# ROOT DYNAMICS OF A SHORTGRASS ECOSYSTEM 

Submitted by
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY Dale Lee Bartos ENTITLED "Root Dynamics of a Shortgrass Ecosystem" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF Doctor of Philosophy.


Head of Department

## ABSTRACT OF DISSERTATION

## ROOT DYNAMICS OF A SHORTGRASS ECOSYSTEM

Seasonal dynamics of roots of a shortgrass system were determined by samples collected at two week intervals for two growing seasons (1969-1970) with a fall and winter sampling period in between. Soil cores were taken to a depth of either 10 cm or 80 cm ; the deep cores were used to determine the entire profile distributions of roots. The cores were washed free of soil particles and then the root mass was dried, weighed, ashed and reweighed. All values were expressed on an ash-free basis.

Sixty percent of the root weight was in the $0-10 \mathrm{~cm}$ segment and $75 \%$ was found in the upper 20 cm of the soil profile. The upper 10 cm increment had significant variations between dates, but the lower levels remained quite constant.

Four grazing treatments (none, light, moderate, heavy) were used to determine if grazing had an effect on the root mass. No significant differences were found among the four treatments.

The usual concept of substrate storage in roots and subsequent utilization was not supported by the data. Losses of root weights did not coincide with periods of leaf initiation. An alternative model was developed which better represented the fluctuations found during the

1969 growing period. This model reflects a hypothesis of root decomposition and growth which is a new approach to understanding root dynamics.

The mathematical model consists of two logistic equations added together. The resultant equation was fitted to the original data via a direct search curve fitting program.

Two curves were separated from the main equation with the declining curve representing decomposition and the rising curve growth. Various constants were added to the equation to limit the indicated amount of decomposition. The various curves presented all have merit, however, more work needs to be done to determine what actually occurs in nature.

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## INTRODUCTION

Virtually all of the 280 million acres of shortgrass prairie in the United States is used as rangeland (Stoddart and Smith 1955). Therefore, understanding the function of a shortgrass ecosystem is not only of scientific interest but is most important from a management viewpoint.

Primary producers are an important compartment of an ecosystem. The role of the primary producer is to fix energy via photosynthesis, which can be self utilized or passed on through different trophic levels.

A majority of the primary producer component in a shortgrass ecosystem occurs underground. Root systems act as the conductive mechanism between the aerial portions of the primary producer and the soil medium; energy and nutrient storage organs; food source for small herbivores; and are essential in the cycling of nutrients within the ecosystem.

A system is a group of objects united by some type of interactions. During the past several years ecologists have become more concerned with studying entire ecological systems or ecosystems. Odum (1965) defines an ecosystem as "any area of nature that includes living organisms and nonliving substances interacting to produce an exchange of materials between the living and nonliving parts." Of
course, no system will be studied in all its detail, but with the use of more quantitative approaches and computer facilities more breath and depth can be added than ever before.

## Study Objectives

The basic purpose of this project was to study the seasonal and annual dynamics of the root mass of a shortgrass ecosystem. This particular study was one facet of an overall ecosystem effort; the specific objectives of this study are:

1. measure and interpret fluctuations in the root mass during the 1969 and 1970 growing season.
2. test the influence of grazing by large herbivores on underground organs.

## LITERATURE REVIEW

In order to understand the entire ecosystem it is essential to have a thorough understanding of the primary producers. The producers are not only important aboveground but also belowground. It has been reported for various grassland ecosystems that from $80 \%$ to $95 \%$ of the vegetation occurs underground (Nilsson 1970; Hanson and Stoddart 1940; and Ovington, Heitcamp and Lawrence 1963). Because of the proportion and role of roots in a grassland ecosystem it seems necessary to study them in more detail.

Methods of root sampling
Pavlychenko (1937a) gives a detailed discussion of root studies during the past two centuries. Many of the early studies were conducted because of agronomic interests (Weaver 1920 and 1926; Weaver and Crist 1922). Studies of root systems, during the first portion of the twentieth century, were non-quantitative and are typified by Markle (1917) and Preston (1900). These two studies dealt with root penetration and distribution of cacti and shrubs.

Weaver (1920 and 1926), Weaver et al. (1922) and Weaver and Crist (1922) reported the use of the laborious and tedious trench and pick method of determining root distribution. This involved digging a
trench approximately 1.8 meters deep and then using an ice-pick to rid the profile of soil particles.

The next major advance in root sampling was reported by Pavlychenko (1937b). His soil-block washing method has been modified to various degrees and is being used at the present time. In his introduction, Pavlychenko gives a thorough account of previously used methods for root studies.

Prior to 1945 the two major soil sampling methods were Weaver's trench and pick method and Pavlychenko's soil-block washing method. A modification of the soil-block washing method was developed in 1947 employing a soil sampling machine mounted on the back of a truck. This apparatus enabled the sampler to collect 2" $4^{\prime \prime}$ diameter samples to a depth of $6^{\prime}$ (Kelley, Hardman and Jennings 1947). These samples were virtually undisturbed and could be sectioned as desired. Roots could be separated from the soil either by dry sieving or a washing process.

A major portion of the root samples collected since 1947 have been taken with various types of hydraulic corers. Uniform samples are obtained rapidly compared to the soil-block or trenching method. Moir and Bachelard (1969) compared coring to excavation and found coring to be more efficient and less tedious.

Boehle, et al. (1963), Kotanska (1967), Feherenbacher and Alexander (1955) and Dahlman and Kucera (1965) are among those
who used soil cores and a washing process to obtain root mass measurements.

One of the easiest and quickest ways of separating the roots from the soil is using water and different size screens for root collection. Comparison of hand washing of samples and a machine developed by Fribourg (1953) showed the machine to be 10 times faster.

McKell, Wilson and Jones (1961) described a floatation method for separation of roots and soil. This method as outlined is widely used today and has been modified (Lauenroth and Whitman 1971).

Milner and Hughes (1968) give a fairly complete summary of root sampling techniques available through 1968 which pertain to production of grasslands.

A recent innovation developed by Blevins, et al. (1968) is the use of liquid nitrogen which freezes the soil, thus a large, undisturbed soil sample can be obtained. This is a modification of the soil-block technique. It is, of course, much quicker than conventional methods of sampling.

Another way of determining root penetration and distribution is by the use of a box with one glass side (Lavin 1961; Muzik and Whitworth 1962; and Crider 1955). These are mainly used for crops or transplanted plants and would be difficult to use under natural conditions. The glass side is placed on the bottom and the box is tilted at
a $30^{\circ}-40^{\circ}$ angle. Geotropism causes the roots to grow against the glass where they can be easily studied.

One of the newest ways of determining root biomass and turnover rates is by the use of radioactive materials. Dahlman and Kucera (1968) allowed growing grass to assimilate ${ }^{14} \mathrm{CO}_{2}$ and then measured the translocated radioactive carbon in various parts of the plant.

In certain agricultural studies radioactive phosphate $\left({ }^{32} P\right)$ has been used. The ${ }^{32} \mathrm{P}$ was placed at various depths in the soil and the aerial portions were monitored to determine when the roots actually reached these particular levels (Hall et al. 1953). When radiophosphorus techniques were compared to the soil-block technique it was found they both gave comparable results, however, the ${ }^{32} P$ was far less laborious (Pettit and Jaynes 1971).

Neilson (1964) used ${ }^{14} C$ and other radioactive materials for determining root activity. Dodd and Van Amburg (1970) tested Andropogon scoparius clones, via ${ }^{134} C_{6}$, to determine tiller activity. It was found that groups of tillers acted as individual plants and most of the ${ }^{134} \mathrm{Cs}$ was concentrated in the upper 5 cm of roots.

## Grazing effects on roots

Many studies have been conducted to determine grazing effects on roots. Some have used clipped vegetation to simulate grazing by herbivores. Troughton (1957) and Jameson (1963) have both reviewed
the literature concerning effects of herbage removal on root growth and root weights. A summary of the more pertinent studies is presented in Table 1.

Most studies of grazing effects on roots showed that grazing (or hand clipping) reduces the amounts of roots. However, in a study of a grass-sagebrush community in eastern Idaho, Pearson (1965) found that grazed areas had more roots than ungrazed areas. He attributed this to (1) differences in species composition of the two areas or (2) root growth stimulated by grazing.

Newly seeded blue grama (Bouteloua gracilis) was utilized to see what effects clipping had on carbohydrate contents of the roots (Dodd and Hopkins 1958). Under controlled conditions increases in underground parts varied inversely with rates of growth; generally, however, this trend did not hold for those plants clipped. In the month after clipping there was a decrease in carbohydrates which was usually restored during the second month after clipping.

Crider (1955), removing varing percents of aerial growth, demonstrated that continuous clipping (grazing) had an adverse effect on root growth. If $70 \%$ or more of the foliage was removed, root growth was completely curtailed. One of the species Crider worked with was blue grama, where he found that root growth stopped for 17 and 13 days when the aerial portion was cut to a 2 "height. This stoppage occurred the first and second day after clipping. Blue grama root production was reduced $85 \%$ by clipping.

