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Effects of Forage Availability on Voluntary Intake and Feeding Behavior of Grazing Heifers

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EFFECTS OF FORAGE AVAILABILITY ON VOLUNTARY INTAKE
AND FEEDING BEHAVIOR OF GRAZING HEIFERS

by
A. S. Nastis

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah
1979
ACKNOWLEDGMENTS

I wish to express my deep appreciation to Dr. John C. Malechek Chairman of the Supervisory Committee, for his professional guidance and support during my entire graduate program. Appreciation is also extended to the members of the Supervisory Committee, Dr. Philip J. Urness for his guidance and continued interest during this study and through my entire program; Dr. Joseph C. Street for his valuable suggestions; Dr. James A. Gessaman for his helpful recommendations; Dr. Donald V. Sisson for the statistical aid.

Thanks are also extended to Kris M. Havstad and Fred D. Provenza for their assistance in preparing facilities, taming animals and collection of samples.

Financial support for this project was provided by the Utah Agricultural Experiment Station, Project No. 764. Partial scholarship funding was provided by the Sophias Chlorou endowment through the National Polytechnical University at Athens, Greece.

Above all I acknowledge my wife Stella, and sons Stefis and Vasos for their patience and support in fulfilling this assignment.

Anastasios Nastis
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ABSTRACT

Effects of Forage Availability on Voluntary Intake and Feeding Behavior of Grazing Heifers

by

Anastasios S. Nastis, Doctor of Philosophy

Utah State University, 1979

Forage intake by animals is an important factor in determining production of livestock products from rangelands. However, relatively little is known of effects of such forage variables as availability and distribution in space upon intake. Even less is known about how the grazing animal modifies its feeding tactics when confronted with diminishing or limited supplies of available forage and how such altered behavior may affect the animal's energetic cost for existence. Forage intake, body weight gain, grazing time and biting rate of Angus heifers was related to forage availability and plant height on semiarid crested wheatgrass rangeland during the late summer.

Forage availability was estimated within 10 percent of the mean (P<0.10) by use of hand-clipped 1 m$^2$ plots. Forage intake was estimated from data on fecal production and in vitro digestibility of forage. Fecal production was determined by total collection, using fecal collection bags, and by a single-dose marker technique, used to estimate fecal production indirectly. Digestibility was
determined by an in vitro procedure. Additionally crude protein and cell contents of forage were determined. Grazing time was measured by mechanical grazing clocks (Vibracorders) mounted on animals' necks. Biting rate was determined visually using a stop watch to time specific grazing intervals during which all bites were counted.

There were a total of four 4-day trials during 1977 and five 4-day trials during 1978. Crude protein content within years was significantly higher during the third period in 1977 and during the fifth period in 1978 when regrowth occurred. Within years, in vitro digestibility was significantly higher only for the fifth trial during 1978. Cell contents decreased as grazing progressed only during 1978. Crude protein content, cell contents and in vitro digestibility were higher during 1977 than 1978.

Forage intake of heifers did not vary significantly among successive grazing trials as forage availability declined from 919 to 143 kg DM/ha. Heifers apparently compensated for the diminishing forage availability by increasing grazing time from 380 to 656 min/day and biting rate from 37 to 50 bites/min.

Grazing time was inversely related to forage availability and was expressed by the relationship $y = 676.8 - 0.3x; r^2 = 0.93$. Biting rate was less correlated with forage availability and was described as $y = 50.4 - 0.02x; r^2 = 0.86$. However, biting rate was more closely correlated with plant height as described by the relationship $y = 53.0 - 0.48x; r^2 = 0.95$. 
Heifers maintained or gained 0.1 to 0.7 kg/head/day weight during all trials except the last trial in 1978 when they lost approximately 1.1 kg/head/day. The weight loss for this trial was apparently not a result of restricted forage intake or limited forage quality but partly due to extra maintenance energy expenditures attributable to increased grazing time and biting rate. Correlation between estimates of fecal output by the single dose marker technique with total fecal collection were not significant ($P<0.05$) using the model $y = a + bx$. More sophisticated two- or three-compartment models estimating the lagtime between injection of indicator and first appearance in feces and observations on the ascending limb of the excretion curve must be considered.
STATEMENT OF THE PROBLEM

Introduction

Evaluation of optimum range use has traditionally been based on plant-related factors. For example, most studies concerned with the time of initiation of grazing or "range readiness" for a particular range have been based largely on plant parameters. Likewise, decisions on when to terminate grazing at the end of the season have been based on physiological factors of the plant community, while animal requirements have not generally been considered. Animal demands need to be considered more carefully in the decision-making processes of range management, particularly where seeded ranges are concerned. These rangelands are more amenable to intensive grazing management than are their native counterparts.

Efficient animal production on rangelands depends to a large extent on maintaining high levels of voluntary intake. Many nutrient deficiencies result first in reduced intake and then in decreased production or clinical symptoms. The basic factors which govern intake, as related to the range forage resource, need to be discussed and integrated. Rice et al. (1974) and Langlands and Bennett (1973b) reported that voluntary intake of range forage is a function of both forage quality and quantity. These two variables are not independent and isolation of causative factors in various situations is difficult.
In natural settings, a change in forage availability usually affects quality. The two variables of forage quality and availability are best studied in such a manner that interactions are eliminated or do not invalidate conclusions.

The act of grazing involves the selection of a diet from a complex mixture of plant species and parts, most of which differ appreciably in nutritional value. The plant species and parts chosen depend to a large extent on the quantity of forage available. Selection is also influenced by the botanical composition and physical structure of the vegetation. Grazing animals, in an effort to maintain homeostasis of intake with varying range conditions, alter both foraging time and bites per unit time (Arnold and Dudzinski 1978). These behavioral responses are thought to allow the animal to maintain intake over diminishing levels of forage availability; however, at some undefined low level of forage availability intake decreases. The conditions (both plant and animal) that define this lower level are not clearly defined. The effects of these changes in feeding behavior on the animal's energy budget are probably large, but are generally undefined.

**Delineation of the Problem**

The relation between forage availability and voluntary intake is probably asymptotic. Any increase in forage availability, at low availability levels, will result in an increase in intake. However, additional increments of availability will result in progressively smaller increases in intake. Finally, a point will be reached beyond which any increase in availability ceases to affect intake. Only at very high but generally undefined, levels of
forage availability will intake be decreased because of interference to feeding from undesired portions of the standing forage crop.

The relationship between forage availability and foraging time is most likely curvilinear. When forage availability decreases, at high availability levels, foraging time will increase slightly. As forage availability continues to decrease, foraging time will increase progressively. Ultimately, a point will be reached beyond which any additional decrease in forage availability has a negative effect on foraging time. Chacon and Stobbs (1975) observed animal responses that generally fit this theoretical pattern, however, their inflection points at low availabilities were at 6400 kg dry matter (DM)/ha and 3360 kg/ha DM in two separate experiments.

The number of bites per unit time should follow a similar pattern to that described for foraging time. However, the inflection point for decreased bite rate at low forage availabilities should be at comparatively lower availability levels. Chacon and Stobbs (1976) found this inflection point to be at 5000 kg DM/ha in their first experiment but in their second experiment, they did not reach the inflection point when forage availability decreased to 2400 kg DM/ha.

Foraging time and biting rate have been measured in pastures with instantaneous forage availability above 2500 kg DM/ha (Stobbs 1973, Chacon and Stobbs 1976). In semiarid rangelands, total annual production is well below 2500 kg DM/ha (Hutchings and Stewart 1953). The extent to which altered behavioral responses can curtail the effect of diminishing forage availability on intake is not well established for semiarid rangelands.
Purpose of the Study

The purpose of this study was to establish the relationship between forage availability and voluntary intake, foraging time and biting rate of cattle grazing on semiarid crested wheatgrass (Agropyron cristatum) lands. These data are required to first understand the mechanics of the grazing process and, secondly, to construct models of grazed ecosystem function, particularly where energy balance of the animal is concerned. Only when the grazing process is better understood can range management be intensified for increasing animal production without detrimental impacts on the plant community.

Objectives

1. To characterize the functional relationship between intake and forage availability on crested wheatgrass rangeland.

2. To determine the relationship between foraging time and biting rate with varying levels of forage availability on crested wheatgrass rangeland.

Hypotheses

The objectives stated were investigated by subjecting the following hypotheses to empirical validation:

A. Hypothesis related to Objective 1.

1. Within the range of forage availability generally observed on semi-arid seeded ranges (0-1,600 kg/ha),
organic matter intake by heifers declines as forage availability decreases.

B. Hypotheses related to Objective No. 2.

1. There is no correlation between grazing time and forage availability levels.

2. There is no correlation between biting rate and forage availability levels.

Significance of the Study

The development of a functional relationship between forage availability and voluntary intake, foraging time, and biting rate is fundamental for analysis of grazing practices, particularly on seeded ranges subject to intensive management. Such relationships can be used to determine time for entering and leaving a pasture, stocking rates, duration of grazing, or the necessity of supplemental feeding.

The possibility of removing constraints on voluntary intake is important because only intake in excess of maintenance can be used for net production. Potentials and limitations that affect maximal forage intake need to be explored. In this way, production per animal and per unit area can be evaluated to obtain the optimum combination in various situations.

Definition of Terms

Availability

The amount of herbage which is potentially consumable per unit area of land at an instant in time is termed availability. This
represents the aerial biomass of gramineous species as determined by harvest-and-weigh-sampling procedures when the clipping height is 1.0 cm above the soil surface.

**Voluntary intake**

The amount of forage consumed per unit of time by an animal which has continuous access to the forage resource. Specifically this represent kilograms of forage ingested per unit of metabolic animal body mass (i.e., body mass $0.75$) per day.
LITERATURE REVIEW

Effect of Forage Availability on Intake

Heady (1975), citing Sharp (1970), stated that mature range cattle can maintain adequate levels of voluntary intake on crested wheatgrass ranges when there is a standing crop of 225 kg DM/ha and an 11 kg DM/ha daily growth increment. Sharp (1970) arrived at these estimates by comparing the grazing animals to a mechanical mower and evaluating the distances the mower needed to travel to harvest a given quantity of forage. Little definitive information is available for arid or semiarid ranges to either support or refute this rather simplistic conclusion.

For grassland swards grown under mesic conditions, Noy-Meir (1975) reported that intake is asymptotic above levels of forage availability in the vicinity of 1500 kg DM/ha. Woodward (1936) reported that cows required about 1100 kg DM/ha of green matter and a plant height of 10-15 cm to maximize intake in a sward composed mainly of orchardgrass (Dactylis glomerata). Willoughby (1959) and Allden (1962) reported that intake for sheep increased to a maximum when forage availability in a temperate sward was 1500 kg DM/ha. Allden and Whittaker (1970), Hamilton et al. (1973), and Langlands and Bennett (1973a and b) also reported that intake increased asymptotically with total herbage available. Additionally, Arnold (1964) and Arnold and Dudzinski (1966) showed that intake
of sheep grazing temperate pastures changed little as the amount of herbage available was increased beyond 1100-1600 kg DM/ha.

