flexuosus* support these views. In 1970, the peak standing crop of *B. eriopoda* was more than 50 g/m² on the ungrazed area compared with less than 15 in 1971 and only 34 g/m² in 1972 (figure 5). *B. eriopoda* never contributed much biomass on the grazed area. The analysis of variance showed a significant difference between treatments for most com-

Table 2. Percentage contribution to peak above-ground standing live by various ecological categories.

Category	1970		1971		1972	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Perennial Warm-Season Grass	14.5	62.7*	36.7	47.1	32.8	50.1*
Perennial Warm-Season Forb	3.5	1.1*	4.3	1.8*	13.1	2.9*
Annual Warm-Season Forb	33.8	11.4*	51.3	45.7*	42.4	44.3
Shrub	48.2	24.8*	6.5	5.0	11.7	2.7*
Other	0	0	1.2	0.4	0	0
Total	100.0	100.0	100.0	100.0	100.0	100.0

*Difference within a year between grazed and ungrazed are significant at P < 0.05.

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partments each year. Even biomass of *S. flexuosus* was considerably lower in 1972 than in 1970 on the ungrazed area (figure 6), which also suggests mortality and loss of vigor. However, on the grazed area (figure 7), peak standing crop of *S. flexuosus* was more than twice as great in 1972 as it was in 1970. Much of this increase may have been contributed by seedlings established during the wet summer of 1972. Besides open spaces for seedling establishment in the grazed area, reasons for the rapid increase in biomass of *S. flexuosus* on the grazed area contrasted to the decrease on the ungrazed area are not clear. Annual warm-season grasses were not encountered in 1970 and made only small contributions to standing live in 1971 and 1972 (figure 4). The analysis of variance indicated few significant differences

Fig. 5. Standing crop of <u>Bouteloua eriopoda</u> on the ungrazed treatment during all 3 years of the study.

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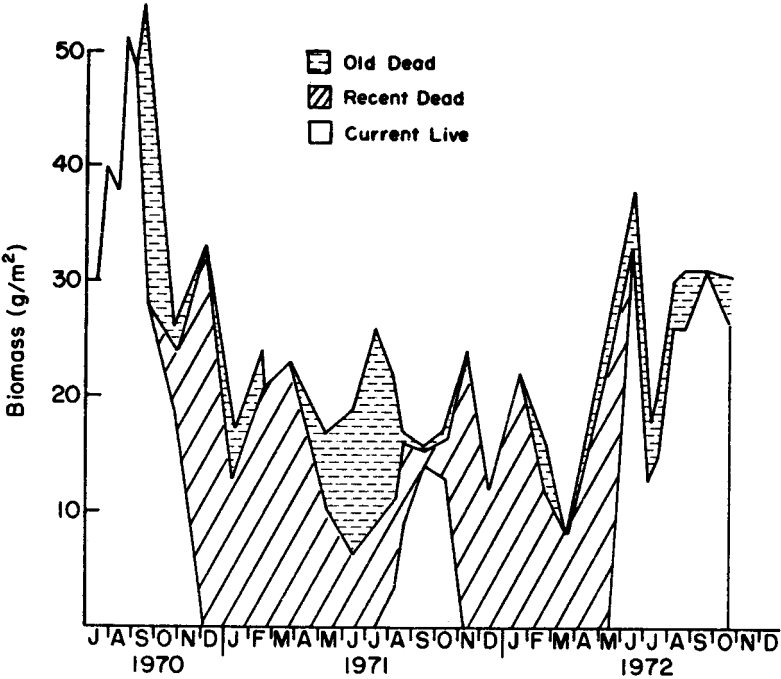
Fig. 6. Standing crop of _Sporobolus flexuosus_ on the ungrazed treatment during all 3 years of the study.
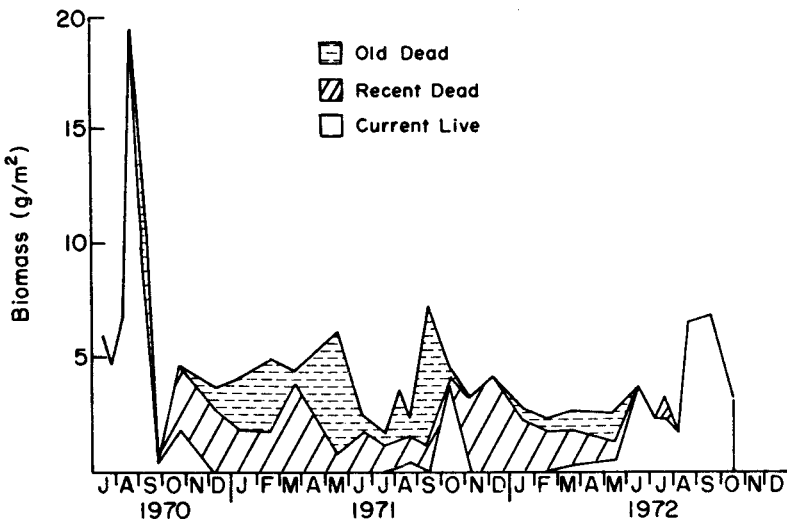
among categories for annual warm-season grasses except among dates for all 3 years. Although there were no grass species classified as cool-season, some species may grow in the spring if soil water is available. _S. flexuosus_ and several species of _Aristida_ often produce new leaves during cool, spring weather. However, during most years much _S. flexuosus_ growth is made during the summer (cf. figs. 6, 7).