Table 1. Literature concerning effects of herbage removal upon root weights.

| Citation | Location \& Major Vegetation Represented | Treatment | Root Mass | Comments |
| :---: | :---: | :---: | :---: | :---: |
| Pearson (1965) | Rexburg, Idaho |  |  |  |
|  | Stipa comata <br> Artemisia tridentata | Grazed (70 yrs.) <br> Ungrazed (11 yrs.) | $\begin{aligned} & 1031 \mathrm{~g} / \mathrm{m}^{2} / 40 \mathrm{~cm} \\ & 704 \mathrm{~g} / \mathrm{m}^{2} / 40 \mathrm{~cm} \\ & \text { (Ovendry wts.) } \end{aligned}$ | $\begin{aligned} & 80 \%(0-20 \mathrm{~cm}) \\ & 18 \%(20-40 \mathrm{~cm}) \end{aligned}$ |
| Schuster (1964) | Colorado Springs, |  |  |  |
|  | Colorado | Heavy grazed (17 yrs.) | $395 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm}$ | $\begin{aligned} & 71 \%(0-31 \mathrm{~cm}) \\ & 18 \%(31-61 \mathrm{~cm}) \end{aligned}$ |
|  | Bouteloua gracilis | Moderately grazed (17 yrs. ) | $482 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm}$ | $\begin{aligned} & 79 \%(0-31 \mathrm{~cm}) \\ & 14 \%(31-61 \mathrm{~cm}) \end{aligned}$ |
|  | Festuca arizonica | Ungrazed (20 yrs.) | $\begin{gathered} 570 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm} \\ \text { (Air-dry wts.) } \end{gathered}$ | 82\% ( $0-31 \mathrm{~cm}$ ) |
|  | Artemisia frigida |  |  | 12\% ( $31-61 \mathrm{~cm}$ ) |
| Lorenz \& Rogler(1967) | Mandan, North Dakota |  |  |  |
|  |  | Heavy grazed | $36407 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm}$ | 78\% (0-31 cm) |
|  | Agropyron smithii | (45 yrs.) |  | $14 \%$ ( $31-61 \mathrm{~cm}$ ) |
|  | Stipa comata |  |  |  |
|  | Bouteloua gracilis | Moderate grazed (45 yrs.) |  | 74\% (0-31 cm ) |
|  | Artemisiz frigida |  | $\begin{gathered} 35702 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm} \\ \text { (ovendry wts.) } \end{gathered}$ | 15\% ( $31-61 \mathrm{~cm}$ ) |
|  |  |  |  | No significant difference between the two treatments. |

Table 1. (continued)

| Citation | Location \& Major Vegetation Represented | Treatment | Root Mass | Comments |
| :---: | :---: | :---: | :---: | :---: |
| Biswell E Weaver (1933) | Lincoln, Nebraska <br> Bouteloua gracilis | Hand clipped <br> Not clipped | $\begin{gathered} 4 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm} \\ 105 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm} \end{gathered}$ | These values were obtained from transplanted plants. <br> Roots of the clipped grass grew very poorly. Length of roots were greatly reduced by clipping. |
| Cook, Stoddart, <br> E Kinsinger (1958) | Logan, Utah <br> Agropyron desertorum | Clipped to $1^{1 "} \mathrm{ht}$. <br> Clipped to 3 " hr . | $\begin{aligned} & 1159 \mathrm{~g} / \mathrm{m}^{2} / 46 \mathrm{~cm} \\ & 1328 \mathrm{~g} / \mathrm{m}^{2} / 46 \mathrm{~cm} \end{aligned}$ | When more is left aboveground there is more belowground. <br> Clipping reduced roots most in the upper 15 cm . |
| Jameson \& Huss (1959) | South Central Texas <br> Andropogon scoparius | Check <br> Leaves removed <br> Stems removed <br> Leaves \& Stems removed | $.63 \mathrm{~g} / \mathrm{pot}$ <br> $.47 \mathrm{~g} /$ pot <br> $.41 \mathrm{~g} /$ pot <br> $.34 \mathrm{~g} /$ pot <br> (ovendry wts.) | Individual plants were used. "Apparently the major influence of clippings on the roots was to stop further root growth rather than to utilize the carbohydrates already in the roots." |
| Blydenstein (1966) | Tucson, Arizona <br> Bouteloua curtipendula <br> Bouteloua filiformis | Grazed <br> Ungrazed <br> Grazed <br> Ungrazed | $\begin{aligned} & 11.7 \# \text { roots in }{ }^{2} \\ & 15.5 \# \text { roots in }{ }^{2} \\ & 11.2 \# \text { roots in }{ }^{2} \\ & 29.0 \# \text { roots in }{ }^{2} \end{aligned}$ | "Root system represents almost $1 / 2$ of the total material produced by that plant." |

Table 1. (continued)

| Citation | Location E Major Vegetation Represented | Treatment | Root Mass | Comments |
| :---: | :---: | :---: | :---: | :---: |
| Hanson $\mathcal{E}$ Stoddart (1940) | Southern Cache Valley, Utah |  |  |  |
|  |  |  |  |  |
|  |  | Grazed | $422 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm}$ |  |
|  | Agropyron inerme |  |  | Average root/shoot $=13: 1$ |
|  |  | Ungrazed | $2585 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm}$ |  |

## Decomposition and temperature

One of the factors associated with root mass fluctuations is that of decomposition. However, a search of the literature reveals that little work has been done concerning root decomposition under natural conditions.

Rodin and Bazilevich (1967) discuss the root-decay process. These workers indicate that during dry years the decomposition process is much slower and that this is why there is more root mass during dry years as opposed to wet years.

An in depth study of root decomposition in undisturbed prairie soils was conducted by Weaver (1947). He was concerned with three species, Andropogon gerardi, Andropogon scoparius and blue grama. Blue grama lost $67 \%$ of its weight in two years and Weaver felt that little decomposition occurs the first year. He also indicated that of the three species blue grama was the most resistant to decay.

In an early study, Weaver and Zink (1946b) used a banding technique to determine how long roots lived. After three growing seasons only $45 \%$ of the blue grama roots were alive. It must be kept in mind that this study was done under very disturbed conditions where sods were moved to the laboratory for observation. An earlier banding study indicated grass roots live at least a year and many in excess of two years (Stoddart 1935).

Pilat (1969) found that decreases in roots coincided with periods of increased soil moisture; he therefore concluded that rates of decomposition were related to soil moisture.

Turnover values were calculated for the root mass in a tall grass prairie (Dahlman and Kucera 1965), by using the following formula:

$$
T=\frac{M-N}{M}
$$

where;

$$
\begin{aligned}
& \mathrm{T}=\text { turnover value } \\
& \mathrm{M}=\text { maximum amount of root mass } \\
& \mathrm{N}=\text { minimum amount of root mass }
\end{aligned}
$$

They calculated that approximately one-fourth of the mass was replaced each year, and concluded that a complete turnover of roots occurred every four years.

Probably the major factor effecting root growth is that of temperature (Tajima 1965; Bommer 1960; Garwood 1965; Takeda and Agata 1966; and Beard 1959).

Stuckey (1941) attributed the stoppage of root growth during the summer months to high soil temperatures. He found that root tip cells of Kentucky bluegrass (Poa pratensis) were actively dividing at $0^{\circ} \mathrm{C}$ which should indicate root growth.

In a Japanese study on Ladino clover (Kumai, Hirose, and Sanada 1965) it was postulated that when top growth was at a maximum root initiation was very slow and decay of old roots occurred. They associated root weight decreases from April to August with flowering and rapid aerial growth.

## Quantitative measurements of root mass

Within the past 20 years considerable work has been done concerning roots and root fluctuations of natural vegetation. This, of course, is quite essential in understanding the function of the entire ecosystem. Some of the major studies pertinent to grassland ecosystems are referenced in Table 2 and quantitative values are given for comparison.

Although quantitative root studies in the grassland ecosystem are somewhat scarce, there is valuable information to be gathered from the literature. Studies by Weaver (1958, 1961) have provided pertinent information on the root systems of shortgrass prairies. Dahlman and Kucera (1965) have provided useful information on root systems of a tallgrass prairie.

## Advances in modelling

Modelling has been proposed as a method of organizing the study of the entire ecosystem and parts thereof (Van Dyne 1969). He suggests an abstraction of the real world situation into mathematical

Table 2. Literature concerning quantitative measurements of roots in various grasslands.

| Citation | Location \& Major Vegetation Represented | Amounts Present | Comments |
| :---: | :---: | :---: | :---: |
| Weaver (1958) | Lincoln, Nebraska to Colorado Springs, Colo. <br> Bouteloua gracilis <br> Buchloe dactyloides | $\text { Avg. } 448 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm}$ | Blue grama and buffalo grass have a shallow root system to benefit from light rain showers. $\begin{aligned} & 79 \%(0-15 \mathrm{~cm}) \\ & 10 \%(15-31 \mathrm{~cm}) \end{aligned}$ |
| Weaver \& Zink (1946a) | Eastern Nebraska <br> Native prairie <br> Bouteloua gracilis | $562 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm}$ | $\begin{gathered} \text { Root/shoot ratios: } \\ 1943=.29 \\ 1944=.25 \\ 1945=.21 \\ 94 \%(0-31 \mathrm{~cm}) \end{gathered}$ |
| Dittmer (1937) | Iowa City, Iowa Secale cereale (winter rye) | Total surface area $639 \mathrm{~m}^{2}$ | Surface area of underground to tops was 130 times greater. |
| Bray (1963) | Summary of 28 temperate angiosperms. Mean yearly, net herbaceous production of belowground parts | $354 \mathrm{~g} / \mathrm{m}^{2} / ?$ | Belowground/aboveground ratio increased from moist to mesic to xeric species. |
| Ovington, Heitcamp, and Lawrence (1963) | Minneapolis and St. Paul, Minnesota Tallgrass prairie <br> Stipa spartea <br> Poa pratensis <br> Andropogon gerardi | $482 \mathrm{~g} / \mathrm{m}^{2} / 50 \mathrm{~cm}$ (ovendry wt.) | 91\% of total biomass was found undergrounds. |