In contrast, Johnstone-Wallace and Kennedy (1944) reported that availability beyond 1100 kg DM/ha in Kentucky bluegrass (Poa pratensis) sward reduced intake for cattle. The higher availabilities were achieved only when the forage crop neared the end of its growth cycle and reduced intake was attributed to poor quality of the mature forage. Wheeler et al. (1963) found no correlation between weight of herbage per unit area and intake of digestible organic matter (OM) by sheep in a pasture composed of Demeter fescue (Festuca arundinacea) and white clover (Trifolium repens) and in a second pasture composed of phalaris (Phalaris tuberosa). Gibb and Treacher (1978) failed to demonstrate an asymptote for ewes grazing perennial ryegrass (Lolium perenne) pastures having availabilities above 400 kg DM/ha. They allowed sheep to graze paddocks with levels of forage available ranging from one to four times the animals' daily requirements and showed a significantly linear effect on intake by lactating ewes and their lambs. This suggests that at allowances of four times animal requirements, maximum intake was not achieved.

On native or seeded ranges under arid or semiarid conditions, season-long herbage yield was usually less than 1500 kg DM/ha (Hutchings and Stewart 1953, Frischknecht and Harris 1968). Consequently, following principles elucidated on mesic pastures, forage intake and animal productivity on arid and semiarid ranges should theoretically be below the animal's potential. However,
animal gains during spring grazing on seeded rangelands, such as crested and intermediate wheatgrass, often equals those observed on temperate pasture situations (Frischknecht and Harris 1968, Cook and Harris 1968). The question arises: Is forage availability a limiting factor for production on seeded rangelands, and if so, at what level(s) does it become limiting?

**Effect of Digestibility on Intake**

Intake is related not only to forage availability but also to forage nutrient content, particularly as the kinds and amounts of nutrients present affect the rate of ingesta disappearance from the reticulorumen. Balch and Campling (1962) and Waldo (1969) suggested that the factor limiting intake for roughage forages in general is rumen capacity. Roughage diets high in fiber components are generally fermented slowly (Van Soest 1965) limiting the capacity of the reticulorumen to pass through large amounts of forage. Conrad et al. (1964), and Van Soest (1965) specified that rumen fill regulates voluntary intake of forages having digestibilities below about 65 percent. During most of the year, forages on western rangelands are characterized by digestibilities considerably less than 65 percent.

Most digestion of the roughage takes place in the reticulorumen (Campling 1964). When rumen capacity is the limiting factor for intake, intake can be increased either by increasing the extent of digestion or the rate of digestion, or both. The extent of digestion determines what proportion of the forage dry matter is absorbed from the digestive tract. Increased intake corresponding
to increased levels of digestibility has been reported by many researchers. Blaxter et al. (1961), feeding hay to ewes, found an increase in daily intake from 50.5 to 94.0 g DM/kg BW$^{73}$ when apparent digestibility increased from 44.7 to 74.2 percent. Blaxter and Wilson (1962) also reported that intake for hay-fed steers increased from 44.4 to 90.3 g DM/kg BW$^{73}$/day when apparent digestibility increased from 45.9 to 69.4 percent. Clancy et al. (1976) feeding alfalfa-concentrate diets to sheep, found an increase in intake from 76.3 to 94.7 g DM/kg BW$^{75}$/day when digestibility increased from 60.2 to 65.9 percent. However, intake subsequently decreased to 80.3 g DM/kg BW$^{75}$/day when digestibility further increased to 73.5 percent. Corbett et al. (1963) reported that intake for cows grazing in a pasture showed a slight increase; from 24.8 to 26.7 g DM/kg BW/day, while digestibility increased from 65 to 80 percent.

Effect of Chemical Composition on Intake

In addition to digestibility, the two factors having the most pronounced effect on intake are nitrogen content (Jones et al. 1970, Jones 1972, Bergen et al. 1973, Fenderson and Bergen 1976) and the proportion of cell contents in the dry matter (Van Soest 1965, Mertens and Van Soest 1973, Clancy et al. 1976). Both factors directly affect the rate of digesta disappearance from the rumen.

Cell contents of forages are generally considered to be almost completely digestible (Van Soest 1965). Additionally, the extent of digestion of this fraction is only slightly affected by lignification.
Van Soest (1965) reported that, although the overall digestibility of selected legumes and grasses was the same, intake was higher for legumes. From this finding and knowing that legumes had higher percentages of cell contents in comparison to grasses in this study, one can speculate that other plants with relatively high concentrations of cell contents are digested at a comparatively fast rate, even though the extent of digestion may be the same as those with lower concentrations of cell constituents.

Cell walls, in excess of 55-60 percent of the dry matter, have a negative effect on voluntary intake (Van Soest 1965) because this fibrous mass occupies substantial rumen volume and is relatively slow to be digested by microbial activity. Additionally, cell wall digestibility is greatly affected by lignification.

Effect of Plant Community Structure on Intake

It is unclear how availability is affected by the spatial distribution of forage over the range and how variation in plant morphology and structure affects intake. Stobbs (1975) suggested that a reason for low animal performance on tropical pastures is the "loose packing" of herbage which makes it difficult for animals to ingest large quantities per bite. Woodward (1936) reported that in an orchardgrass pasture with 2800 kg DM/ha biomass, intake was closely related to plant height over the range of 5 to 25 cm. Rice et al. (1974), without specifying plant height or production, proposed in their model that intake for cattle was related to plant height for green forage but independent of height for dry forage.
However, Cox et al. (1956) showed no correlation between kg DM/m$^2$ of forage and intake of grazing cows over the availability range of 2270 to 4540 kg DM/ha. Wheeler et al. (1963) also found that height and density (plants/m$^2$) of various temperate pastures with forage availability ranging from 170 to 3290 kg DM/ha had no effect on OM intake of grazing sheep.

However, Arnold and Dudzinski (1969) reported that intake for plants of the same height in a pasture can vary as much as 50 percent because of differences in density (plants/m$^2$). The way physical characteristics relate to intake of grazing animals under low forage availability levels is not well established.

**Effect of Forage Availability on Behavior**

The effects of diminishing forage availability on grazing time and biting rate have been reported by many researchers. Atkeson et al. (1942) and Hodgson (1933) reported increased grazing time for pastures with low forage availability. Arnold (1960b) reported a linear increase in foraging time from 7.0 to 10.3 h/day when forage availability decreased from 3000 to 1000 kg DM/ha in a *Phalaris* pasture. Arnold in a later paper (1964) suggested that foraging time decreased at availabilities below 560 kg DM/ha, also a *Phalaris* pasture. However, Chacon and Stobbs (1976) found that the inflection point for decreased grazing time for cattle at low availabilities was at 3360 kg DM/ha in *Setaria* pasture. Biting rate similarly increased (Chacon and Stobbs 1976) from 56 to 62.4 bites/min and
from 51.4 to 59.4 bites/min with forage availability from 7200 to 1500 kg DM/ha and 3900 to 2400 kg DM/ha, respectively.

Most behavioral experiments have been conducted in temperate or tropical pastures with herbage biomass greatly above the highest level possible under semiarid conditions. The behavioral tactics employed by cattle grazing diminishing quantities of forage under semiarid conditions is not known, but must be established before models can be constructed depicting the energy dynamics of the grazing animal.
MATERIALS AND METHODS

Purpose of the Experiment

This experiment was designed to evaluate the relation between forage intake and decreasing levels of forage availability under semiarid conditions. Additionally, relationships of behavioral measurements (grazing time and biting rate) to plant height and forage availability were investigated.

Area and Animals

The study was conducted during the summers of 1977 and 1978 on the Tintic experimental area near Eureka, Juab County, in central Utah. The elevation of the area is approximately 1650 m. Average annual precipitation in Eureka (approximately 10 km from the study area) during the last 45 years has been 400 mm. Precipitation is nearly evenly distributed during all months of the year. Precipitation during 1977 and 1978 was 339 mm and 603 mm, respectively. Average temperatures range from -3.2°C during January to 21.3°C during July. Records for precipitation and temperature were obtained on the study site during the course of the experiment.

Two crested wheatgrass-dominated pastures (pasture 17 and 18), both with sandy loam soil, served as experimental units. During 1977, the entire 28-ha area of pasture 18 was grazed by 20 1.5-year-old Angus heifers (obtained from a local rancher). This pasture
was grazed from August 9 until September 18 at an average stocking rate of 1 Animal Unit Month (AUM)/ha (Range Term Glossary Committee 1964). During 1978, 10 ha of uniform area in the adjacent pasture 17 were fenced and were grazed by 16 experimental animals and, periodically, by 18 other animals all similar to those used in 1977. The additional animals were used to achieve desired levels of forage utilization. This 10 ha pasture was grazed on the average of 22 heifers from August 9 until September 29 at the average stocking rate of 3.7 AUM/ha.

Prior to the initiation of grazing trials in both years, a sub-group of heifers was selected from the main herd and transported to Logan for taming and training. In 1977, 10 such animals were trained and, in 1978, 18 were trained. During 1977, six of the 10 heifers were trained to wear fecal bags (Kartchner and Rittenhouse 1977) and grazing clocks (Vibracorders) similar to those described by Stobbs (1970). These six heifers, the remaining four, and 10 additional untrained heifers constituted the population of animals studied during the first year.

During 1978, six of the 18 heifers were trained to wear fecal bags and harnesses and six others to wear the grazing clocks. These two sets of six animals, plus the four remaining animals formed the experimental population. The remaining two were returned to the owner and not used in the experiment.

Once heifers were trained, they were returned to the Tintic area where they were placed in a holding pasture for conditioning to crested wheatgrass. This preliminary period began 10 days prior to the initiation of the experiment following the recommendations.
of Church (1971). Animals had continuous access to water and salt mineral licks during periods on pasture.

Animal weights were recorded at the start of the experiment and approximately every 10 days thereafter. During 1978 the second weighing followed the first by six days, and the sixth weighing preceded the last weighing by five days.

**Grazing Trials**

**Grazing periods**

There were a total of four 4-day experimental periods during 1977 and five 4-day periods during 1978. Each period was separated by a six day interval when animals grazed undisturbed to achieve successively heavier levels of forage utilization. Thus, treatments were repeated every 10-days. However, occurrence of snow necessitated an 11-day interval between the fourth and fifth periods in 1978.