Warm-season forbs were a major component of the standing crop of vegetation throughout the study (table 2). On the grazed area the biomass of warm-season forbs seemed directly related to precipitation, with the lowest production occurring in 1971 and the highest in 1972. On the ungrazed treatment, however, production of warm-season forbs was greater in 1971 than in 1970. Apparently, the annual forbs were able to utilize the available soil water in 1970 before the perennial grasses. The most important annual warm-season forb was _S. kali_, which followed similar growth patterns on both treatments in 1971 and 1972. In 1970, _S. kali_ peak standing live was significantly (P < 0.05) greater on the

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Fig. 7. Standing crop of Sporobolus flexuosus on the grazed treatment for all 3 years of the study.
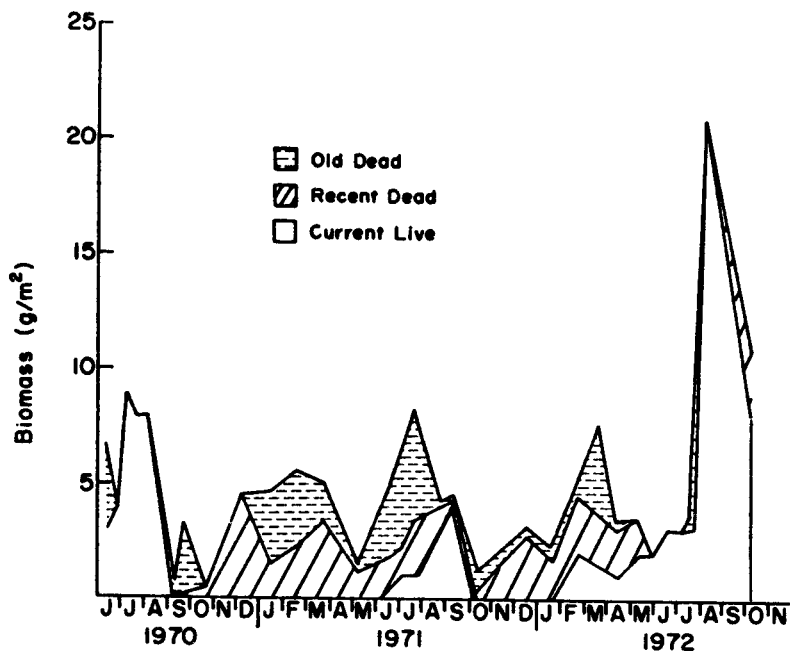
grazed area than on the ungrazed area but there was no difference in 1971 or 1972. Competition from perennial grasses, which were fairly vigorous in 1970, may have reduced productivity of *S. kali* on this treatment.

Annual cool-season forbs were important only during 1972, 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 annaul warm-season forbs were just beginning growth. One species, *Cryptantha crassisepala,* contributed most of the biomass for cool-season annual forbs. The peak biomass of *C. crassisepala* and cool-season annual forbs was greater on the grazed treatment than on the ungrazed treatment, especially in 1972 (table 3).

Perennial warm-season forbs contributed little to community standing live biomass in either 1970 or 1971, but

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Table 3. Peak standing crop of current live material (G/m^2) of important species on the ungrazed and grazed treatments during all three years of the study.

Species	1970		1971		1972	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Bouteloua eriopoda	51	5*	27	1*	31	1*
Sporobolus flexuosus	19	9*	5	4	7	21*
Xanthocephalum sarothrae	19	32*	1	3	7	7
Salsola kali	7	25*	3	3	37	41
Cryptanthus crassisepala	4	1	1	>1	15	24*
Croton corymbulosus	4	3	2	2	6	5
Dithyrea wislizeni	0	>1	0	>1	5	7

*Difference within a year between ungrazed and grazed significant at $P < 0.05$.

were somewhat more important in 1972, especially on the grazed treatment (figure 8). Growth patterns of this group were similar on both treatments.

The standing crop of shrubs other than *Yucca elata* and *Prosopis juliflora* varied from one sampling period to another (figure 8). These variations and relative large standard errors associated with each mean are probably related to the circular quadrats used and the distribution patterns of the shrubs. The major shrub on both treatments was *Xanthocephalum sarothrae*. Differences in biomass among years were similar for shrubs and *X. sarothrae* (figure 8, table 3). In 1970, *X. sarothrae* populations were high and biomass exceeded 30 g/m² on the grazed treatment and approached 20 g/m² on the ungrazed treatment. This difference was significant (P < 0.05) in 1970, but the differences were not significant during the other years. During the drought of 1971 mortality of *X. sarothrae* was high and biomass of shrubs and *X. sarothrae* were very low. Many seedlings became established during 1972, but live biomass did not reach the highs of 1971. The standing crop of recent and old dead material of *X. sarothrae* also varied widely and was generally fairly high in early 1971 and much lower in 1972.