Table 2. (continued)

| Citation | Location \& Major <br> Vegetation Represented | Amounts Present | Comments |
| :---: | :---: | :---: | :---: |
| Dahlman 8 Kucera (1965) | Columbia, Missouri <br> Tallgrass Prairie | $\begin{aligned} \text { Spring } & =1449 \mathrm{~g} / \mathrm{m}^{2} / 86 \mathrm{~cm} \\ \text { Summer } & =1860 \mathrm{~g} / \mathrm{m}^{2} / 86 \mathrm{~cm} \\ \text { Fall } & =1901 \mathrm{~g} / \mathrm{m}^{2} / 86 \mathrm{~cm} \\ \text { Winter } & =1755 \mathrm{~g} / \mathrm{m}^{2} / 86 \mathrm{~cm} \end{aligned}$ | $80 \%(0-25 \mathrm{~cm})$ <br> Root turnover every 4 years. |
| Nilsson (1970) | Smaland, South Sweden Hay Meadow | $\begin{aligned} & \text { Peak }=1700 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm} \\ & \text { Low }=900 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm} \\ & \text { Peak }=1950 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm} \end{aligned}$ | $\begin{array}{ll} 77-82 \% & (0-10 \mathrm{~cm}) \\ 97 \% & (0-72 \mathrm{~cm}) \end{array}$ <br> 94\% of the organic matter in the hay meadow consisted of humus. |
|  | Wet Site | $\text { Low }=940 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm}$ | A thorough study of a natural system. |
| Andersson (1970) | Lund, Sweden | $\begin{aligned} \text { Aerial } & =470 \mathrm{~g} / \mathrm{m}^{2} \\ \text { Roots } & =1300 \mathrm{~g} / \mathrm{m}^{2} / 50 \mathrm{~cm} \\ \text { Litter } & =240 \mathrm{~g} / \mathrm{m}^{2} \\ \text { Humus } & =30405 \mathrm{~g} / \mathrm{m}^{2} / 50 \mathrm{~cm} \\ \text { Total } & =32405 \mathrm{~g} / \mathrm{m}^{2} \\ \text { Dry } & \text { weight } \end{aligned}$ | Ratio of aboveground to belowground organic matter $=1 / 49$. |
| Weaver (1961) | Lincoln, Nebraska |  |  |
|  | Stipa spartea <br> Andropogon scoparius | $\begin{aligned} & 605 \mathrm{~g} / \mathrm{m}^{2} / 31 \mathrm{~cm} \\ & 986 \mathrm{~g} / \mathrm{m}^{2} / 31 \mathrm{~cm} \end{aligned}$ |  |
|  <br> Koelling (1967) | Columbia, Missouri <br> Tallgrass prairie | The root system contributed ca. $469 \mathrm{~g} / \mathrm{m}^{2}$ of the total net productivity during 1962. | 1962 roots had ca. $2.18 \times 10^{6} \mathrm{cal} / \mathrm{m}^{2}$ energy. <br> Turnover of roots every 4 years. |

Table 2. (continued)

| Location \& Ma jor <br> Citation | Vegetation Represented | Amounts Present |
| :--- | :--- | :--- |

notation which will in turn be interpreted to applicable conclusions for the real world.

Models are a means of studying complex phenomena (Forrester 1964). It is quite conceivable to have word, picture or box and arrow type of models, any of which could be developed further into mathematical expressions. Most mathematical models of dynamic systems are either of the difference or differential equation type.

Van Dyne (1969) and Watt (1968) suggest the use of models as a tool to better understand the entire ecosystem. Indeed, if such a large undertaking is accomplished it will have to be done with the use of some simplifying abstraction.

The use of models in predicting root mass changes or in fitting root data is quite limited. Bledsoe and Jameson (1969) discuss plant growth in a mathematical equation and root material was one particular variable considered. Both a constant and a varying coefficient model were used by Kelley, et al. (1969) to represent actual collected root biomass data. It was found that the best fit was obtained by the varying coefficient model.

## Description of study site

The study area is located on the Pawnee Site, US-IBP Grassland Biome. ${ }^{1}$ Study plots are located in Weld County, Colorado, 40 miles N.E. of Fort Collins in Section 15 and 23, Township 10N, Range 66 W .

The Pawnee Site was established in 1968 to serve as the Intensive Site for the US-IBP Grassland Biome. Sections 15 and 23 were designated for study purposes of all major trophic levels in a shortgrass ecosystem. A further description and past history of the Pawnee Site and adjacent areas is given by Jameson and Bement (1969). A complete soils map of sections 15 and 23 is presented in Appendix 1.

Four different grazing intensities were used in this study. These treatments were initiated in 1939 and have been maintained to the present time (Jameson and Bement 1969). The four different treatments and their location are given in Table 3.

Hydrologic studies required establishment of 0.5 ha microwatersheds to be established. Eight microwatersheds were
${ }^{1}$ The Pawnee Site is located on the Central Plains Experimental Range (Agricultural Research Service, USDA) and adjacent areas of the Pawnee National Grassland (Forest Service, USDA).
constructed to represent two replications of each treatment as outlined above (Smith and Striffler 1969). All eight microwatersheds were located on sandy-loam soils of the Ascalon Series. ${ }^{2}$

Table 3. Location of grazing treatments used in the primary producer studies on the Pawnee Site during 1969 and 1970.

| Treatment <br> Number | Replicate | Type of <br> grazing | Macroplot <br> Number | Location |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 1 | Ungrazed | 2 | $23 \mathrm{E}^{*}$ |
| 1 | 2 | Light | 8 | $15 \mathrm{~W}^{*}$ |
| 2 | 1 | $"$ | 4 | 23 W |
| 2 | 2 | Moderate | 5 | 23 W |
| 3 | 1 | $"$ | 6 | 15 E |
| 3 | 2 | Heavy | 7 | 15 E |
| 4 | 1 | 1 | 1 | 23 E |
| 4 | 2 |  | 23 E |  |

## * Exclosure

Complete growing season precipitation values for the study area are given by Smith (1971). Average precipitation and temperature values for 1969 and 1970 are presented in Figs. 1, 2, 3, and 4.

The Ascalon soil series has a uniform vegetation cover. Major species are blue grama, Bouteloua gracilis; red threeawn, Aristida longiseta; buffalograss, Buchloe dactyloides; western wheatgrass, Agropyron smithii; sun sedge, Carex heliophila; fringed sagewort, Artemisia frigida; scarlet guara, Gaura coccinea; broom snakeweed,

[^0]

Figure 1. Monthly precipitation, Central Plains Experimental Range (CPER), 1969.

CPER 30 year mean
Pawnee Site 1970


Figure 2. Monthly precipitation, Pawnee Site, 1970
(Striffler 1971).
----- Maximum Air Temperature - CPER (degrees F)
—— Minimum Air Temperature - CPER (degrees F)


Figure 3. Maximum and minimum air temperatures for 1969, recorded at Central Plains Experimental Range (CPER) weather station.

---- Maximum Air Temperature - CPER (degrees F)<br>———Minimum Air Temperature - CPER (degrees F)



Figure 4. Maximum and minimum air temperatures for 1970 , recorded at Central Plains Experimental Range (CPER) weather station.

Gutierrezia sarothrae; evening-primrose, Oenothera coronopifolia; plains pricklypear, Opuntia polyacantha; scarlet globemallow, Sphaeralcea coccinea; and slimflower scurfpea, Psoralea tenuiflora. Sample herbarium specimens are filed at the Pawnee Site Headquarters, Nunn, Colorado, and voucher specimens are at the CSU Herbarium in Fort Collins, Colorado. A complete plant list is given by Jameson and Bement (1969).

Macroplots were established adjacent to each of the microwatersheds (example, Fig. 5). These plots were selected to be representative of vegetation found within the microwatersheds. All primary production work was initiated within or adjacent to these macroplots. The terms macroplots and watersheds will be considered to be synonymous.

## General sampling scheme

In order to accomplish the objectives of this study it was necessary to have a general sampling procedure (Fig. 6). Essentially the 1969 sampling period was considered as a pilot study to get an efficient sampling scheme worked out for the 1970 and later seasons.

To better understand the workings of the primary producer section of the shortgrass ecosystem it was necessary to obtain good estimates of the root mass. From this data production figures could


## TOTAL CROWN MASS



Figure 6. Flow diagram of field and laboratory sampling procedures for 1969.
be obtained and, therefore, a most important compartment of the primary producer would be better understood.

Root measurements were conducted in conjunction with the aboveground vegetative sampling (Uresk 1971) and plots clipped for aerial samples were also sampled for roots. Besides root data, other variables were sampled, i.e. crown mass, total organic matter and roots for chemical analysis; thus, the primary producer was thoroughly sampled.

## Specific sampling methods (1969)

In order to determine root mass, soil cores were obtained using a hydraulic corer which was mounted on the back of a pickup truck. Because the motor heat from the truck scorched and the tires broke the vegetation the sampling was limited to the peripheral areas of the macroplot (see Fig. 5 dotted areas).

Soil cores were taken in $0.25 \mathrm{~m}^{2}$ plots that had been clipped for aboveground standing crop measurements (Uresk 1971). Four clipped plots were utilized for root samples during the eight sampling periods for summer 1969 (May 24 - September 10).

The ranked-set method was utilized in determining the plots to be sampled for root mass (Halls and Dell 1966). The two plots at either end of the macroplot were ranked as to high and low amounts of aboveground vegetation. If the high production plot was selected at one end, the low production plot was used on the opposite end. Thus,
only two of the four plots were used to determine root mass. All four plots were used to determine crown mass and organic matter.

In determination of root mass a 7.62 cm diameter core was used to a 40 cm depth and a 2.54 cm diameter core was used to continue to a depth of 80 cm . It was assumed that at least $95 \%$ of the roots would be sampled by going to a depth of 80 cm (Weaver 1958; Shantz 1911).

The total 80 cm core was divided into 5 sections of 10 and 20 cm length as outlined in Fig. 6. The core sections were placed in paper sacks and properly marked with the necessary identifying information.

The samples were transported to the headquarters building where the cores were washed to extract the roots. Generally, root washing was done the same day as the cores were collected to prevent drying of cores prior to washing.