**Measurements of plant community**

Biomass of forage available was determined every 10 days during 1977 and every 5 days during 1978 by harvesting and weighing all forage in stratified-random 1.0 m$^2$ plots. The sample size was determined so that the experimental error was within 10 percent of the mean with a probability of >90 percent. During 1977 the sample size was determined to be 90 1-m$^2$ plots for the 28-ha pasture and during 1978 30 1-m$^2$ plots for the 10-ha pasture. A slightly larger number of plots was clipped each year (100 and 35 plots, respectively) to provide a margin of reliability.
Plants were clipped at approximately 1.0 cm above ground level with hand shears. Samples were dried for 24 h at 105°C and weighed to determine total forage available. Regrowth within each experimental period was measured by protecting 30 clipped plots with exclosure cages and reclipping them at the end of the period.

Plant height and species frequency was also recorded. Two plants occurring in or near predetermined positions of the 1-m² sampling ring were selected for height measurements. Species of these plants were noted for determination of pasture botanical composition.

**Procedures for Estimating Intake**

**General equation**

Forage intake of grazing animals was estimated according to the equation:

\[
\text{Intake of OM} = \frac{\text{Total fecal organic matter content}}{1 - \text{organic matter digestion coefficient}}
\]

Fecal production was determined directly during 1978 by total fecal collection with fecal bags and was estimated indirectly during both 1977 and 1978 by the use of the indigestible external indicator Erbium. The digestion coefficients were determined through an in vitro analysis of hand-harvested forage samples according to the procedures of Tilley and Terry (1963).

**Indigestible marker**

Estimation of fecal output by use of indigestible indicators is a well-established technique of grazing animal nutrition.
research. Conventionally-used external indicators such as Cr$_2$O$_3$ appear to produce questionable results (Cordova et al. 1978), however. Such indicators place stress on the grazing animal because they must be force-fed at least once, and preferable, twice daily. Additionally, there is a tendency for nonuniform excretion, leading to biased estimates of fecal production.

Huston and Ellis (1968) proposed the use of indigestible rare earth elements as external indicators. They suggested that rare earth elements bind to solid particles of the ingesta while conventional indicators such as Cr$_2$O$_3$ and polyethylene glycol are carried by the liquid phase. Theoretically, flow of rare earth elements through the gastrointestinal tract therefore is more closely associated with the flow of undigested dry matter.

Based on these assumptions, and with the associated advantage of minimizing animal handling during administration of the indicator, the single-dose marker technique of Ellis et al. (1977) was employed during 1977 and 1978.

The indicator was administered once at the beginning of each four-day experimental period. In this experiment a total of 16.59 g of Er (as hydrous ErCl$_3$) was dissolved in 75 ml H$_2$O and was quantitatively injected intra-rumenally into each heifer via an infusion apparatus at the beginning of each experimental period.

The injection during 1977 was made early in the morning following an overnight fast from food and water. During 1978, the injection was made immediately after the early morning grazing session and water was not restricted.
In order to find a relationship between the pattern of indicator excretion when the animals were fasted in comparison to when the animals were not fasted, a separate test was conducted. During 1978, four heifers were selected and, during each trial, two of them were deprived of food and water overnight before the injection.

Following the injection, fecal grab samples were collected in the early morning and late afternoon for four consecutive days. Samples from the bagged animals were obtained by subsampling from their bags. Grab samples from the nonbagged animals were collected in the pasture whenever animals defecated while grazing.

**Determination of Fecal Production**

**Total collection**

Determination of fecal output by total collection procedures was attempted during 1977, but failed because insufficiently trained animals refused to wear the fecal collection apparatus. During 1978, fecal output was determined by total collection procedures as well as by the indigestible indicator approach. Six heifers were equipped with collection bags and harnesses similar to those described by Kartchner and Rittenhouse (1977). Collection periods lasted 96 h during each trial. Fecal bags were emptied twice daily at 0830 and 1700 hours and at these times the plastic lining with the fecal contents was removed and fecal bags were washed with water to eliminate remaining traces of feces. New bag liners were installed and the bags were remounted on the heifers. Liners with their contents were placed in metallic buckets and transferred
to a temporary laboratory. Each individual sample was thoroughly mixed and then two subsamples were taken and placed in water-proof containers and refrigerated immediately at -18°C. Samples were later dried at 105°C for 3-4 days until a constant weight was attained. Then they were ground and stored until analyzed.

The major advantage of such double sampling, using both total collection and indigestible markers to estimate fecal output, is that sample size can be increased markedly without a large additional investment of the investigator's field time or labor. It is generally recognized that variation inherent in the marker technique is larger than with total collection, but with limited data from total collections, adjustments can be made on data based on the indicator technique.

**Laboratory Determination of Erbium**

The rare earth element Erbium (Er) can be detected at very low concentrations in the feces either by flame spectroscopy or atomic absorption.

Fecal subsamples were prepared for analysis by first digesting them with an acid mixture composed of 3.5/1 nitric/perchloric acid, both 70 percent by weight. One-gram samples of dried, ground feces were placed into 125-ml flat bottom conic beakers and 15 ml of digestion solution in each beaker. For reducing acid evaporation a funnel was placed in each beaker. In this way, a substantial proportion of the acid vapours were condensed and returned to the digestion flasks. Samples were heated slowly until the solution
was cleared. The liquid was then evaporated to a moist salt. This residue was cooled and diluted to 100 ml with distilled water. The clear supernatant was transferred to test tubes after solids settled from suspension. Then Er concentration was determined by flame emission according to Kinnunen and Lindsjo (1967).

Calculations of fecal output from indicator data

Concentration of indicator in the rumen over time follows a pattern similar to that of a decaying radioactive isotope. Assuming instantaneous mixing, the concentration of indicator at any time will be given by the equation:

$$C_t = C_0 e^{-\frac{t}{v}}$$  \hspace{1cm} (1)

where

- $C_t =$ concentration of indicator at time "t"
- $C_0 =$ concentration of indicator at time zero
- $e =$ base of the natural logarithm
- $i =$ average rate of intake of indigestible dry matter
- $v =$ rumen volume of undigestible material
- $\frac{i}{v} =$ turnover rate (k)
- $t =$ time

Equation (1) can be rewritten as $\ln C_t = C_0 + kt$ (2), which is of the general form $Y = a + bX$, the model used by Ellis et al. (1977). This linear regression between concentration of indicator in the feces and time has a Y-intercept "a" which is the concentration
of indicator at time zero and a slope "b" which is the turnover rate of indigestible material entering the rumen.

The rumen volume of undigested dry matter (RUDM) was calculated for each animal and period by dividing the indicator dose in mg by the concentration of indicator (mg/liter) at time zero. Then, fecal output was calculated by multiplying RUDM times the turnover rate.

In order to evaluate the applicability of the single-dose marker technique, an attempt to develop a relationship with measured (via total collection) fecal production was made.

**Nutritional Quality Measurements**

**Forage sampling and sample preparation**

Forage samples were collected daily during the experimental periods by hand-harvesting plant material similar to that grazed by cattle. Differences in hand-collected and esophageal-collected samples have been reported by many researchers (Weir and Torrell 1959, Bredon et al. 1967, Guthrie et al. 1968, Rao et al. 1974). However, William and Rittenhouse (1975) reported that no significant difference was found (P<.10) between clipped samples and samples collected from eight fistulated steers grazed on crested wheatgrass pasture. Seeded ranges have a relatively homogeneous forage, and variation in dietary chemical composition due to selective grazing is generally small compared to that seen on native range. Additionally, when samples are collected from cured forage stands as in this study, forage quality does not vary greatly. Clipped samples were dried at 60°C for 24 hours and then ground and stored for analysis.
Determination of In Vitro Digestibility

Digestibility estimates were obtained by the Tilley and Terry (1963) in vitro procedure utilizing clipped forage samples similar to the grazed forage. Inoculum for the in vitro procedure was obtained from heifers grazing the crested wheatgrass pastures. Four animals were each tranquilized with 5 cc Rompun (Haver-Lockhart Laboratories, Shawnee, Kansas). Inoculum was then obtained by vacuum aspiration via stomach tube and pooled into two preheated 1-liter thermos bottles. The bottles were stoppered with Bunsen valves and were placed in a preheated Coleman ice chest maintained at approximately 39°C with warm water. Inoculum was immediately transferred to the laboratory where the in vitro digestion trials were conducted.

Chemical Determinations

The hand-clipped forage samples were analyzed for nitrogen content by a macro-Kjeldahl procedure (Harris 1970), and for cellular constituents (Van Soest and Wine 1967). Ash content of forage and feces was determined by combusting representative samples according to Harris (1970).

Behavioral Determinations

Grazing time

Vibracorders similar to those described by Stobbs (1970) were fitted to six of the nonbagged heifers during 1978. Readings of
grazing time and periodicity of grazing were obtained every third day by changing the paper charts.

Data on grazing time were also collected in 1977 by the same procedure, but as part of another study already reported by Scarnecchia (1979). Hence, only 1978 data on grazing time are reported in the present discussion.

**Biting rate**

Biting rate for the six heifers that carried Vibracorders was determined ocularly. A stop-watch was used to measure time intervals of five minutes during which all bites were counted. Timing and counting was interrupted when heifers ceased grazing or when they walked with their head raised. These observations were generally made during the early morning and early evening period when animals grazed continuously for 2-3 hours. Heifers used for these observations were accustomed to being handled by the observer and were apparently not disturbed or frightened by his presence.

Biting rate data for the 1977 season were also reported by Scarnecchia (1979).

**Statistical Analysis**

The data related to forage nutritional measurements (crude protein, cell constituents, and in vitro digestibility) were analyzed according to a completely randomized design (Snedecor and Cochran 1971). A two-way analysis of variance was conducted (Snedecor and Cochran 1971) for data related to animal measurements.
(weight gains, fecal production, intake by heifers of OM, grazing time and biting rate). Comparisons between years were made for in vitro OM digestibility, crude protein content and cell constituents with a "t" test. Intake between fasted and nonfasted animals were analyzed in a \(4^2\) factorial design.

For evaluating significant differences among means, Duncan's New Multiple Test was used (Steel and Torrie 1960). Differences between means at the \(a<0.05\) level of probability were considered statistically significant.

Intake of OM estimates were regressed on forage availability and plant height. Foraging time and biting rate were regressed on forage availability and plant height and tested for linear and quadratic significance using orthogonal polynomials (Snedecor and Cochran 1971). Coefficients of correlation were tested for significance at the \(P<0.05\) level.
RESULTS AND DISCUSSION

Forage Production

Forage availability ranged from 474 to 170 kg/ha during 1977 and from 929 to 114 kg/ha during 1978 (Table 1). Forage biomass per unit area in 1978 was almost twice that for 1977. This was mainly due to differences in amounts and distribution of precipitation during these two years. The total amounts of precipitation from October until September were 317 and 577 mm for the years 1976-1977 and 1977-1978, respectively.