The analysis of variance of individual species indicated a significant difference between grazing treatments for most *B. eriopoda* compartments and for *C. crassisepala, S. kali,* and *X. sarothrae* current-live compartments. For the annual species the dead compartments were often missing. There was no significant difference between treatments for *S. flexuosus* for any compartment any year.

Biomass differences were significant for most species and compartments among dates except for *X. sarothrae*. The date x treatment interaction was not significant for the current-live compartment for most species, except *C. crassisepala* indicating that treatment differences were consistent across sampling dates.

B. eriopoda had the highest peak standing crop of any species on the ungrazed treatment in 1970 and 1971, but was exceeded slightly by that of *S. kali* in 1972 (table 3). Peak standing crops of *S. flexuosus* and *X. sarothrae* were nearly 20 g/m² in 1970, but declined considerably in 1971. In

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Fig. 8. Aboveground current live standing crop of shrubs and perennial warm-season forbs on the ungrazed and grazed treatments.
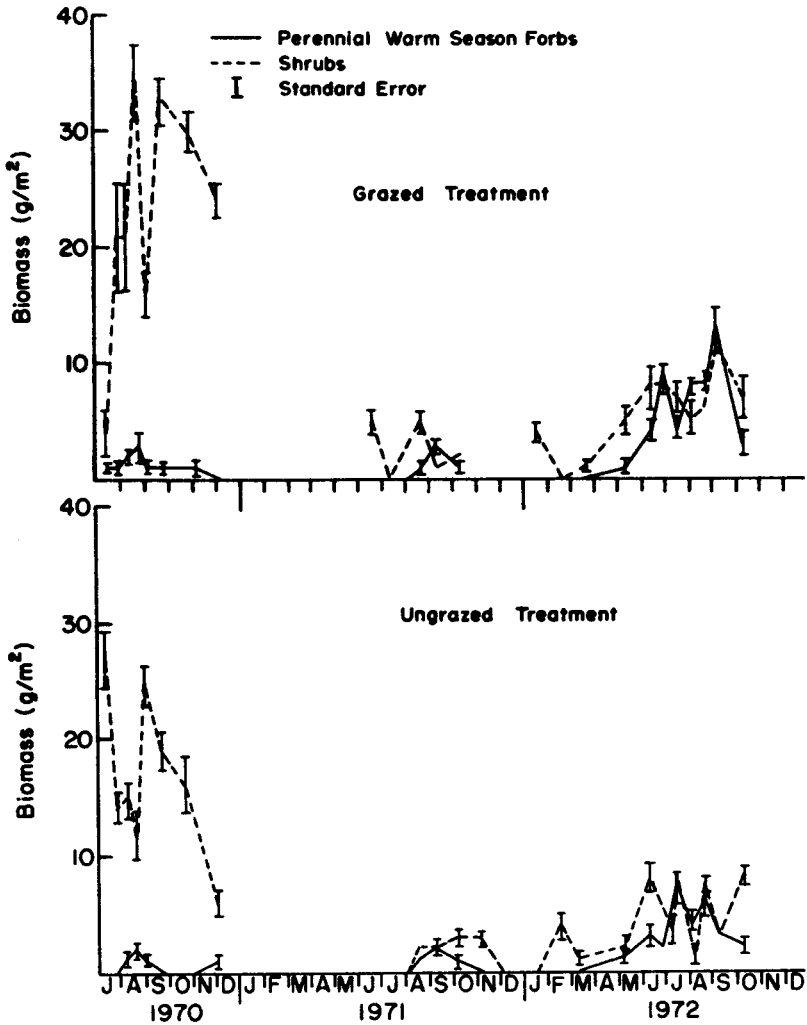
1972 the peak standing crop was 15 g/m² or more for *B. eriopoda, S. kali,* and *C. crassisepala* on the ungrazed treatment. The major warm-season forb was *Croton corymbulosus*

Engelm. *Dithyrea wislizenii* Engelm. was fairly abundant in 1972 on the site and more abundant off the site. *B. eriopoda* was never very abundant on the grazed treatment where the peak standing crop was only 1 g/m² in both 1971 and 1972.

Seasonal dynamics of belowground biomass. Although the data for belowground biomass were quite variable, with large standard errors associated with the means, some seasonal patterns repeated themselves during the 3 years of the study. In general belowground biomass declined in the winter and spring on both treatments (figure 9). For example, belowground biomass declined from 221 g/m² on the ungrazed treatment on February 20, 1971, to 118 g/m² on May 18, 1971 and from 231 to 94 g/m² on the grazed treatment. These general declines were evident for all depths, but perhaps more pronounced for the 0 to 10 cm depth. Root respiration during the dormant season may account for some of this decline. 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/m² on the grazed treatment from February to May 1971 but increased from 146 to 178 g/m² on the ungrazed treatment during the same period. Belowground biomass appeared to increase during the growing season, probably because of root growth and perhaps 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 recorded.