The cores were soaked in pails between 15-30 minutes and then the mixture was poured through a 32 mesh screen. It was assumed that less than $1 \%$ of the root mass was being lost. Gist and Smith (1948) stated that some roots were lost through a 20 mesh screen and they assumed that a similar proportion was lost from all samples. In 1946a (Weaver and Zink) reported a small fraction of $1 \%$ lost via washing of intact root systems.

All attempts were made to get the roots as clean as possible, however, even after a clean water "rinse" they were still not
absolutely clean. To reduce the errors from adhering soil particles the root mass was converted to an ash-free basis. Therefore, after being oven-dried for 48 hrs at $105^{\circ} \mathrm{C}$ they were weighed, ashed at $610^{\circ} \mathrm{C}$ for 8 hrs and then reweighed. The underground material was expressed on an ash-free basis and the values were converted to grams per square meter. A sample of the data sheets used is presented in Fig. 7.

Four organic matter samples per macroplot were taken using a $2.54-80 \mathrm{~cm}$ core. This core was subdivided into sections in the same manner as the root sample cores (Fig. 6). A 1 cm horizontal section of soil was taken from the center of each subdivision, oven-dried at $105^{\circ} \mathrm{C}$ for 48 hrs , and weighed, ashed at $610^{\circ} \mathrm{C}$ for 8 hrs , and reweighed. This organic matter was expressed on a grams per meter square basis. The remainder of the cores were combined by depth for each macroplot, washed and dried at $105^{\circ} \mathrm{C}$ for 48 hrs and saved for future chemical analysis.

The samples for chemical analysis were stored until June 1971. At this time the $0-10 \mathrm{~cm}$ increments were combined by treatment and the lower depths were all combined by sampling dates. The combined material was ground in a Wiley Mill through a 20 mesh screen.

Samples of crown material, i.e., the vegetation above the roots which was not removed by clipping, was obtained by coring. The crown material, approximately 1 cm thick, was oven-dried at $105^{\circ} \mathrm{C}$

ROOT PRODUCTION
DATE
$\qquad$
$\qquad$

| Depth (cm) | Weights <br> I | $\xrightarrow{\text { cRu }}$ | $\begin{gathered} \text { Weights } \\ 2 \end{gathered}$ | CRU | Weights <br> 1 | CRU | $\begin{gathered} \text { Weights } \\ 2 \end{gathered}$ | crum |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 0-10 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
| 10-20 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
| 20-40 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
| 40-60 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
| 60-80 |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |

Figure 7. Example of data sheet used during the 1969 sampling period for recording root biomass values.
for 48 hrs and ashed at $610^{\circ} \mathrm{C}$. A portion of the crown mass measurements were obtained from the cores used for root samples.

During the last sampling period detailed time measurements of the various sampling steps in Fig. 6 were recorded (Table 4). Values are given by depth for the various steps involved. Different time values for weighing and ashing the various depths are due to the varying volume and fineness of roots.

Table 4. Average time cost in man minutes for field and laboratory steps necessary to obtain one core sample. (Based upon times taken during the 9 September 1969 sampling period.)

| FIELD |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Travel Between Plots 2.7 min | Anchoring Truck 5.5 min |  |  |  | Coring$3.0 \mathrm{~min}$ |  |
| LABORATORY |  |  |  |  |  |  |
| Root level (cm) | 0-10 | 10-20 | 20-40 | 40-60 | 60-80 | Total |
| Washing (min) | 18.5 | 20.3 | 22.7 | 14.2 | 11.5 | 87.2 |
| Weighing and Handling (min) | 2.9 | 2.4 | 2.4 | 1.7 | 1.7 | 11.1 |

Root estimates were also obtained in November and December 1969. Samples were taken using a small core within the large one just as was done in the summer 1969. Number of samples were increased and taken within the macroplot as opposed to the peripheral area. Four clipped plots were utilized and three cores within each of the clipped plots were obtained. This was three times the number of cores procured during the summer sampling period. Crown
material, organic matter, and chemical samples were not collected during this sampling period.

Specific sampling methods (1970)
Belowground material was sampled eleven times during the 1970 growing season at approximately two week intervals. Modifications of the 1969 sampling was implemented to facilitate rapid and efficient collection of roots.

Observation of 1969 data indicated that approximately $60 \%$ of the root mass occurred in the upper 10 cm and that variability of the lower depths was slight compared to the $0-10 \mathrm{~cm}$ increment. Therefore, it was decided to sample the $0-10 \mathrm{~cm}$ depth with greater accuracy (more samples per plot) and more often during the growing season. The lower depths were sampled only twice during the growing season.

A rapid, $T$ shaped sampler was designed that would take 10 cm cores with a diameter of 7.5 cm (Fig. 8). With the use of this corer, a sample could be obtained in approximately 30 seconds.

Root samples were collected on eight $0.25 \mathrm{~m}^{2}$ plots, which were located randomly within the macroplot and had been clipped to determine the amount of herbage (Uresk 1971), thus the actual aboveground standing crop was known for the sampled area.

During two sampling periods (July 2 and August 18) deep cores were taken to a depth of 80 cm . These were collected to obtain a

Figure 8. Root core sampler used for rapid collection of samples during the 1970 growing season.

more accurate estimate of the distribution of the root mass. To collect the deep cores a pneumatic hammer ${ }^{3}$ was adapted to fit a 5 cm diameter corer which was a meter in length. These cores were divided into 5 sections as outlined in Fig. 9.

The motor driven pneumatic hammer was used to collect cores within the macroplot with minimal destruction to the vegetation. A handy-man jack was modified to aid in extracting the cores from the ground (Fig. 10).

All core samples for 1970 were handled the same irrespective of how they were collected. The samples were placed in paper sacks and given an identification number. The collected cores were then taken to the IBP Grassland Biome Field Laboratory where the roots were separated from the soil.

The 1969 washing process was employed in 1970. No dispersing agents were used and the cores were washed the same day as collected or shortly thereafter. The root mass was collected on a 32 mesh ( 500 micron) screen and ovendried at $105^{\circ} \mathrm{C}$ for 48 hours. This material was weighed, ashed at $610^{\circ} \mathrm{C}$ and reweighed. Root mass was expressed on an ash-free basis to correct for any adhering soil particles and the data were converted to grams per square meter.

[^1]

Figure 9. Flow diagram of field and laboratory sampling procedures for 1970.

Figure 10. Adapted handy-man jack used in removing an 80 cm core from the ground.


The root mass values were not corrected for the ash content of the roots.

Data manipulation and compilation
Because of the voluminous amount of data collected and the inherent chance for error, it was necessary to develop a rapid, computer compatible data handling system. Examples of the three data sheets are given in Fig. 11. All root data for 1969 were converted to this form for uniform presentation.

The basic premise of the data acquisition system was that a single number was easier to keep track of than a detailed description and therefore gave less chance of error. Data sheet no. 3 was used in the field and each sample was given a number and pertinent identification information. Through the washing and ashing steps the sample was identified only by this number. Data sheets one and two were used in the laboratory for recording weights before ashing (no. 1) and after ashing (no. 2).

It was found that the various procedures were easily explained to technicians and a minimal amount of data was lost. The threesheet system was particularily useful when more than 200 samples were being processed because of the time that would be required to locate particular samples on a single data sheet, but would be unnecessary for fewer samples.


[^2]A computer program ( $\mathrm{R} \varnothing \varnothing$ TAS) was written which is a sort and condensation program. Three arrays are used to store data for manipulation. The primary purpose of the program is to take the identification information contained on card 3 and sort through cards 1 and 2 to find the rest of the data for a particular sample. A complete listing of $R \varnothing \varnothing$ TAS is presented in Appendix 2.

RФФTAS is adaptable for use on similar types of data. For example, variations of this program were used in calculations of crown material and for presentation of organic matter values.

After the initial weight difference is determined, the program calculates the grams of root material on a square meter basis. These values are then arranged in tables by macroplot and include such pertinent information as; site (PAWNEE, abbreviated PAW), date (year-month-day), watershed number (1-8), microplot number ( $0-100$ ), core number within plot, and weight ( $\mathrm{g} / \mathrm{m}^{2} / \mathrm{cm}$-depth) for various increments when applicable. Where data are missing, average values are automatically substituted. Means and standard errors are calculated for each macroplot.

The program also presents all data, by treatments, summarized into tables for each date. These particular tables contain the following:

1. Number of plots contained in each treatment mean.
2. Mean root weight by depth (where applicable) and total means.
3. Standard errors for each mean.

All data (sorted, tabular and FФRTRAN usable) are preserved in the central IBP data bank under file number A2 U003B.

## RESULTS

## Treatment effects

Individual samples for root measurements were taken on 21 sampling dates between May 24, 1969, and September 12, 1970. All data are presented in tabular form via RФФTAS; a sample of the various tables is contained in Appendix 3.

No pattern was observed for the mean root weights for the various macroplots. In the summer of 1969 weights ranged from a low of $793 \mathrm{~g} / \mathrm{m}^{2} / 80 \mathrm{~cm}$ on July 31 to a high of $2068 \mathrm{~g} / \mathrm{m}^{2} / 80 \mathrm{~cm}$ on August 27. Generally, a decrease in the amount of root material occurred between the November and the December sampling period. This decrease is approximately $400 \mathrm{~g} / \mathrm{m}^{2} / 80 \mathrm{~cm}$. Maximum and minimum amounts of total root mass for the various treatments occurred on different dates. The 1970 data which includes both crowns and roots also appears to vary erratically. The high and low both occurred on July 2 with $2768 \mathrm{~g} / \mathrm{m}^{2} / 80 \mathrm{~cm}$ measured in macroplot 6 and $1753 \mathrm{~g} / \mathrm{m}^{2} / 80 \mathrm{~cm}$ in macroplot 5 .

