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Primary production of a rough fescue ecosystem in Western Montana

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PRIMARY PRODUCTION OF A ROUGH FESCUE ECOSYSTEM IN WESTERN MONTANA

By

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I wish to dedicate this manuscript to the memory of my mother whose love of the outdoors and encouragement toward higher education have been a constant inspiration to me.

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CHAPTER I

INTRODUCTION

Presently the terrestrial biosphere is undergoing rapid change due to an increase in demand for land for more industrial development and expansion of cultivated land. These changes cause transformation of ecosystems, the consequences of which are unpredictable. In order to minimize the unfavorable consequences, it is necessary to undertake large-scale research on the structure and function of these naturally occurring ecosystems (Eckardt, 1968). In view of the large area of the world occupied by grasslands (approximately 44% of the earth's surface according to Lewis [1969]) and their importance to man, the study of their primary productivity and factors limiting this are of prime importance (Milner et al., 1969).

The grassland ecosystem is valuable to man for food and human habitat, for forage and feed for wild and domestic herbivores, for watershed values and scenic beauty, for the opportunities it affords for recreation and the scientific study of natural and semi-natural ecosystems, as a source of medicinal and industrial products, and as a source of germ plasm for use in domestication or in genetic improvement of cultivated species (Lewis, 1970). Efficient and sustained use of grassland ecosystems demands careful management based on a knowledge of their structure and function.

On many of Montana's mountain range lands, rough fescue (Festuca scabrella Torr.) is the dominant species in the fescue grassland type. Rough fescue is generally associated with a mesic grassland environment characterized by soils with dark surface horizons (of the Chernozem or Chestnut Great Soil Groups), annual precipitation of approximately 14 or more inches, and a cool, short growing season. In the southern, more zeric parts of its range, rough fescue tends to be confined to the cooler and more moist exposures (Stickney, 1961).

Rough fescue is desirable to maintain as a dominant species because it produces abundant forage palatable to cattle, horses, and elk and possesses an extensive fibrous root system excellent for providing soil stability. By understanding the structure and function of such an ecosystem through a study of its primary productivity, the efficient and sustained use of this grassland type might be achieved.

The National Bison Range provides a suitable location for such a study. The vegetation and soils are representative of western Montana rough fescue grasslands.

Climatically and physiographically, these rough fescue stands are a southwest extension of the Fescue Grasslands as described by Coupland and Bradshaw (1953). In addition, the area is protected from outside influences and has a controlled number of grazing animals.

The objectives of this study are (1) to estimate the net primary productivity of two rough fescue ecosystems, one that has been heavily grazed and one in an ungrazed condition; (2) to estimate other qualities, such as biomass, associated with net primary productivity; and (3) to evaluate environmental conditions which are most closely associated with functioning of the ecosystem in relation to net primary production.

CHAPTER II

REVIEW OF LITERATURE

The primary producers of a grassland ecosystem include the entire gamut of autotrophic plants that form the basis of all food chains (Lewis, 1970).

In any ecological study, terminology tends to be a major problem in communicating what is being described or evaluated. The study of primary productivity involves two basic concepts that must not be confused: production or productivity and biomass.

Primary production is commonly expressed as the amount of energy bound or plant matter incorporated into the ecosystem during a specified time interval (Milner, 1970; Whittaker, 1970; Kormondy, 1969). It is commonly designated as $g/m^2/yr.$, Kg/ha/yr., or pounds/acre/year. Whittaker (1970) has further defined primary productivity as the rate at which energy is bound or organic matter created by photosynthesis per unit area, per unit of time (i.e., $g/m^2/year$ or $cal/cm^2/year$). Biomass, however, is generally considered as that amount of organic matter present at a given time per unit of area (Whittaker, 1970) (i.e., g/m^2 or pounds/acre).

Primary production must be further defined as falling into two categories: net primary production and gross primary production. Green plants use for their own respiration part of the organic matter they create. The total energy bound or organic matter created by green plants per unit surface and time is their gross primary production. The amount of energy bound or organic matter created per unit surface and time that is left after plant respiration is termed their net primary production (Whittaker, 1970; Milner, 1970).

The general terminology as defined above will be utilized throughout this discussion.

Much research has been done on primary productivity of terrestrial vegetation. Working with cultivated crops was the beginning of studies in primary productivition. One of the first such studies in 1926 was conducted by Edward Transeau in estimating the accumulation of energy of a midwestern cornfield. He calculated the net productivity and, by establishing certain premises, he was able to estimate gross productivity.

Due to the difficulties in harvesting underground plant parts many early studies were based only on above-ground primary production. Larson and Whitman (1942) found that at the end of the growing season grassland mesas of South Dakota produced 138.0, 177.5, and 199.0 g/m^2[1] for

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[1]See Appendix, p. 114, for abbreviations and symbols used.

heavy, medium, and light grazing conditions. Odum (1960) estimated seasonal productivity of an old field in Michigan to vary from 1 to 5 g/m^2/day over the six-month growing season, with the highest productivity from July to September. These figures approximate the world average for corn, wheat, or native prairie, indicating that productivity does not necessarily change with species or increase with succession as is often assumed. In the tall grass prairie of North Dakota, Hadley (1967) estimated the peak green herbage production to be between 109 and 353 g/m^2.

Ovington et al. (1963) in a central Minnesota prairie, Pearson (1965 and 1966) studying a desert grassland-shrub community, and Chew and Chew (1965) in a desert shrub community concluded that an estimate of both roots and shoots was necessary to evaluate the primary production of plant communities. In all cases, there were more roots than shoots produced, with roots averaging 27 to 64% of the total net primary production.

Many of the environmental factors which influence plant growth and development have been studied. Gates (1965) concludes that light and temperature are the most important factors affecting productivity of green plants. Bray et al. (1959) show that the efficiency of organic matter accumulation ranges from 0.04 to 0.53% depending on the stage of succession of a Minnesota plant community. Kucera et al. (1967), also comparing available solar energy with net primary production, estimated the average conversion to be 1.21% for a tall grass prairie community in Missouri. Botkin et al. (1968) estimated 10% efficiency for a one-year-old field in the New Jersey Piedmont. Whitman (1969) and Whitman and Wolters (1967) provide the most conclusive studies, which attempted to relate all factors of the grassland microenvironment to specific plant functions (leaf turgidity, etc.) and they developed a formula for the balance of energy within the microenvironment.

A limited number of studies have been conducted which deal with primary productivity of grasslands and the relationship of environment to primary productivity. Blaisdell (1958), in a 23-year study on the Upper Snake River Plains of eastern Idaho, concluded from vegetation and climatic records that both height and weight generally followed the common sigmoid pattern, being relatively slow at the beginning and end of the growing season and rapid during the intermediate period. Precipitation, particularly precipitation prior to the growing season, was most highly correlated to forage weights of grasses, forbs, and shrubs. Plant growth in general was found to be apparently regulated by weather, particularly temperature, with early growth being caused mainly by high temperatures. Height was directly related to precipitation and inversely related to mean temperature.

Smoliak (1956) studied grass productivity and various climatic data in an attempt to derive a regression equation for predicting range production. He concluded that May and June precipitation was most highly correlated with grass production. Seasonal mean temperature, hours of bright sunlight, and wind speed were all significantly correlated with forage production. Seasonal evaporation and forage production were the most poorly correlated.

Rogler and Hass (1947), working in the northern Great Plains rangelands, concluded that there was a high correlation between the preceding fall soil moisture and April to July precipitation, with range productivity. A much higher correlation was obtained when these two factors were added than when they were used separately.

CHAPTER III

DESCRIPTION OF THE STUDY AREA

LOCATION

The National Bison Range is the area for the study. The Bison Range is essentially a low group of mountains covered with a variety of habitat types including forest, grassland, and mixed shrub-tree types along the major drainages. It is located in Lake county about 20 miles south of Ronan, Montana. The area includes the approximately 18,000 acres which are managed by the Bureau of Sport Fisheries and Wildlife as a wildlife refuge and to perpetuate the plains bison. The general location of the study area is shown in Figure 1.

STUDY SITE SELECTION

While it would have been desirable to have had the two treatments adjacent to each other, this was impossible due to the historical use of the area and the previous lack of cross-fencing. The two 1.62 hectare sites were selected as near to each other as possible. In addition, each site was selected to be as similar as possible to the other with respect to aspect, slope and elevation, and inner uniformity.

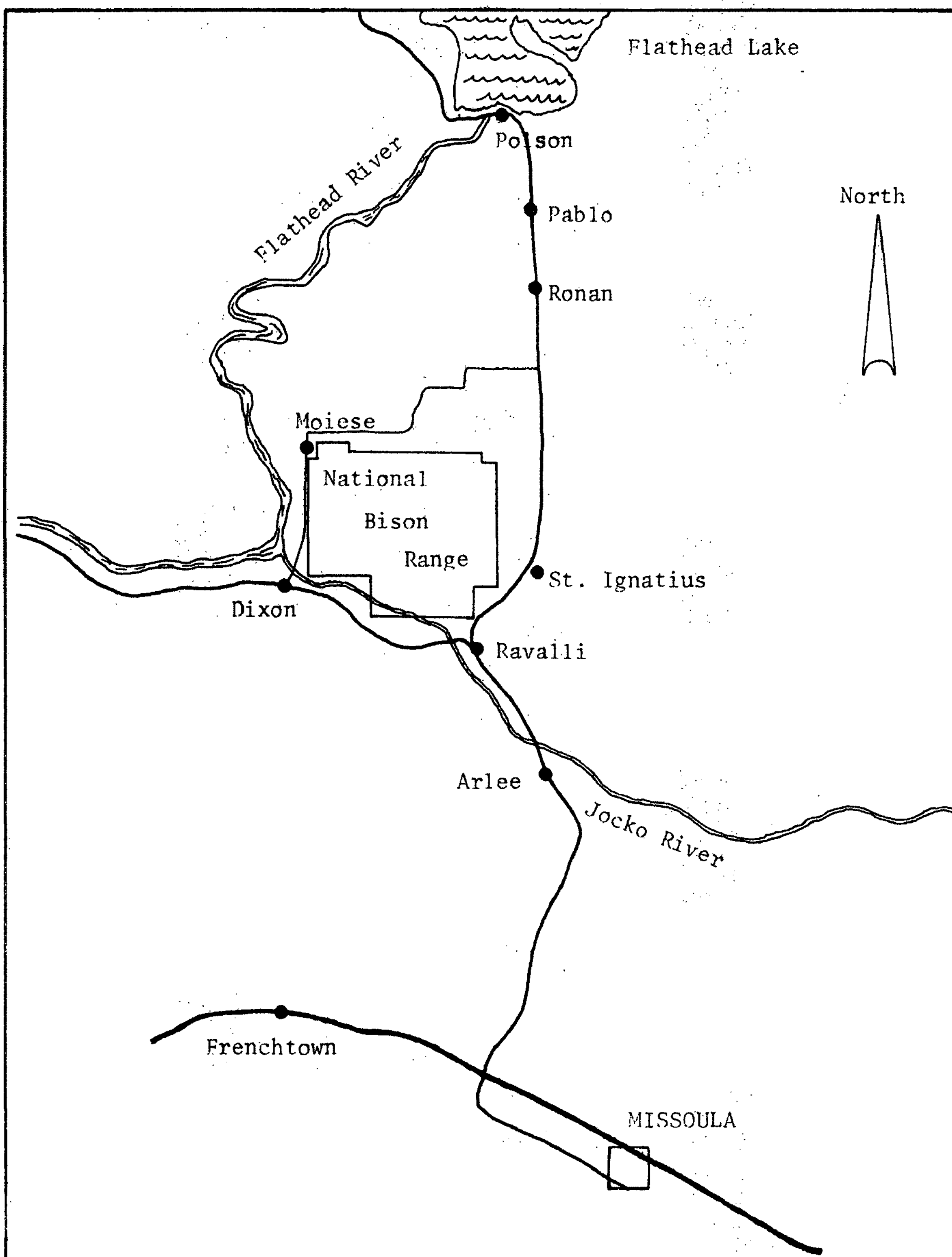


FIGURE 1 . General location map of the National Bison Range in western Montana. Approximate scale is 1 inch = 10 miles.

RELIEF AND ASPECT

The ungrazed treatment, a 121.8 x 121.8 meter exclosure, is located on an absolute north (0^{o}) exposure. The slope varies from 40% to 60% with an average slope of 55%. Its elevation is 963 meters.

The grazed treatment is a 182.8 x 76.2 meter exclosure located on an aspect of N34^{o}W. The slope varies from 13% to 20%, with an average of 17%. The elevation of this site is 945 meters.

CLIMATE

Climatological data which would best characterize this study area are available from the weather station at the National Bison Range Headquarters. This station is slightly lower in elevation than the study sites, but receives the general weather patterns which affect the study sites.

The 21 years of temperature records (1950-1970) show a mean annual temperature for the station of 7.5^{o}C (Weather Records, National Bison Range). January is the coldest month with an average temperature of -4.0^{o}C, while July is the warmest month with an average temperature of 19.4^{o}C. The average frost-free period of 112 days extends from May 26 to September 16.

The mean annual precipitation for the National

Bison Range is 382.19 mm. Normally about 38% of the annual precipitation falls during the months of April, May, and June. August usually is the driest month with an average of 1% of precipitation for the year.

Table 1 shows the 21-year mean monthly and annual precipitation and temperature and the monthly and annual precipitation and temperature for January 1968 to January 1970 as an average of the daily precipitation and maximum and minimum temperatures of the National Bison Range.

The general weather during 1970 deviated from the average in several ways. The precipitation was 58.32 mm above normal during 1968-1969 and 30.80 mm above normal in 1969-1970. The annual average temperature for the 1969-1970 year period was 0.3°C below normal.

SOILS

The soils under these grasslands are Typic haploboroll (Morris[1]) or the Chernozem great soil group. Table 19, p. 110, gives the classification by depth of soil as to Munsell color rating, texture, -15 bar soil moisture retention, and bulk density of the soils studied. They are characterized by fairly deep silt loam with very dark surface horizons. The soil series on the ungrazed treatment is Rattle Cobbly Silt Loam. Based on the information given in Table 19, the grazed treatment would also fall

[1]Personal communication.

Table 1. Mean monthly and annual precipitation and temperature for 1968-1970 and the 21-year average (1950-1970) based on weather records of the National Bison Range.

Precipitation in Millimeters			
Month	1968-69	1969-70	Average
Sept.	72.05	17.43	27.43
Oct.	16.15	25.13	25.38
Nov.	15.13	2.82	21.02
Dec.	28.21	9.74	21.28
Jan.	64.62	39.49	26.15
Feb.	4.10	22.56	15.13
Mar.	7.69	26.92	16.67
Apr.	13.08	34.87	28.72
May	31.28	58.46	42.05
June	136.92	54.10	59.92
July	1.79	65.13	24.62
Aug.	0.00	5.88	2.33
Average	391.02	362.50	331.70

Temperature in Centigrade Degrees			
Month	1968-69	1969-70	Average
Sept.	12.6	13.4	13.5
Oct.	6.4	5.4	7.4
Nov.	3.0	1.3	1.2
Dec.	-4.6	-5.4	-2.1
Jan.	*	-3.1	-4.0
Feb.	*	0.9	-0.6
Mar.	-2.6	1.8	1.3
Apr.	8.7	1.7	6.7
May	11.6	11.6	11.6
June	14.7	18.3	15.7
July	18.3	20.1	19.4
Aug.	15.6	19.2	18.1
Average	--	7.1	7.4

*Missing data.

into this series. These soils are derived from weathered limestones and range from exposed surface bedrock to 1.5 meters in depth.

VEGETATION

The vegetation of the study area is characterized by open grasslands, stands of ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) at the higher and more moist locations, and stands of snowberry (*Symphorcarpos albus*) and hawthorn (*Crategous douglasii*) in the draws and drainages at lower elevations. On rocky hillsides, chokecherry (*Prunus virginiana*) also occurs (Morris and Schwartz, 1957).

The grasslands upon which the study sites are located are of the Palouse Prairie type described by Daubenmire (1943). The dominant plant species on the ungrazed treatment is rough fescue (*Festuca scabrella*). Lupine (*Lupinus serecius*) was the second highest producer on the ungrazed treatment. Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Agropyron spicatum*) share dominance on the grazed treatment. Rough fescue is considered to be the climax dominant on both sites. The dominance of Idaho fescue and bluebunch wheatgrass on the grazed treatment is most likely a seral stage of the rough fescue type created by past heavy grazing.

PAST GRAZING HISTORY

The ungrazed treatment has had very little past grazing. The primary use seemed to be by elk (Cervus canadensis). The drainage bottom of this north-facing slope was used heavily as a salting ground for bison (Bison bison), but this had little effect on vegetation of this study site. It remains a relatively pristine stand of Festuca scabrella.

The grazed treatment has been subjected to heavy past grazing. Prior to cross-fencing, it was one of the major driveways to the slaughter house during the annual bison roundup. Also, from observations during the past field season, it seems to be a preferred feeding and loafing area for the bison when they are in this pasture on the rotation system.

Evidence that this area is a seral stage of a rough fescue ecosystem is that the botanical composition is quite similar, and that the remaining rough fescue plants are primarily small portions of larger clumps which are now dead. These clumps are quite evident throughout the grazed treatment.

PRESTUDY CONSTRUCTION

During the month of March, exclosures were constructed to preclude grazing by wild ungulates during the 1970 study period. These exclosures were built to standard fence dimensions as to post and pole spacings. In addition, the fence was eight feet high and constructed entirely of woven wire (sheep fence). Corners were reinforced to prevent damage by bison.

The only structures within these exclosures were weather instrument shelters constructed to approximate U.S. Weather Bureau standards, and plant-drying racks used to air-dry plant material before laboratory processing.

CHAPTER IV

METHODS AND PROCEDURES

BIOTIC STUDIES

Plant nomenclature follows Booth and Wright (1966) for dicotyledons and Booth (1950) for monocotyledons except for grasses which follow Hitchcock (1950).

In estimating aboveground net primary production, an error is introduced when sampling the peak standing crop and using this as the production estimate. The error is that not all species reach their peaks at the same time. It is valid to use an estimate of net primary shoot production based on community peak standing crop only when the dominant species have similar phenologies. Otherwise the separate peaks of the dominant species must be used (Malone, 1968; Wiegert and Evans, 1964). To facilitate the determination of primary productivity of these sites, periodic measurements of aboveground plant biomass were made. To further understand net primary production, plant moisture content and plant height growth of certain plant species were measured.

Aboveground Measurements

Production and biomass. The estimation of net primary production was by the harvest method. It has been described by Kormondy (1969) and Whittaker (1970) as one of the oldest and most reliable methods of determining plant production. Random plot lines were established on each treatment by harvest date. The sample plots were located systematically on these lines. Figures 2 and 3 show the location of plot lines by harvest date within each treatment. By design, some lines contain more than one harvest date. The study sites are divided into replicates and sections to facilitate statistical analysis. In addition, each section is divided into three equal areas to correspond to the proposed three-year U S I B P Grasslands Biome Study. Only data from the 1970 sections were utilized for this study. Plots were located equidistant along the line, with the first plot at one meter below the beginning of the line.

The area of each plot was one-half square meter. To remove the effect of slope, each plot frame was leveled with a hand level and the corrected corners established. All live vegetation that contributed to more than 5% of the total plot weight (oven dried) was clipped and placed in paper bags by species. Those species comprising less than 5% were lumped into a miscellaneous category. Rough fescue, Idaho fescue, bluebunch wheatgrass, lupine,

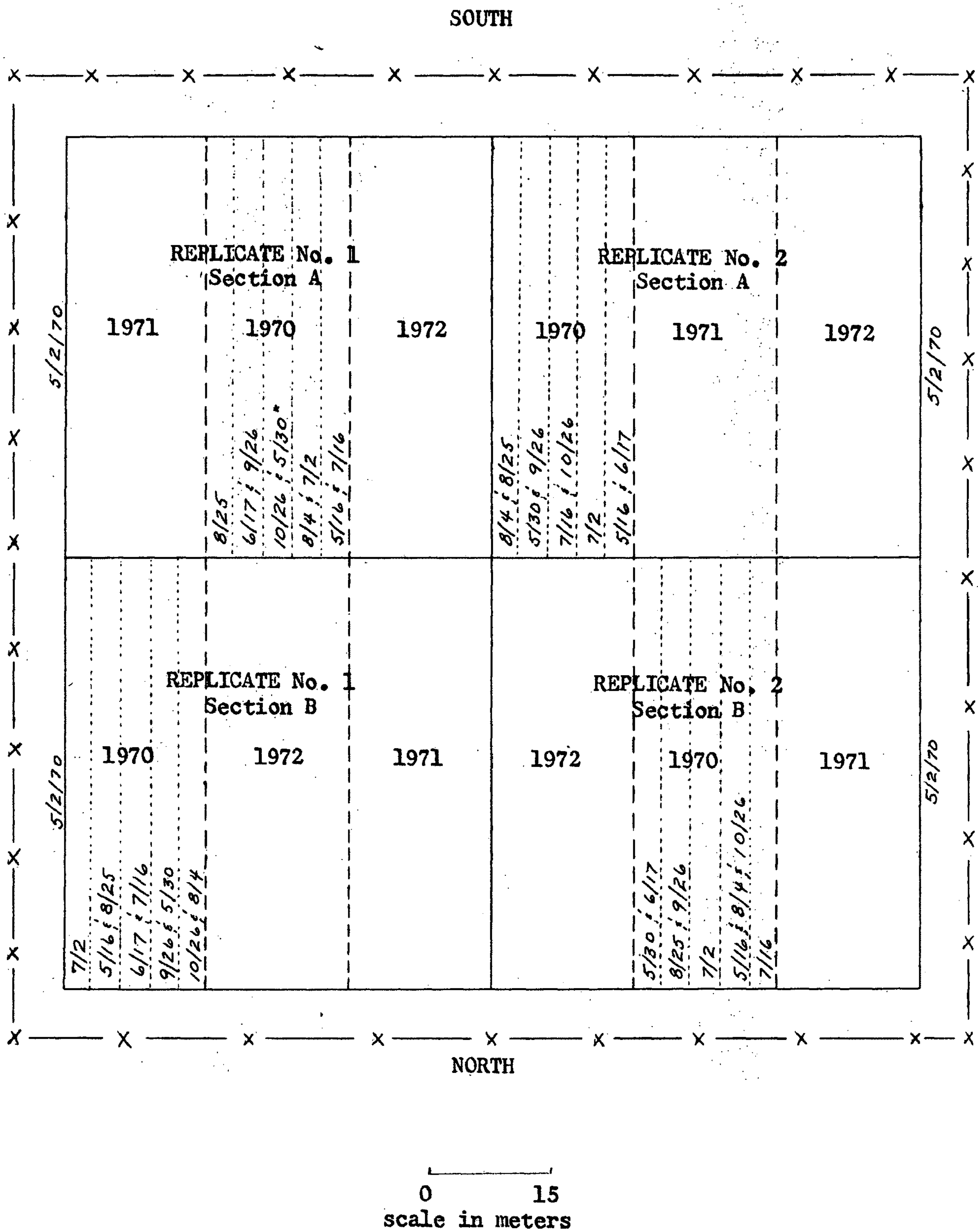


Figure 2. Ungrazed treatment. Schematic layout of plot lines by harvest date for 1970.