Belowground biomass was consistently higher in the ungrazed than in the grazed treatment at the 0 to 10 cm depth (figure 9). Over the 3-year study, belowground biomass averaged 16 g/m² more at each sampling date on the ungrazed treatment than on the grazed treatment. There were only small and inconsistent differences in belowground biomass between treatments for the other depths (figure 9). 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, *X. sarothrae* was more abundant on the grazed treatment.

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Fig. 9. Belowground standing crop by depth for the ungrazed and grazed treatments.
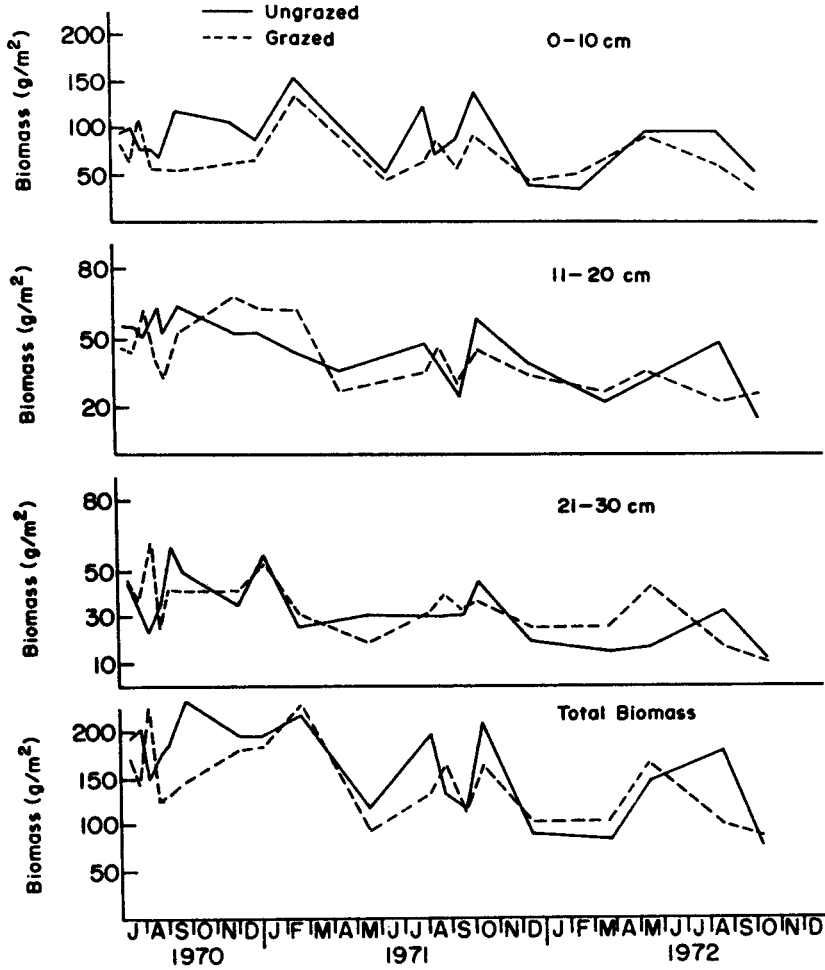
Belowground biomass differed little between 1970 and 1971. However, somewhat surprising was the general decline, primarily in the 0 to 10 cm depth, in belowground biomass from 1971 to 1972 (figure 9) in view of the aboveground growth in 1972. Perhaps there was more root mortality in

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the 1971 drought and increased decomposition of below-ground 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. There was no evidence of root accumulation 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 cm, and 20% in the 21 to 30 cm depths.

Belowground:aboveground ratios: Belowground:aboveground ratios were calculated by the use of current-live, recent-dead, old-dead and litter. *Y. elata* and *P. juliflora* were included since these could not be separated in below-ground biomass. All belowground organic matter was sampled, and compared with all aboveground organic matter. The data revealed no consistent seasonal changes, but some ratios varied between sampling dates. Consequently, only yearly and treatment means are shown in table 4. Ratios were consistently higher on the grazed treatment than on the ungrazed treatment since there were only small differences in belowground biomass between treatments and relatively large differences in aboveground biomass. Average ratios for 1970 and 1972 were not significantly different (P < 0.05) but ratios in 1971 were higher because of the relatively large belowground biomass and the small aboveground biomass (table 4).

Table 4. Belowground:aboveground ratios averaged over all sampling dates for each year[1].

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

[1] Aboveground biomass includes current live, recent dead, old dead, litter, and *Yucca elata* and *Prosopis juliflora.*
[2] Means with the different small letters are significantly different (P < 0.05) within a year; those with different capital letters are significantly different (P > 0.05) among years.