Date summaries for the grazing treatments are presented in Table 5. The treatment means and standard errors are useful for comparative purposes. In 1969 all treatments were found to reach the minimum value on July 31, except for the moderate grazed

Table 5. Grazing treatment means and atandard errors of root biomest for $\mathbf{2 1}$ sampling dates.

CIUAAFY TADIF OF AIL WATFOCMEDSIWTSI DY TGFATMFNT ITRTI









GITF = DAW OATF =69071

|  |  |  |  | ----- | PFR | ORR CM | DEPTHE | - | 6/1950 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | $\cdots$ | 4 | MEAN NF 4 DLOTE STANDARO ERROR | $\begin{array}{r} 47.74 \\ 7.30 \end{array}$ | $\begin{array}{r} 14.07 \\ .67 \end{array}$ | $7.3 n$ .35 | 4.17 .61 | 2.95 .53 | $\begin{array}{r} 1127.51 \\ 22.7 \end{array}$ |
| 2 | n | 1 | uFAN OF 4 DLITS GTh*napn ERDOD | $\begin{array}{r} 64.75 \\ \times .71 \end{array}$ | $\begin{array}{r} 16.27 \\ 1.47 \end{array}$ | $\begin{array}{r} 10.0 \mathrm{~A} \\ .50 \end{array}$ | 4.72 .35 | $\begin{aligned} & 5.63 \\ & 1.34 \end{aligned}$ | $\begin{array}{r} 1557.93 \\ 92.06 \end{array}$ |
| 4 | 5 | 7 | *EAR DF 4 Plats STANABRD ERWNO | $\begin{array}{r} 51.85 \\ 4.31 \end{array}$ | $\begin{array}{r} 18.72 \\ 1.50 \end{array}$ | $\begin{array}{r} 8.09 \\ .45 \end{array}$ | 2.85 .15 | $\begin{array}{r} 1.74 \\ .15 \end{array}$ | $\begin{array}{r} 1190.09 \\ 74.78 \end{array}$ |
| $A$ | 7 | 7 | MEAN OF 4 DIOT CTANOAPD ERQOP | $\begin{array}{r} 4 R, 63 \\ S, K 0 \end{array}$ | $\begin{array}{r} 13.9 \% \\ 1.10 \end{array}$ | $\begin{array}{r} 9.10 \\ .78 \end{array}$ | $\begin{array}{r} 5.05 \\ .66 \end{array}$ | $\begin{array}{r} 3.02 \\ .20 \end{array}$ | $\begin{array}{r} 1211.25 \\ 108.44 \end{array}$ |


SITF = PAW NATE $\$ 890731$

WTS AND WTS = TRI $\quad 0-10 \mathrm{CM} 10-20 \mathrm{CM} 20-40 \mathrm{CM} 40-60 \mathrm{~cm} 60-80 \mathrm{CM} \quad \mathrm{TOTAL}$



Table 5 (Continued).
SUMMAOY TAALE OF ALL WATFPSAENS(WTS) DV TREATMFNT (TRT,





STTF = PAW DATF $=691104$





Table 5 (Continued).

 STTF = UAW OATF=7nの\#??

 STTF PAW OATE =700619

| 1 | 3 | 4 |  | 6/4s\%/rm | 6/4 |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | MfAN OF 14 OITC | 119.09 | 2361.81 |
|  |  |  | STANDAOn EPRop | 3.92 | 35.49 |
| 7 | A | 1 | WFAH OF is Plote | 120.19 | 2375.45 |
|  |  |  | STANOARD ERROD | 1.7 .3 | 21.61 |
| 4 | 5 | $?$ | 4FAN OF 14 PInte | 46.94 | 2083.71 |
|  |  |  | STAMnaOD ERROA | 7.07 | 25.97 |
| 6 | 7 | 3 | WEAN OF IS PLOTS | 119.08 | 2349.24 |
|  |  |  | STANDARO FPODR | 7.08 | 7K. 05 |



|  |  | STTE = PAW natf s700717 |
| :---: | :---: | :---: |
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|  |  |  |


| 1 | 3 | 4 | wFAN NF it olinte ETMannon fapop | r/uSn/ru | G/uco |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | $\begin{array}{r} 104.79 \\ 1.52 \end{array}$ | $\begin{array}{r} 2208.90 \\ 10.97 \end{array}$ |
| $?$ | A | 1 | vfin of is Dinta | 127.75 | 2474.04 |
|  | - |  | CTANTACD Fpond | 1.47 | 77.41 |
| 4 | 5 | $?$ | MFAN OF im Piotc | 117.10 | 2337.01 |
|  |  |  | STGMOADOn coond | 1.47 | 17.77 |
| 6 | 7 | 7 | MFA* OF if PInt | 130.41 | 2503.31 |
|  |  |  | Clanliad foonp | 3.79 | 29.85 |

## Table 5 (Continued).

GIMMARY TARIF OF ALI MATECGWFOS(WTS) FY TOFATMFNTITRT)
 STTF = OAW NATE =7nn779
WTS AND WTS = TOT O-10 CM TOTA!.


| 1 | 3 | 4 |  | rıMSN/C:A | G/MSO |
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|  |  |  | - 4 FAN ОF IK DI OTS | 112.76 | 2295.24 |
|  |  |  | CTA:InaOl FODOO | 2.00 | 75.02 |
| $?$ | R | 1 | UFAツ OF 14 - OTE | 114.27 | 2326.64 |
|  |  |  | <TAMDADN FDROD | $>.17$ | 27.1? |
| 4 | 5 | 2 | mean of 14. Ointe | 172.21 | 2150.45 |
|  |  |  | STAPinadr: FuOnc | 1.70 | 71.21 |
| 6 | 7 | 3 | UFAN OF 1G PLOTV | 115.00 | 2310.75 |
|  |  |  | GTAVnauj founu | 2.31 | 20.9n |


SITF = DAW NATE $=70041 ?$
WTS AND WTS = TOT O-1م CM TOTAL


| 1 | 3 | 4 |
| :--- | :--- | :--- |
| 2 | 9 | 1 |
| 4 | 5 | 2 |
| 6 | 7 | 3 |


| MFAN OF IA DİOTC GTANMARII FRPOR | $\begin{array}{r} 105.51 \\ 1.64 \end{array}$ | $\begin{array}{r} 2204.55 \\ 20.53 \end{array}$ |
| :---: | :---: | :---: |
| -AFAN OF $1 / 4$ PLOTS | 114.7 ? | 2307.26 |
| STAMNADO FOQOD | 1.35 | 16.87 |
| MFAN OF 14 PL_OTS | 107.90 | 2271.91 |
| STANDADN FDUOD | 1.71 | 21.31 |
| MFAN OF 15 PI_OTS | 44.62 | 2055.94 |
| STANDAOS FRROP | 1.53 | 19.0R |


SITE = DAW DATE =70091?
WTS AND WTS = TPT
0-10 CM
TOTAL

G/ASN/CM G/MSO

| 1 | 3 | 4 | MFAN OF in pl.nts STANDAOD FROOR | $\begin{array}{r} 113.32 \\ 7.26 \end{array}$ | $\begin{array}{r} 22 R 9.67 \\ 2 R .22 \end{array}$ |
| :---: | :---: | :---: | :---: | :---: | :---: |
| $?$ | 8 | 1 | MEAN OF IS PLIOTS | 94.46 | 2054.00 |
|  |  |  | STANDARD FPROR | 1.45 | 18.07 |
| 4 | 5 | $?$ | MEAN OF IG PLOTG | 97.56 | 209?.70 |
|  |  |  | STANDARD FRROP | 1.10 | 13.80 |
| 6 | 7 | 3 | MFAN OF IA PLOTS | 110.33 | 2252.36 |
|  |  |  | STANOARD FROOR | ?. 13 | 26.67 |


treatment 3 (Table 6). It should be noted that the value for treatment 3 was only slightly larger on July 31 than on June 21.

Table 6. Maximum and minimum amount of root mass present during the 1969 growing season for four grazing treatments.

| Treatment Number |  | Root Weight |  | Date |
| :---: | :---: | :---: | :---: | :---: |
| 1 | Maximum | 2007 g | $\mathrm{g} / \mathrm{m}^{2} / 80 \mathrm{~cm}$ | 6/21/69 |
| 1 | Minimum | 1411 | ' | 7/31/69 |
| 2 | Maximum | 2050 | " | 9/10/69 |
| 2 | Minimum | 1226 | " | 7/31/69 |
| 3 | Maximum | 1889 | " | 9/10/69 |
| 3 | Minimum | 1350 | " | 6/21/69 |
|  |  | (1480) | " | (7/31/69) |
| 4 | Maximum | 2155 | " | 8/27/69 |
| 4 | Minimum | 1065 | " | 7/31/69 |

The data from the November sample indicates that total root mass in all treatments increased during the fall. The December sampling period shows a uniform root mass which is lower than the November period for all treatments except the heavy grazed pasture (treatment 4).

Summer 1970 root material for the $0-10 \mathrm{~cm}$ increment varied as follows: heavy grazing $884 \mathrm{~g} / \mathrm{m}^{2}$ (May 22) to $1138 \mathrm{~g} / \mathrm{m}^{2}$ (July 29); moderate grazing $916 \mathrm{~g} / \mathrm{m}^{2}$ (May 22) to $1305 \mathrm{~g} / \mathrm{m}^{2}$ (July 2 and 17); light grazing $792 \mathrm{~g} / \mathrm{m}^{2}$ (July 2 ) to $1171 \mathrm{~g} / \mathrm{m}^{2}$ (July 17 ); and no grazing $725 \mathrm{~g} / \mathrm{m}^{2}$ (July 2) to $1278 \mathrm{~g} / \mathrm{m}^{2}$ (July 17).