Forage in the pasture grazed during 1977 was composed of 88 percent crested wheatgrass and 12 percent western wheatgrass (Agropyron smithii). It did not reach full phenological development and was prematurely cured by draughty conditions. Before the initiation of grazing, the forage had an average plant height of 15.1 cm (Appendix Table 39) and 56 percent by weight was leaves (Appendix Table 38). Forage in the grazed pasture during 1978 was 56 percent crested wheatgrass (Appendix Table 40), 36 percent western wheatgrass, and 8 percent Indian ricegrass (Oryzopsis hymenoides). During this year forage reached full phenological development. Before the initiation of the experiment, average plant height was 31 cm and leaves were 42 percent by weight.

A substantial amount of regrowth occurred during the study period in 1977. Fifty mm of rain occurred on August 25. This moisture, in combination with favorable temperatures (averaging...
Table 1. Biomass available (kg/ha) during 1977 and 1978.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Mean Herbage Yield</th>
<th>SD</th>
</tr>
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<tbody>
<tr>
<td>1977 1/</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8-9</td>
<td>474</td>
<td>13.6</td>
</tr>
<tr>
<td>8-19</td>
<td>359</td>
<td>14.3</td>
</tr>
<tr>
<td>8-29</td>
<td>272</td>
<td>12.1</td>
</tr>
<tr>
<td>9-8</td>
<td>236</td>
<td>12.8</td>
</tr>
<tr>
<td>9-18</td>
<td>170</td>
<td>9.4</td>
</tr>
<tr>
<td>1978 2/</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8-9</td>
<td>929</td>
<td>39.5</td>
</tr>
<tr>
<td>8-13</td>
<td>909</td>
<td>32.7</td>
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<tr>
<td>8-18</td>
<td>864</td>
<td>34.1</td>
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<tr>
<td>8-23</td>
<td>652</td>
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<tr>
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<td>4.7</td>
</tr>
<tr>
<td>9-28</td>
<td>114</td>
<td>6.6</td>
</tr>
</tbody>
</table>

1/ N = 100. 1.0 m² quadrats at each sampling date.
2/ N = 35. 1.0 m² quadrats at each sampling date.
18°C in Eureka for the 18 days following the rainfall) resulted in 62 kg DM/ha regrowth during the third trial. In 1978, a total of 72 mm of precipitation occurred during the study period. However, this moisture was apparently not as effective for plant regrowth as that of 1977. On August 14th, 25 mm of rain fell, but high temperatures (29, 43, and 40°C maximum on the study area during the 3 days following the rainfall) quickly evaporated most of the moisture from the surface soil. A slight, but unmeasurable, amount of plant regrowth was observed, but only in the swales following this rainfall event.

An additional 47 mm of precipitation fell as snow on September 18th. Despite this relatively large amount of precipitation, cool temperatures averaging 10.5°C in Eureka for the rest of the experiment (11 days) resulted in only 5 kg DM/ha plant regrowth for 1978.

The amount and distribution of precipitation has a definite impact on crested wheatgrass regrowth. Forage production is closely related to precipitation (Hutchings and Stewart 1953, Robertson et al. 1970, Alfred 1970). Additionally, favorable temperatures have to occur on the days following precipitation for substantial plant growth. Richardson et al. (1975) suggested that growth for cool season grasses is proportional to temperature within the range 4.5 to 25°C, when other factors are not limited.

Fierro (1977) reported 33.0 and 12.7 kg DM/ha regrowth of crested wheatgrass on a grazed pasture with 75 and 31 mm of precipitation in 1975 and 1976, respectively, and with temperatures less than 1°C
higher than recorded in Eureka during the present study. In the same pasture studied by Fierro (1977) the following year (1977) Austin (1979) recorded 311.4 kg DM/ha regrowth with comparable temperatures and 97 mm of precipitation.

The fact that plants attained full maturity at Tintic during the 1978 spring growing season, whereas they were forced into premature dormancy during 1977 may have also contributed to the difference observed in late-summer regrowth responses.

**Forage Quality**

**In vitro digestibility**

Comparison of digestibilities between years resulted in significantly ($P \leq 0.05$) higher digestibility for 1977 (49.3 percent) than for 1978 (35.3 percent) (Table 2 and Appendix Table 30). Samples from both years were digested in the same trial with the same inoculum source. Hence the difference between years was attributed to differences in forage quality.

Cook and Harris (1968) reported that in vivo digestibility with sheep for crested wheatgrass was 53.0, 57.0, and 53.4 percent during the boot, dough, and seed stage of development. Fierro (1977) reported a 63 percent digestibility for early spring growth of crested wheatgrass consumed by deer. Handl (1972) reported that in vitro digestibility of crested wheatgrass declined from 68 to 62 percent during the spring growth. Determination of digestion coefficients in the above studies were all made on immature or partially mature but not cured grass. Therefore, it was not
Table 2. In vitro organic matter digestibility (% of DM) for hand-harvested crested wheatgrass forage during 1977 and 1978.

<table>
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<td>1977</td>
<td>46.2(1^\text{/})</td>
<td>46.1</td>
<td>47.9</td>
<td>45.9</td>
<td>--</td>
</tr>
<tr>
<td>--</td>
<td>49.6</td>
<td>55.8</td>
<td>50.6</td>
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<tr>
<td>--</td>
<td>47.4</td>
<td>54.8</td>
<td>48.8</td>
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</tr>
<tr>
<td>Means±SD(2^\text{/})</td>
<td>46.2a</td>
<td>47.7±1.8a</td>
<td>52.8±4.3a</td>
<td>48.4±2.4 a</td>
<td>--</td>
</tr>
<tr>
<td>1978</td>
<td>33.8</td>
<td>35.8</td>
<td>34.1</td>
<td>33.9</td>
<td>31.8</td>
</tr>
<tr>
<td>36.7</td>
<td>35.2</td>
<td>31.1</td>
<td>32.0</td>
<td>38.6</td>
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</tr>
<tr>
<td>34.1</td>
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<td>35.5</td>
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<td>30.7</td>
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<td>34.1</td>
<td>29.7</td>
<td>35.2</td>
<td>46.0</td>
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<tr>
<td>Means±SD</td>
<td>34.9±1.6a</td>
<td>34.5±1.7a</td>
<td>32.9±2.0a</td>
<td>33.5±2.0a</td>
<td>40.2±4.8b</td>
</tr>
</tbody>
</table>

\(1^\text{/}\) Each data entry represents a single hand-harvested herbage sample. Sample size varied depending on other demands on observer's time.

\(2^\text{/}\) Means in the same row followed by a common letter are not significantly different (P<0.05).
surprising that digestibilities were higher than those found in the present study. Differences in digestibilities between years has to be partially attributed to the difference in plant composition (13 percent more western wheatgrass and 7 percent more Indian ricegrass in 1978 than in 1977) and partially to the more mature stage of development during the second year. Digestibility apparently increased during both years when regrowth occurred. Statistically, this increase was not significant during 1977, probably because of the small sample size with high variation. However, during 1978, when regrowth occurred, digestibility was significantly higher during the fifth period than in previous periods.

**Crude protein content**

Crude protein content of forage fluctuated significantly through the trials during both years. The increment of regrowth occurring during the third period of 1977 and during the fifth period of 1978 resulted in distinct increases in crude protein content (Table 3) of the entire diet.

Crude protein content during 1977 was almost twice that of 1978. As previously mentioned, extremely dry conditions during spring and early summer of 1977 caused cessation of growth before most grass plants entered the stage of culm elongation. Thus, the forage crop was cured at a physiologically immature stage when protein levels were high. In contrast, plants reached full maturity in 1978 and protein levels were low at the time grazing began.
Table 3. Crude protein content (\% of DM) for hand-harvested crested wheatgrass during 1977 and 1978.

<table>
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<tbody>
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1/ Each data entry represents a single hand-harvested herbage sample. Sample size varied depending on other demands on observer's time.

2/ Means in the same row followed by a common letter are not significantly different (P<0.05).
Hedrick et al. (1969) reported that crude protein content of crested wheatgrass was higher during dry years in comparison to wet years. The slightly different botanical composition of the pasture used during 1978 might also have affected total forage protein content.

Sneva (1973) reported crude protein content of mature crested wheatgrass in late fall varying from 4.6 to 6.1 percent depending on the year. Cook and Harris (1968) reported that crude protein content at seed stage was 10.8 percent. Findings from the present research were within the limits of these reported values.

It is not surprising that crude protein content increased during periods when regrowth occurred. Fierro (1977) reported that crude protein content of regrowth may vary between 15 and 35 percent. Even a small increment of regrowth can alter the overall crude protein content of standing cured forage with low crude protein content.

Cell contents

No significant (P<0.05) difference in cell contents was found among forage samples collected during the grazing trials in 1977 (Table 4). However, cell contents decreased significantly (P<0.05) as grazing progressed during 1978.

Forage during 1977 had significantly (P<0.05) higher cell contents during 1978. Immature cured forage during 1977 had a relatively higher and even distribution of cell contents within the plant biomass. Additionally, regrowth occurring during the

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1/ Each data entry represents a single hand-harvested herbage sample. Sample size varied depending on other demands on observer's time.

2/ Means in the same row followed by a common letter are not significantly different (P<0.05).
third trial contributed to the cell contents (regrowth was mainly leaves high in cell contents). Therefore, cell contents were maintained at about 40 percent through the grazing trials. Contrarily, a decline in cell contents from 39 percent during the first trial to 33 percent during the fourth and fifth trial was measured during 1978 (Table 4). This indicates that grazing was selective even in the floristically simple pasture. Selective grazing (Cook and Harris 1950, Arnold 1960b) typically removes leaves in preference to stems. However, no significant difference in the present study in leaves/stem ratios by weight was found among trials in either year (Appendix Table 38). This limited selection of leaves is first attributed to the physical structure of the plant community studied. Crested wheatgrass typically grows in dense bunches and has relatively short leaves. Additionally, its stems are relatively soft and small in diameter when compared to other grass species such as Phalaris evaluated by Arnold (1960b). Secondly, heifers are generally less selective for leaves versus stems when compared with sheep used in the experiments conducted by Cook and Harris (1950) and Arnold (1960b).

Grazing Behavior

Measurements of grazing behavior during 1977 have been reported by Scarnecchia (1979). Only the behavioral measurements obtained during 1978 are presented here.
Grazing time

Grazing time continuously increased throughout the trials (Table 5). Time spent grazing during the first and second trials was significantly less ($P<0.05$) than the third and fourth trial. But, grazing time for the third and fourth trial was significantly less ($P<0.05$) than the fifth. This progressively increasing grazing time was significantly ($P<0.05$) but inversely correlated with forage availability (Figure 1) yielding an $r^2$ value of 0.93. However, grazing time was not significantly correlated with average plant height. The relationship between grazing time and forage availability was hypothesized to be curvilinear. However, according to the procedures of Snedecor and Cochran (1971), no difference from a linear relationship was found within the range of forage availabilities studied.