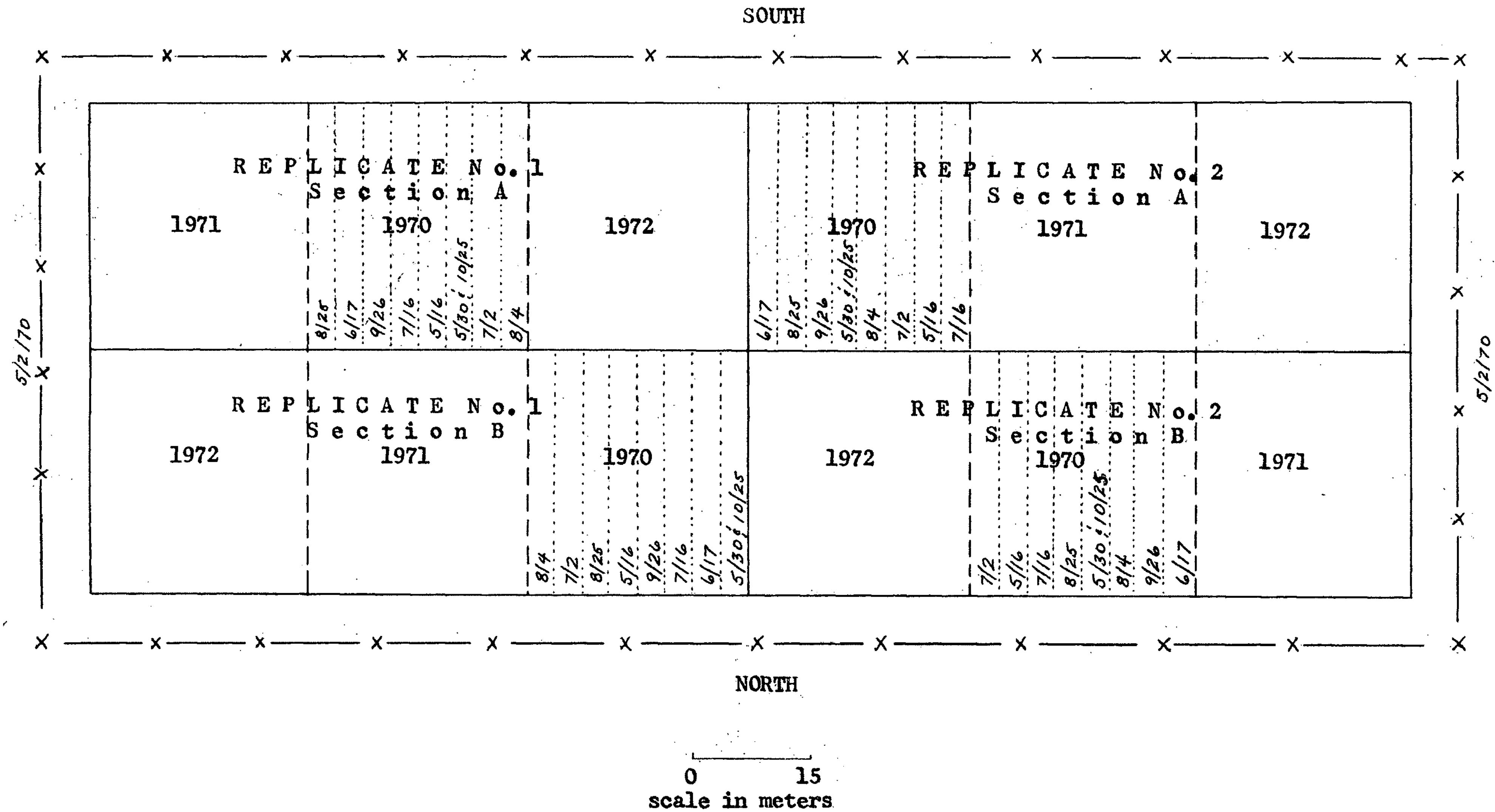


Figure 3. Grazed treatment. Schematic layout of plot lines by harvest date for 1970.

arnica (*Arnica fulgens*), agoseris (*Agoseris glauca*), yarrow (*Achillea millifolium*), and death camas (*Zigadenus paniculatus*) were always separated regardless of percent of the plot contributed.

Moss (*Brachythecium albicaus*) was harvested at only one date, which approximated the peak of the growth period.

Dead plant material was field separated into standing dead and litter categories. Litter and previous year's standing dead were placed in paper bags. Standing dead from 1970 was clipped with the live vegetation and a percent estimate of live to dead vegetation was made in the field at the time of clipping. These estimates were then used to calculate the 1970 standing dead plant material.

All aboveground plant material was brought to the laboratory, allowed to air dry for one to three days, and then oven dried at 65 C for 24 hours or until a moisture equilibrium was reached. The oven-dry material was then weighed and recorded as grams per square meter (g/m^2). Sub samples of moss and litter were placed in an ashing oven at 600 C for four to eight hours to separate plant material from the intermixed soil.

It is realized that some aboveground biomass was removed by rodents and insects. Both rodent and insect activity were observed during the study, but the amount of plant material utilized in this manner was not measured.

It is felt that it comprised no major reduction in plant biomass or production.

Plant moisture content. Plant moisture content was determined by clipping the 1970 aboveground plant production. Rough fescue, Idaho fescue, and bluebunch wheatgrass were clipped by species at two-week intervals. The clippings were placed in airtight plastic bags in the field. In the laboratory, the plants were weighed before and after oven drying. The percent of moisture was determined by the formula:

$$\% \, H_2O = \frac{\text{green weight} - \text{oven dry weight}}{\text{oven dry weight}} \times 100$$

Plant height growth. Plant height growth was studied by measuring the longest vegetative part of rough fescue, Idaho fescue, and bluebunch wheatgrass. Approximately 50-100 plants were measured in an undisturbed portion of each exclosure. Measurements were made at two-week intervals to the nearest whole centimeter.

Belowground Measurements

Root material was sampled at the time of peak aboveground production. This single sample was due to the difficulty of sampling extremely stony soil where a soil sampling core is not functional. To obtain the root samples a pit was dug and 10 x 10 cm squares were removed (intact as much as possible) in 5 to 10 cm intervals in the vertical profile. The roots were soaked in a mild solution of water and sodium hexametaphosphate (Calgon) for one to three hours and washed on 2 mm screens to remove the remaining soil from the root material. When all visible soil was removed, the roots were weighed, ashed, and re-weighed in a similar fashion as the moss and litter to separate the plant material from any remaining soil.

ABIOTIC STUDIES

Abiotic studies include the measurement of several environmental factors at both study sites. These data are used to show relationships between these factors and net primary production or other biotic measurements. In addition, the measurement of these factors is of value in revealing environmental differences or similarities of the two treatments. All measurements were made at both treatments unless otherwise specified.

Precipitation

Precipitation was measured with a standard U.S. Weather Bureau rain gauge. Weekly measurements of precipitation were totaled for given harvest periods. A "t" test was used to determine if a significant difference in total rainfall existed at the two sites for the study period.

Soil Moisture

Soil moisture was measured gravimetrically at biweekly intervals throughout the soil profile at each study site. Soil samples were secured at 0-5 cm, 5-10 cm, and thereafter at 10 cm intervals throughout vertical soil profile to 100 cm. Soil moisture was calculated by the formula:

$$\% \ H_2O = \frac{\text{fresh soil weight} - \text{oven dry soil weight}}{\text{oven dry soil weight}} \times 100$$

The soil was dried at an oven temperature of 100°C for approximately 24 hours.

Soil analysis included texture analysis, bulk density, and -15 bar moisture retention percentage. These analyses were made for soil profiles at the same intervals that soil moisture was determined. The soil texture analysis was made by the hydrometer method. The -15 bar determinations were made with a pressure plate apparatus.

Temperature

Temperature was measured at five levels; three in the soil (at 2.5, 25, and 75 cms) and two in the air (at 2.5 and 100 cm). Temperature was measured in several ways. Chromel-alumel thermocouples were placed at all five levels and measured at weekly intervals to detect trends in growing seasons. Continuous recording hygrothermographs were maintained throughout the growing season at the 100 cm air level. At the ungrazed treatment site, a three-point thermograph maintained continuous temperature records at the 2.5 cm air temperature level and at the 2.5 and 25 cm soil temperature level. Continuous records of temperature were summarized for daily, weekly, and monthly means for descriptive and comparative purposes. For comparison of continuous and interval records (i.e., chart vs. thermocouple) between sites, the temperature for the given time was taken from the chart and compared to interval temperature. All instruments and thermocouples were checked at weekly intervals by use of a maximum-minimum thermometer installed on the site.

Relative Humidity

Relative humidity was measured and recorded by continuous recording of a hygrothermograph. Daily, weekly, and monthly means were calculated for descriptive and comparative purposes.

Wind Speed

Wind speed was measured at 100 cm only in the ungrazed exclosure with a three-cup anemometer. Wind velocity was calculated in meters per second (m/sec) by weekly intervals.

Solar Radiation

Solar radiation, which is the driving force of the ecosystem and related directly to primary production, could not be measured due to lack of equipment. However, U.S. Weather Bureau records from Great Falls, Montana, of total incoming solar radiation were averaged to approximate the solar radiation received. When solar radiation is compared to the net primary production, an energy efficiency ratio is established. Energy efficiency ratios are very important in comparing primary production of different ecosystems.

CHAPTER V

RESULTS

BIOTIC STUDIES

Aboveground Biomass

Aboveground plant biomass is classified as: (1) 1969 standing dead; (2) 1970 standing live; (3) 1970 standing dead; and (4) litter. The results of the study of aboveground biomass will be described in terms of herbage dynamics (changes in the class of plant biomass), maximum production, plant moisture content, plant height growth, and botanical composition.

Herbage dynamics. The dynamics of the aboveground herbage are graphically represented in Figures 4 and 5. On the ungrazed treatment at the first clipping date (4/15/70) the 1969 standing dead crop comprised 45.5% of the aboveground plant biomass; 1970 live production 2.5%; and litter 52.0% of the total aboveground biomass present. At the peak of production harvest (7/3/70) the 1969 standing dead crop was 19.1%; 1970 live production 39.9%; and litter 39.9% of the total aboveground biomass. The remaining 1.7% was contributed by dead plant material from 1970. At the last harvest date (10/31/70), the 1969

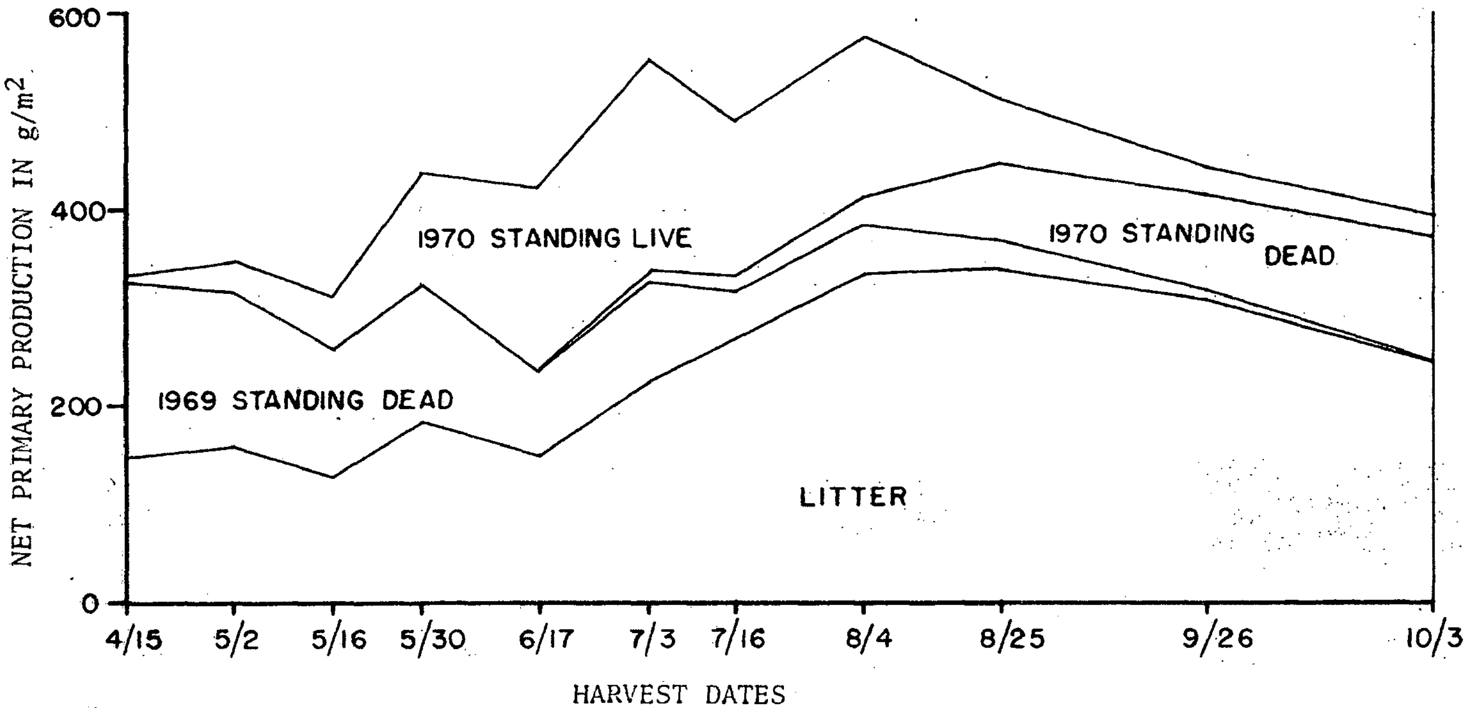


FIGURE 4 . Ungrazed treatment. 1970 seasonal trends of aboveground plant biomass.

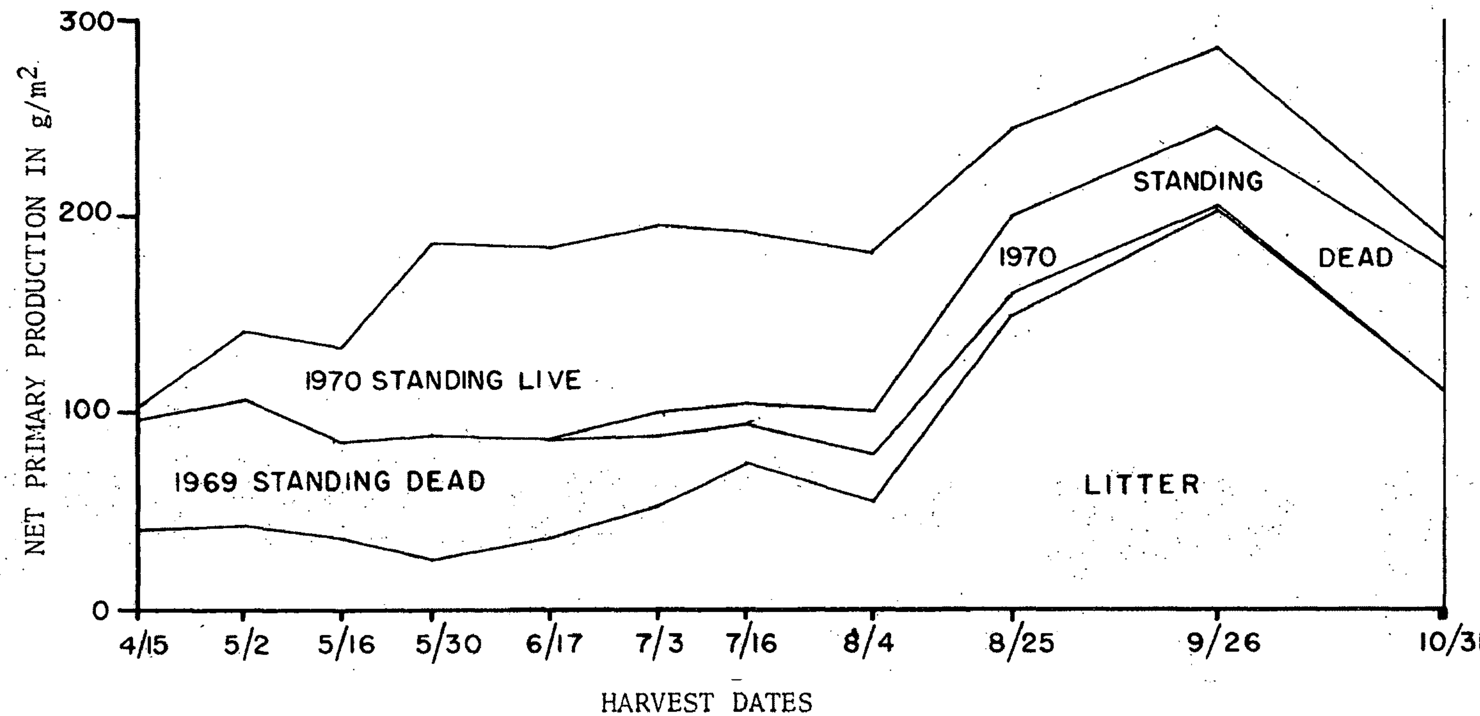


FIGURE 5 . Grazed treatment. 1970 seasonal trends of aboveground plant biomass.

standing dead crop was less than 1%; 1970 live production 6.6%; 1970 standing dead was 31.7%; and litter was 61.7% of the total aboveground biomass.

On the grazed treatment at the first clipping date (4/15/70) the 1969 standing dead was 54.7%; 1970 live production was 6.8%; and litter 38.5% of the total aboveground biomass. At the peak production harvest (7/3/70) 1969 standing dead crop contributed 18.7%; 1970 live production 48.9%; 1970 standing dead 6.3%; and litter 26.1% to the total aboveground biomass. At the last clipping date (10/31/70) the 1969 standing dead contributed less than 1% to the total aboveground biomass. The 1970 live production was 8.8%; 1970 standing dead was 32.4%; and litter was 58.8% of the remaining aboveground biomass.

Since the 1970 plant production was harvested by species, a comparison of the changes in grass and forb production at each clipping can be easily illustrated. Initially (4/15/70), grasses contributed 87.5% of the aboveground biomass on the ungrazed treatment and 79.7% on the grazed treatment. By the peak of the growing season (7/3/70) grasses contributed 69.4% and 58.1% on the ungrazed and grazed treatments respectively. At the end of the growing season (based on 10/31/70 clipping) grasses made up 77.8% and 72.2% on the ungrazed and grazed areas respectively. Figures 6 and 7 show the g/m^2 of 1970 standing live herbage production harvest dates.

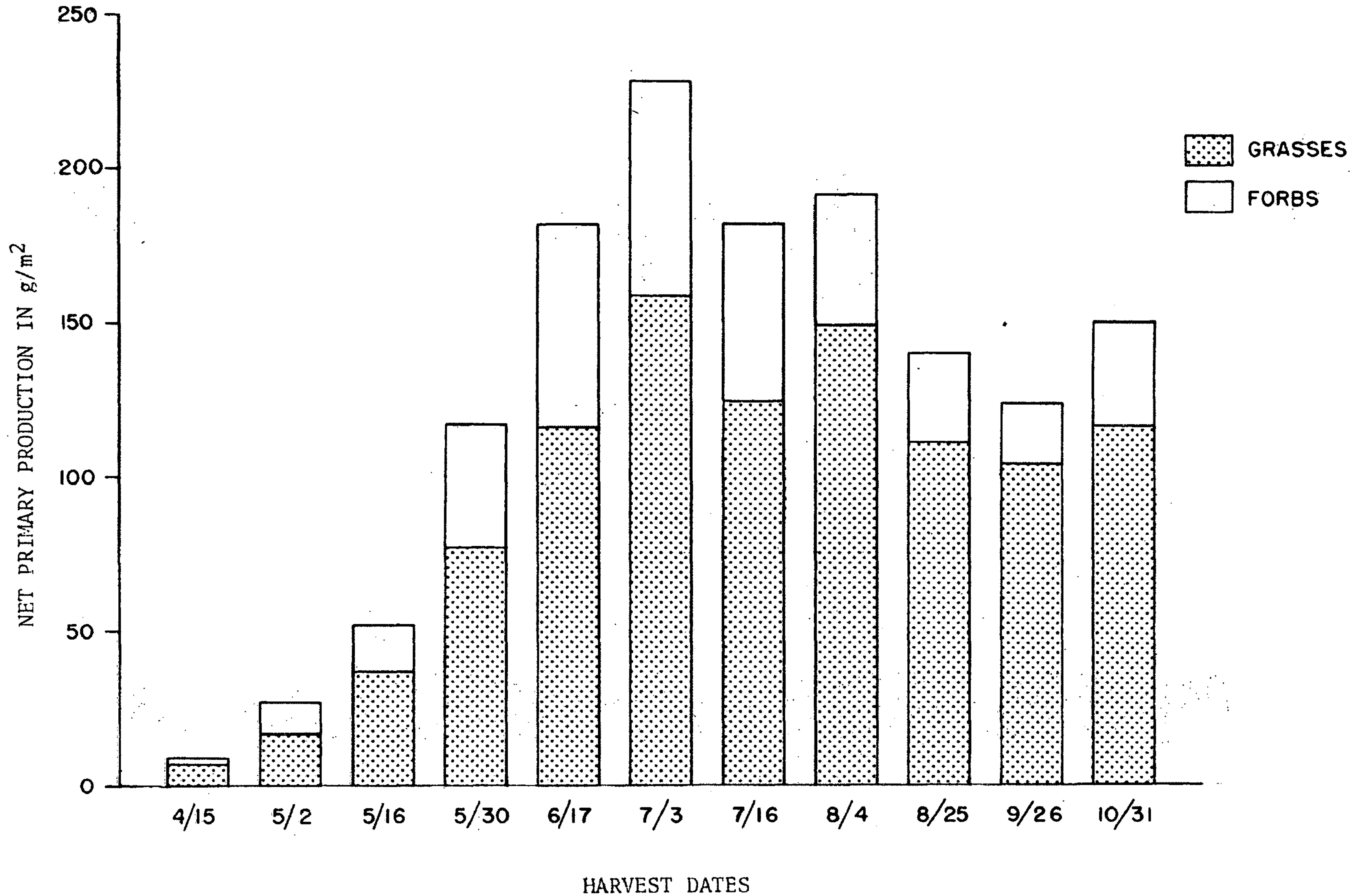


FIGURE 6 . Ungrazed treatment. Standing herbage production for 1970.