A marked difference in sampling error was noted by comparing the summer and winter errors. The range of standard errors of the means for the summer 1969 was $1 \%-12 \%$ with an average of $5.4 \%$, this range was reduced for the fall and winter sampling periods to $1.5 \%$ $4 \%$ with an average of $2.9 \%$. This could indicate that 1969 fluctuations were not measured very accurately, however, the standard errors reported are acceptable. The 1970 sampling period had an average of $1.3 \%$ and a range of $.5 \%-3.5 \%$. The standard errors improved for the 1970 sampling period which can be attributed to more samples taken.

Analysis of variances were carried out to test if differences existed in the individual samples of roots. A computer program, STAT02V, developed by Dixon (1970) has been converted for use on the Colorado State University computer.

Because of the design of the experiment (four treatments with two replications each) statistical analysis was easily accomplished via the factorial design program (STAT02V). For this program to work all factors have to be balanced; a five increment sample cannot be tested against a single increment sample.

The data were segregated into three main periods (Summer 1969, Fall-Winter 1969, and Summer 1970) allowing for utilization of STAT02V. Generally, during these particular periods balanced samples were collected. All individual samples could not be used in STAT02V because the limits of the program were exceeded.

Individual samples for the two 1969 data sets were utilized to detect any treatment differences. These two periods were balanced and small enough to use STAT02V. The six main effects considered in this run were dates, treatments, depth increments, watersheds within treatments, plots within watersheds-treatments, and cores within watersheds-treatments-plots. These particular components plus all possible interactions were considered for summer 1969 (Table 7) and fall-winter 1969 (Table 8).

An observation of these two analysis of variance tables indicates significance (. $05 \%$ level) for only dates, depth increments, and dateincrement interaction. Because of these results it did not appear necessary to test the 1970 data using individual observations.

## Vertical distribution of roots

Observation of treatment means (Table 5) shows the vertical distribution of underground plant material. Sixty percent of the root weight was in the upper 10 cm , and this proportion held across treatments, sampling dates and years.

During the 1969 summer sampling period crown material was separated from the $0-10 \mathrm{~cm}$ increment. Crown mass contributed $15 \%$ of the total material. This percentage should hold for the other sampling periods where crowns and roots were not separated.

Table 7. Analysis of variance table containing six main effects and all possible combinations which were run on individual samples for the 1969 summer sampling period.

| Source | D.F. | S.S. | M.S. | F |
| :---: | :---: | :---: | :---: | :---: |
| D | 7 | 5765.0 | 823.6 | 4.587 (7,28) ** |
| T | 3 | 152.2 | 50.7 | . 139 (3,4) N.S. |
| I | 4 | 525837.8 | 131459.5 | $1158.473(4,16)$ ** |
| TI | 12 | 1255.2 | 104.6 | . $922(12,16)$ N.S. |
| W ( T) | 4 | 1464.4 | 366.1 | $1.608(4,8)$ N.S. |
| $\mathrm{P}(\mathrm{WT}$ ) | 8 | 1821.5 | 227.7 | $1.677(8,16) \quad$ N.S. |
| $C$ (PWT) | 16 | 2172.6 | 135.8 | $1.826(16.448)$ * |
| DT | 21 | 4724.4 | 225.0 | $1.253(21,28)$ N.S. |
| DI | 28 | 9422.8 | 336.5 | $3.013(28,112)$ ** |
| DW (T) | 28 | 5017.0 | 179.5 | . $876(28,56)$ N.S. |
| $D \cdot P(W T)$ | 56 | 11470.2 | 204.8 | $1.863(56,112)$ ** |
| D. C (PWT) | 112 | 12312.0 | 109.9 | $1.478(112,448)$ ** |
| DIT | 84 | 9731.4 | 115.9 | $1.037(84,112)$ N.S. |
| I- W ( T ) | 16 | 1815.6 | 113.5 | . $970(16,32) \quad$ N.S. |
| $\mathrm{I} \cdot \mathrm{P}(\mathrm{WT}$ ) | 32 | 3744.4 | 117.0 | $1.086(32,64) \quad$ N.S. |
| I-C (PWT) | 64 | 6898.2 | 107.8 | $1.449(64,448)$ * |
| IDW ( T ) | 112 | 12511.6 | 111.7 | . $830(112,224) \mathrm{N} . \mathrm{S}$. |
| IDP(WT) | 224 | 30145.3 | 134.6 | $1.809(224,448)$ ** |
| IDC (PWT) | 448 | 33320.0 | 74.4 |  |

where; $D=$ Dates, $T=$ Treatments, $W=$ Watershed, $P=$ Plots, $C=$ Core, and $I=$ Increments.

* = Significant at 5\% level
** $=$ Significant at $1 \%$ level

Table 8. Analysis of variance table containing six main effects and all possible combinations which were run on individual samples for the 1969 fall-winter sampling period.

| Source | D.F. | S.S. | M.S. | F |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| D | 1 | 4082.3 | 4082.3 | 12. $589(1,4)$ | * |
| T | 3 | 547.1 | 182.4 | . $232(3,4)$ | N.S. |
| I | 4 | 607113.9 | 151778.5 | $313.619(4,16)$ | ** |
| TI | 12 | 2228.5 | 185.7 | . $384(12,16$ ) | N.S. |
| W ( T ) | 4 | 3147.2 | 786.8 | $2.268(4,24)$ | N.S. |
| P(WT) | 24 | 8326.2 | 346.9 | $1.652(24,64)$ | N.S. |
| C(PWT) | 64 | 13440.9 | 210.0 | $1.648(64,280)$ | ** |
| DT | 3 | 892.4 | 297.5 | . $917(3,4)$ | N.S. |
| DI | 4 | 9060.9 | 2265.2 | $9.193(4,16)$ | ** |
| DW (T) | 4 | 1297.1 | 324.3 | $1.117(4,24)$ | N.S. |
| D.P(WT) | 24 | 6967.6 | 290.3 | $1.719(24,64)$ | * |
| D.C (PWT) | 64 | 10806.4 | 168.9 | $1.325(64,280)$ | N.S. |
| DIT | 12 | 2269.1 | 189.1 | . $767(12,16$ ) | N.S. |
| $\mathrm{I} \cdot \mathrm{W}(\mathrm{T})$ | 16 | 7743.3 | 484.0 | $1.747(16,96)$ | * |
| I-P(WT) | 96 | 26591.6 | 277.0 | $1.411(96,232)$ | * |
| I•C(PWT) | 232 | 45561.7 | 196.4 | $1.541(232,280)$ | ** |
| IDW ( T ) | 16 | 3942.6 | 246.4 | . $909(16,96)$ | N.S. |
| IDP ( WT) | 96 | 26035.6 | 271.2 | $2.129(96,280)$ | ** |
| IDC (PWT) | 280 | 35677.0 | 127.4 |  |  |

where; $D=$ Dates, $T=$ Treatments, $W=$ Watersheds, $P=$ Plots, $C=$ Cores, and $I=$ Increments.

* $=$ Significant at $5 \%$ level
** $=$ Significant at $1 \%$ level

Approximately $73 \%$ of the roots were present in the upper 20 cm of the soil profile. The following increments contributed these percentages:

$$
\begin{aligned}
& 20-40 \mathrm{~cm}=14 \% \\
& 40-60 \mathrm{~cm}=8 \% \\
& 60-80 \mathrm{~cm}=5 \%
\end{aligned}
$$

Where depth increments were sampled ( 12 dates) the data were fit to a negative exponential in an attempt to determine if the depth distribution varied by treatment. This regression equation takes the form:

$$
Y=a+b e^{-c x}
$$

where;

$$
\begin{aligned}
a= & \text { determines the asymptote (the distance the parallel } \\
& \text { portion of the curve is from the } x \text {-axis). } \\
b= & Y \text { intercept }-a . \\
c= & \text { controls the curvature of the line. }
\end{aligned}
$$

Treatment means for dates by depths were fit to this equation with the aid of a computer program (TAYLN). ${ }^{4}$ The iterative calculations for solving this equation can be found in Williams (1959).

Values were obtained for the three parameters ( $a, b$, and $c$ ). First, a factorial analysis of variance of parameters a and bindicated that no treatment differences existed (Table 9). This is comparable to an analysis of total root weight.

[^3]Table 9. ANOV table for parameters (A + B) obtained from a negative exponential fit.

| Source | D.F. | S.S. | M.S. | F |
| :--- | ---: | ---: | ---: | ---: |
| Dates | 11 | 91283.8 | 8298.5 | .806 |
| Treatments | 3 | 12177.5 | 4059.2 | .394 |
| N.S. |  |  |  |  |
| Error | 33 | 339754.4 | 10295.6 |  |
| Total | 47 | 443215.7 |  |  |

N.S. = Non-significant

The next step was to do analysis of variance of the c parameter, which controls the curvature of the line. This is essentially a test of the depth distribution. Various combinations of the data were tested, with the following tests conducted:

1. Summer 1969 crowns present (Table 10)
2. Summer 1969 crowns absent (Table 11)
3. Summer and Fall $1969+$ two dates in 1970 (Table 12).

For comparative purposes the various negative exponential equations were plotted. Eight date means for 1969 summer sampling period were plotted, the data had crown meterial absent from the $0-10 \mathrm{~cm}$ increment. Three equations for the more diverse situations during the summer 1969 are presented (Fig. 12). Individual graphs are in Appendix 4.