Grazing time during the first trial was 40 percent less than that reported by Allden (1962) and 9.5 percent less than that reported from Arnold (1960a) on temperate pastures with about the same level of forage availability. Also, Scarnecchia (1978) reported a 17 percent higher investment in grazing time in the adjacent pasture during 1977. This difference in grazing time was attributed to 55 percent less forage availability in his study than in the present study.

Stobbs (1975) reported that fatigue limits the time spent by a grazing cow to about 720 min/day. Grazing time during the last trial was only 9.4 percent less than this proposed maximum indicating
Table 5. Daily grazing time (min) of heifers during 1978 as influenced by decreasing forage availability over time.

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Means ± SD1/
380±73c 423±92c 521±32b 531±31b 656±44a

1/ Means in the same column or row followed by a common letter are not significantly different (P<0.05).
Figure 1. Grazing time in relation to forage availability. Vertical lines represent the range; means indicated by the dot.
that heifers were grazing very close to their potential maximum grazing time, if indeed Stobbs' estimate is an accurate one.

Scarnecchia (1979) showed that foraging time increased from 462 min/day to a maximum of 618 min/day when forage availability decreased from 416 kg/ha to 254 kg/ha. When forage availability further decreased to 203 kg/ha, he observed a subsequent slight decrease in grazing time to 600 min/day.

In the present research, foraging time increased continuously as forage availability decreased from 919 to 143 kg MD/ha. A decrease in grazing time would be expected only under a negative energy balance. Presumably, heifers will then conserve energy by restricting their abilities.

Grazing began daily between 6:40 and 7:15 a.m. during all trials, depending on the time of sunrise and seemed to be independent of other environmental conditions such as temperature, wind, and humidity. Initiation of afternoon grazing was delayed during days with maximum temperatures above 27°C, when the heifers did more grazing during the night than on days with lower day temperatures. During the first night when minimum temperatures were below 10°C, grazing was sporadic. Night grazing did not occur the following days when minimum temperatures were below 10°C. Arnold and Dudzinski (1978) proposed that night grazing is a function of the difference between the maximum and minimum temperature within a day. However, no such effect was found in this experiment, probably because of the narrow range of variation (17-23°C with the exception of four days when variation was out of this range).
Biting rate

Biting rate ranged from 37 to 50 and averaged 42 bites/min over the entire experiment. During the first three trials no increase in biting rate was detected (Table 6). However, biting rate increased significantly ($P < 0.05$) during the fourth trial in comparison to the previous trials. Subsequently, biting rate again increased significantly during the fifth trial in comparison to all previous trials.

Biting rate was significantly correlated ($P < 0.05$) with forage availability (Figure 2) and plant height (Figure 3) yielding $r^2$ values of 0.86 and 0.95, respectively. Both relationships were hypothesized to be curvilinear. However, when tested (Snedecor and Cochran 1971) no difference from a linear relationship was found within the range of values studied. A multiple regression-correlation was developed relating biting rate to both forage availability (FA) and plant height (PH). This relationship, expressed by the equation $y = 53.1 + 0.0007 \ (FA) - 0.5 \ (PH)$ accounted for 95 percent of the variation. This indicated that in the multiple regression forage availability contributed very little toward increasing the power of the regression equation for predicting grazing time.

Biting rate apparently depends on both quantity and quality of forage (Arnold 1964). The lowest biting rate was observed when forage was abundant and dry during the first three trials. The highest biting rate was observed when forage was limited, especially when there was regrowth available during the fifth trial. Arnold
Table 6. Biting rate (bites/min) for heifers grazing crested wheatgrass pasture during 1978.

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Means ± SD 1/ 37±3.4a 40±3.0a 39±2.2a 45±4.8b 50±2.8c

1/ Means in the same column or row followed by a common letter are not significantly (P≤0.05) different.
Figure 2. Biting rate in relation to forage availability. Vertical lines represent the range; means indicated by the dot.
Figure 3. Biting rate in relation to average plant height. Vertical lines represent the range; means indicated by the dot.

\[ y = 53.0 - 0.48x \quad r^2 = 0.95 \]
(1960) reported sheep biting rates of 25-40/min for dry abundant pasture and 60-80/min for short green pasture.

Allden (1962) showed that biting rate increased to 65/min for sheep grazing ryegrass (Lolium perenne)-subterranean clover (Trifolium subterraneum) pasture when forage availability decreased to less than 1000 kg/ha. Additionally, Chacon and Stobbs (1976) reported that their maximum biting rates for cows, 62 and 58 bites/min in two separate experiments, were observed when forage availability was lowest at 5900 kg DM/ha and 2400 kg DM/ha, respectively. In the present experiment, biting rate did not change significantly ($P<0.05$) when forage availability decreased from 919 to 500 kg DM/ha, however, when availability declined below 500 kg/ha, sharp increases in biting rates were observed. The maximum biting rate of 50/min was observed at 143 kg DM/ha. It can be concluded that in the crested wheatgrass pastures, maximum biting rate occurs at much lower levels of forage availability than in tropical pastures.

The maximum biting rate obtained was approximately 20 percent less than the one observed by Allden (1962) and Chacon and Stobbs (1976). Biting rate in the present experiment probably did not increase to its maximum potential because of the patchy configuration of vegetation present in pasture 17. Heifers spent considerable time moving from one patch to another, hence reducing biting rate as measured in this experiment. This was probably also the main reason for a lower biting rate compared to that of Scarnecchia (1979), who studied similar animals in pasture 18 during 1977. There the
grass sward was relatively uniform and continuous because individual bunches were not widely spaced.

Heifers apparently compensated for the decreased forage supply by increasing the overall number of bites per day from 14,060 to 32,800, comparing first and last trials. In relative terms, grazing time increased 75 percent over the course of the study, whereas biting rate increased only 35 percent.

The pattern of compensation was not uniform over all levels of forage availability. For example, when forage available diminished from 919 to 500 kg/ha, foraging time increased but biting rate remained relatively unchanged. As forage available further diminished to 143 kg/ha, foraging time continued to increase and biting rate also increased sharply (from 37 to 50 bites/min).

All biting rates during the present study were below the lowest rate recorded by Scarnecchia (1979). One would expect higher biting rates during the fifth trial of the present experiment than Scarnecchia's because forage availability and plant height were comparatively lower than those observed by Scarnecchia (1979). Biting rate apparently depends on plant community structure and plant parts (leaves/stems) and their arrangement in space. As previously discussed, it was subjectively estimated that pasture 18 had uniformly continuous forage while pasture 17 had patchy configuration. In contrast, foraging time for the pasture studied was independent of spatial arrangement. Grazing time obtained in the two experiments were comparable and proportional to forage availability. It can be speculated that foraging time is mainly controlled by appetite drive.
Intake

Attempts based on indigestible indicator prediction of fecal output

Linear regression equations were calculated by regressing the natural logarithm of indicator concentration on time for those feces produced after administration of the single dose indicator. The pattern of indicator excretion in the feces after a single dose injection is theoretically described by a rapid increase in indicator concentration up to a maximum and then a relatively slow decrease over time. However, the manner in which data were collected in this experiment permitted only the descending part of the curve to be described by this regression. A separate such regression equation was calculated for each animal and trial. All regression equations calculated in this way were significant at P<0.05 level. Additionally more than 95 percent of all r² values were above 0.90. These data suggest that the pattern of indicator excretion is well described by the regression of the general form y = a + bx.

From each of the above equations the rumen volume of undigested material was estimated. By multiplying rumen volume with the turnover rate "b" an estimate of the fecal output was obtained. However, when fecal output as predicted by the marker was regressed on measured fecal output (total collection) no significant relation (P<0.05) was obtained. Only 6 percent of the variation was explained by the regression equation.

The equation of the general form y = a + bx does not consider the lagtime between the injection of the marker and the appearance
of detectable levels of indicator in the feces. Also, it does not consider the ascending part of the excretion curve. When lagtime is not considered, estimates of concentration of the indicator at time zero were always over-estimated because slope of the regression is always negative.

As a possible approach for rectifying this problem, a total of 16 lagtimes were measured during 1978. This was done by initiating grab sampling within 3 hours post-injection and determining the length of time from injection to the time when the first measurable concentrations of Erbium occurred in fecal samples. When an average of these measured lagtimes was considered, no improvement in the correlation between measured and estimated fecal production was found. Grovum and Williams (1973) and Grovum and Phillips (1973), developing the theoretical model for the single-dose indicator excretion technique have proposed a two-compartment model of the form \[ y = A e^{-k_1(t-TT)} - A e^{k_2(t-TT)}. \] This considers both the lag-time and the ascending part of the excretion curve. However, Ellis (1979) found no close agreement when using this model with actual measurements. More sophisticated two- or three-compartment models must be considered. Without doubt the single-compartment model used in this experiment did not adequately predict fecal output. Unfortunately, sufficient data were not available to test the applicability of the two-compartment models.

Estimates based on measured fecal output

Intake during 1978 (estimated from total fecal collections and in vitro digestibility) was not (P<0.05) significantly different
(Table 7) among grazing trails. Values ranged from 44.4 to 50.6 g/kg OM BW$^{.75}$/day over a broad spectrum of available forage ranging from 919 to 143 kg DM/ha. No significant correlation ($P < 0.05$) was found between intake of forage, availability and plant height. These intake values were below the NRC tabulated standards of 57 g OM/kg BW$^{.75}$/day. An intake of 5.4-7.2 kg DM/day was reported by Handl and Rittenhouse (1972) for steers grazing crested wheatgrass pastures and 8.2-17.5 kg DM/day by Kartchner (1975) for lactating cows. The lowest of these values correspond to more than 70 g OM/kg BW$^{.75}$/day. However, in the cited studies, forage consumed was immature, with digestibility levels above 60 percent as compared to digestibility levels of only 35 percent in the present study.

Intake of forage was significantly different ($P < 0.05$) among animals (Table 7). The reason why one heifer consumes more forage than a similar heifer is not well understood. The most efficient animals in terms of net energy production are those that do eat large quantities of food per unit of body weight (Graham and Searle 1975). Research on the biochemical and physiological changes occurring within the animal may lead to an understanding as to why intake is irregular among animals.

Allden (1962), Willoughby (1959), and Arnold (1964) reported that forage intake increases as forage availability increased at relatively low availability levels (Figure 4). The average rate of increase in intake for the above studies ranged from 1.5 to 4.4 g OM/100 kg DM of forage available. In the present study this
Table 7. Daily intake of organic matter (g/kg BW^75) by heifers grazing crested wheatgrass pasture during 1978. Estimates based on total fecal collection and in vitro digestibility.