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Net Primary Productivity

Aboveground. Aboveground net primary productivity (ANPP) has been calculated by many approaches with the use of harvest data for herbaceous species such as those collected in this study. Many studies have shown that the use of peak community standing crop as a measure of ANPP may seriously underestimate ANPP since the contribution of individual species of groups that grow at different times may not be taken into account (Odum 1960; Malone 1968; Sims and Singh 1971; Kelly, Van Dyne and Harris 1974; Pieper, Dwyer and Banner 1975; Singh, Lauenroth and Steinhorst 1975). Adding the peak standing crop by species may underestimate ANPP if there are periods of no growth with reduction of aboveground live material followed by a period of renewed growth. Adding all positive increments by species would take these declines and growth spurts into account, but could result in some overestimations of ANPP, especially if sampling variation is high and positive increments were added that were merely random sampling fluctuations from one period to the next.

A wide variation in ANPP can be obtained from the data for the IBP Desert Grassland Site by using different methods of calculation (Singh, Lauenroth and Steinhorst 1975). In general, use of peak community live standing crop gave the lowest values, especially for the wet year of 1972. However, some lower values were obtained with other methods and treatments. There was considerable variation among the methods by year and treatment. Recommendations of Singh, Lauenroth and Steinhorst (1975) were followed and the sum of species peaks was used for the following discussion.

ANPP was condiderably higher for the ungrazed treatment than for the grazed treatment in 1970 and 1971. In 1971, ANPP was nearly 60% higher on the ungrazed than on the grazed treatment (table 5). However, in 1972, ANPP differed little between the two treatments, because of the contribution by annual forbs and *S. flexuosus* as discussed earlier.

Ecological groups contributing most to ANPP were warm-season species (table 6), with grasses most important on the ungrazed treament in 1970 and 1972, and shrubs on the grazed treatment in 1970 and 1971. Cool-season forbs

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Table 5. Aboveground net primary (g/m^2/year) calculated by adding species peaks of standing live biomass.

Year	Ungrazed	Grazed	Average
1970	134	97*	115.5
1971	125	51*	88.0
1972	186	180	183.0
Average	148	109*	128.5

*Difference between ungrazed and grazed significant at P < 0.05.

Table 6. Contribution (%) to net primary production by various ecological categories, based on time-weighed seasonal biomass means.

Ecological Category	1970		1971		1972	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Warm season grasses	53.0	14.6	37.1	21.0	41.5	18.6
Warm season forbs	8.0	26.6	31.7	28.0	31.4	37.0
Cool season forbs	1.0	0.2	0	0	10.1	15.0
Warm season shrubs	18.5	40.4	31.2	51.0	17.0	29.4

were important only in 1972, when *C. crassisepala* was abundant on all areas.

The highest primary productivity for any period occurred in August 1970, when productivity on the ungrazed treatment was 2.4 g/m² /day (table 7) which corresponds to the period following precipitation. When soil water became available in 1972, productivity was only modest on the ungrazed treatment. This low amount is probably a result of lack of photosynthetic tissue following the drought of 1971. Productivity was sustained longer in 1972 than in the other years, resulting in the high biomass and ANPP on the un-grazed treatment in 1972.

Highest productivity on the grazed treatment occurred when more than 2.15 g/m² /day were produced between August 23 and September 12, 1972 (table 8). Much of this amount was contributed by warm-season species, especially

Table 7. Aboveground net primary productivity (g/m^2/day) for all species, some groups of species and individual species for the ungrazed treatment.

Period	All Species	PWSG¹	AWSF¹	ACSF¹	SHRUBS	BOER¹	SPEL¹	SAKA¹	CrCr¹	XASA¹
1970										
7/14 – 7/30	2	0.50	0.27	0.19					0.36	
7/31 – 8/10	0.73	0.10	0.50		0.09	0.63	0.18	0.18		
8/11 – 8/20	2.40	2.60	0.08			1.30	1.20	0.20		
8/21 – 9/1	0.50				1.17			0.17		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		0.12	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					0.08	0.08
3/29 – 5/13	0.11		0.02	0.09	0.02				0.09	
5/14 – 6/14	1.17	1.23	0.10		0.50	1.03	0.13	0.02		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					
8/23 – 9/12	1.10	0.35	0.70		0.25			0.70		
9/13 – 10/7					0.19	0.15				0.19

¹ Symbols are as follows: PWSG-perennial warm season grass; AWSF-annual warm season forb; ASCF-annual cool-season forb; BOER-*Bouteloua eriopoda*; SPEL-*Sporobolus flexuosus*; SAKA-*Salsola kali*; CrCr – *Cryptantha crassisepala*; XASA-*Xanthocephalum sarothrae*.

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Table 8. Aboveground net primary productivity (g/m^2/day) for all species, some groups of species and some individual species for grazed treatment.

Period	All Species	PWSG[1]	AWSF[1]	ACSF[1]	SHRUBS	BOER[1]	SPEL[1]	SAKA[1]	CrCr[1]	XASA
1970										
7/14 – 7/30	1.19	0.06	0.06		1.06		0.06	1.13	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	2		0.42					0.58		
9/2 – 9/26		0.12								
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		0.29					
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	0.05		0.70			0.05	0.30			
7/20 – 8/2	0.08						0.23			
8/3 – 8/22	0.78	0.28	0.50		0.17		0.50	0.08		
8/23 – 9/12	2.15	0.95	0.45		0.25	0.90	0.05		0.15	
9/13 – 10/7							0.38			

[1] Symbols are as follows: PWSG-perennial warm season grass; AWSF-annual warm season forb; ACSF-annual cool season forb; SPEFL-Sporobolus flexuosus; SAKA-Salsola sali; CrCr-Cryptantha crassisepala; XASA Xanthocephalum sarothrae.
[2] Blank spaces indicate a decrease or no change in biomass for the period.