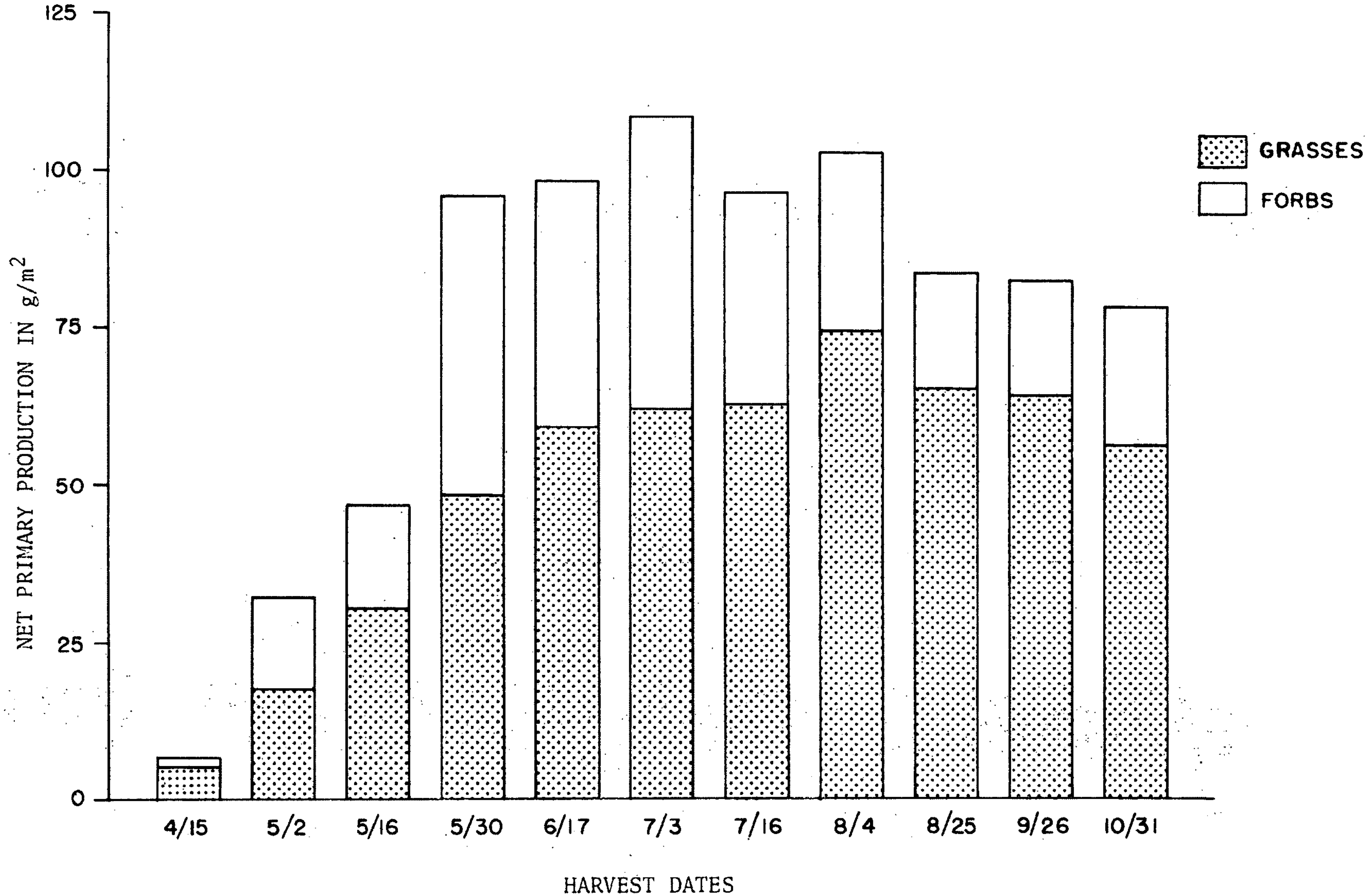


FIGURE 7 . Grazed treatment. Standing herbage production for 1970.

To more fully understand the dynamic nature of the aboveground 1970 production, Figures 8 and 9 illustrate the change in mean production throughout the growing season, including the standard errors of the means for the ungrazed and grazed treatments respectively. Tables 12 and 13, pp. 99 and 101, present a complete assessment of dynamics and production of aboveground biomass for 1970.

Maximum production. Maximum production may be viewed in two ways: as the point of highest production of the treatment as a whole during the growing season, or as the sum of the maximum production of the primary species during the growing season. As will be seen in a later section, this is one of the most important decisions in computing the net primary production and site efficiency. For the purpose of this study, both types will be discussed.

In terms of maximum treatment production, the ungrazed treatment produced 228.12 g/m^2 and the grazed treatment produced 108.18 g/m^2. The ungrazed treatment produced 2.1 times as much plant material as the grazed treatment. These peaks in 1970 production are based on the 7/3/70 clipping in both treatments. Table 2 shows the contribution of the major species to the peak community production. The sum of these primary species does not equal the total because minor species and miscellaneous category figures are not included.

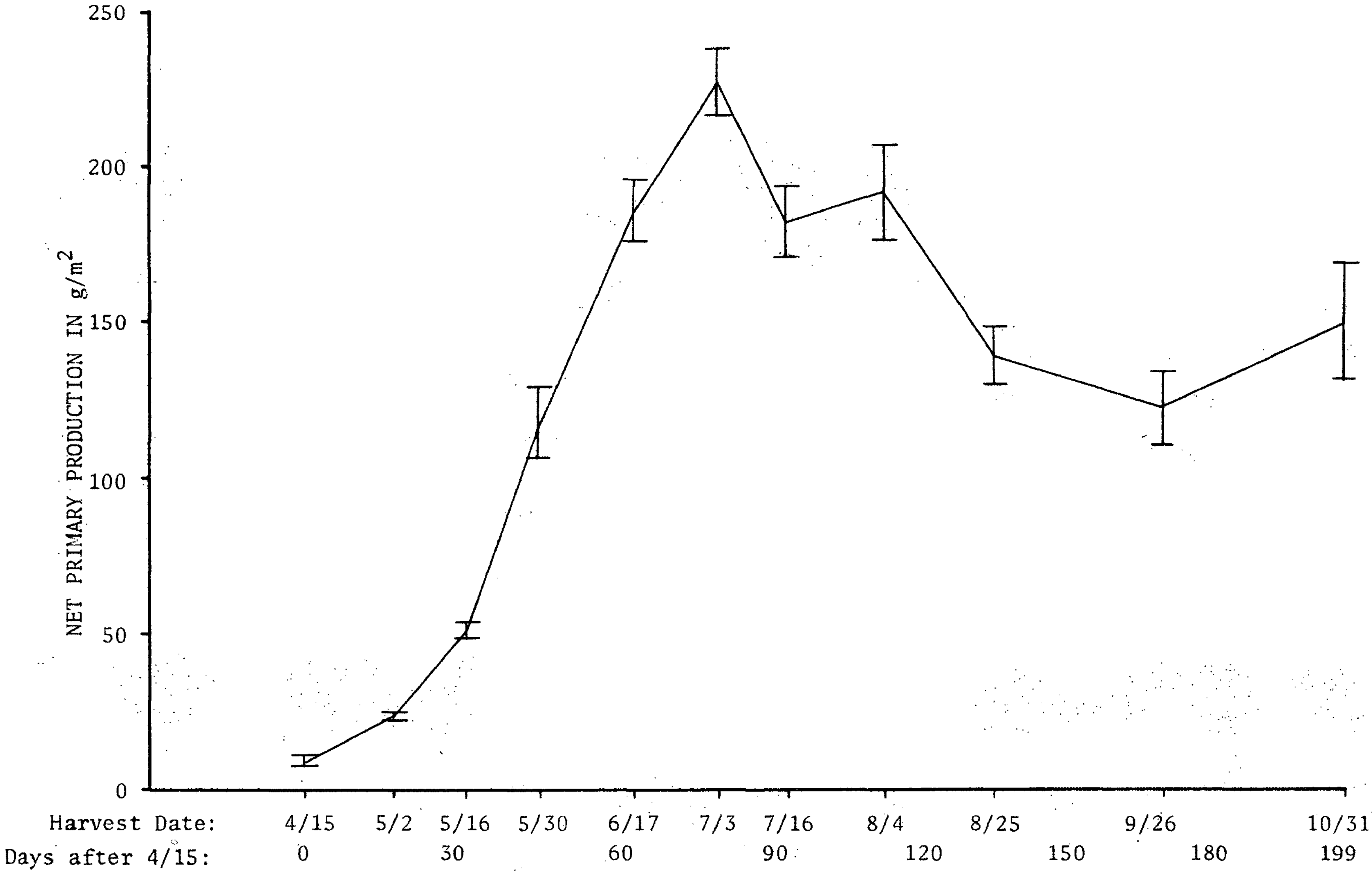


FIGURE 8 . Ungrazed treatment. 1970 mean production of all species with associated standard errors.

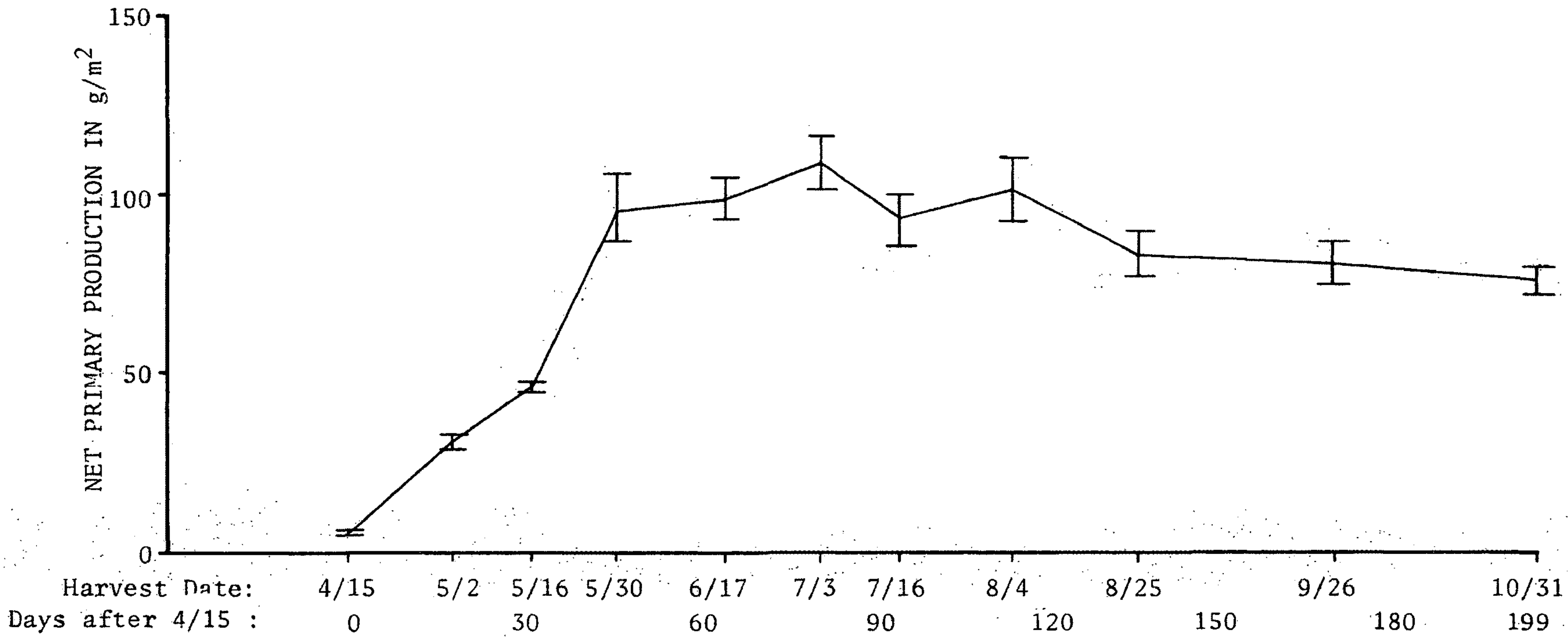


FIGURE 9 . Grazed treatment. 1970 mean production of all species with associated standard errors.

When the sum of the peak productions of individual species is considered as the maximum production of a community, a higher figure is derived. On the ungrazed treatment, 250.41 g/m^2 was produced, and on the grazed treatment 156.57 g/m^2. In this case, the ungrazed treatment produced 1.6 times as much as the grazed treatment. These figures were arrived at by taking the maximum species production figures from Tables 12 and 13 and summing.

Table 2. Production of primary species measured at the peak of treatment production (7/3/70) in grams per square meter.

Species	Ungrazed Treatment	Grazed Treatment
Fesc	140.71	3.29
Feid	10.26	25.85
Agsp	3.08	26.25
Luse	34.26	20.72
Acmi	7.78	6.34
Aggl	4.03	3.32
Arfu	1.56	1.14
TOTAL	228.12	108.18

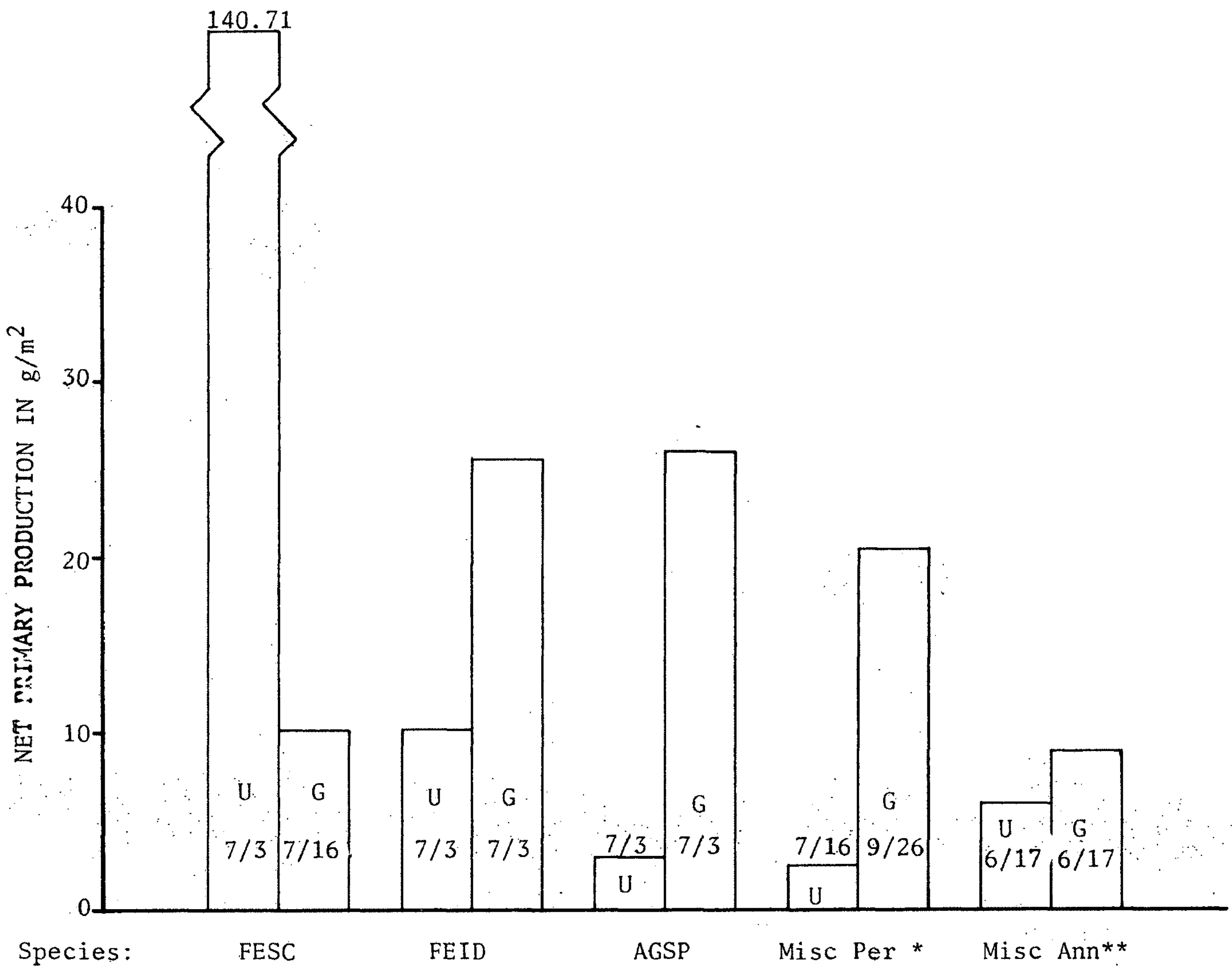
Table 3 shows the contribution of the primary species to the maximum production based on the peak of individual production. Again, the total presented is not a sum of the individual species since the miscellaneous categories and minor species are not shown.

A comparison of maximum production between the ungrazed and grazed treatments is also illustrated in

Figures 10 and 11. Figure 10 compares grass production, and Figure 11 compares forb production. Rough fescue on the ungrazed treatment produced more plant material than any other species. It was the top producing grass on the ungrazed treatment, but was overshadowed by Idaho fescue and bluebunch wheatgrass on the grazed treatment. Lupine was the highest producing forb on both treatments, but produced nearly twice as much plant material on the ungrazed treatment. Yarrow was the next highest consistent producer being similar on both treatments. _Lithospermum ruderale_ became a fairly high producer late in the season, but only on the ungrazed treatment. Moss was sampled only once during the study period and only on the ungrazed treatment. Some moss did grow on the grazed treatment, but was in very small quantity. On 7/16/70, the average moss production was 90.75 g/m^2 after ashing.

Table 3. Production of primary species as they contribute to maximum production based on peaks of individual species in grams per square meter.

Species	Ungrazed Treatment	Grazed Treatment
Fesc	140.71	10.18
Feid	10.26	25.85
Agsp	3.08	26.25
Luse	41.30	20.72
Acmi	7.78	9.04
Aggl	4.75	4.86
Arfu	4.66	4.77
TOTAL	250.41	156.57



*Miscellaneous perennial grasses (KOCR, POSE, and POPR primarily)
**Miscellaneous annual grasses (BRTR, BRJA, and APIN primarily)

FIGURE 10 . Comparative maximum grass production during 1970 for the ungrazed (U) and the grazed treatments with dates of measurements. Species designations in Appendix D

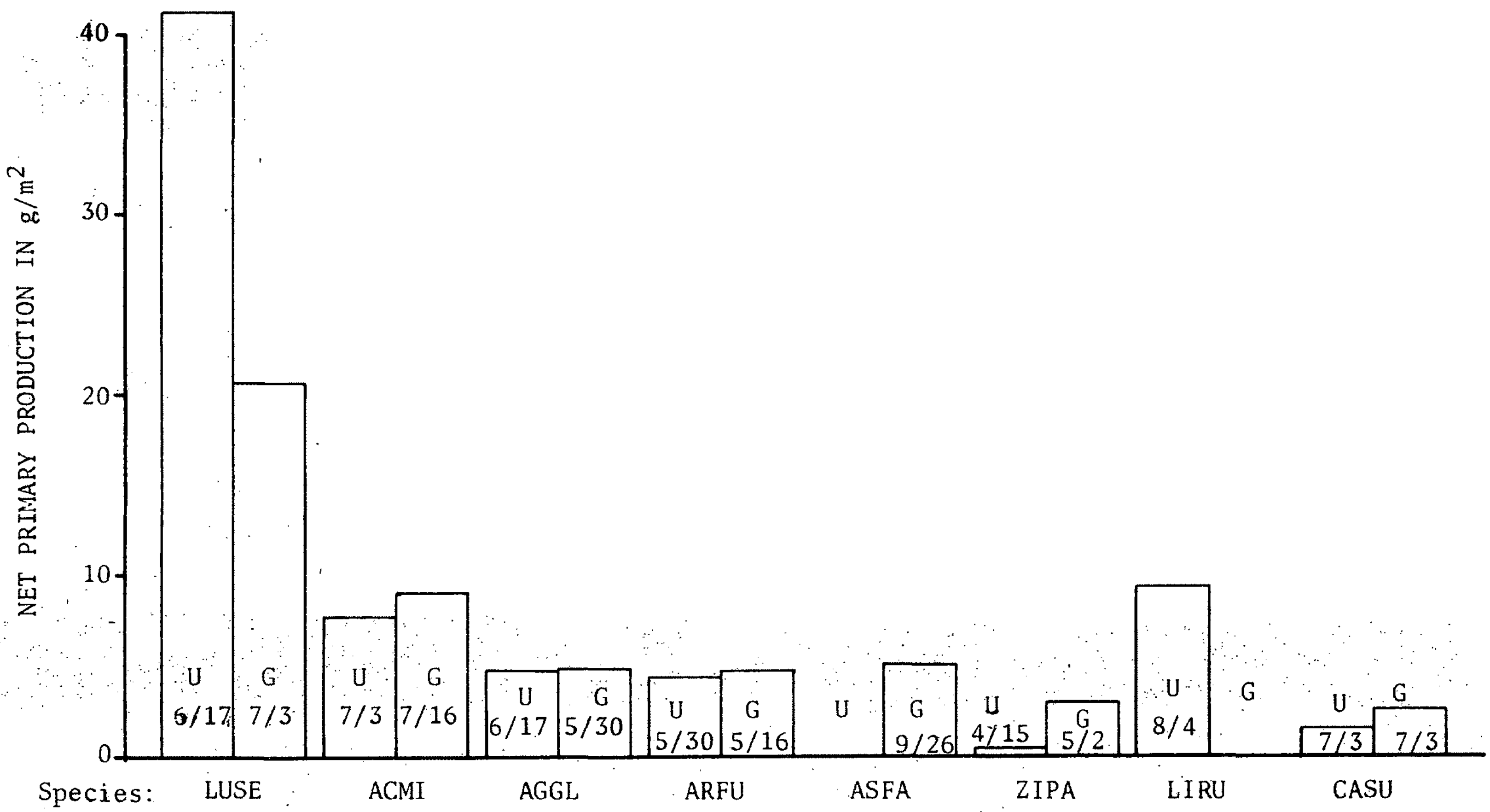


FIGURE 11. Comparative maximum forb production during 1970 for the ungrazed (U) and the grazed (G) treatments with dates of measurement. Species designations are listed in Appendix D

<u>Plant moisture content</u>. Plant moisture content was measured for the primary grass species on each treatment. The results are illustrated in Figures 12 and 13 for the ungrazed and grazed treatments respectively. As expected, the moisture content was very high in the beginning of growth during the period of rapid growth. As the plants matured the moisture content decreased rapidly and a final equilibrium was reached on about 8/27/70 for both treatments. The drop in moisture was not a gradual or an equal phenomenon for all species. In the ungrazed treatment both rough fescue and Idaho fescue had approximately 40% decreases in moisture content between 7/30 and 8/7/70. In the grazed treatment rough fescue showed a similar sudden decline in moisture between 8/20 and 8/27/70 (approximately 35%). Idaho fescue and bluebunch wheatgrass in the grazed treatment show more gradual decreases in moisture content. All species in both treatments showed large decreases in moisture between 4/15 and 5/2/70. Table 15, p. 104, summarizes plant moisture content for both treatments.