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Means ± SD^1/ 44.4±7.0a 49.8±5.4a 46.3±6.8a 50.1±8.9a 50.6±8.5a

^1/ Means in the same column or row followed by a common letter are not significantly (P<0.05) different.
Figure 4. Consumption as a function of forage availability.
1. Allden (1962), sheep, ryegrass, clover;
2. Willoughby (1959), sheep, Phalaris-clover;
3. Arnold (1964), sheep, Phalaris-annuals-clover;
4. Arnold (1964), winter shorn sheep, Phalaris-annuals-clover;
5. Data from the present study, heifers (Tables 1 and 7).
rate was 35 g OM/100 kg DM. Similar rates can be calculated from data reported by Handl (1972) for steers grazing immature crested wheatgrass. These differences in increase of forage intake as forage availability increases at low availability levels is probably a result of the different plant species studied and the different animals (sheep versus cattle) used.

The maximum intake levels determined in the literature illustrated in Figure 4 were obtained at availability levels ranging from 1200 to 4000 kg DM/ha. In the present study intake apparently was not limited when forage availability was equal to or above 143 kg DM/ha. Similar results have been reported in a 2-year study by Handl (1972) on crested wheatgrass pasture. There, the quantity of forage did not limit intake during the first year in spring or early summer when it was in excess of 167 kg DM/ha and during the second year (spring) when it was in excess of 176 kg DM/ha.

These findings suggest that on mature crested wheatgrass pasture having levels of forage availability above 143 kg DM/ha, intake cannot be increased by increasing the quantity of forage available. However, increases in intake may possibly be obtained by increasing the quality of the diet (Greenhald 1967, Hodgson and Wilkinson 1968).

Most published works on grazing models for domestic livestock have shown intake as a function of forage availability. Rice et al. (1974) used a negative exponential equation to describe the relationship of intake with forage availability. Vera et al. (1977) used a Mitcherlich-type function to describe the above relationship.
Findings of the present study suggest that considerably more work is needed to define these functions over a broader range of forage and animal conditions. Published models would not have adequately predicted relationships observed in the present study.

**Live Weight Changes of Heifers**

Weight gains during 1977 (Table 8) were small but significantly higher (P<0.05) during the last two trials than in the second one. During 1978 (Table 9), there were not significant differences among trials except the last one when heifers lost weight. This weight loss cannot be attributed to either reduced forage intake or to limitations on quality, since a relatively constant intake level was maintained throughout the trials (Table 7) and measurements of forage quality (Tables 2, 3, and 4) indicated either higher or equal nutritional levels during trial five in comparison to the initial four trials. However, limited forage availability forced heifers to increase their muscular activity especially for locating, prehending, and ingesting food. This was evidenced by prolonged foraging times (Table 5), increased biting rates (Table 6), and subjectively estimated increased standing time.

Daily minimum temperatures (Appendix Table 42) were not below the critical temperature (Blaxter 1962) where animals would be required to use endogenous energy for thermoregulation. The overall weight loss, although statistically significant, was only about 1.2 percent of the animals' body weight during the last trial.
Table 8. Weight gains (kg/head/day) by heifers grazing crested wheatgrass pasture during 1977.

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<tr>
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</tbody>
</table>

¹/ Data for the initial period was in obvious error when compared to those for subsequent dates. A malfunction in the livestock scale was later discovered. These data were therefore omitted.

²/ Means followed by a common letter are not significantly different (P<0.05).
Table 9. Weight gains (kg/head/day) by heifers grazing crested wheatgrass pasture during 1978.

<table>
<thead>
<tr>
<th>Animal Nos.</th>
<th>Periods</th>
<th>Mean ± SD</th>
</tr>
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<tbody>
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<tr>
<td>16</td>
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<td>1.2</td>
</tr>
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</table>

Means ± SD¹/   0.8±1.0a  0.7±0.4a  0.4±0.4a  0.4±0.4a  -1.1±1.2b

¹/ Means followed by a common letter are not significantly different (P<0.05).
This change was considered small and no attempt was made to account for the various activity costs that may have been associated with the weight loss. The general body of scientific information is limited in regard to the processes and rates associated with catabolism of body tissue to meet energy demands. Unit costs of such activities as grazing, walking, and standing are poorly quantified for cattle.
SUMMARY AND CONCLUSIONS

A two year study was conducted on mature crested wheatgrass pasture during the late summer to investigate the relationships between forage intake of Angus heifers and body weight change with forage nutritive value and availability. Additionally, the relationships between grazing time and biting rate with forage availability and plant height were examined.

During 1977 there were a total of four 4-day trials and during 1978 there were five 4-day trials. Consecutive trials were conducted in the same pasture, thus forage availability was decreasing from the first to the last trial. Forage availability before and after each trial was estimated from $1-m^2$ hand-clipped plots within 10 percent of the mean with a $P<0.10$ level of significance. Availability ranged from 474 to 170 kg DM/ha during 1977 and from 929 to 114 kg DM/ha during 1978. Hand-harvested forage samples similar to the forage grazed during each trial were analyzed for crude protein content, in vitro digestibility, and cell contents.

Foraging time and periodicity of grazing were determined with mechanical clocks (Vibracorders) mounted on animals' necks. Biting rate was determined by visual counts during timed periods of five minutes duration. Biting rate measurements were made during the early morning or early evening period of intensive grazing.

Intake of forage was estimated from fecal output and in vitro digestibility data. Determination of fecal output was attempted in
1977 and 1978 using a single dose indicator method. During the second year, fecal output was also measured by total collection. In vitro digestibility of organic matter was determined by the Tilley and Terry (1963) procedure.

Within years, crude protein content increased significantly (P<0.05) during the third trial in 1977 and during the fifth trial in 1978. This resulted from forage regrowth occurring immediately before and during those trials. No difference in cell contents was found among trials during 1977. This was a result of the regrowth (mainly leaves high in cell contents) which occurred during the third trial. During 1978 cell contents decreased as grazing progressed and the quantity of forage available diminished. Cell contents during 1977 were significantly higher (P<0.05) than 1978.

Foraging time was inversely related to forage availability. It increased from 380 min/day to 656 min/day as forage availability decreased from 919 to 143 kg DM/ha through the course of the experiment. Consequently, the hypothesis that no correlation existed between forage availability and grazing time was rejected. Similarly, biting rate increased from 37 to 50 bites/min from the first to the last trial and the hypothesis that no correlation existed between forage availability and biting rate was rejected. However, biting rate was more closely related to plant height than to forage availability (expressed as kg/ha). The relationship of grazing time and biting rate to forage availability was hypothesized to be curvilinear. However, no difference from a
linear relationship was found within the range of forage availabilities studied. Thus, when forage availability decreases animals alter their behavior linearly by increasing both their foraging time and biting rate. Biting rate apparently depends on pasture structure, specifically plant density, while grazing time mainly depends on appetite drive. These conclusions are based on a comparison of grazing time and biting rate of the present study in pasture 17 with data for 1977 obtained in pasture 18 (Scarnecchia 1979). Pasture 18 had a relatively homogeneous plant cover while pasture 17 had a patchy plant cover and two times as much forage availability as pasture 18. Foraging time was described satisfactorily by the same function for both years. However, biting rate was much lower in pasture 17 than 18 even when comparing trials with similar forage availability and plant height. Biting rate was lower in pasture 17 because animals spent considerable time moving from one patch to the other.

Significant differences \((P \leq 0.05)\) in in vitro OM digestibilities were found only for the fifth trial in 1978. Forage digestibility during 1977 was significantly higher \((P \leq 0.05)\) than in 1978. Forage did not reach full development during the first year when it was prematurely cured due to drought conditions. Additionally, the contribution of forage regrowth to increased digestibility was significant.

Intake data obtained when fecal output was estimated by the single-dose marker technique were inconclusive. No significant correlation was found between measurements of total fecal production
and estimates by the single-dose marker technique. The single-dose indicator technique does not satisfactorily predict fecal output using the model \( \ln y = a + bx \). More sophisticated two- or three-compartment models using estimates of marker lagtime and observations on the ascending limb of the excretion curve must be considered.

Intake of OM determined from total fecal collection and in vitro OM digestibility ranged from 44.4 to 50.6 g/kg \( BW^{0.75} \)/day and did not vary significantly (\( P < 0.05 \)) among trials during 1978. The relationship between forage availability and voluntary intake was hypothesized to be asymptotic according to published findings from temperate pasture situations (Johnston-Wallace and Kennedy 1944, Allden and Whittaker 1970, Hamilton et al. 1973, Langlands and Bennett 1973a and b). However, in this study, intake of g OM/kg \( BW^{0.75} \)/day was independent from forage availability within the range 919 to 143 kg DM/ha. Consequently, the hypothesis that organic matter intake by heifers decreased as forage availability decreases was rejected.

Weight gains of heifers was significantly higher (\( P < 0.05 \)) during the last two trials in 1977 when forage regrowth occurred in comparison to the previous trial. Most heifers gained weight for all trials in 1978 except the last. Then, weight loss of approximately 1.1 kg/head/day was probably a result of additional energy expenditures for foraging rather than limited forage intake or lower forage quality.

The general form of the findings of this study applies to the free-grazing animal on mature crested wheatgrass pasture and the
relationships will no doubt vary with other types of ranges and animals. Work on the relationship of forage availability and intake summarized by Noy-Meir (1975) indicates that optimum intake was obtained on the average at approximately 1800 kg DM/ha forage availability. Those reports have been extensively used in range modeling. Findings of the present study indicated that 143 kg DM/ha are adequate for maximum intake of heifers. These suggest that a reexamination of the function used is needed on a wider array of forage and animal conditions.
LITERATURE CITED


Ellis, W. C. 1979. Personal communication.


Wier, W. C., and D. T. Torell. 1959. Selective grazing by sheep as shown by a comparison of the chemical composition of the range and pasture forage obtained by hand clipping and that collected by esophageal fisulated sheep. J. Animal Sci. 18:641-649.


APPENDIX
Table 10. Weight (kg) of heifers grazing crested wheatgrass pasture during 1977.

<table>
<thead>
<tr>
<th>Animals</th>
<th>8/9</th>
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1/ Data from the initial weighing was obviously in error when compared to those for subsequent dates. A malfunction of the livestock scale was later discovered.
Table 11. Weight (kg) of heifers grazing crested wheatgrass pasture during 1978.

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1/ Missing record.
Table 12. Analysis of variance for weight gains by heifers grazing crested wheatgrass pasture.

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<th>Degrees of Freedom</th>
<th>Mean Squares</th>
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<tr>
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<tr>
<td>Error</td>
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</tbody>
</table>

<sup>1/</sup> *Statistically significant (P<0.05).*
Table 13. Comparison of weight gains by heifers grazing crested wheatgrass pasture using Duncan's New Multiple Range test.