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Sporobolus flexuosus and annual forbs. Surprisingly, *Salsola kali* contributed very little during this period.

Shrub productivity was highest in 1970 on both treatments and was reduced thereafter because of the drought (table 7 and 8) on both treatments. For any single species, productivity was highest for *Bouteloua eriopoda* in August 1970 and from May 14 to June 14, 1972, on the ungrazed treatment when productivity was more than 1 $g/m^2/day$. *S. flexuosus* productivity also approached and exceeded 1 $g/m^2/day$ on both treatments. *S. kali* and *C. crassisepala* had the highest productivity of any forbs. Most of the warm-season species probably follow the C^4 photosynthetic pathway, but the main cool-season forb, *C. crassisepala* is a C^3 plant (Lewis 1974). Primary productivity of this desert grassland is lower than that of all other ungrazed grasslands reported by Lewis (1971) for the 1970 season except for the Pawnee Shortgrass Site. Productivity of over 6 $g/m^2/day$ was calculated for two tall grass sites and over 5 $g/m^2/day$ for two mixed grass sites. Productivity for the Pawnee Site was about 2.0 $g/m^2/day$. The reason for the low productivity at the Jornada was probably related more to limited leaf area and photosynthetic tissue than to lack of soil water. In late summer of 1972, soil water was probably not restricting photosynthesis and yet productivity was only about 2 $g/m^2/day$. However, even on good condition desert grassland, the 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) (Singh and Yadava 1974). The four methods yielded variable results, particularly in 1972 (table 9). BNPP values were lowest when the difference between the peak and the preceding minimum value was used. 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 result seems unrealistic in view of the favorable growing conditions during 1972. One method that takes

Table 9. Estimates of annual belowground productivity calculated by four methods for the Jornada (g/m²).

Method	1970 Ungrazed	1970 Grazed	1971 Ungrazed	1971 Grazed	1972 Ungrazed	1972 Grazed
1	84	68	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	13

[1] 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.

into account changes in biomass by depth did show some belowground biomass productivity for 1972 and slightly lower values for 1970 and 1971 than do the other methods.

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 separate living and dead portions. If a substantial portion of the belowground biomass were dead, changes in the living portion would be masked. Separation by species was not possible either and if roots of one species had been decreasing while those of another were increasing, the net change might be zero. Some of these species shifts might have been occurring in 1972. No direct measure of belowground decomposition was made, and this was certainly a complicating factor.

Method 3 in table 9, with the sum of positive increments by depth, was 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. It

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is not possible to explain these relationships with the present data, but they are probably related to differences and changes in species composition, 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 reported by Smith (1973). Plant biomass was converted to caloric values by multiplication of aboveground biomass by 4 and belowground biomass by 4.7. Thus, net primary productivity values presented (table 10) are in direct relation to ANPP (table 5).

Efficiency of energy capture by desert grassland plants on the 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 10).

Aboveground efficiency was always higher on the ungrazed treatment than on the grazed treatment. Efficiency for total net primary productivity ranged from 0.11% on the grazed treatment in 1970 to 0.21% on the ungrazed treatment

Table 10. Net primary productivity and efficiency for utilization of solar energy on ungrazed and grazed treatments.

Treatment	1970	1971	1972	Average
Aboveground net primary productivity (kcal/m²)				
Ungrazed	536	500	744	593
Grazed	388	204	720	437
Efficiency (%)				
Ungrazed	0.07	0.07	0.10	0.08
Grazed	0.05	0.03	0.09	0.05
Belowground net primary productivity (kcal/m²)				
Ungrazed	526	917	390	611
Grazed	531	912	362	602
Total net primary productivity (kcal/m²)				
Ungrazed	1,062	1,417	1,134	1,204
Grazed	912	1,116	1,082	1,039
Efficiency (5)				
Ungrazed	0.13	0.21	0.15	0.16
Grazed	0.11	0.16	0.14	0.14

in 1971 (table 10). 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 by use of the biomass data (table 5) following methods outlined by Sims and Singh (1971) and Singh and Yadava (1974). These data indicate some of the lag effects in these transfers. For example, the transfer from ANPP to standing dead in the 1970 ungrazed treatment exceeded ANPP that year by more than 40 g/m² and was probably a result of aboveground biomass produced the previous year (table 11). Transfers from ANPP to standing dead in 1972 were considerably less than ANPP, probably reflecting relatively low ANPP the previous 2 years. Although these transfers have not been measured directly, it is likely that standing material may remain several years, since there seldom is snow cover to accelerate transfer to litter. Wind is a factor for some species such as *Salsola kali* and *Sporobolus flexuosus*, which are easily broken off and added to the litter.