<u>Plant height growth</u>. Plant height growth was measured for the primary grass species occurring on each treatment. Figures 14 and 15 illustrate the change in plant height on the ungrazed and grazed treatments. The maximum leaf length of rough fescue was 47.4 cm on the ungrazed treatment and 43.9 cm on the grazed treatment.

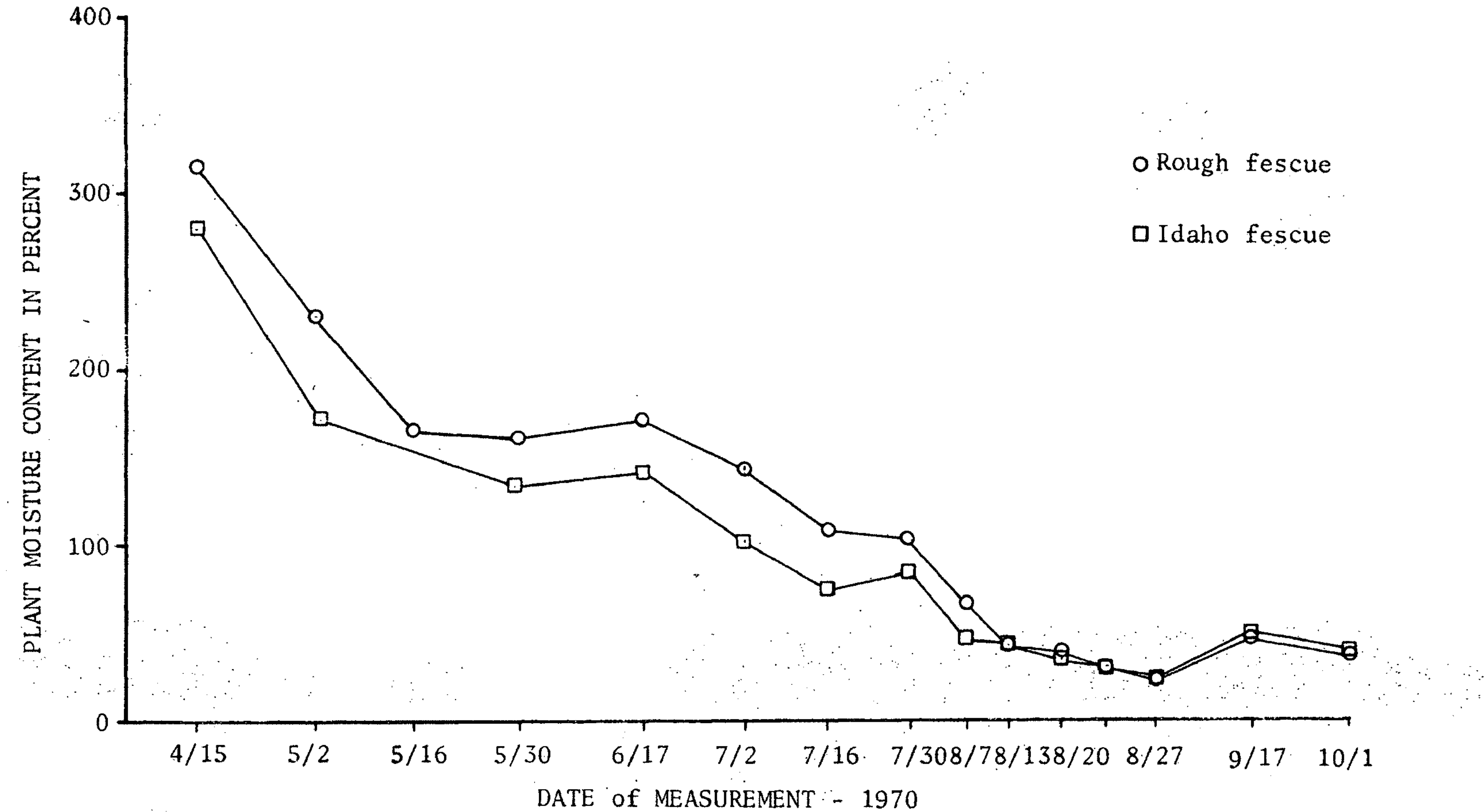


FIGURE 12. Ungrazed treatment. Plant moisture content. Measurements are percent of oven dry wieght.

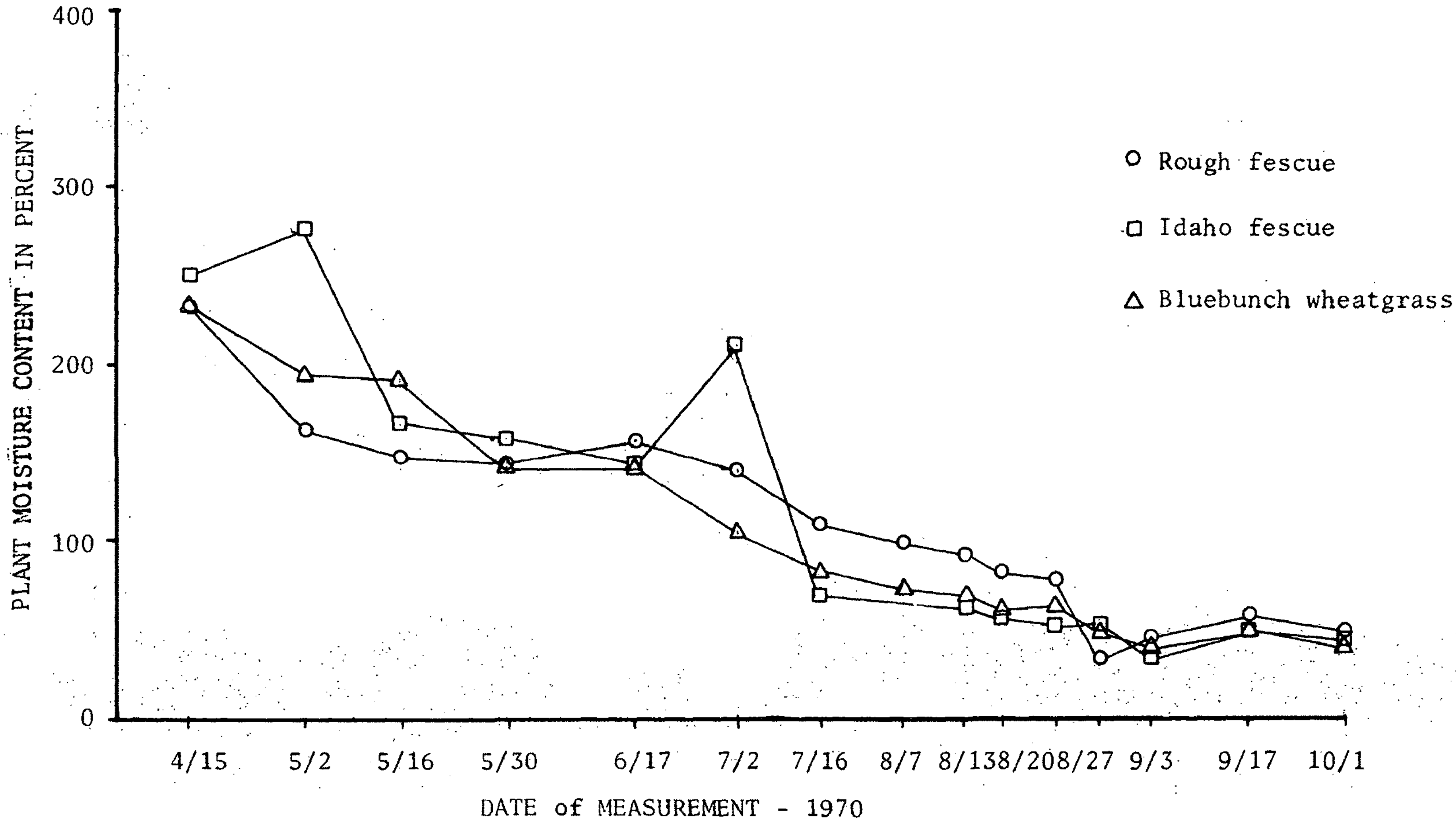


FIGURE 13 . Grazed treatment. Plant moisture content. Measurements are percent of oven dry weight.

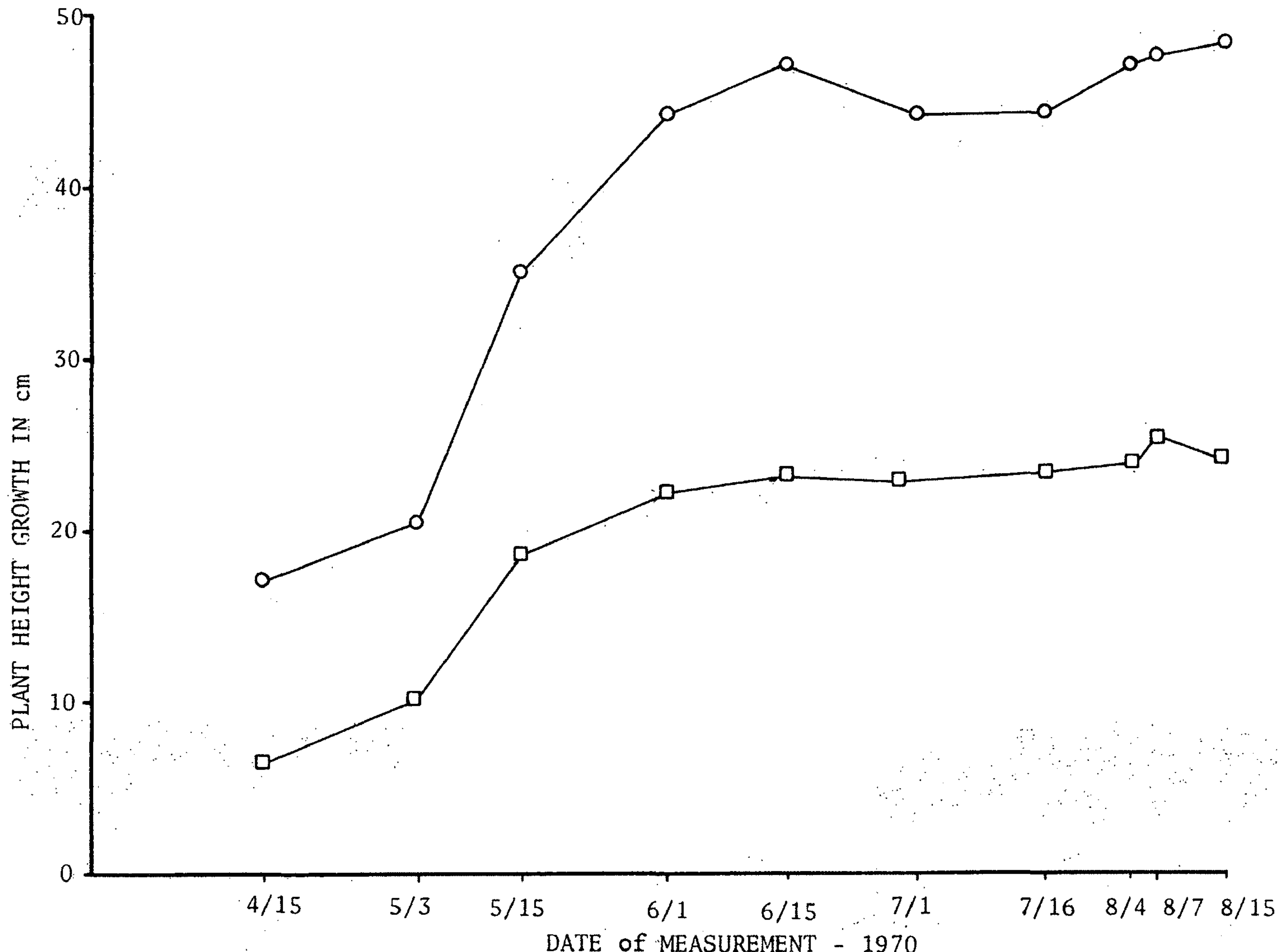


FIGURE 14. Ungrazed treatment. Plant height growth. Rough fescue is ○ ; Idaho fescue is □ . Measurement is maximum leaf length in centimeters.

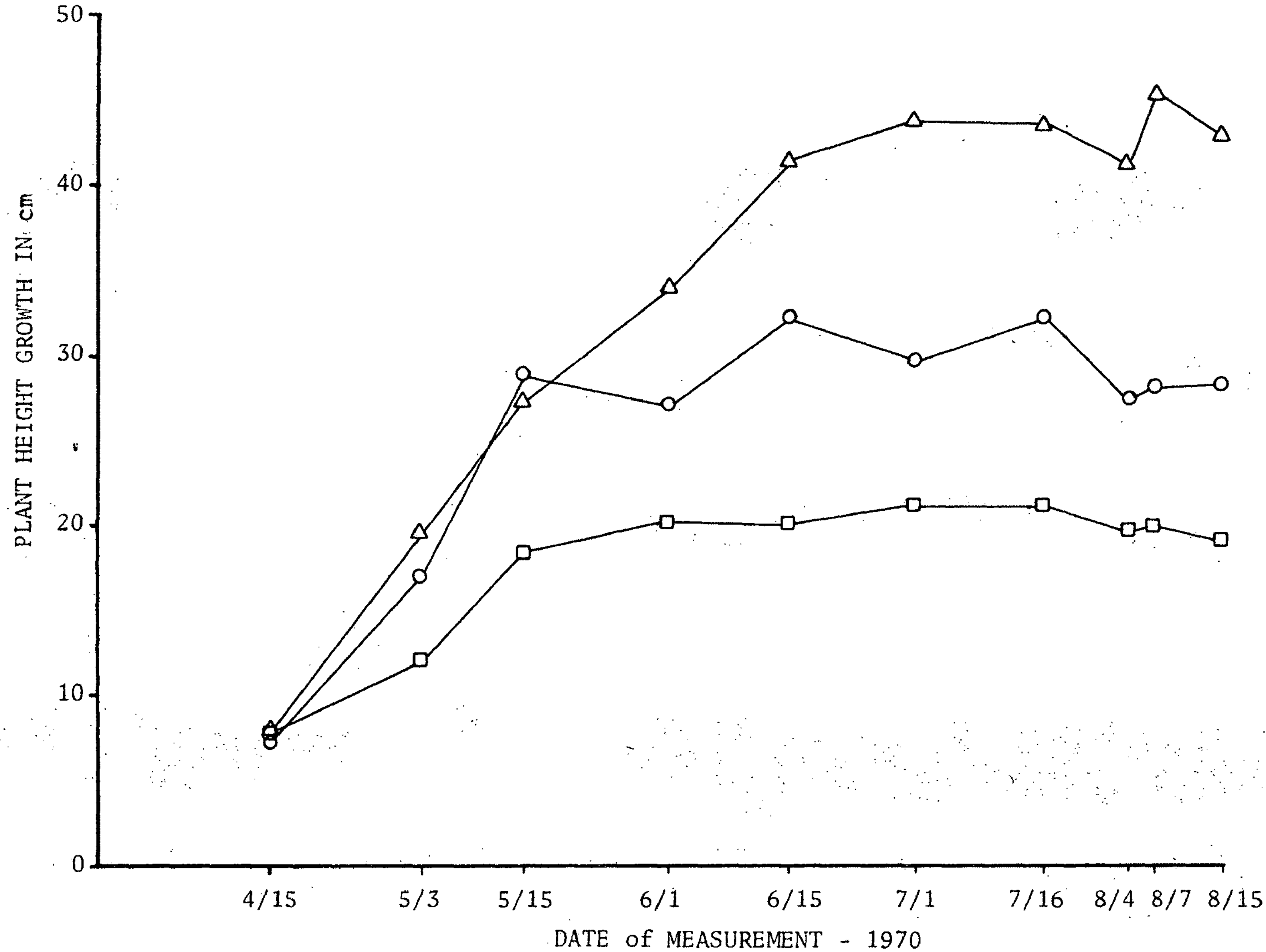


FIGURE 15. Grazed treatment. Plant height growth. Rough fescue is ○; Idaho fescue is □; bluebunch wheatgrass is △. Measurement is maximum leaf length in centimeters.

Idaho fescue's maximum leaf length was 23.3 cm and 20.1 cm on the ungrazed and grazed treatments respectively. Bluebunch wheatgrass, measured only on the grazed treatment, was 43.8 cm at its maximum height. Both rough fescue and Idaho fescue appeared to have reached maximum height by the 6/15/70 sample date on the ungrazed treatment. On the grazed treatment, rough fescue and Idaho fescue again appeared to have reached their highest points by 6/15/70. Bluebunch wheatgrass, however, continued growth until 7/1/70.

Maximum height growth and dates of maximum height growth are only estimates based on the samples taken. Fluctuations in sample means which occurred after the dates cited as maximum height growth are considered as due to sampling error. As the rate of growth becomes slower towards the end of plant growth, measurements by the technique used become less able to distinguish growth. This is especially obvious when negative growth patterns are seen after peak height growth is reached.

Plant height growth was compared to production of the dominant grasses on each treatment. Figure 16 is a scatter diagram with functional lines fitted by inspection. It is apparent that height and weight are related, and that the measurement of height as the longest leaf length is a functional description of production to the point where the longest leaf matures and ceases elongation.

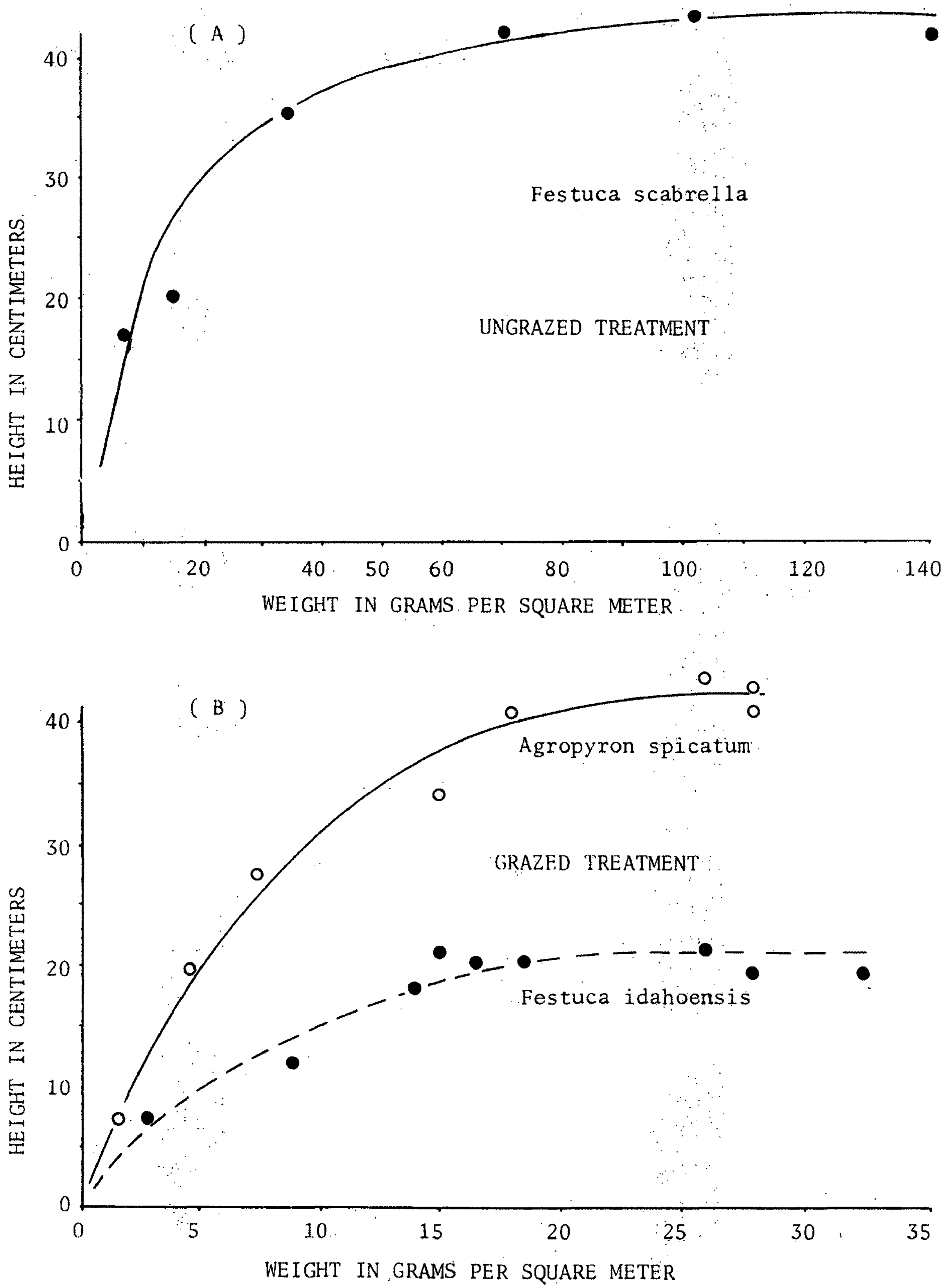


FIGURE 16 . Scatter diagram for plant height in relation to aboveground net primary production of the dominant grasses on each treatment for the 1970 growing season. Lines are fitted by inspection.

From this point, until production reaches its peak, increases in weight are due to elongation of immature leaves, synthesis of carbohydrates, or tillering. The latter is all but eliminated since very little tillering was noted on any species during the study period.

Botanical composition. Botanical composition, as used here, is the percentage that each species contributes to maximum net primary production. It provides a good measure for vegetative comparison of the two treatments. Table 4 shows the maximum production of each species and the percent that it contributes to the total. Rough fescue comprises 56% of the production on the ungrazed treatment. Bluebunch wheatgrass and Idaho fescue shared dominance on the grazed treatment being 37% of the total production. Annual and perennial grass were 15% higher on the grazed treatment.

On both treatments, *Lupinus sericeus* was the highest producing forb and, along with *Achillea millifolium*, *Agoseris glauca*, and *Arnica fulgens*, produced almost one-fourth of the total vegetation. The primary vegetative differences were: the presence of *Lithospermum ruderale* and *Geum triflorum* on the ungrazed treatment and their absence on the grazed treatment; and the presence of *Antennaria rosea* and *Aster falcatus* on the grazed treatment and absence on the ungrazed treatment. I suspect that

Table 4. Botanical composition of the ungrazed and grazed treatments based on the percent of maximum production of each species.