To further examine the date-increment interaction separate analysis were done on each depth increment with the use of watershed means. These means were used because it was shown earlier that


Table 10. ANOV of depth distribution parameter (c) obtained from a negative exponential fit run on 8 dates (1969) with crowns present.

| Source | D.F. | S.S. | M.S. | F |
| :--- | :---: | :---: | :---: | :---: |
| Dates | 7 | .00369 | .00053 | 1.3589 N.S. |
| Treatments | 3 | .00297 | .00099 | 2.5385 N.S. |
| Error | 21 | .00827 | .00039 |  |
| Total | 31 | .01494 |  |  |

Table l1. ANOV of depth distribution parameter (c) obtained from a negative exponential fit run on 8 dates (1969) without crowns.

| Source | D.F. | S.S. | M.S. | F |
| :--- | :---: | :---: | :---: | :---: |
| Dates | 7 | .00358 | .00051 | 1.2143 N.S. |
| Treatments | 3 | .00276 | .00092 | $2.1905 \mathrm{~N} . \mathrm{S}$. |
| Error | 21 | .00873 | .00042 |  |
| Total | 31 | .01507 |  |  |

Table 12. ANOV of depth distribution parameter (c) obtained from a negative exponential fit run on 12 dates (1969 and 1970) with crowns present.

| Source | D.F. | S.S. | M.S. | F |
| :--- | :---: | :---: | :---: | :---: |
| Dates | 11 | .01000 | .00091 | 2.022 N.S. |
| Treatments | 3 | .00316 | .00105 | 2.333 N.S. |
| Error | 33 | .01483 | .00045 |  |
| Total | 47 | .02799 |  |  |

no differences existed when individual sample values were used.

Table 13 shows which tests were made and the results of same.

Table 13. Summary of ANOV's run on various depth increments using watershed means. Complete ANOV tables are in Appendix 5.

| Data | F Value <br> (Dates) | Results |
| :---: | :---: | :---: |
| Crowns | .873 | N.S. |
| $0-10 \mathrm{~cm}$ depth + crowns | 2.975 | $*$ |
| $0-10$ | $\prime \prime$ | $"$ |
| $10-20$ | $"$ | $" 1$ |
| $20-40$ | $"$ | $" 1$ |

[^4]The results of these analyses indicate that the major reason for significant differences between dates was change in the weight of the $0-10 \mathrm{~cm}$ increment. Crowns had essentially no change, and the lower depth has less change than the $0-10 \mathrm{~cm}$ increment.

## Seasonal trends

All twenty-one dates were plotted using treatment means and numbering the dates from 1 (January 1, 1969) - 730 (December 31, 1970). SNФФP, a computer program for two dimensional plotting was used (Frayer 1968).

First, plottings were done with crowns added into the 0.10 cm increment and these plots are in Fig. 13-16. After observing the erratic fluctuations in these particular figures it appeared desirable to subtract the crown weights. All data were again plotted with crowns deleted from the first 8 sampling periods of 1969 (Fig. 17-20). Data of the summer of 1969, when plotted without crowns presented a general curve which appears to have some biological interpretation. Because there are no significant differences among treatments or watersheds an average value across treatments was used for each of the eight dates. These data points were plotted (Fig. 21).
 TWO-OIMENS IONAL GAAPH




Figure 14. Root woights $(0-10 \mathrm{~cm})$ for light graxing treatment plotted for 21 eampling pariod.--crown* present.






OOT WEIGHT (O-10 CM) FOR MODERATE GRAZING FOR 21 DATES


[^5]Figure 19. Root weight ( $0-10 \mathrm{~cm}$ ) for moderate grasing treatment ploted for 21 hampling periode.-crowne aboent.

JOA NIMARER ©
ROOT WEIGHF (0-10 (m) TOR heavy grazing for 21 dates



Figure 21. Raw data for summer 1969 representing root fluctuations.

## DISCUSSION

## Effects of herbivores on root mass

A main objective of this project was to measure the effects large herbivores have upon the roots in a shortgrass ecosystem. A simple ANOV run on individual samples using a factorial design showed no treatment differences in the root mass. Significant differences were found only among dates, increments, and combinations of the two.

The lack of grazing treatment effect is in contrast to most results in the literature. Most grazing studies have shown decreased root mass with grazing (Schuster 1964; Lorenz and Rogler 1967; Biswell and Weaver 1933; Cook, Stoddart and Kinsinger 1958; and Jameson and Huss 1959); the only reported increase was that described by Pearson (1965). Schuster (1964) indicated the aerial portion of blue grama was reduced by heavy grazing although Lang and Barnes (1942) present contradictory results.

It is of particular interest to note that all studies of blue grama have reported decreasing root weights with grazing. It appears that some of the data is questionable, however, Lorenz and Rogler (1967) found ca. $36,000 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm}$ in a mixed grass area and Biswell and Weaver (1933) in a greenhouse experiment found a maximum
$105 \mathrm{~g} / \mathrm{m}^{2} / 61 \mathrm{~cm}$. This a wide range of values; therefore, caution should be used in making conclusive statements concerning them.

Research has shown that grass roots stop growing when the aerial portions are clipped. Crider (1955) found that these periods of no root growth occurred for periods of 6-18 days for various species. He found that roots of clipped plants weighed one-eighth as much as the roots of the unclipped plants. Clipped blue grama, for example, produced approximately $85 \%$ less root mass than unclipped blue grama.

Possible explanations for lack of treatment effects include:

1. All samples were taken on the same soil type, thus, this may be a unique feature of the Ascalon soil type.
2. The major plant species is blue grama and it has been reported as having a very dense root system (Hopkins 1953) which might be effected less by the influence of grazing animals.
3. There were no treatment differences in the aerial portion (Uresk 1971) and there may be a close correlation between the aerial and belowground compartments.
4. This phenomenon might have been peculiar for the two years sampled.
5. Inherent "feedback" mechanisms adequately compensated for any grazing effect.

## Vertical distribution of roots

On the Pawnee Site, 60 percent of the root weight occurred in the upper 10 cm of the soil profile compared to about 75 percent in the upper 20 cm . These values correspond very closely with values
observed for blue grama-buffalo grass communities by Weaver (1958), $79 \%$ in the upper 15 cm and Weaver and Zink (1946a), $80 \%$ in the upper 35 cm .

These figures show that shortgrass prairies have a shallow root system maintained by the low and erratic precipitation (Stoddart and Smith 1955). Weaver (1958) substantiates this finding by stating that blue grama and buffalo grass have a shallow root system which probably provides maximum benefit from moisture furnished by light showers. Earlier Weaver and Albertson (1943) indicated root depth corresponded to rainfall penetration.

As early as 1911 (Shantz) indicated that the shortgrass root system was limited to the upper 18 inches of the soil. Markel (1917) suggested that a superficial root system is due to soil moisture content and Weaver and Crist (1922) said the main factor was available water. Most of the roots occur in the upper levels of the soil profile (Weaver 1958 and Nilsson 1970) and decrease rapidly with depth (Dahlman and Kucera 1965). Nilsson (1970) stated that grass roots concentrate in the upper soil layers because grass plants are shallow rooters and grass roots are thicker in their proximal parts even if not functional.

It was observed in this study that the shortgrass ecosystem has a greater fraction of the vegetative mass below the soil surface than above it. Distribution of this mass follows a distribution hypothesized
by other investigators. Concentration of shortgrass roots in the upper layers of the soil can be attributed to frequent small and shallow penetrating rain showers.

Negative exponential curves were fitted to the data to show how root weights decreased by depth and the parameters of the equations were used to see if any treatment differences existed. The series of curves reflected the root weight fluctuations over the growing period. In general all curves have approximately the same asymptotes; the major difference can be seen to occur in the upper most increment. During May the $Y$-intercept of these curves is at a high point, dropping considerably during the end of July. The Y-intercept rose to a point comparable to the May value.

Analysis of variance run on the various parameters showed no significant treatment effect. Inspection of the data indicated differences in increments which were confirmed when an analysis of variance was run using data by depth increments. The major date difference was confined to the $0-10 \mathrm{~cm}$ increment and the root mass below 10 cm varied little.

## Dynamic model of seasonal variations

With crowns present (Figs. 13-16) the root mass data were very erratic. With crown weights deleted, however, the graphs at least had an observable trend during the 1969 growing season (Figs. 17-20).

These graphs show a very slight increase in roots between May and June with a marked decrease of roots occurring the last of July. Following the root decrease, there was a rapid increase of root material to a point slightly greater than the early season value of $616 \mathrm{~g} / \mathrm{m}^{2} / 10 \mathrm{~cm}$.

Four studies of grass root decomposition that were reviewed are applicable here. First, Weaver and Zink (1946b) approximated the length of life of root systems at 4 years. Weaver (1947) reported that blue grama roots lost $67 \%$ of their weight during a two year period and presumed that a majority of this mass was lost during the second growing season. Working in a tallgrass prairie Dahlman and Kucera (1965) calculated turnover rates of roots to be 4 years. Nilsson (1970) calculated a turnover rate for hay meadows to be $50 \%$ or a new root system every two years.

Weaver (1958) stated that "complete decomposition of the roots, to a condition in which no particles could be distinguished by the naked eye from the soil, required 3 to 5 years."

Quantitative measurements of roots have been discussed by various investigators and it is apparent that the fluctuations of grass roots are not the same. Nilsson (1970) working in southern Sweden found a peak belowground mass occurring at the end of June with gradual decrease till the following growing season. It was shown by Pilat (1969) that decreases in roots coincided with periods of
increased soil moisture. Kucera et al. (1967) indicated that lack of soil moisture impeded root decomposition. Dahlman and Kucera (1965) sampled only four times during the year and found peak root material occurring during the summer.

Crider (1955) stated that "the growth and rest periods of the roots alternated with growth and rest periods of the tops." Dodd and Hopkins (1958) agree that when aerial growth is occurring there is little storage in the roots and vice-versa. Clipping the aerial vegetation caused the carbohydrate content of the roots to be low for a month.

The general pattern observed by Dodd and Hopkins was an increase in root growth during June (slow aerial growth) and less root growth in July (rapid aerial growth).

The usual explanation of the mid-season dip in root weight and subsequent recovery is that stored carbohydrates are utilized for growth and that new carbohydrates are stored later in the season. Pilat (1969), however, observed that there was no evidence of any gradual accumulation of underground biomass that could be attributed to assimilate storage. This view is supported by May (1960) but is quite opposite from those given by Dodd and Hopkins (1958) and others. It is clear, however, that it is possible to make equally valid interpretations of root dynamics using concepts of growth and decomposition, without requiring a concept of storage for subsequent translocation to tops.