Table 11. Compartmental transfers for growing season (g/m²) for ungrazed and grazed treatments.

Year	Treatment	ANPP	SD[1]	L[2]	LD[3]	BNPP[4]	RD[5]
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

[1] Transfer to standing dead
   ANPP + initial live biomass - final live biomass = SD
[2] Transfer from SD to litter compartment
   SD + initial biomass of standing dead - final live biomass of litter = L
[3] Litter disappearance
   L + initial biomass of litter - final live biomass of litter = LD
[4] Summation of significant positive increases in biomass by depth.
[5] BNPP + initial belowground biomass - final belowground biomass = RD

Root disappearance was calculated by two methods as shown in table 12. Some differences between the methods were small and others were rather large. The data for method 2 were used for calculations in table 13. In 1970 and 1971 the root death or disappearance value was less than that for BNPP, but in 1972, the reverse was true. Root disappearance was greater on the ungrazed treatment in 1970, but greater on the grazed treatment in 1971 and 1972.

Although climatic variations in desert grasslands are great, as are yearly variations in primary productivity, the data indicated that over the 3-year period, some types of equilibria were present. On the ungrazed treatment, there was little difference in the biomass transferred from ANPP to standing dead or that transferred from standing dead to mulch (table 13). ANPP and mulch disappearance were nearly equal for the 3 years. On the grazed area, transfer to standing dead and mulch disappearance were equal for the 3 years. There were some differences in BNPP and root disappearance, but these were not great. Apparently the 2 dry years followed by 1 wet year resulted in balances for these productivity characteristics.

Table 13 shows the compartmental transfer functions as decimals or percentages of transfer from one box to another. For example, in 1970 on the ungrazed treatment, 54% of the total net primary production was accounted for by above-

Table 12. Annual rate of belowground biomass diasappearance (g/m^2) calculated by two methods for the Jornada.

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

[1] Methods used were the following:
   (1) Peak biomass minus succeeding biomass minimum = RD
   (2) BNPP + Initial root biomass – Final root biomass = RD

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Table 13. Comparmental transfer functions for all 3 years on ungrazed and grazed treatment. Values are ratios between compartment values and the value transferred to next compartment. See text for full explanation.

Transfer	1970		1971		1972	
	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
TNPP to ANPP[1]	0.54	0.46	0.39	0.21	0.69	0.70
TNPP to BNPP	0.46	0.54	0.61	0.69	0.31	0.30
ANPP to SD	1.33	0.95	1.06	1.31	0.54	0.45
SD to M	0.79	0.86	0.93	0.79	1.30	0.90
ANPP to M	0.95	0.81	1.05	1.21	0.64	0.37
M to MD	1.34	1.41	1.07	1.17	0.90	0.91
BNPP to RD	0.92	0.59	0.75	0.82	1.28	2.40

[1] TNPP is total net primary productivity; ANPP is aboveground net primary productivity; BNPP is belowground net primary productivity; SD is standing dead; M is mulch; MD is mulch disappearance; RD is root disappearance.

ground net primary productivity and 46% by belowground net primary productivity. Values close to unity indicate that the input in a particular compartment equals output. For example, the transfer to ANPP to SD in 1970 and 1971 was about 1 for' both treatments, indicating nearly complete transfer of live material to standing dead (figure 10). 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 mulch to mulch disappearance exceeded 1 in 1970 and 1971, indicating a net loss of mulch, probably because of low ANPP for those 2 years and higher rates of mulch disappearance.

Belowground turnover rates indicate the dynamics of root and other belowground organic matter. As defined by Kucera (1973), turnover is the proportion of total biomass (dead material + annual net productivity) decomposing each year. In this respect, turnover is equivalent to the decay constant, k, of Jenny (1961). Turnover rates were calculated as given by Dahlman and Kucera (1965) as the ratio of annual increment to total average belowground biomass. Annual turnover rates determined by this method are presented in table 14. Turnover rates were lower in 1970 and 1972 than they were in 1971. Belowground biomass was highest in 1971 and lowest in 1972; thus, it appears that turnover rate is inversely related to belowground biomass. However, belowground sampling was confounded by our inability to separate live from dead and difficulty in determining annual increment. In 2 of the 3 years, belowground turnover was higher on the ungrazed treatment than on the grazed treatment. Apparently much more experimental work is needed to determine belowground dynamics and their relation to grazing.

Table 14. Turnover of belowground biomass on ungrazed and grazed treatment for three years.