Species	Ungrazed Treatment		Grazed Treatment	
	Grams/m^2	Percent	Grams/m^2	Percent
Festuca scabrella	140.71	56.03	10.18	6.20
F. idahoensis	10.83	4.31	32.35	19.70
Agropyron spicatum	3.08	1.22	28.54	17.38
Misc. Per. Grasses	2.74	1.09	20.88	12.72
Misc. Ann. Grasses	6.30	2.50	9.06	5.52
TOTAL GRASSES	163.66	65.15	101.01	61.52
Lupinus sericeus	41.30	16.45	20.72	12.62
Achillea millifolium	7.78	3.09	9.04	5.50
Agoseris glauca	4.75	1.89	4.86	2.96
Arnica fulgens	4.66	1.85	4.77	2.91
Lithospermum ruderale	9.59	3.85	--	--
Geum triflorum	5.60	2.24	--	--
Castellea sulphurea	1.82	0.73	2.86	1.76
Zigadenus paniculatus	0.47	0.18	3.02	1.84
Antennaria rosea	--	--	2.10	1.28
Aster falcatus	--	--	5.22	3.19
Misc. Forbs	11.47	4.57	10.53	6.42
TOTAL FORBS	87.44	34.85	63.12	38.48
TOTAL	251.10		164.13	

these differences are due primarily to the slight differences in slope and aspect of the two treatment areas. However, this difference could be caused by past grazing histories.

In general, the composition of species seems to be quite similar. The percentages of grasses and forbs is remarkably uniform. Only the quantity of vegetation is significantly different.

To statistically test the difference between the two treatments at maximum aboveground primary production, a one-way analysis of variance was done. The following table of analysis of variance shows the significance level of the difference between the two treatments.

Table 5. Analysis of variance comparing net primary production between the ungrazed and grazed treatments.

Source of Variation	df	SS	Variance	F
Total	39	53712.85	--	
Between Treatments	1	35348.97	35348.97	73.15[a]
Within Treatments	38	18363.88	483.26	

[a]Significant at the .01 probability level.

These data show the significance of past grazing histories on net primary production. Production was significantly reduced on the grazed treatment when compared to the ungrazed treatment.

Belowground Biomass

Belowground biomass was measured in a single sample on 8/18/70 consisting of two subsamples at each study site. Figure 17 illustrates the means in grams per square meter of the two subsamples for given soil depths. The numbers in parenthesis are the percent of the total in that depth. In the ungrazed treatment, 93.3% of the roots are in the first 50 cm of the soil profile. Approximately 98.6% of the roots were in the first 50 cm on the grazed treatment. The ungrazed treatment had a mean of 2540 g/m^2 whereas the grazed treatment had 1470 g/m^2.

These measurements were taken past the peak of vegetative production. Due to the dryness of the soil, and hence low microbial activity, it is felt that deterioration of root material was not significant.

As 1970 root production could not be separated from that portion of the root system remaining from previous years, an estimate of 1970 production was made based on the studies of Dahlman and Kucera (1965 and 1968). They found, based on pre- and post-growing season root measurements and the use of ^{14}C for labeling prairie grasses, that approximately 25% of the root system is replaced each year. With this estimate as a guide, Table 6, the 1970 production of root material, is presented.

TREATMENT

Soil Depth in cm	Ungrazed	Grazed
0-5	1070 (42.1)	950 (64.6)
5-10	650 (25.6)	240 (16.3)
10-20	340 (13.4)	160 (10.8)
20-30	170 (6.7)	30 (2.0)
30-40	140 (5.5)	30 (2.0)
40-50	40 (1.6)	40 (2.7)
50-60	60 (2.4)	20 (1.4)
60-70	70 (2.8)	
Total	2540	1470

FIGURE 17. Maximum root weights for 1970 on ungrazed and grazed treatments. Top number is g/m^2 ; bottom number in () is th percent of total weight.

Table 6. Estimated 1970 production of root material in g/m^2 based on 25 percent annual turnover.

Soil Depth in cm	Ungrazed Treatment	Grazed Treatment
0- 5	298.0	237.5
5-10	162.5	60.0
10-20	90.0	40.0
20-30	45.0	7.5
30-40	35.0	7.5
40-50	10.0	10.0
50-60	15.0	5.0
60-70	17.5	---
TOTAL	635.0	367.5

ABIOTIC STUDIES

Precipitation

Precipitation was measured in millimeters at weekly intervals throughout the study period. Precipitation differences between the two sites were minimal throughout the study period. A "t" test of the mean weekly precipitation was not significant.

Table 7 shows the precipitation on the ungrazed and grazed treatments. Also, for comparison, the 1967, 1968, 1969, and 1970 precipitations and the four-year mean for the same time interval are presented. Approximately 60% of the growing season precipitation falls from 4/15 to 7/3. From 7/3 to 9/3 only about 10% fell. The remaining 30% falls between 9/3 and 10/31. The four-year mean, 226.67 mm, is slightly higher than the 205.13 mm and 219.23 mm for the ungrazed and grazed treatments respectively.

Table 7. Precipitation in millimeters on the ungrazed and grazed treatments for the 1970 study period. For comparison, the 1967 to 1970 precipitation and four-year mean from the National Bison Range Headquarters are given.

Period	Bison Range Headquarters					Ungrazed Treatment 1970	Grazed Treatment 1970
	1967	1968	1969	1970	Four-year Mean		
4/15-4/25	12.56	7.18	11.54	9.49	10.26	8.97	9.49
4/26-5/3	32.31	3.33	6.92	5.38	12.05	3.59	2.82
5/4-5/10	22.31	3.59	12.31	13.33	9.74	18.72	17.18
5/11-5/17	3.59	2.05	0.00	36.67	13.59	22.05	37.95
5/18-5/22	0.00	8.97	5.64	6.41	5.38	4.87	5.38
5/23-5/30	18.21	5.64	6.41	2.05	8.21	0.00	0.00
6/1-6/5	17.95	3.08	0.00	1.03	5.64	17.95	0.77
6/6-6/12	7.95	28.21	69.49	22.82	32.05	25.38	17.95
6/13-6/19	0.77	4.36	1.79	9.23	4.10	11.79	11.79
6/20-6/25	41.28	7.44	35.64	0.00	21.03	0.00	0.00
6/26-7/3	0.00	5.89	31.54	21.03	14.62	13.59	16.41
7/4-7/10	0.00	0.00	0.26	0.00	0.07	0.00	0.00
7/11-7/16	0.26	0.00	0.00	19.74	5.13	0.00	13.33
7/17-7/23	1.03	0.77	0.00	17.18	4.62	0.00	4.36
7/24-7/30	0.00	0.00	0.00	25.89	6.41	14.10	17.69
7/31-8/6	0.00	1.03	0.00	5.89	1.79	4.62	3.33
8/7-8/13	0.00	3.59	0.00	0.00	1.03	0.00	0.00
8/14-8/18	0.00	39.49	0.00	0.00	10.00	0.00	0.00
8/19-8/25	0.00	2.05	0.00	0.00	0.51	0.00	0.00
8/26-8/27	0.00	6.15	0.00	0.00	1.54	0.00	0.00
8/28-9/3	0.00	29.49	0.00	0.00	7.44	0.51	0.77
9/4-9/10	2.31	0.00	2.56	16.41	5.38	14.87	11.79

Table 7 (continued)

Period	Bison Range Headquarters					Ungrazed Treatment	Grazed Treatment
	1967	1968	1969	1970	Four-year Mean	1970	1970
9/11-9/17	6.15	18.97	0.00	1.54	6.67	0.00	0.00
9/18-9/24	0.00	23.59	10.25	3.08	9.74	4.62	6.92
9/25-10/1	7.44	0.00	4.62	0.00	3.08	0.00	0.26
10/2-10/16	10.51	15.38	8.72	37.44	20.26	37.44	37.44
10/17-10/31	20.00	0.77	16.15	2.56	10.00	2.05	3.58
TOTAL	204.62	221.03	223.85	257.18	226.67	205.13	219.23

Soil Moisture

For the 1970 study period, the soil moisture means were not significantly different between the two treatments. A "t" test of mean biweekly soil moisture percents as an average of 0 to 50 cm samples proved nonsignificant.[1] The permanent wilting percent, estimated at the moisture percent retained at -15 bars of moisture stress, were similar between treatments, but varied from 26.9 to 4.6% moisture within a 100 cm soil profile. The -15 bar moisture percent was reached by both treatments at most soil depths between 7/3 and 7/16. After reaching this point, soil moisture continued to gradually decline and level off at 3 to 6% on 8/27.[2] Fall rain showers between 8/28 and 10/16 totalled 59.49 mm and 60.76 mm on the ungrazed and grazed treatments respectively, and brought the soil moisture of the upper five cms up to 25 to 28% by 10/22.

Figures 18 and 19 illustrate the percent soil moisture change within a profile from 4/12 to 10/22/70 for the ungrazed and grazed treatments respectively.

Temperature

Temperature measurements were made throughout the study period at five levels: 100 cm and 2.5 cm air

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[1]See Table 20, p. 111.

[2]See Tables 17 and 18, pp. 106 and 108, for all soil moisture values for the study period and values at 15 bars of moisture stress.

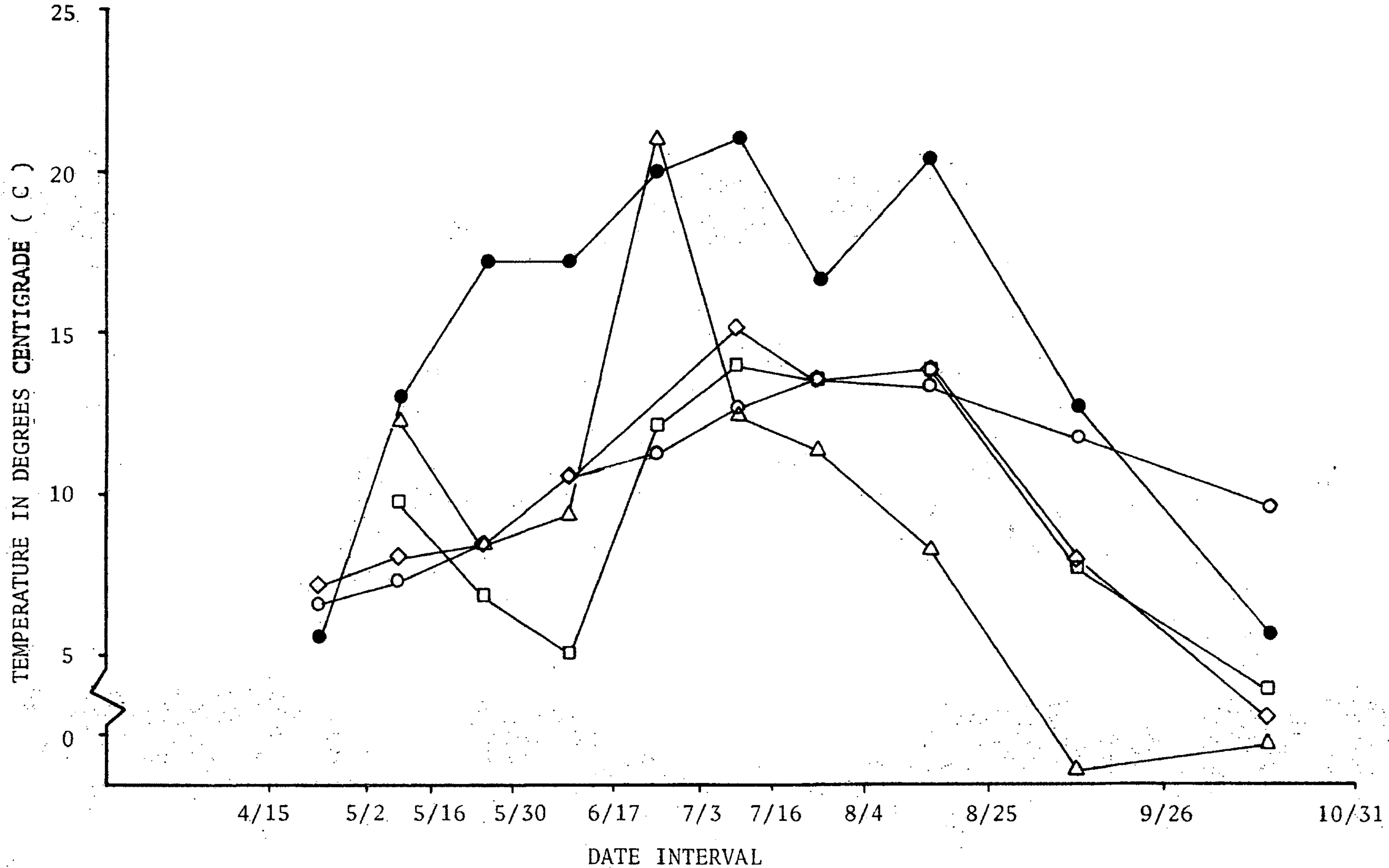

FIGURE 20. Ungrazed treatment. 1970 seasonal temperature trends in degrees centigrade for 5 measurement levels: 100 cm air** ● ; 2.5 cm air* △ ; 2.5 cm soil* □ ; 25 cm soil* ◇ ; 75 cm soil* ○ . (*mean of 1000 hrs. reading made weekly by thermocouple; **mean of bihourly summary of hygrothermograph chart.)

temperatures and 2.5 cm, 25 cm, and 75 cm soil temperatures. The means of the 100 cm air temperature are a daily summary of bihourly temperatures recorded continuously on a hygrothermograph. The means of the other four levels are averages of a 10:00 a.m. reading made weekly at the grazed treatment, and the 10:00 a.m. thermograph recording on the ungrazed treatment which corresponds to the reading time and date at the grazed treatment. This method was followed to allow for comparison of the means.

Figures 20 and 21 illustrate the 1970 seasonal trends of temperature for the ungrazed and grazed treatments. A comparison of each level was made by a "t" test. The test indicated that all soil temperature means and the 100 cm air temperature means were not significantly different at the .05 level. However, a "t" test of the 2.5 cm air temperature means indicated that the two treatments were very significantly different ($t_{.01}$). This is also quite evident from Figures 20 and 21.

The temperature trends for all levels were generally bell-shaped through the study period. The air temperatures showed the widest fluctuations, while soil temperatures were more subdued, but still followed the general air temperature fluctuations. As expected, the 75 cm soil temperature had the smoothest curve and had the warmest temperatures for the end of the study period. Freezing temperatures were noted at the 2.5 cm soil level on the

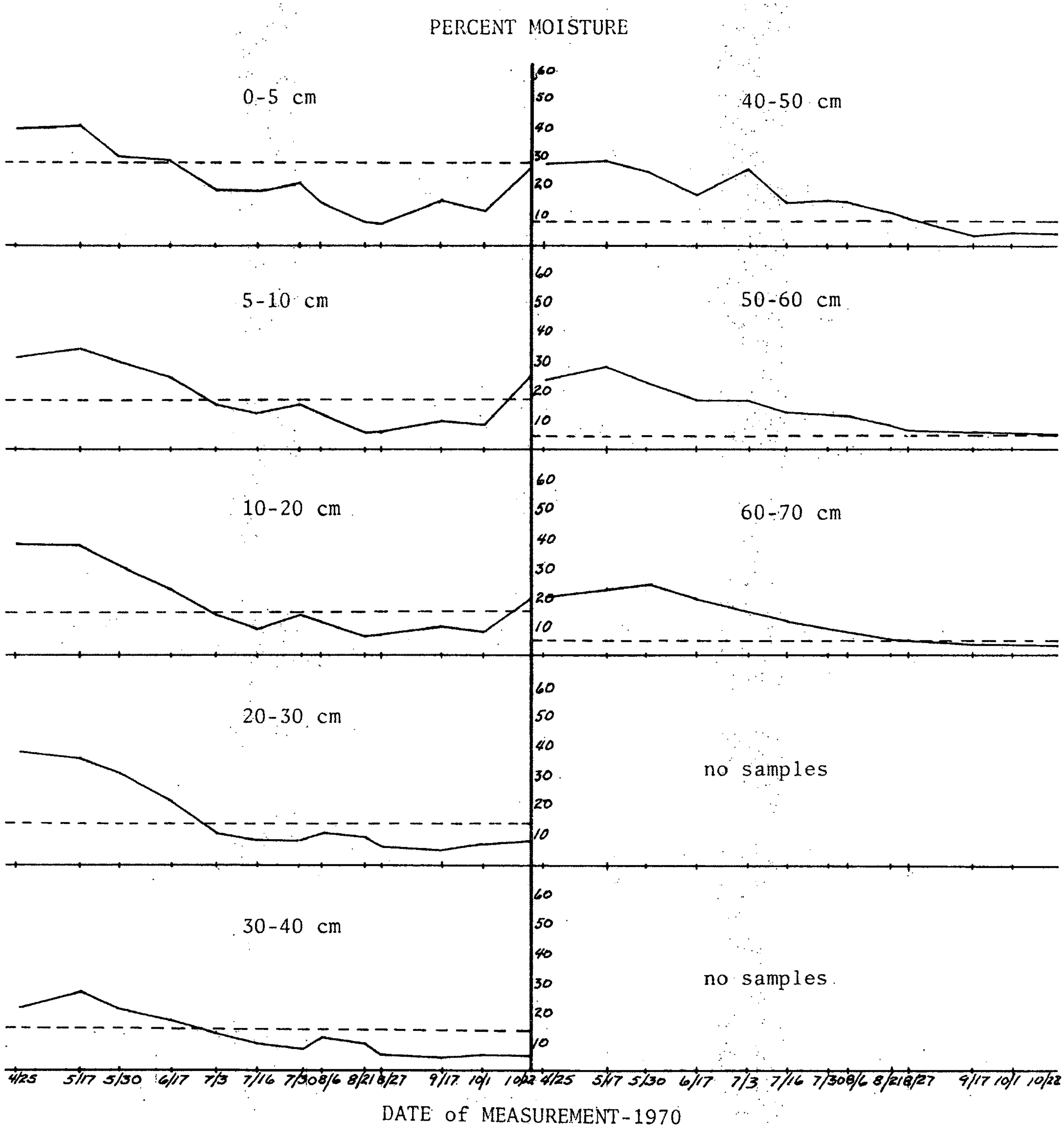

FIGURE 19. Grazed treatment. 1970 percent soil moisture patterns at specified depths. Dashed line represents the 15 atmosphere moisture percent. Soil moisture determined gravimetrically based on oven dry weight.

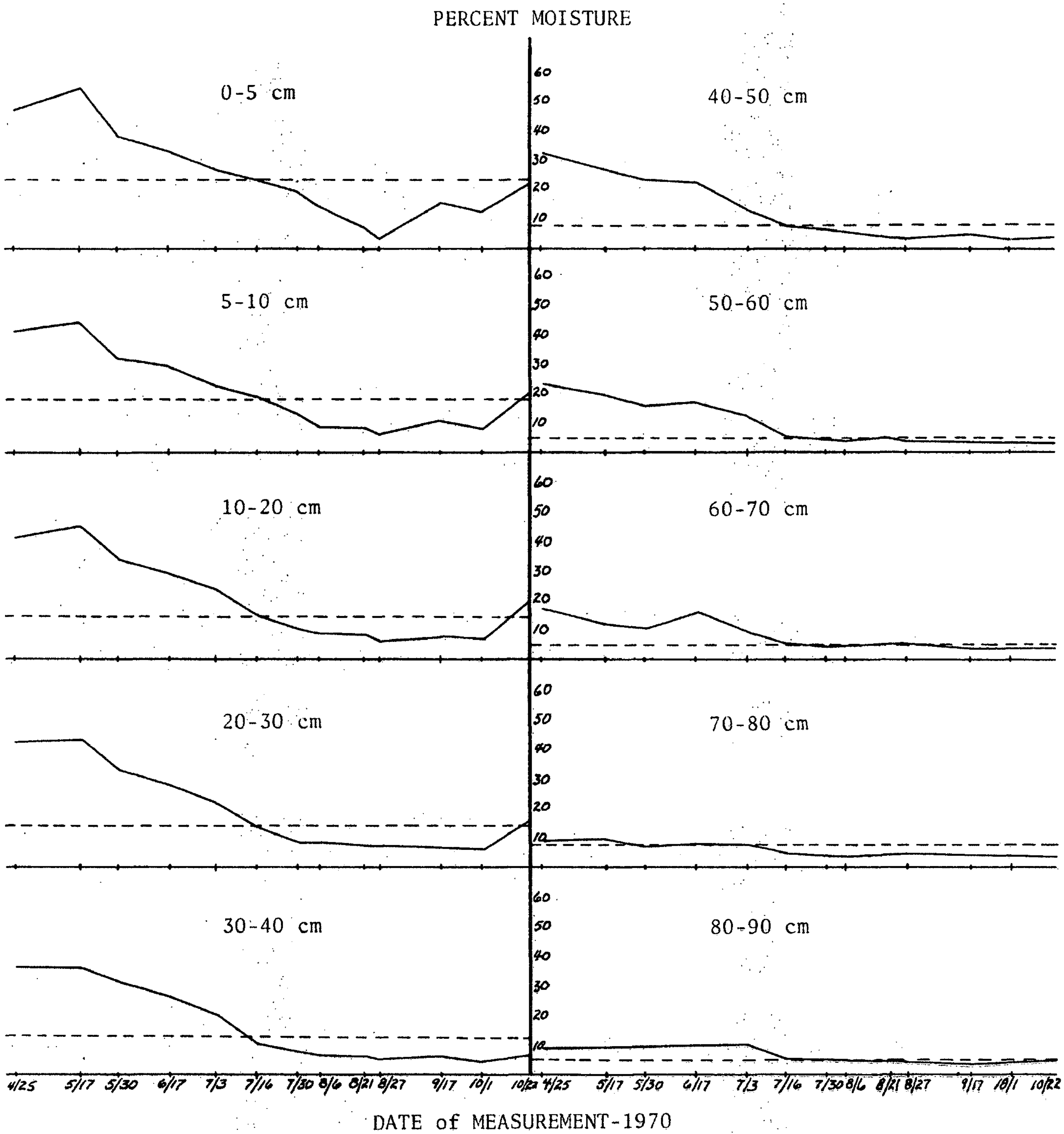

FIGURE 18 . Ungrazed treatment. 1970 percent soil moisture patterns at specified depths. Dashed line represents the 15 atmosphere moisture percent. Soil moisture determined gravimetrically based on oven dry weight.