<table>
<thead>
<tr>
<th>Periods</th>
<th>Mean Weight Gain (kg/head/day)</th>
<th>Mean Difference</th>
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</thead>
<tbody>
<tr>
<td></td>
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</tr>
<tr>
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<td></td>
<td>0.5 0.5</td>
</tr>
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<td>8/9-8/19</td>
<td>--</td>
<td>+</td>
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<tr>
<td>8/29-9/8</td>
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</tr>
<tr>
<td>9/8-9/18</td>
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</tr>
<tr>
<td>8/19-8/29</td>
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<td></td>
</tr>
<tr>
<td>8/8-8/14</td>
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<td></td>
</tr>
<tr>
<td>8/14-8/24</td>
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<td></td>
</tr>
<tr>
<td>8/24-9/3</td>
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<td></td>
</tr>
<tr>
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<td></td>
</tr>
<tr>
<td>9/24-9/29</td>
<td>-1.1</td>
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</tr>
</tbody>
</table>

1/ (+) = significant differences (P<0.05). (-) = no significant difference (P>0.05).
Table 14. Fecal production (kg/head/day) determined by total collections from heifers grazing crested wheatgrass pasture during 1978.

<table>
<thead>
<tr>
<th>Periods</th>
<th>Animals 1</th>
<th>Animals 2</th>
<th>Animals 3</th>
<th>Animals 4</th>
<th>Animals 5</th>
<th>Animals 6</th>
<th>Means</th>
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<td>2.3</td>
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<tr>
<td>8/19-8/23</td>
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<td>2.8</td>
<td>3.2</td>
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<td>2.5</td>
<td>2.7</td>
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<td>3.0</td>
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Table 15. Analysis of variance for total fecal produced by heifers grazing crested wheatgrass pasture during 1978.

<table>
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<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Mean Squares</th>
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<td>0.2</td>
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<tr>
<td>Error</td>
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</table>
Table 16. Estimates of undigested material (feces) produced (kg/head/day) by heifers using a single-dose marker technique during 1977.

<table>
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<th>Animal Nos.</th>
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Means ±SD 5.4±1.3 5.5±1.8 6.2±2.4 5.9±0.7

1/ Missing record.
Table 17. Estimates of undigested material (feces) produced by heifers (kg) using a single-dose marker technique during 1978.

<table>
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<td>6.4</td>
<td>4.1</td>
<td>5.4±1.3</td>
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<td>6.0±1.6</td>
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<td>3.7</td>
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<td>5.1</td>
<td>6.1</td>
<td>4.8±1.1</td>
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<td>4.1±0.5</td>
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<td>4.8±1.7</td>
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<td>6.8</td>
<td>-</td>
<td>5.1±1.2</td>
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<td>4.7</td>
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<td>4.0±1.0</td>
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<td>4.2</td>
<td>4.0</td>
<td>4.4±1.3</td>
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<td>4.7</td>
<td>-</td>
<td>7.1</td>
<td>5.4±1.6</td>
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<td>3.7</td>
<td>10.5</td>
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<td>4.0</td>
<td>5.2±3.0</td>
</tr>
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<td>3.9±1.2</td>
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</table>
Table 18. Fecal output (kg/head/day) estimates by the single-dose marker technique for heifers fasted (F) and nonfasted (NF).

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<td>-</td>
</tr>
<tr>
<td>8/29-8/2</td>
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<td>-</td>
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<td>-</td>
<td>*1/</td>
<td></td>
<td>3.6</td>
<td>-</td>
</tr>
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<td>9/8-9/12</td>
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<td>3.8</td>
<td>-</td>
<td>-</td>
<td>3.9</td>
<td>3.9</td>
<td>-</td>
</tr>
<tr>
<td>9/24-9/28</td>
<td>-</td>
<td>4.4</td>
<td>*</td>
<td>-</td>
<td>1.6</td>
<td>-</td>
<td>3.9</td>
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1/ * Missing data.

Table 19. Analysis of variance for fecal production by fasted and nonfasted animals estimated by the single-dose marker technique.

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<th>Mean Squares</th>
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<td>1</td>
</tr>
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<td>Fasted-Nonfasted</td>
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<tr>
<td>Error</td>
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Table 20. Ash content of fecal samples collected from heifers grazing crested wheatgrass pasture during 1977.

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<td>26.4</td>
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<td>23.9</td>
<td>23.6</td>
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<td>28.0</td>
<td>26.7</td>
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Table 21. Ash content of fecal samples collected from heifers grazing crested wheatgrass pasture during 1978.

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<td>18.8</td>
</tr>
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<td>18.3</td>
</tr>
<tr>
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<td>25.9</td>
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<td>26.7</td>
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<td>22.5</td>
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<tr>
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<td>21.0</td>
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Table 22. Analysis of variance for ash content (%) of feces collected from heifers grazing crested wheatgrass pasture.

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<td></td>
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\(^1/\) *Statistically significant (P<0.05).
Table 23. Comparison of ash content (%) of fecal samples collected from heifers grazing crested wheatgrass pasture by Duncan's New Multiple Range test.

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<td>Mean Difference</td>
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<td>1.9</td>
<td></td>
</tr>
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<td>-</td>
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<td>8/11</td>
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<td></td>
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<td>2.0</td>
<td>2.0</td>
<td>2.0</td>
</tr>
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<td>+</td>
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<tr>
<td>8/31</td>
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</table>

1/ (+) = significant differences (P<0.05). (-) = no significant difference (P>0.05).

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<th>Source of Variation</th>
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<td>1978</td>
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<tr>
<td>Error</td>
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1/ *Statistically significant (P<0.05).

Table 25. Individual mean for in vitro organic matter digestibility (%) of hand-harvested crested wheatgrass forage over five periods.

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<td>2.2</td>
<td>2.1</td>
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1978

<table>
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1/ (+) = significant differences (P<0.05). (-) = no significant difference (P<0.05).
Table 26. Analysis of variance for crude protein content of hand-harvested crested wheatgrass forage.

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<tr>
<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Mean Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Periods</td>
<td>3</td>
<td>6.7*1/</td>
</tr>
<tr>
<td>Error</td>
<td>7</td>
<td>0.6</td>
</tr>
<tr>
<td>1978</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Periods</td>
<td>4</td>
<td>17.3*</td>
</tr>
<tr>
<td>Error</td>
<td>23</td>
<td>1.4</td>
</tr>
</tbody>
</table>

1/ *Statistically significant (P<0.05).
Table 27. Comparison of crude protein content of hand-harvested crested wheatgrass using Duncan's New Multiple Range test.

<table>
<thead>
<tr>
<th>Range</th>
<th>(Number of means within a comparison)</th>
<th>5</th>
<th>4</th>
<th>3</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periods</td>
<td>Mean Protein Content (%)</td>
<td>Mean Difference</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1977</td>
<td></td>
<td>1.9</td>
<td>1.9</td>
<td>1.8</td>
<td></td>
</tr>
<tr>
<td>8/29-9/2</td>
<td>13.2</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>8/8-9/12</td>
<td>11.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>8/9-8/12</td>
<td>10.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>8/19-8/23</td>
<td>9.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>1978</td>
<td>1.7</td>
<td>1.7</td>
<td>1.6</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>9/24-9/28</td>
<td>9.5</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>8/19-8/23</td>
<td>6.2</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>8/9-8/13</td>
<td>5.9</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>9/8-9/12</td>
<td>5.8</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>8/29-9/2</td>
<td>5.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

1/ (+) = significant differences (P<0.05). (-) = no significant difference (P>0.05).
Table 28. Analysis of variance for cell contents of hand-harvested crested wheatgrass forage.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Mean Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1977</td>
<td></td>
</tr>
<tr>
<td>Periods</td>
<td>3</td>
<td>0.2</td>
</tr>
<tr>
<td>Error</td>
<td>5</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>1978</td>
<td></td>
</tr>
<tr>
<td>Periods</td>
<td>4</td>
<td>41.3*1/</td>
</tr>
<tr>
<td>Error</td>
<td>22</td>
<td>5.2</td>
</tr>
</tbody>
</table>

1/ *Statistically significant (P<0.05).

Table 29. Comparison of cell contents of hand-harvested crested wheatgrass forages using Duncan's New Multiple Range test.

<table>
<thead>
<tr>
<th>Range</th>
<th>(Number of means within a comparison)</th>
<th>5</th>
<th>4</th>
<th>3</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Cell Constituents</td>
<td>3.3</td>
<td>3.2</td>
<td>3.1</td>
<td>3.0</td>
</tr>
<tr>
<td>Periods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1978</td>
<td>38.8</td>
<td>+1/</td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>38.1</td>
<td></td>
<td>+</td>
<td>+</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>35.2</td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>32.6</td>
<td></td>
<td></td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>32.6</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1/ (+) = significant differences (P<0.05). (−) = no significant difference (P>0.05).
Table 30. Comparison between years for in vitro digestibility, crude protein content, and cell contents using a "t" test.

<table>
<thead>
<tr>
<th>Years</th>
<th>In Vitro Digestibility</th>
<th>Crude Protein</th>
<th>Cell Constituents</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sample (%)</td>
<td>Size</td>
<td>Sample (%)</td>
</tr>
<tr>
<td>1977</td>
<td>10</td>
<td>49.3</td>
<td>11</td>
</tr>
<tr>
<td>1978</td>
<td>26</td>
<td>35.3</td>
<td>28</td>
</tr>
<tr>
<td>S² pooled</td>
<td>0.8</td>
<td>0.2</td>
<td>0.3</td>
</tr>
<tr>
<td>&quot;t&quot;</td>
<td>125.2*¹/</td>
<td>1640.2*</td>
<td>39.0*</td>
</tr>
</tbody>
</table>

¹/ Statistically significant (P<0.05).

Table 31. Analysis of variance for daily intake of organic matter (g/kg BW⁻⁰·⁷⁵) during 1978. Estimates based on total fecal collection and in vitro digestibility.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Mean Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periods</td>
<td>4</td>
<td>60.7</td>
</tr>
<tr>
<td>Animals</td>
<td>5</td>
<td>136.1*¹/</td>
</tr>
<tr>
<td>Error</td>
<td>20</td>
<td>34.8</td>
</tr>
</tbody>
</table>

¹/ Statistically significant (P<0.05).
Table 32. Comparison for daily intake of organic matter by heifers grazing crested wheatgrass using Duncan's Multiple Range test. Estimates based on total fecal collection and in vitro digestibility.

<table>
<thead>
<tr>
<th>Range</th>
<th>(Number of means within comparisons)</th>
<th>6</th>
<th>5</th>
<th>4</th>
<th>3</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean Intake (g/kg BW\textsuperscript{75})</td>
<td>Mean Differences</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>56.5</td>
<td>+\textsuperscript{1/}</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>51.5</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>49.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>1</td>
<td>48.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>43.6</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>42.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

\textsuperscript{1/} (+) = significant differences (P \leq 0.05). (-) = no significant difference (P \leq 0.05).