Treatment	1970	1971	1972
Ungrazed	0.39	1.21	0.54
Grazed	0.57	0.79	0.34

Fig. 10. Rates of transfer from one compartment to another.[1]

Ungrazed—1970

Grazed—1970

Ungrazed—1971

Grazed—1971

Ungrazed—1972

Grazed—1972
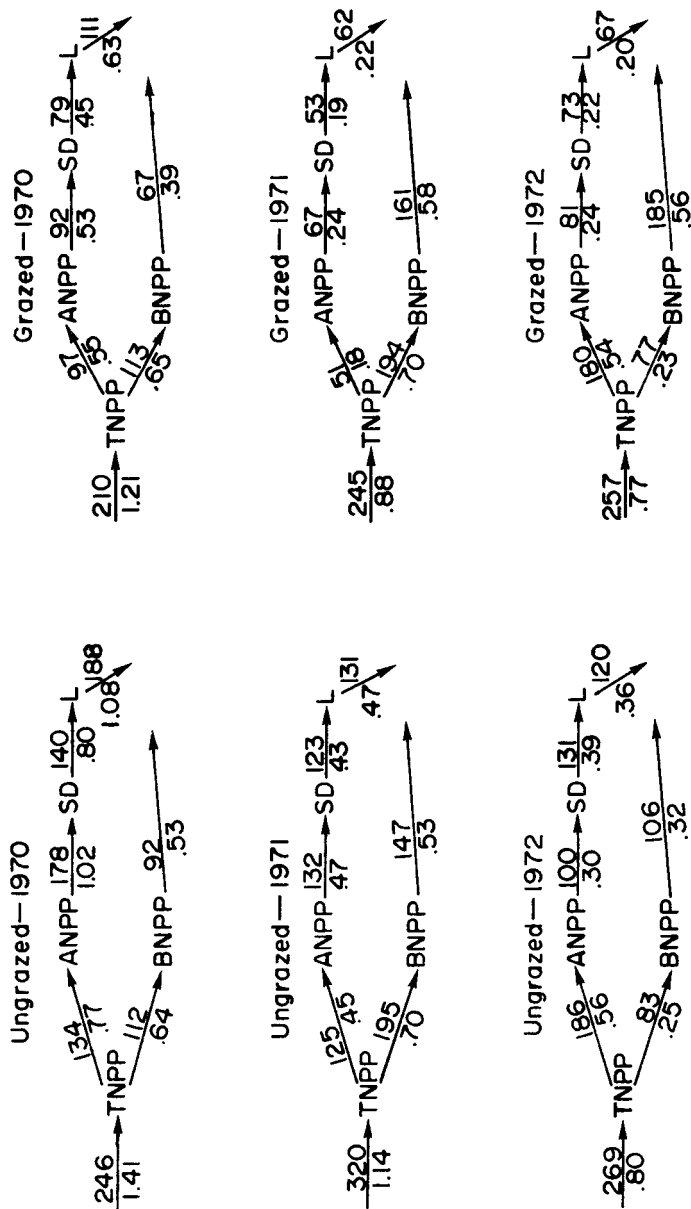
[1] Figures above the line are annual rates in g/m², while those below the line are daily rates in g/m²/day. Rates per day were calculated on a sampling season of 174 days in 1970 and a growing season of 280 days for 1971 and 333 days for 1972 (taken from table 1).

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DISCUSSION AND CONCLUSIONS

Primary production on desert grasslands tends to occur in irregular patterns and can occur during any month. Availability of soil water appears to be the primary environmental variable that triggers plant growth, although temperature may determine distribution of growth among the taxa present on an area. Production during the hot summer months was contributed mainly by grasses, forbs and shrubs, but production during cooler portions of the year is primarily by forbs such as *C. crassisepala*.

Annual aboveground net primary productivity of desert grasslands appears to be lower than that of most other U.S. grasslands (Sims and Singh 1971). Both tall grass and midgrass ecosystems exhibited higher annual aboveground productivity than the desert grassland, but a sagebrush-grass shrub-steppe ecosystem had the lowest annual productivity reported (98 kg/m² compared to 148 g/m²) for the desert grassland.

Root system biomass of desert grasslands apparently is much lower than that of other grasslands (Sims and Singh 1971). Average belowground biomass of desert grassland was only 205 g/m² compared to more than 1000 g/m² for all other grasslands on the ungrazed treatments (Sims and Singh 1971). Average annual belowground productivity was only 123 g/m² for the desert grassland compared to about 600 for other grasslands. Explanations for the low belowground: aboveground ratios on desert grasslands are not apparent.

Domestic livestock grazing at heavy rates reduces aboveground productivity and results in shifts in species composition. On the ungrazed treatment, perennial warm-season grasses contributed over 50% of the peak aboveground standing crop compared to less than 30% on the grazed treatment. Annual warm season forbs were more important contributors to aboveground standing crop on the grazed treatment than on the ungrazed treatment.

Desert grasslands are characterized by high solar radiation and fairly low productivity. Consequently, efficiency of solar energy capture by plants is low -- in the order of 0.1% for aboveground productivity. This compares to about

0.25% for tall grass prairie and mixed prairie (Sims and Singh 1970). However, efficiencies for shrub-steppe vegetation is in the same order.

Even during the relatively short period of the three years of this study, the desert grassland seemed to be in equilibrium with respect to compartmental transfers. Two dry years followed by one wet year may have nearly equalized the factors influencing these transfers. The presence and absence of annuals may allow the system to adjust to some of the environmental variations fairly rapidly.

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