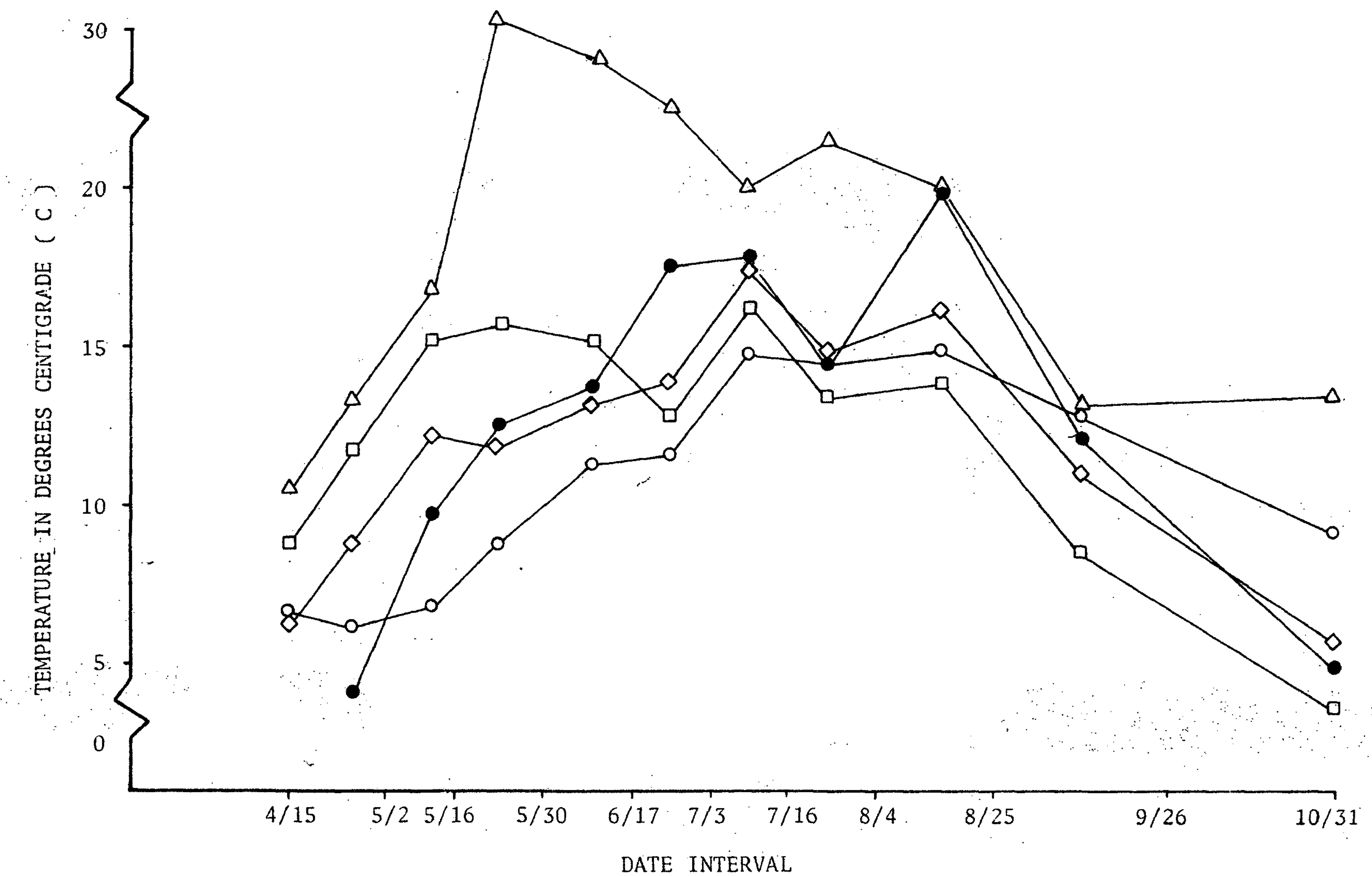

FIGURE 21 . Grazed treatment. 1970 seasonal temperature trends in degrees centigrade for 5 measurement levels: 100 cm air** ● ; 2.5 cm air* △ ; 2.5 cm soil* □ ; 25 cm soil* ◇ ; 75 cm soil* ○ . (*mean of 1000 hrs. reading made weekly by thermocouple; **mean of bihourly summary of hygrothermograph chart.)

ungrazed treatment at the end of the study period.

While seasonal trends are of general interest in the study of vegetation, they are averages, and they subdue the magnitude of temperature change which plants must endure during the growing season. Utilizing a combination of a hygrothermograph and a three-point thermograph on the ungrazed treatment, daily temperature fluctuations at 100 cm-air, 2.5 cm-air, 2.5 cm-soil, and 25 cm-soil were measured. Figure 22 gives a 72-hour section from 7/4, 7/5, and 7/6. The tremendous change of 34 C at the 2.5 cm air level is the most pronounced. The 2.5 cm-soil level also shows a large magnitude of temperature change. The 100 cm air level shows a constant, but smaller amounts of temperature change than the 2.5 cm air. The 25 cm soil shows quite small changes compared to the other three.

Relative Humidity

The biweekly averages of percent relative humidity are presented for both treatments in Figure 23. Both treatments showed extremely similar percentages for all measurement periods. A "t" test used to compare the seasonal means showed no significant difference at the .05 level. Relative humidity ranged from an average low of 46.6% to an average high of 80.7% for both treatments. The lowest levels being from 8/4 to 8/25 and the highest during 9/26 to 10/31.

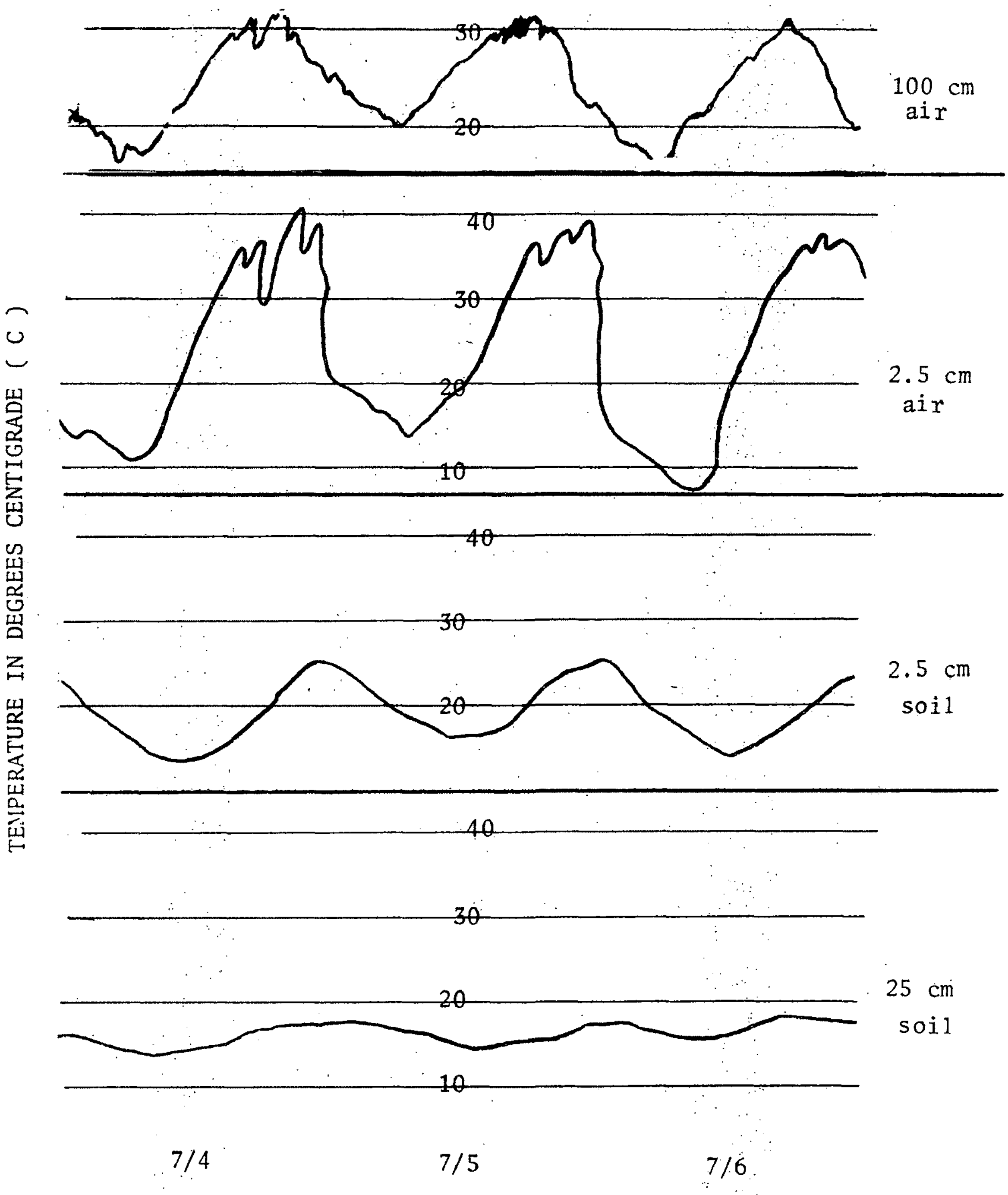

FIGURE 22. Ungrazed treatment. Daily temperature fluctuations for 7/4, 7/5, and 7/6/70 at four levels of measurement. Temperature in degrees centigrade.

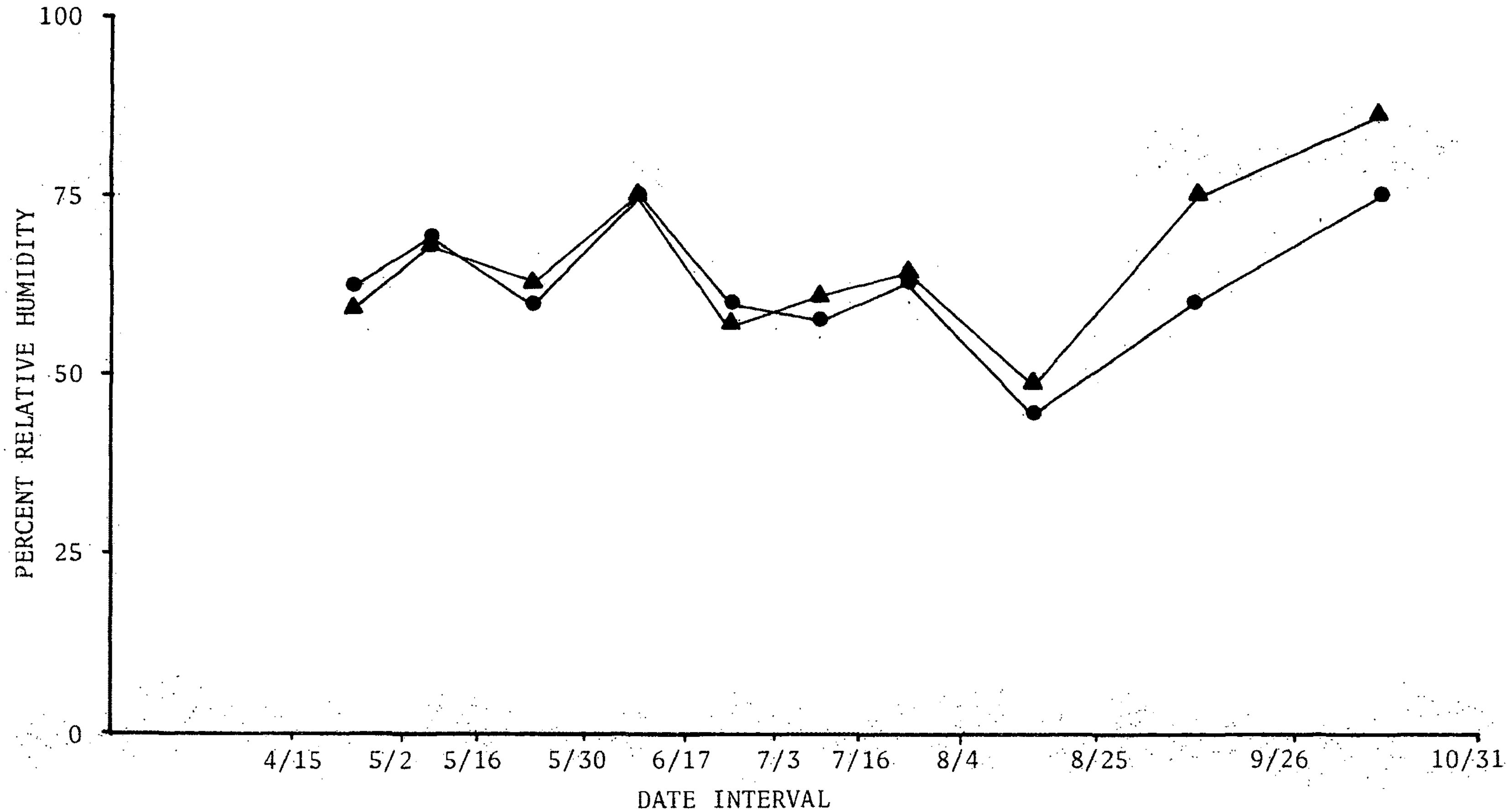

FIGURE 23 . Ungrazed (●) and grazed (▲) treatments. 1970 mean relative humidity based on daily means derived from hygrothermograph charts.

As with temperatures, seasonal trends in relative humidity are of general interest, but the magnitude of fluctuations in relative humidity in which vegetation must grow and survive was examined. To provide some continuity, the daily change in relative humidity in the ungrazed treatment for 7/4, 7/5, and 7/6/70 are shown in Figure 24. The range from almost 100% during the night to 40% during the day exemplifies the magnitude of change endured by plants during the peak of production.

Wind Velocity

Wind velocity was measured at the ungrazed treatment only. Average wind velocity pattern during the study period is given in Figure 25. Velocity ranged from 0.75 to 1.202 m/sec.[1] Lowest velocity was during the 6/17 to 7/3 interval, and the highest was during the 8/25 to 9/26 interval.

Solar Radiation

Solar radiation was not measured on site, and U.S. Weather Bureau data for 1970 were not available. However, a 17-year average for Great Falls, Montana, the closest measuring station, is shown graphically in Figure 26. Mean monthly averages from April to October show July as the

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[1] m/sec x 2.237 = miles per hour.

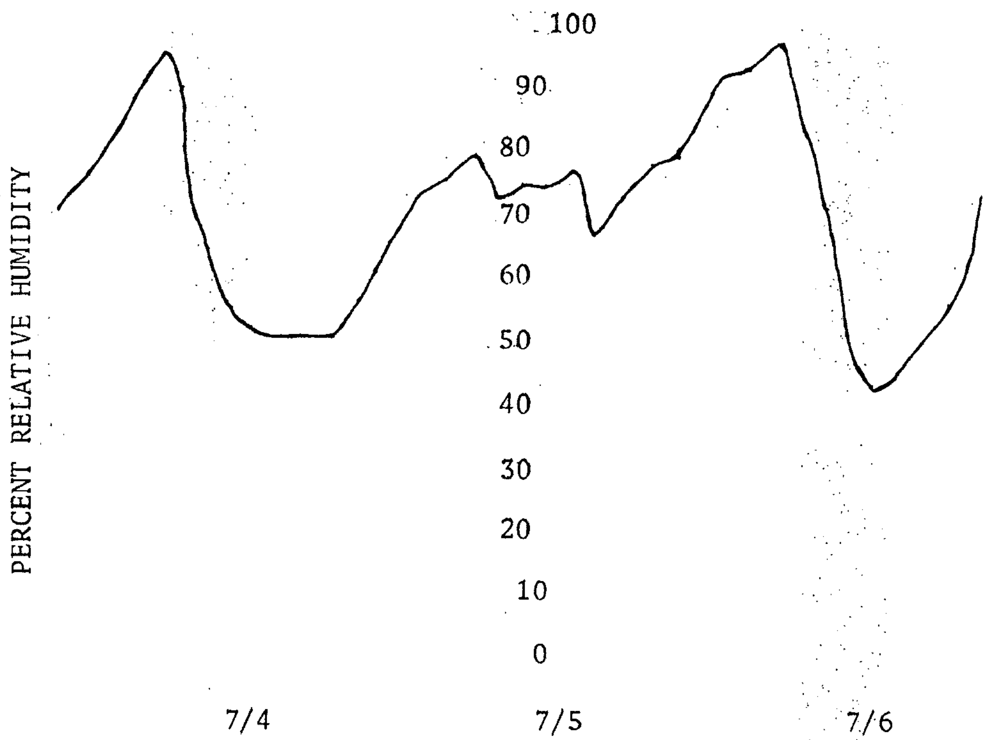


FIGURE 24 . Ungrazed treatment. Daily relative humidity fluctuations for 7/4, 7/5, and 7/6 at the 100 cm air level.

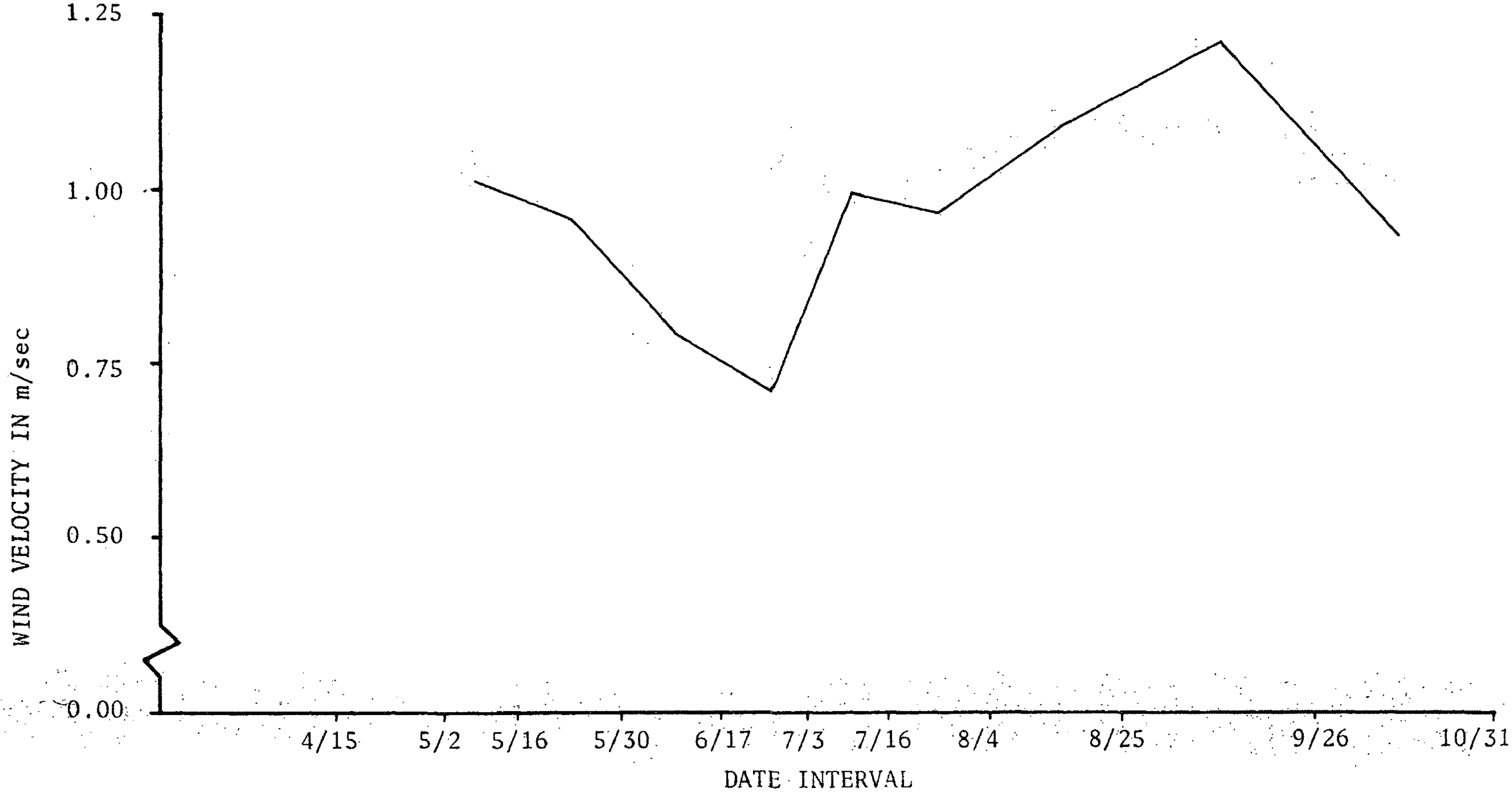
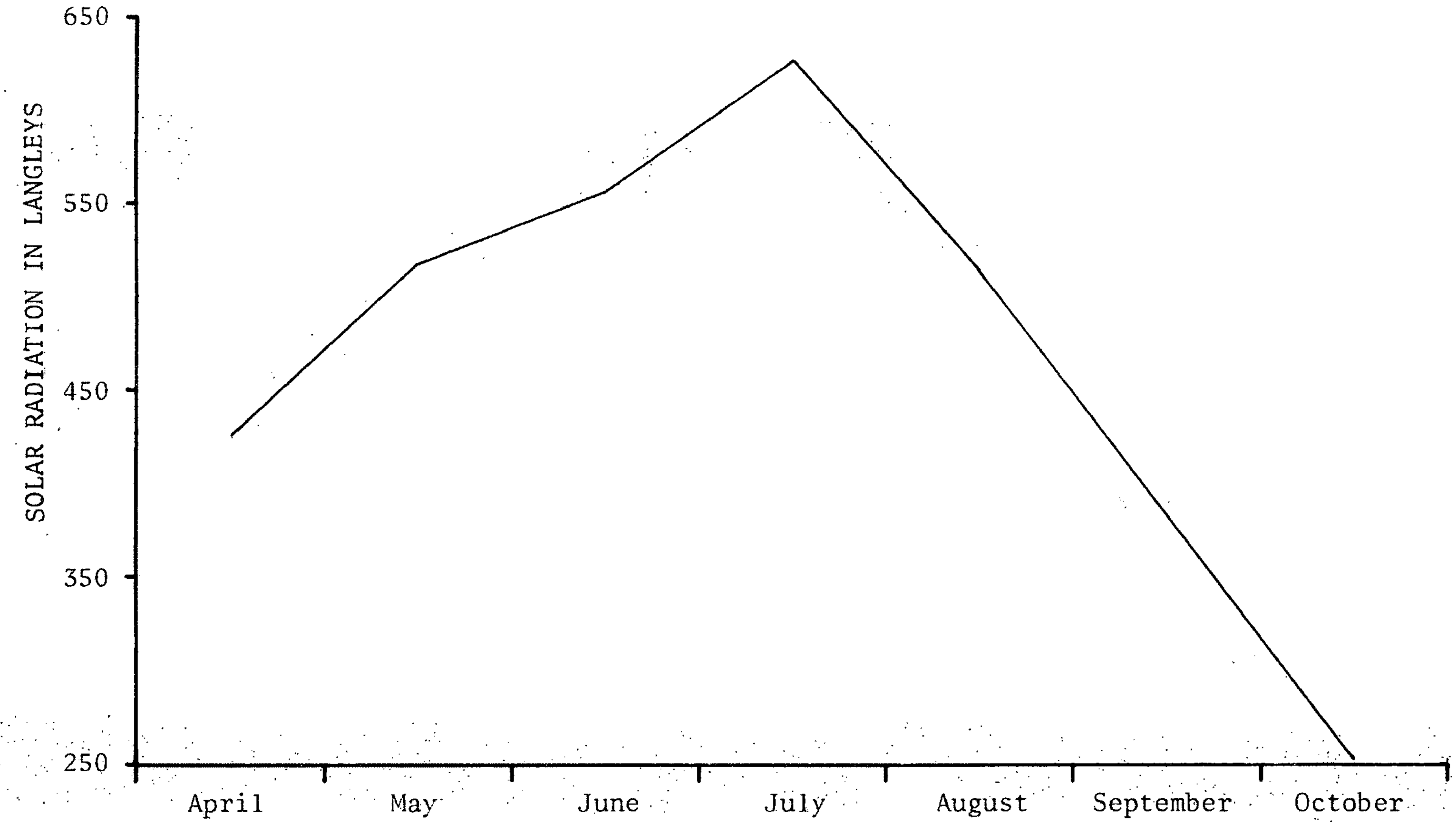


FIGURE 25 . Ungrazed treatment. 1970 mean wind velocity expressed in meters per second.