Table 33. Analysis of variance for daily grazing time (min) of heifers during 1978 as influenced by decreasing forage availability over time.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Mean Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periods</td>
<td>4</td>
<td>69428.1*\textsuperscript{1/}</td>
</tr>
<tr>
<td>Animals</td>
<td>5</td>
<td>8023.9*</td>
</tr>
<tr>
<td>Error</td>
<td>20</td>
<td>2447.1</td>
</tr>
</tbody>
</table>

\textsuperscript{1/} *Statistically significant (P \leq 0.05).
Table 34. Comparison of grazing time (min/day/heifer) influenced by decreasing forage availability during 1978 using Duncan's New Multiple Range test.

<table>
<thead>
<tr>
<th>Animals</th>
<th>Mean Grazing Time</th>
<th>Mean Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>541</td>
<td>+</td>
</tr>
<tr>
<td>1</td>
<td>539</td>
<td>+</td>
</tr>
<tr>
<td>3</td>
<td>513</td>
<td>+</td>
</tr>
<tr>
<td>6</td>
<td>504</td>
<td>+</td>
</tr>
<tr>
<td>5</td>
<td>484</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>433</td>
<td></td>
</tr>
</tbody>
</table>

1/ (+) = significant differences (P<0.05). (-) = no significant difference (P<0.05).

Table 35. Comparison of average grazing time (min/day) of heifers as influenced by decreasing forage availability during 1978 using Duncan's New Multiple Range test.

<table>
<thead>
<tr>
<th>Periods</th>
<th>Mean Grazing Time</th>
<th>Mean Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>9/24-9/28</td>
<td>656</td>
<td>+</td>
</tr>
<tr>
<td>9/8-9/12</td>
<td>531</td>
<td>+</td>
</tr>
<tr>
<td>8/29-9/2</td>
<td>521</td>
<td>+</td>
</tr>
<tr>
<td>8/19-8/23</td>
<td>423</td>
<td>+</td>
</tr>
<tr>
<td>8/9-8/13</td>
<td>380</td>
<td></td>
</tr>
</tbody>
</table>

1/ (+) = significant differences (P<0.05). (-) = no significant difference (P<0.05).
Table 36. Analysis of variance for bites per minute by heifers grazing crested wheatgrass pasture.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Degrees of Freedom</th>
<th>Mean Squares</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periods</td>
<td>4</td>
<td>166.8*(^1/)</td>
</tr>
<tr>
<td>Animals</td>
<td>5</td>
<td>23.6</td>
</tr>
<tr>
<td>Error</td>
<td>20</td>
<td>8.7</td>
</tr>
</tbody>
</table>

\(^1/\) *Statistically significant (P<0.05).

Table 37. Comparison of bites per minute by heifers grazing crested wheatgrass pasture using Duncan's New Multiple Range test.

<table>
<thead>
<tr>
<th>Range (Number of means within a comparison)</th>
<th>5</th>
<th>4</th>
<th>3</th>
<th>2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periods</td>
<td>Mean Bites Rate</td>
<td>Mean Differences</td>
<td>3.9</td>
<td>3.8</td>
</tr>
<tr>
<td>9/24-9/28</td>
<td>50</td>
<td>+(^1/)</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>9/8-9/12</td>
<td>45</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>8/19-8/23</td>
<td>40</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8/29-9/2</td>
<td>39</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8/9-8/13</td>
<td>37</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

\(^1/\) (+) = significant differences (P<0.05). (-) = no significant difference (P≥0.05).
Table 38. Percent of leaves (by weight) of crested wheatgrass pastures under continuous grazing.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Leaves (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1977</strong></td>
<td></td>
</tr>
<tr>
<td>August 9</td>
<td>56</td>
</tr>
<tr>
<td>August 19</td>
<td>62</td>
</tr>
<tr>
<td>August 29</td>
<td>56</td>
</tr>
<tr>
<td>September 8</td>
<td>46</td>
</tr>
<tr>
<td>September 18</td>
<td>68</td>
</tr>
<tr>
<td><strong>1978</strong></td>
<td></td>
</tr>
<tr>
<td>August 8</td>
<td>42</td>
</tr>
<tr>
<td>August 13</td>
<td>42</td>
</tr>
<tr>
<td>August 18</td>
<td>54</td>
</tr>
<tr>
<td>August 23</td>
<td>49</td>
</tr>
<tr>
<td>August 28</td>
<td>39</td>
</tr>
<tr>
<td>September 2</td>
<td>42</td>
</tr>
<tr>
<td>September 8</td>
<td>41</td>
</tr>
<tr>
<td>September 12</td>
<td>47</td>
</tr>
<tr>
<td>September 23</td>
<td>59</td>
</tr>
<tr>
<td>September 28</td>
<td>56</td>
</tr>
</tbody>
</table>
Table 39. Average plant height and moisture content of crested wheatgrass stands under continuous grazing.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Plant Height (cm)</th>
<th>SE</th>
<th>Moisture (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1977</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 9</td>
<td>15±0.8</td>
<td></td>
<td>22</td>
</tr>
<tr>
<td>August 19</td>
<td>12±0.5</td>
<td></td>
<td>28</td>
</tr>
<tr>
<td>August 29</td>
<td>10±0.4</td>
<td></td>
<td>37</td>
</tr>
<tr>
<td>September 8</td>
<td>8±0.4</td>
<td></td>
<td>40</td>
</tr>
<tr>
<td>September 18</td>
<td>6±0.3</td>
<td></td>
<td>40</td>
</tr>
<tr>
<td><strong>1978</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 9</td>
<td>31±1.3</td>
<td></td>
<td>33</td>
</tr>
<tr>
<td>August 13</td>
<td>33±0.6</td>
<td></td>
<td>40</td>
</tr>
<tr>
<td>August 18</td>
<td>33±2.1</td>
<td></td>
<td>33</td>
</tr>
<tr>
<td>August 23</td>
<td>27±1.7</td>
<td></td>
<td>41</td>
</tr>
<tr>
<td>August 28</td>
<td>29±2.0</td>
<td></td>
<td>43</td>
</tr>
<tr>
<td>September 2</td>
<td>22±1.8</td>
<td></td>
<td>43</td>
</tr>
<tr>
<td>September 8</td>
<td>19±3.2</td>
<td></td>
<td>35</td>
</tr>
<tr>
<td>September 12</td>
<td>17±2.6</td>
<td></td>
<td>50</td>
</tr>
<tr>
<td>September 23</td>
<td>6±1.3</td>
<td></td>
<td>55</td>
</tr>
<tr>
<td>September 28</td>
<td>6±1.1</td>
<td></td>
<td>40</td>
</tr>
</tbody>
</table>
Table 40. Average plant frequency in seeded crested wheatgrass pastures under continuous grazing.

<table>
<thead>
<tr>
<th>Dates</th>
<th>Agropyron cristatum</th>
<th>Agropyron smithii</th>
<th>Oryzopsis hymenoides</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1977</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 9</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>August 19</td>
<td>--</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>August 29</td>
<td>88</td>
<td>12</td>
<td>*2/</td>
</tr>
<tr>
<td>September 8</td>
<td>83</td>
<td>17</td>
<td>*</td>
</tr>
<tr>
<td>September 18</td>
<td>89</td>
<td>11</td>
<td>*</td>
</tr>
<tr>
<td>Means</td>
<td>87</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>1978</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>August 9</td>
<td>56</td>
<td>36</td>
<td>8</td>
</tr>
<tr>
<td>August 13</td>
<td>56</td>
<td>38</td>
<td>6</td>
</tr>
<tr>
<td>August 18</td>
<td>60</td>
<td>31</td>
<td>8</td>
</tr>
<tr>
<td>August 23</td>
<td>59</td>
<td>38</td>
<td>3</td>
</tr>
<tr>
<td>August 28</td>
<td>65</td>
<td>24</td>
<td>11</td>
</tr>
<tr>
<td>September 2</td>
<td>63</td>
<td>26</td>
<td>11</td>
</tr>
<tr>
<td>September 8</td>
<td>73</td>
<td>16</td>
<td>11</td>
</tr>
<tr>
<td>September 12</td>
<td>81</td>
<td>15</td>
<td>4</td>
</tr>
<tr>
<td>September 23</td>
<td>87</td>
<td>10</td>
<td>3</td>
</tr>
<tr>
<td>September 28</td>
<td>80</td>
<td>14</td>
<td>6</td>
</tr>
<tr>
<td>Means</td>
<td>68</td>
<td>25</td>
<td>7</td>
</tr>
</tbody>
</table>

1/ Not recorded.
2/ Not present.
<table>
<thead>
<tr>
<th>Months</th>
<th>Temperature °C</th>
<th>Precipitation in mm</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Average for 15y</td>
<td>1977</td>
</tr>
<tr>
<td>January</td>
<td>-3.2</td>
<td>-3.3</td>
</tr>
<tr>
<td>February</td>
<td>1.3</td>
<td>0.6</td>
</tr>
<tr>
<td>March</td>
<td>1.3</td>
<td>0.1</td>
</tr>
<tr>
<td>April</td>
<td>6.7</td>
<td>8.6</td>
</tr>
<tr>
<td>May</td>
<td>13.3</td>
<td>9.2</td>
</tr>
<tr>
<td>June</td>
<td>15.7</td>
<td>18.9</td>
</tr>
<tr>
<td>July</td>
<td>22.2</td>
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<td>20.7</td>
</tr>
<tr>
<td>September</td>
<td>16.2</td>
<td>16.0</td>
</tr>
<tr>
<td>October</td>
<td>8.6</td>
<td>10.3</td>
</tr>
<tr>
<td>November</td>
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<tr>
<td>December</td>
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<sup>1/</sup> M = Records missing.
Table 42. Temperatures (°C) measured on the Tintic study area.

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<tr>
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<td>29</td>
<td>9</td>
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</table>
Figure 5. Intake of organic matter in relation to average daily temperature. Vertical lines represent the range; means indicated by the dot.
Figure 6. Biting rate in relation to average daily temperature. Vertical lines represent the range; means indicated by the dot.
VITA

Anastasios S. Nastis

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Effects of Forage Availability on Voluntary Intake and Feeding Behavior of Grazing Heifers

Major Field: Range Science

Biographical Information:

Anastasios Stefanon Nastis was born October 30, 1942, at Archangelos, Pellis, Greece. He graduated from Arideas High School, Pellis Greece in 1960. He entered Aristotelion University of Thessaloniki, School of Agriculture and Forestry, Department of Forestry in 1961 and graduated in 1967. He worked for six months as a consultant in forest management. In 1967 he joined the army for two years. In 1969 he continued working as a consultant in forest management. In 1970 he became a faculty member as a research and teaching assistant at the Laboratory of Range Management, University of Thessaloniki. He worked in this position for four years. In 1974 he enrolled as a graduate student in the Department of Range Science at Utah State University. In 1977 he completed the requirements for the Master of Science degree. At present he is a candidate for the degree of Doctor of Philosophy in the Department of Range Science at Utah State University.