* a langley is equivalent to one gram calorie per square centimeter of irradiated surface.

FIGURE 26 . Mean monthly solar radiation recieved at the U.S. Weather Bureau, Great Falls, Montana. Mean is based on a 17-year average.

highest month with an average of 627 langleys[1] per day, and October the lowest for the study period. Amounts of solar radiation rise to and fall rapidly from the July zenith.

NET PRIMARY PRODUCTION

Net primary production is that amount of plant matter incorporated or energy bound into the ecosystem during a specified time interval. The time interval considered here is the growing season.

Primary production can be based on the peak of production for the ecosystem, or as the sum of the individual species' peaks of production. Table 8 shows net primary production as the peak of the treatment production.

Table 9 presents net primary production as the sum of the individual species' peaks of production.

It is apparent from Tables 8 and 9 that considerably higher production figures are derived by presenting net primary production as the sum of the individual species' peak production. The ungrazed treatment is 22.29 g/m^2 (2.5%) higher, and the grazed treatment is 48.39 g/m^2 (9.2%) higher in net primary production when this method is used.

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[1]A langley is equivalent to one gram calorie per square centimeter of irradiated surface.

Table 8. Net primary production in g/m^2 based on peak treatment production for 1970.

Category of Plant Material	Treatment	
	Ungrazed	Grazed
Aboveground	228.12	108.18
Belowground	635.00	367.50
Moss	90.75	--
TOTAL	958.87	475.68
TOTAL w/o moss	863.12	475.68

Table 9. Net primary production in g/m^2 based on the sum of individual plant species peak production for 1970.

Category of Plant Material	Treatment	
	Ungrazed	Grazed
Aboveground	250.41	156.57
Belowground	635.00	367.50
Moss	90.75	—
TOTAL	976.16	524.07
TOTAL w/o moss	885.41	524.07

Tables 12 and 13, pp. 99 and 101 of the Appendix, reveal that the difference between the two sites is due to the larger number of species (with inherently different peaks of production) which are major contributors to production on the grazed treatment as opposed to the relatively few species (rough fescue contributed 56%) which are major contributors to maximum production on the ungrazed treatment. The writer feels that the sum of the peak production of individual species constitutes a more accurate method of measuring net primary productivity, and all subsequent calculations of productivity and efficiency will be based upon these data.

The amount of moss which contributes to net primary production is unknown for this study, and the literature gives no indication of annual moss production. For this reason, and since the small amount of moss on the grazed treatment was not harvested, all production figures which follow will not include moss.

The difference in net primary production between the ungrazed and grazed treatments (Table 9) is 361.34 g/m^2. The ungrazed treatment produced 37.5% more aboveground plant material and 42.2% more belowground plant material than the grazed treatment in 1970. Overall, the ungrazed treatment produced 40.9% more plant material than the grazed treatment.

Productivity

Another aspect of net primary production is productivity. Productivity, according to Kormondy (1969), is the amount of energy bound by the ecosystem. A review of literature has found no reference to the caloric content of the species studied. However, Lieth (1968) and Golley (1961) found that prairie grasses have approximately

4.1 kcal per gram, forbs have 4.2 kcal per gram, and root material has 4.0 kcal per gram.

From these data, the caloric content of the study area plant species was estimated. Table 10 shows the productivity in kcal/m^2 of the two treatments. The ungrazed treatment incorporated or bound approximately 41% more energy into the ecosystem than the grazed treatment.

Table 10. Productivity in kcal/m^2 on the ungrazed and grazed treatments for 1970.

Category of Plant Material	Treatment	
	Ungrazed	Grazed
Grass	671.00	414.14
Forb	295.55	256.28
Root	2540.00	1470.00
TOTAL	3506.55	2140.42

Efficiency

Efficiency of each treatment is defined in terms of energy and water utilization. Energy efficiency is a ratio of the amount of incoming solar radiation received by the ecosystem during the growing season to the amount of energy bound into the ecosystem in net primary production. Water efficiency is the ratio of the amount of water used for the production of plant growth to the amount of plant material produced. A most important consideration in determining efficiency is the length of the growing season. For the purposes of this study, the growing season is considered to extend from 1 April to 30 September.

Solar radiation, as received by the earth's surface, consists mostly of visible radiation or light, infrared or thermal radiation, and ultraviolet radiation--the relative quantities being in that order.

The U.S. Weather Bureau at Great Falls, Montana (the closest recording station), reports that 92,377 langleys (923,770 kcal/m^2) is the average total solar radiation for the study period (1 April to 30 September). Energy efficiency based on the total incoming solar radiation is calculated as follows:

Ungrazed Treatment:

$$\frac{3506.55 \text{ kcal/m}^2 \text{ (productivity)}}{923{,}770 \text{ kcal/m}^2 \text{ (total solar radiation)}} = 0.38\%$$

Grazed Treatment:

$$\frac{2140.42 \text{ kcal/m}^2 \text{ (productivity)}}{923{,}770 \text{ kcal/m}^2 \text{ (total solar radiation)}} = 0.23\%$$

Light is the radiation with wavelengths between 400 and 760 millimicrons. Light also is the effective radiation in photosynthesis and makes up almost half of the solar radiation reaching the earth's surface. Efficiency of energy use based on the solar range of radiation utilized in photosynthesis, 400 to 760 millimicrons, is defined for the two treatments as:

Ungrazed Treatment:

$$\frac{3506.55 \text{ kcal/m}^2 \text{ (productivity)}}{369508 \text{ kcal/m}^2 \text{ (solar radiation - 400 to 760 millimicrons)}} = 0.95\%$$

Grazed Treatment:

$$\frac{2140.42 \text{ kcal/m}^2 \text{ (productivity)}}{369508 \text{ kcal/m}^2 \text{ (solar radiation - 400 to 760 millimicrons)}} = 0.58\%$$

While this latter method is now most commonly used to measure energy efficiency, other studies have used total radiation. For this reason, both methods have been described and utilized.

In a most recent study described by Whitman (1969) energy efficiency in a mixed-grass prairie was 1.0% and 0.6% for two consecutive years (1965 and 1966). These are based on a 60-day growing season from 20 May to 20 July and the visible spectrum of solar radiation (400 to 760 millimicrons). Although the growing season is considerably shorter, the efficiencies are comparable to those found for this study.

Water efficiency is based on water used in evapotranspiration compared to the amount of net primary production. Total water used during the growing season is determined by adding the amount of precipitation to the quantity of soil water used in evapotranspiration. Soil moisture in percent was converted to centimeters of water by using the average soil bulk density. On the ungrazed treatment 16.4 cm of precipitation plus the net loss of 36.3% soil moisture during the growing season amounted to 166,960 grams of water used in evapotranspiration. When compared to the net primary production of 976.16 grams, it is found that 171.05 grams of water were required to produce one gram of net primary production.

On the grazed treatment, 17.6 cm of precipitation plus the net loss of 20.4% soil moisture amounted to 177,861 grams of water used in evapotranspiration. When compared to 524.07 grams of net primary production, 339.39 grams of water were required to produce one gram of net primary production. This shows that the ungrazed treatment was 49.6% more efficient in water use than the grazed treatment.

RELATIONSHIPS BETWEEN NET PRIMARY PRODUCTION AND ABIOTIC FACTORS

It is generally acknowledged that plants have three "cardinal temperatures for growth; a minimum, an optimum, and a maximum," and that these so-called cardinal points vary greatly between species (Meyer et al., 1960). In general, however, most species of temperate zone origin do not grow appreciably at temperatures below 5 C. Their optimum growth usually occurs between 20 C and 30 C, and the maximum temperature at which growth continues is about

35 to 40 C. Some of the grass species which are found on this study have been observed to grow at temperatures well below 5 C.[1]

Another generally accepted implication is that many plants appear to cease growth when the percent soil moisture drops below that percent soil moisture retained at −15 bars of soil moisture stress. This is by no means an absolute value for all soil types or all plant species, but does provide a reference point for study of plant growth and responses to soil moisture changes.

Figures 27 and 28 illustrate the changes in 1970 production and standing crop and the associated changes in temperature, soil moisture, and relative humidity for the ungrazed and grazed treatments throughout the study period. A very obvious conclusion from Figures 27 and 28 is that relative humidity remained at a fairly constant level throughout the study and appears to have very little effect on production. Simple coefficients of determination, r^2, for rate of production in $g/m^2/day$ and relative humidity were 0.13 and 0.15 for the ungrazed and grazed treatments respectively. This indicates that only about 13 to 15% of the variation in the rate of production can be accounted for by relative humidity assuming that a linear relationship exists. Also obvious from Figures 27

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[1]Personal communication with Dr. Lee E. Eddleman.

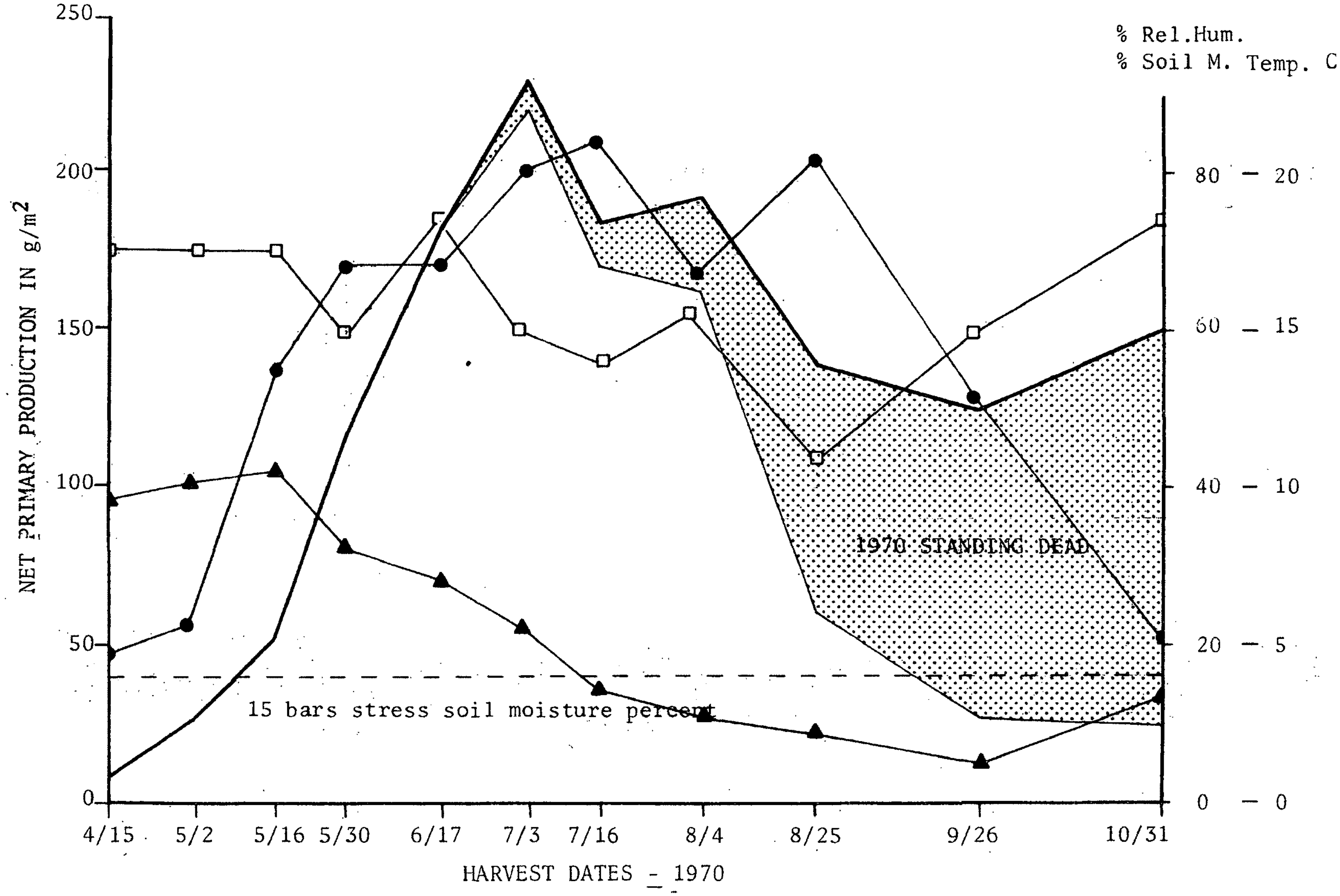

FIGURE 27 . Ungrazed Treatment. Seasonal trends in air temperature(100 cm) ● , relative humidity □, and soil moisture ▲ in relation to the 1970 standing crop ——.

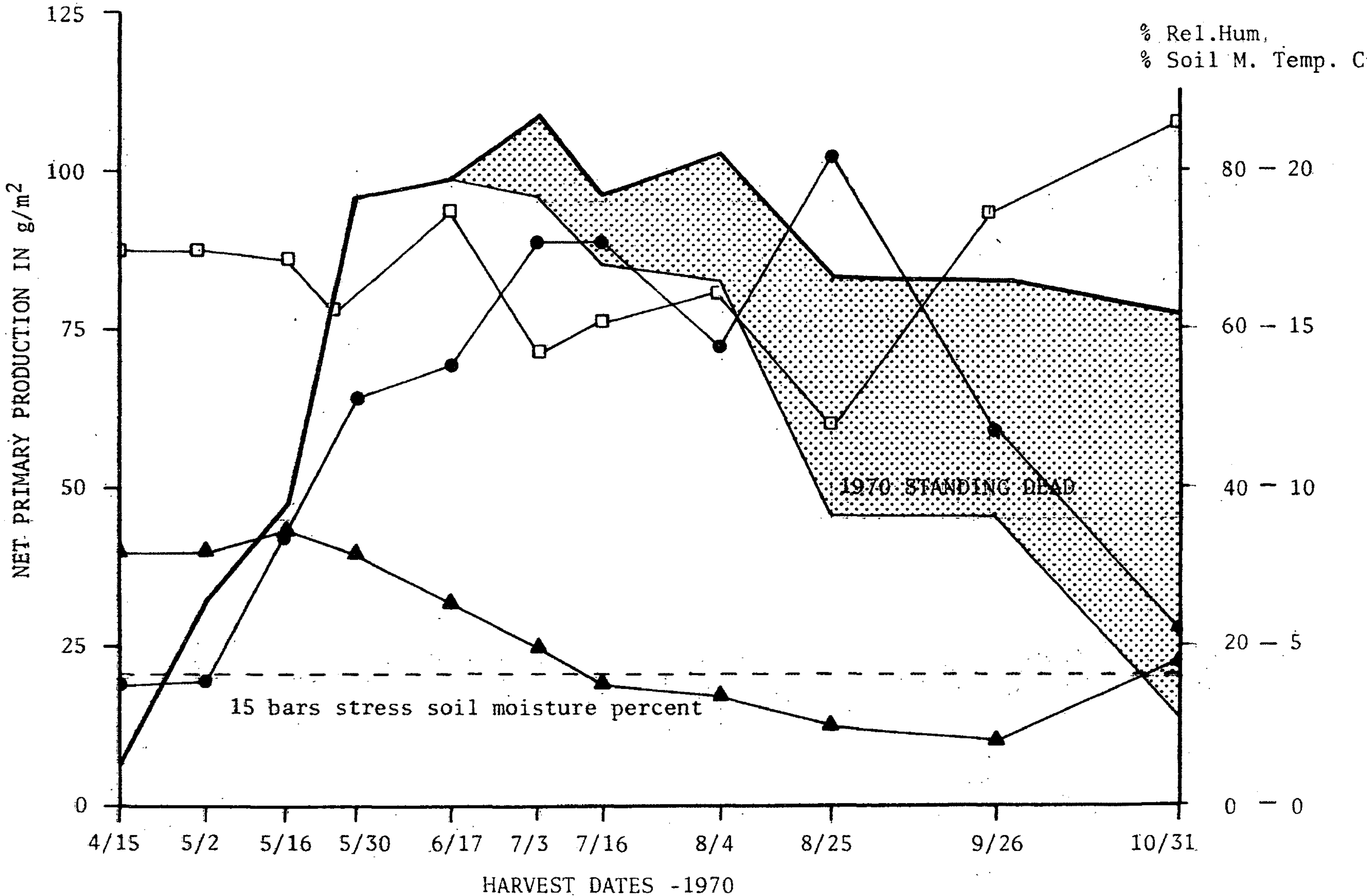

FIGURE 28 . Grazed treatment. Seasonal trends in air temperature(100 cm) ●, relative humidity □, and soil moisture ▲ in relation to the 1970 standing crop ▬.

and 28 are the corresponding trends of ambient air temperature and soil moisture to increases in aboveground production. Generally, as temperatures rise, production increases. With this increase in production, soil moisture decreases. The slight increase in soil moisture near the beginning of the study period is due to precipitation. However, coefficients of determination, r^2, measuring the impact of temperature on the rate of production were .659 and .0005 for the ungrazed and grazed treatments. For soil moisture and rate of production the r^2's were .375 and .229. On the ungrazed treatment r^2 of wind speed and production was .241. Since the range for r^2 is 0 to 1, it seems that little of the variation in production rate is caused by any of these factors. This can be explained by the fact that during the active production period temperatures fluctuated within the optimum range of temperatures for plant growth and, therefore, caused little corresponding change in the rate of growth. Also, during the active growth period soil moisture was adequate for plant growth. Decreases in soil moisture caused no overt reduction in plant growth rate during the active growth period.

It is apparent that if either temperature or availability of soil moisture is beyond the range of plant metabolism, plant growth will not occur. This was the phenomenon that occurred on both treatments at the beginning and the cessation of production. At the beginning of the growing season, soil moisture was high and not a limiting factor; however, temperatures ranged from 3.9 to 5.0 C and, due to these lower temperatures, growth proceeded at a very slow rate. By 5/15, temperatures averaged 9.4 to 13.9 C, and growth rate increased rapidly. This high growth rate was maintained until 7/3 when the average temperatures were 17.8 to 20.0 C. From this point, measurable growth ceased, and 1970 standing dead plant material increased. The highest periodic rate of growth was from 5/16 to 5/30 for both treatments. It is apparent that temperatures less than 3.9 to 5.0 C suppressed plant growth, and that temperatures about 9.4 to 13.9 C were optimum for plant growth and production in these two ecosystems. Maximum temperature for growth was not attained.

Soil moisture content throughout the growth period shows a general decline. This decrease is a function of plant growth and soil surface evaporation (evapotranspiration). The largest periodic decrease in soil moisture corresponds with the highest periodic rate of plant growth. This is particularly noticeable on the ungrazed treatment. At some date between 7/3 and 7/16 soil moisture decreased below the -15 bar moisture retention percentage. Cessation of plant growth and the decrease of soil moisture below the -15 bar soil moisture retention percentage appeared highly correlated in time of occurrence.

It is apparent that these ecosystems function primarily through temperature and soil moisture availability. Temperature is the controlling factor for the initiation of growth, and availability of soil moisture controls the cessation of growth.

A quantitative evaluation of temperature change, soil moisture, and solar energy utilized to produce one gram per square meter of plant material is summarized in Table 11. The values for solar energy are very high and account for the very low efficiencies of each treatment. The grazed treatment utilized almost three times as much solar energy to produce one gram of plant material.

Table 11. Temperature change, soil moisture, and solar energy utilized to produce one gram per square meter of plant material from 5/15 to 7/3/70.

Factor	Ungrazed Treatment	Grazed Treatment
Temperature	.003 C	.007 C
Soil Moisture	.003 cm	.010 cm
Solar Energy	1.286×10^5 cal	2.312×10^5 cal

The use of soil moisture represents not only the change in soil moisture during the period, but also accounts for the amount of precipitation received. Evaporation is included in the soil moisture use figures as it could not be separated from evapotranspiration. There was 7.18 cm and 5.10 cm of precipitation with decreases of 16.6% and 12.0% soil moisture on the ungrazed and grazed treatments respectively. This amounts to 7.31 cm and 6.10 cm of water used for plant growth as evapotranspiration.

The temperature change at 100 cm aboveground was 6.1 C and 7.8 C on the ungrazed and grazed treatments respectively for this period (5/15 to 7/3/70).

The figures in Table 11 indicate that during the period of maximum growth rate (5/15 to 7/3/70) the ungrazed treatment utilized approximately one-third as much moisture and heat (temperature) and one-half as much solar energy in the production of plant material. This does not indicate that more of any of these factors was required for unit increases in plant growth. It is very probable that, on the grazed treatment, plants could be more efficient as individuals due to a decrease in plant numbers which results in decreased competition. However, per unit area this is not true. The differences in temperature and solar energy utilization could account for the large differences in mean air temperature at 2.5 cm. These two factors are lost into the atmosphere as heat and reflected radiation from exposed soil, which has a higher percentage on the grazed treatment.

CHAPTER VI

DISCUSSION

That a large amount of variation is more often the rule rather than the exception in biological phenomena is generally accepted. Species, as well as individuals within a species, respond to environmental factors in a variety of ways manifested in adaptation and survival. In addition, factual evidence concerning many biological phenomena which, due to the infinite variety encountered in nature, holds true only in a very limited number of circumstances. With these thoughts as guidelines, the following discussion is presented.

It is desirable to examine the relationships that exist between the two treatments. What are the abiotic similarities and differences between these two treatments? What is the relationship between the differences of net primary production on these two treatments? What are the relationships between production and the abiotic factors? In a study of this type, the total ecology of each ecosystem, not to mention each species, and of all the interrelated factors cannot be explained. However, estimates of net primary production of these ecosystems and the general relationships of production to certain abiotic factors may be obtained.

When "t" tests were applied to compare the abiotic factors for differences between the two treatments, all differences were found not to be significant except the 2.5 cm air temperatures. This difference can be explained as being the function of several factors. The two sites, as mentioned, were selected to be similar in all respects. However, the grazed treatment had less percent slope and a more westerly aspect, and therefore it would be assumed to receive more direct radiant energy. It must be realized, also, that differences in amount of plant cover, type of plant cover, and soil color all play an important role in the amount of reflection or albedo of radiant energy from the earth's surface. There is approximately half as much plant material per square meter on the grazed treatment as on the ungrazed treatment. In addition, rough fescue, the main plant species on the ungrazed treatment, is in very low abundance on the grazed treatment. The absorbent, transmittant, and reflectant qualities of these main species must be studied to factually account for the differences in temperature at the 2.5 cm level. It is felt that this difference is more a function of differences in vegetative cover and species composition than differences in physiography.

It can be concluded that while these two locations are not precisely the same in terms of abiotic factors, they are similar enough to be considered as having equal potential for plant production.

A comparison of the species' presence reveals remarkable similarities. This, coupled with the fact that there is evidence of a previous stand of rough fescue on the grazed treatment, lends strong evidence to the conclusion that the lower net primary production of the grazed treatment is the manifestation of past heavy grazing and removal of rough fescue as the preferred forage plant.

Additionally, in view of the large differences in net primary production between the two treatments, it can be concluded that, in this case, production does increase considerably when moving from a seral to a climax stage. This is contrary to one of the conclusions of Odum (1960). He found that in a Michigan old field the production of this successional stage was equal to native prairie of the same region.

One of the most difficult aspects of this study was the determination of the relationship of production and the abiotic factors. It would seem obvious, since the trends in temperature and soil moisture are apparent, that there would be a high correlation between them and the trend in plant production. However, this does not explain any physiological response of plants to their environments. The r^2 values which were determined were an attempt to relate rate of production and the abiotic factors. It was shown that there was no relationship for the time period observed. This was due to one primary event: all measurements of production were made during a time interval when the abiotic factors were at an optimum state. Consequently, fluctuations in abiotic factors within this optimum range had little effect on production. The only apparent response of plant growth to an abiotic factor was the time period when soil moisture dropped below the -15 bar soil moisture retention percentage which corresponded to cessation of production and permanent wilt of the grasses. Since temperature and relative humidity showed no major changes and remained within the apparent tolerance limits of these plants, it must be concluded that soil moisture was the limiting factor in the cessation of growth. Additionally, it can be hypothesized that at the beginning of the growing season temperature operates to control growth since soil moisture is abundant at this time. This particular relation could be substantiated by earlier harvest and earlier seasonal abiotic records. To get more reliable and more meaningful relationships between production and abiotic factors, more samples by harvest must be made during the initial and terminal stages of production. In addition, the abiotic phase should be sampled more thoroughly to determine exactly which attributes of the environment are most closely associated with production.

The results found in this study concerning net primary production compare favorably with those reviewed in the literature. However, due to differences in vegetation it seems more realistic to compare efficiency or other relative values rather than production.

Information obtained in this study seems to point out the amount of variability in a natural ecosystem. The study results illustrate the need for more intensive observation of plant reactions at points of environmental stress rather than during optimum conditions for growth. Also, these points of environmental stress must be analyzed and quantified. To separate these interrelating factors is a challenge for all students of the science.

Since good management of grasslands must be integrated with a knowledge of the structure and function of grassland ecosystems, several management-oriented principles are evident from this study. The limitation is realized that, because of the natural variation mentioned earlier, implications drawn from these study data must be applied only to areas of similar soil and other environmental factors as those found on the study area. Implications made are those based on one study conducted during one growing season. Keeping these limitations in mind, some possible management implications will be presented.

When the maximum amount of standing crop production is considered, the advantage of maintaining a fescue grassland at or near climax is obvious. In a climax condition, the ungrazed treatment produced an average of 250.41 g/m^2 (2226.25 pounds per acre) while the grazed treatment yielded 156.57 g/m^2 (1394.47 pounds per acre). Based on a proper use of 60%, there is approximately 58.4 g/m^2 or 500 pounds per acre more on the climax site. This increase in forage availability makes practical the maintenance of climax conditions.

Since availability of soil moisture seems to cause growth cessation at about mid-summer, it seems that where feasible irrigation could sustain this grassland type in a productive state. To substantiate this possibility, research should be conducted as to the feasibility and practicability of such an undertaking.

The main point of this discussion is net primary production and its relationship to the abiotic factors studied. It must be understood, however, that the plants in these ecosystems have evolved and adapted within the framework of the existing abiotic conditions. In doing so, they have been genetically selected to complete life-cycles and survive. Thus, the plant processes which appear to be strongly related to certain environmental factors respond to these factors not due to the factor alone, but to an entire host of interrelated biotic and abiotic factors not dealt with in this study.

It is felt that this study and the methods employed can be used to determine net primary productivity. However, each phase of the study must be intensified to obtain better and more quantified data. The most hindering aspect of the study area is the inability to obtain below-ground information needed due to the stoniness of the soil.

CHAPTER VII

SUMMARY AND CONCLUSIONS

During the period from April to October 1970, field data were collected on two rough fescue (*Festuca scabrella*) ecosystems: one with a history of heavy-moderate grazing, and the other with little or no grazing history. The object was to measure the net primary production and several other concluding factors, and to attempt to relate the effects of abiotic factors on net primary production. Comparisons of the two treatments for abiotic similarities or differences and for biotic similarities or differences were also made.

The study area is located on the National Bison Range which is approximately 50 miles northwest of Missoula, Montana. The two study treatments are located on approximately north aspects at an elevation of 950 meters. A Rattle Cobbly Silt Loam soil ranges from exposed bedrock to 1.5 meters deep. The climate is characterized by a mean annual temperature of 7.5 C and an annual precipitation of 382.19 mm.

Vegetation was harvested on 20 0.5 m^2 quadrats on each treatment at approximately two-week intervals. It was separated in the field into individual species, 1969 standing dead, or litter. Estimates of 1970 standing dead were made and recorded for each species. All above-ground biomass was oven dried at 65 C and converted to g/m^2 for each date. The date of peak production for each treatment was 7/3; the ungrazed treatment had 228.12 g/m^2; the grazed treatment had 108.18 g/m^2. Based on a summary of the maximum production of each species, the ungrazed treatment produced 250.41 g/m^2 and the grazed treatment produced 156.57 g/m^2. Root production for 1970 was calculated at 635.0 and 367.5 g/m^2 for the ungrazed and grazed treatments respectively. Net primary production is estimated at 885.41 g/m^2 for the ungrazed treatment and 524.07 g/m^2 for the grazed treatment. Net primary production was based on the maximum production of each species.

The efficiency of each treatment was calculated on a solar-energy and water-use basis. The growing season was concluded to be from 1 April to 30 September. Total solar radiation efficiencies of 0.38% and 0.23% were calculated for the ungrazed and grazed treatments. By using that light wavelength range utilized in photosynthesis (400 to 760 millimicrons), efficiencies were 0.950% and 0.575% for the ungrazed and grazed treatments. Water-use efficiencies were 171.05 grams and 339.39 grams of water for each gram of plant material produced on the ungrazed and grazed treatments respectively. Net primary productivity or the amount of energy bound into the ecosystem was calculated as 2506.66 kcal/m^2 and 2140.42 kcal/m^2 for the ungrazed and grazed treatments. These data include both aboveground and belowground plant production.

The botanical composition of each treatment was remarkably similar. There were 61 to 65% grasses and 34 to 38% forbs. Composition was estimated as the percent of total maximum species production. Plant moisture content was measured by placing field-clipped Fesc, Feid, and Agsp[1] in airtight plastic bags which were weighed, oven dried, and reweighed to determine moisture content. Plant moisture was very high at growth initiation, but declined rapidly toward the peak of growth. Plant height growth was the measurement of the longest leaf. Fesc attained 47.4 cm and 43.9 cm; Feid attained 20.1 cm and 23.5 cm; and Agsp was 43.8 cm on the ungrazed and grazed treatments respectively. Height-to-weight curves indicated that production continued after leaf elongation had ceased.

Precipitation was 205.13 mm and 219.23 mm on the ungrazed and grazed treatments, the majority coming in April-May and September. Temperature was measured at 100 cm and 2.5 cm in the air and 2.5 cm, 25 cm, and 75 cm in the soil. A summary of temperatures is given in Table 16, p. 105. Relative humidity remained relatively

[1]See Appendix, p. 112.

constant throughout the study period with daily means ranging from 40 to 80%. Soil moisture ranged from 35 to 40% at the beginning of plant growth, decreased below the 15 bar moisture retention percentage between 6/17 and 7/3/70, and reached a low of 3 to 8% prior to recharge by fall rains in September. Wind was measured by a three-cup anemometer on only the ungrazed treatment. Wind velocity ranged from .7 to 1.25 m/sec with no apparent trends. Solar radiation used for various data calculations was a 17-year monthly average of solar radiation received at Great Falls, Montana.

Simple linear correlations of determination, r^2, were calculated to determine the amount of variation in rate of production which could be accounted for by each of the abiotic factors. Very little variation could be accounted for by this method. It was concluded that this was due to the fact that most measurements were made during optimum growing conditions and, consequently, changes in these abiotic factors caused no apparent changes in production.

To achieve a quantitative value of the relationship of the abiotic factors to production, data for temperature, soil moisture, and solar energy were calculated. It was found that each gram of plant material produced on a square meter between 5/16 and 7/3 utilized .003 C temperature rise, .003 cm of water, and 1.286×10^5 calories of solar energy on the ungrazed treatment. On the grazed treatment, each gram of plant material produced per square meter utilized .007 C temperature rise, .01 cm of water, and 2.312 x 10^5 calories of solar energy. These figures do not indicate that more of any of these factors was necessary for unit increases in production on the grazed treatment than on the ungrazed treatment. They only show that the ungrazed treatment was able to use the environmental factors more efficiently.

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APPENDIX

in grams per square meter for the 1970 study period.

Square Meter						
6/17	7/3	7/16	8/4	8/25	9/26	10/31
102.31	140.71	117.08	134.88	100.93	90.87	108.00
4.48	10.26	3.76	8.66	8.96	10.83	8.74
1.22	3.08	0.84	2.49	0.47	0.86	--
1.72	1.73	2.74	1.49	0.45	1.63	0.58
6.30	2.55	0.30	0.68	0.52	--	--
116.03	158.33	124.72	148.20	111.33	104.19	117.32
41.30	34.26	27.36	16.63	11.46	9.83	14.12
3.37	1.56	1.26	1.49	0.93	--	--
4.75	4.03	0.72	0.60	0.83	--	--
2.88	7.78	6.90	4.00	4.68	4.19	2.48
0.06	0.47	--	0.03	--	--	--
2.02	5.60	2.06	2.96	--	--	--
--	4.32	8.46	9.59	3.83	--	--
0.93	1.82	0.42	1.64	--	--	--
11.47	9.95	9.68	6.76	6.59	4.85	16.92
66.78	69.79	56.86	43.70	28.32	18.87	33.52
182.81	228.12	181.58	191.90	139.65	123.06	150.84
91.25	106.63	39.14	46.45	31.53	11.42	--
--	9.10	13.34	30.87	78.83	95.37	124.89
148.11	222.10	269.16	335.06	338.22	308.60	243.40
422.17	556.85	489.88	573.41	509.40	443.08	394.24

in grams per square meter for the 1970 study period.

Square Meter						
6/17	7/3	7/16	8/4	8/25	9/26	10/31
3.72	3.29	10.18	4.71	3.24	3.95	4.04
18.42	25.85	14.92	28.62	32.35	19.67	24.78
18.42	26.25	28.16	28.54	25.35	19.36	21.40
8.94	6.23	8.74	9.46	1.86	20.88	5.98
9.06	1.28	0.17	3.03	2.63	0.32	--
58.56	62.90	62.17	74.36	65.43	64.18	56.20
11.06	20.72	9.94	8.09	2.70	--	0.92
3.68	1.14	0.94	--	0.03	--	--
4.06	3.32	3.90	0.74	0.68	--	--
7.14	6.34	9.04	7.51	3.09	3.41	4.82
2.16	0.41	--	0.17	1.16	--	--
--	0.67	--	0.43	0.37	--	--
--	--	--	--	--	5.22	4.12
1.08	2.86	2.12	0.61	--	--	--
10.53	9.82	8.50	10.21	9.46	9.49	11.76
39.71	45.28	34.44	27.76	17.49	18.12	21.62
98.27	108.18	96.61	102.12	82.92	82.30	77.82
48.52	36.56	20.27	22.82	12.22	1.13	--
--	12.19	11.50	20.68	40.19	39.01	61.14
36.34	51.22	74.14	55.96	148.16	201.82	110.88
183.13	195.96	191.02	180.90	243.30	285.25	188.70

Table 14. Maximum leaf length of *Festuca scabrella*, *F. idahoensis*, and *Agropyron spicatum* on both treatments during the 1970 growing season.

Treatment and Species	Sample Date—1970								
	4/15	5/3	5/15	6/1	6/15	7/1	7/16	8/4	8/15
Ungrazed									
Festuca scabrella	17.1	20.6	35.4	44.3	47.4	44.5	44.7	47.5	48.6
F. idahoensis	6.7	10.1	18.9	22.4	23.5	23.1	23.6	24.0	24.6
Grazed									
F. scabrella	--	17.0	28.9	27.3	32.3	29.6	32.4	27.3	28.4
F. idahoensis	7.7	12.0	18.4	20.3	20.3	21.3	21.4	19.6	19.2
Agropyron spicatum	7.7	19.9	27.5	34.0	41.5	43.9	43.6	41.3	42.9

Table 15. Plant moisture content as a percent of oven-dry plant material from the ungrazed and grazed treatments during the 1970 growing season.

Date	Ungrazed Treatment		Grazed Treatment		
	Fesc	Feid	Fesc	Feid	Agsp
4/15	316.6	280.0	233.3	252.7	233.3
5/2	230.8	173.3	161.5	277.8	195.2
5/16	164.8	*	149.8	166.4	191.6
5/30	161.4	134.7	144.9	157.1	141.2
6/17	172.5	142.8	155.4	142.5	142.5
7/2	142.7	101.5	139.7	210.9	106.3
7/16	109.1	75.8	107.1	67.8	80.2
7/30	107.6	83.5	99.2	*	72.1
8/7	66.3	46.6	91.1	61.3	68.9
8/13	42.3	42.8	82.4	57.2	60.8
8/20	39.7	36.8	78.7	50.3	62.0
8/27	30.8	29.7	32.5	51.1	49.9
9/3	22.9	23.6	46.6	31.6	38.1
9/17	46.7	49.7	57.3	48.1	47.5
10/1	36.8	38.7	48.6	43.0	39.5

*Missing data.

Table 16. Mean temperatures in degrees centigrade for the ungrazed and grazed treatments for the 1970 growing season based on harvest periods.

Location/ Height or Depth cm.	Dates										
	4/15	4/16 5/2	5/3 5/16	5/17 5/30	5/31 6/17	6/18 7/3	7/4 7/16	7/17 8/4	8/5 8/25	8/26 9/26	9/27 10/31
					Ungrazed Treatment						
Air											
100*	--	5.6	13.9	17.2	17.2	20.0	21.1	16.7	20.5	12.8	5.7
2.5*	--	--	13.9	12.9	12.1	21.2	26.2	17.4	19.4	5.9	-0.8
2.5**			13.5	8.4	9.4	21.1	12.5	11.5	8.5	-1.1	-0.2
Soil											
2.5*	--	--	12.3	9.3	11.9	15.0	17.4	18.4	22.1	9.8	4.1
25*	--	--	8.6	8.6	10.3	13.2	15.5	14.8	15.0	8.6	2.7
2.5**	6.9	8.6	9.8	6.9	5.0	12.1	14.0	13.7	13.9	7.9	3.8
25**	6.1	7.2	8.0	8.4	10.4	12.7	15.1	13.6	14.0	8.0	2.7
75**	--	6.8	7.3	8.8	10.6	11.1	12.6	13.4	13.8	11.9	9.8
					Grazed Treatment						
Air											
100*	--	4.1	9.7	12.6	13.7	17.5	17.9	14.4	19.9	12.0	4.8
2.5**	10.5	13.3	16.8	31.3	28.4	25.5	20.4	23.9	20.2	13.1	13.3
Soil											
2.5*	8.9	11.8	15.3	15.6	15.2	12.8	16.2	13.4	13.9	8.6	3.3
25**	6.1	8.7	12.2	11.9	13.1	13.9	17.5	14.9	16.2	10.9	5.6
75**	6.7	6.4	6.8	8.7	11.4	11.7	14.9	14.7	14.9	12.9	9.1

*Temperatures are an average of two-hour readings recorded on a continuously recording thermograph.

**Temperatures are an average of weekly readings made by thermocouple at 1000 hours. These temperatures can be used to compare treatments.

content as a percent of oven-dry soil. Fifteen bar moisture percents are given for comparison.

Sample								
7/16	7/30	8/6	8/21	8/27	9/17	10/1	10/22	15 bar Percent
23.0	19.3	14.1	7.4	3.7	16.2	13.7	25.5	26.9
18.6	12.3	9.4	8.1	5.9	10.7	8.6	23.5	17.8
14.0	10.4	9.9	8.0	5.8	7.6	6.8	22.6	16.6
12.7	9.3	9.1	7.5	7.1	7.2	6.0	18.2	16.6
10.4	8.4	7.7	6.4	5.6	6.2	4.1	6.9	14.8
7.7	6.3	5.1	3.6	3.4	4.9	3.1	3.9	8.5
5.6	3.9	4.5	4.2	3.9	3.4	3.6	3.4	5.6
4.9	4.0	3.8	4.6	4.3	3.7	3.7	3.9	5.7
4.7	4.5	3.9	4.2	4.7	4.1	--	4.1	7.0
5.5	5.3	4.8	4.3	4.4	4.2	--	4.8	4.9
5.6	5.7	5.1	4.9	5.2	4.9	--	6.4	4.6

as a percent of oven-dry soil. Fifteen bar moisture percents are given for comparison.

Sample								
7/16	7/30	8/6	8/21	8/27	9/17	10/1	10/22	15 bar Percent
17.7	22.4	15.1	8.1	6.0	15.9	11.9	28.2	20.0
13.5	17.7	14.1	7.3	8.2	10.6	9.9	27.8	17.4
10.4	15.5	13.2	6.8	7.1	10.4	8.0	20.5	17.2
9.9	9.2	11.8	9.2	7.1	6.4	7.6	8.9	15.0
9.9	8.2	12.2	9.5	6.0	5.5	6.7	5.4	13.2
14.0	15.6	13.1	10.7	8.1	4.9	5.2	5.4	13.2
11.7	--	11.1	9.4	6.9	5.3	--	--	11.4
--	--	--	7.1	7.1	5.9	--	--	11.6
--	--	--	--	--	6.1	--	--	10.8
--	--	--	--	--	--	--	--	--
--	--	--	--	--	--	--	--	--

Table 19. Soil characteristics for the ungrazed and grazed treatments.

Soil Depth(cm)	% Sand	% Silt	% Clay	Munsell (Dry)	Bulk Density	15 bar % Moist. Ret.
			Ungrazed Treatment			
0- 5	24.0	61.6	14.4	10YR 3/1	.91	20.0
5- 10	24.4	66.0	9.6	10YR 3/2	.63	17.4
10- 20	24.4	70.0	9.6	10YR 3/2	.79	17.2
20- 30	22.8	70.2	7.0	10YR 3/3	.83	15.0
30- 40	22.0	70.0	8.0	10YR 4/4	.36	13.2
40- 50	36.4	49.6	14.0	10YR 5/4	1.73	13.2
50- 60	28.0	54.8	17.2	10YR 5/4	--	11.4
60- 70	40.0	43.8	16.2	10YR 6/4	--	11.6
70- 80	--	--	--	--	--	10.8
80- 90	--	--	--	--	--	--
90-100	--	--	--	--	--	--
			Grazed Treatment			
0- 5	16.0	68.8	15.2	10YR 3/2	.91	26.9
5- 10	13.9	62.3	23.8	10YR 3/2	.89	17.8
10- 20	15.6	65.6	18.8	10YR 3/2	.59	16.6
20- 30	21.6	58.6	19.8	10YR 3/3	.72	16.6
30- 40	21.6	61.0	17.4	10YR 4/4	--	14.8
40- 50	35.6	39.0	25.4	10YR 5/4	--	8.5
50- 60	7.6	67.0	25.4	10YR 5/4	--	5.6
60- 70	16.0	62.0	22.0	10YR 6/4	--	5.7
70- 80	--	--	--		--	7.0
80- 90	--	--	--		--	4.9
90-100	--	--	--		--	4.6

Table 20. Summary of "t" test comparison of treatment biweekly means for measured abiotic factors.

Abiotic Factors Compared	Significance at $t_{.05}$
Precipitation	N.S.
Soil Moisture: (average 0-50 cm)	N.S.
Temperature:	
100 cm aboveground	N.S.
2.5 cm aboveground	**
2.5 cm belowground	N.S.
25 cm belowground	N.S.
75 cm belowground	N.S.
Relative Humidity:	
100 cm aboveground	N.S.

N.S. = nonsignificant

** = significant

Plant List of Species on the Ungrazed and Grazed Treatments for 1970 with Appropriate Symbols

Symbol	Species
	SHRUBS AND HALF SHRUBS
Ardr	Artemesia dracuncula
Arfr	Artemesia frigida
Syal	Symphoricarpus albus
	GRASSES
Agsp	Agropyron spicatum
Agin	Agrostis interrupta
Brja	Bromus japonicus
Brte	Bromus tectorum
Feid	Festuca idahoensis
Fesc	Festuca scabrella
Kocr	Koeleria cristata
Popr	Poa pratensis
Pose	Poa secunda
	FORBS
Acmi	Achillea millifolium
Aggl	Agoseris glauca
Anma	Anaphalis margaritacea
Anro	Antennaria rosea
Arfu	Arnica fulgens
Asfa	Aster falcatus
Asda	Astragalus dasyglottis
Basa	Balsamorrhiza sagittata
Brgr	Brodea grandiflora
Casu	Castelleja sulfurea
Cema	Centaurea maculata
Chvi	Chrysopsis villosa
Ciar	Cirsium arvense
Crac	Crepis accuminata
Debi	Delphinium bicolor
Diam	Dianthus armeria
Doco	Dodecatheon conjugens
Dra	Draba spp
Frpu	Fritillaria pudica
Gatr	Galium triflorum
Gaco	Gaura coccinea
Getr	Geum triflorum
Hecy	Heuchera cylindrica
Hial	Hieracium albertinum

Symbol	Species
	FORBS (continued)
Lapu	Lactuca pulchella
Lipa	Lithophragma parviflora
Liru	Lithospermum ruderale
Luse	Lupinus sericeus
Sarh	Saxifraga rhomboidea
Taof	Taraxicum officinale
Trdu	Tragopogon dubius
Vebl	Verbascum blattaria
Veam	Veronica americana
Zipa	Zigadenus paniculatus
	MOSS
Bral	Brachythecium albicaus

Symbols Used for Metric Nomenclature and the Conversions to the English System

Metric Nomenclature	Symbol	English Equivalent
kilometer	km	0.612 miles
meter	m	3.28 feet
centimeter	cm	0.394 inch
millimeter	mm	0.0394 inch
square meter	m^2	10.758 square feet
gram	g	0.0352 ounces
centigrade degrees	C	F = C x 1.8 + 32