In order to understand variations in root material it is first necessary to recognize two major components, i.e. the total mass is composed of a dead or dying root fraction and a living or actively growing part.

A model was hypothesized that would attempt to explain these data (Fig. 21). Certain assumptions must be made in order for this model to be valid. The following ideas should be kept in mind:

1. The decomposing material is highest at the beginning of the growing season, dropping to a low value as the season progresses and only more resistant material remains. This rapid loss early in the season coincides with sufficient soil moisture (Pilat 1969).
2. New roots are minimal at the first of the season and increase to a high point later in the growing period.

With these two major points established it is possible to write an equation that behaves similarly to the variation in the root mass. Both processes should give a sigmoid curve such as the logistic curve. The decomposition rate can be represented by a decreasing logistic growth curve (Fig. 22) and root growth as an increasing logistic curve (Fig. 23) (Pielou 1969). If these two formulae are added together the following equation results:

$$
Y=\frac{a_{1} / b_{1}}{1+e^{-a_{1}\left(x-x_{1}\right)}}+\frac{a_{2} / b_{2}}{1+e^{a_{2}\left(x-x_{2}\right)}}
$$

where

$$
a_{1} \text { and } a_{2}=\frac{Y}{X} \text { at the point } x_{1} \text { and } x_{2}
$$



Figure 22. Decreasing logistic growth curve $Y_{t}=\left(a_{2} / b_{2}\right) /\left(1+e^{a_{2}\left(x-x_{2}\right)}\right)$
with $a_{2}=16.5, b_{2}=2.6, Y_{0}=631$, and $x_{2}=2.03$.


Figure 23. Increasing logistic growth curve $Y_{t}=\left(a_{1} / b_{1}\right) /\left(1+e^{-a_{1}\left(x-x_{1}\right)}\right)$ with $a_{1}=11.5, b_{1}=1.8, Y_{0}=0$, and $x_{1}=2.13$.
$b_{1}$ and $b_{2}=$ incorporated into determination of the upper asymptote by $\frac{a_{1}}{b_{1}}$ and $\frac{a_{2}}{b_{2}}$ $x_{1}$ and $x_{2}=$ inflection point of the two curves
and

$$
a_{1}, a_{2}, b_{1}, b_{2}, x_{1}, \text { and } x_{2}>0
$$

The particular program (MAIN) used to solve this non-linear model was written by Ibbitt (1970) and it utilizes Rosenbrock's (1960) hill-climbing optimization method. ${ }^{5}$ The model parameters are found automatically by minimizing the differences between the measured and model derived values.

The model was fit to the data and required the following constraints:

$$
\begin{aligned}
& 0<a_{1}<50 \\
& 0<\mathrm{b}_{1}<10 \\
& 210<x_{1}<260 \\
& 0<a_{2}<50 \\
& 0<\mathrm{b}_{2}<10 \\
& 150<x_{2}<210
\end{aligned}
$$

${ }^{5}$ This program was adapted to the CSU Scope 3 system by Freeman Smith. He also provided valuable help in writing the subroutines required and supplied general information concerning the running of the program.

The parameters changed as follows:

|  | Initial | Calculated |
| :---: | :---: | :---: |
| $\mathrm{a}_{1}$ | 13 | 11.47 |
| $\mathrm{~b}_{1}$ | 2.05 | 1.78 |
| $\mathbf{x}_{1}$ | 225 | 213 |
| $\mathrm{a}_{2}$ | 21 | 16.52 |
| $\mathrm{~b}_{2}$ | 3.36 | 2.62 |
| $\mathbf{x}_{2}$ | 200 | 203 |

A good indication of the goodness of fit is indicated by the estimated values calculated via the program as opposed to the given values. For comparative purposes Table 14 was constructed.

Table 14. Original data and values calculated by the Rosenbrock direct search optimization technique.

| Day | Data | Value | Calculated Value |
| :---: | :---: | :---: | :---: |
| 144 | 616 g | $\mathrm{g} / \mathrm{m}^{2}$ | $631 \mathrm{~g} / \mathrm{m}^{2}$ |
| 172 | 637 | " | 633 " |
| 183 | 642 | " | 628 " |
| 197 | 541 | " | 547 " |
| 212 | 431 | 11 | 424 " |
| 225 | 518 | " | 534 " |
| 239 | 646 | " | 616 " |
| 253 | 620 | " | 638 " |

The calculated parameters were used in the model and the function was plotted with the measured values (Fig. 24). To represent the two subprocesses that occurs, the main equation was separated into the two logistic curves and these were plotted (Fig. 24).

With the relative free constraints the curve representing process 1 fell to zero. This does not appear to represent the natural situation, and three more sets of curves were calculated. The decomposition curve was restricted to $60 \%$ (Fig. 25), $33 \%$ (Fig. 26), and $50 \%$ (Fig. 27) of the total mass.

These curves were calculated via the optimization program with a constant value added into the decreasing logistic portion of the function which accounted for the varying percentages that remained. With this change the values for the various parameters varied (Table 15).

Table 15. Various parameters calculated by the Rosenbrock direct search optimization technique for various portions remaining of the decomposition curve.

| Parameters |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\mathrm{a}_{1}$ | $\mathrm{~b}_{1}$ | $\mathrm{x}_{1}$ | $\mathrm{a}_{2}$ | $\mathrm{~b}_{2}$ | $\mathrm{x}_{2}$ |
|  | 10.3 | 2.4 | 215 | 21.1 | 5.1 | 200 |
|  | 13.6 | 4.2 | 220 | 21.2 | 6.8 | 201 |
|  | 23.9 | 9.4 | 224 | 18.4 | 7.3 | 201 |



Figure 24. Plots of the original data points of root mass, the sum of two logistic curves, and the separated curves.


Figure 25. Plots of the original data points of root mass, the sum of two logistic curves, and the separated curves with decomposition becoming asymptotic at $60 \%$ of the total.


Figure 26. Plots of the original data points of root mass, the sum of two logistic curves, and the separated curves with decomposition becoming asymptotic at $33 \%$ of the total.


Figure 27. Plots of the original data points of root mass, the sum of two logistic curves, and the separated curves with decomposition becoming asymptotic at $50 \%$ of the total.

The pair of curves which has the decomposition logistic accounting for $40 \%$ root loss (Fig. 25) shall be considered first. The decomposition curve seems quite realistic and has a slope similar to decomposition rates of buried cellulose (Clark 1970). However, it does reach an asymptote at a value considerably higher than Clark reported. The beginning of decay + respiration losses occurs on the first of July, which seems to be late.

This curve indicates that growth commences on July 20, which is indeed late in the season, and continues for a thirty-day period. The average growth rate of $14 \mathrm{~g} / \mathrm{m}^{2} /$ day is slightly higher than the maximum daily photosynthetic material produced in a shortgrass ecosystem; Dye ${ }^{6}$ found that $9-12 \mathrm{~g} / \mathrm{m}^{2} /$ day is the rate during the peak of the season. It must be kept in mind that $1-2 \mathrm{~g} / \mathrm{m}^{2} /$ day will be retained in the aboveground standing crop which leaves approximately $10 \mathrm{~g} / \mathrm{m}^{2} /$ day being shunted to the root compartment.

For the second pair of curves to be considered, $67 \%$ of the roots decomposed over a growing season (Fig. 26). Growth initiation appears to be more realistic with June 15 being the starting date. The growth rate per day ( $10 \mathrm{~g} / \mathrm{m}^{2} / \mathrm{day}$ ) is within limits observed by Dye. ${ }^{6}$ This curve would require over $450 \mathrm{~g} / \mathrm{m}^{2}$ to be produced per growing season which appears to be to high to be explained by photosynthesis.
${ }^{6}$ Information supplied by A. J. Dye, Graduate Student, Range Science Dept. Colorado State University, Fort Collins.

Decomposition begins early and drops to a point which is quite close to that reported by Clark (1970), but he reported only on cellulose which decomposes rapidly. More resistant materials in the roots should prevent root decomposition from being as complete.

The last pair of curves (Fig. 27) are in between the previous pairs. The separated curves both start on July 1 and come to equilibrium around September 1. The growth curve produces $10 \mathrm{~g} / \mathrm{m}^{2} /$ day at its peak period which is comparable to the previous curve. The curve representing decomposition follows cellulose decay (Clark 1970), but does not drop to as low a level as was reported.

It is quite difficult to say which of the various pairs of curves most closely represent the root growth and decomposition that occurs in nature. In any event, however, the root mass has no significant long term trend over several years; an amount equal to that produced in one year will be decomposed in one year. During the first year of decomposition the more easily broken down fractions would disappear while the resistant fractions would accumulate. Lignin could persist for long periods of time, but if present as fragments it would not be included in the root harvesting procedure.

The basic assumptions of the general model are straight forward and a method of further research to evaluate specific pairs of curves suggests itself. To evaluate the hypothetical curves actual data values of the growth and decomposition components need to be
obtained. Although the dynamic model is quite crude at this point, it does represent a hypothesis which can be tested.

## SUMMARY AND CONCLUSIONS

This study was designed to investigate the root fraction of the primary producer compartment of a shortgrass ecosystem. The two primary objectives of this study were (1) to estimate and interpret root mass fluctuations and (2) to determine if grazing herbivores had an effect on the root mass.

Data were collected for two growing seasons (1969 and 1970) with a fall and winter sampling period in between. Sampling was adequate as indicated from the low standard errors calculated (within $5 \%$ of the mean). The sampling scheme for the second season was modified according to information obtained from the first sampling season.

Summer 1969 data showed a seasonal sequence in root weights, but in 1970 the data fluctuated erratically because crowns were not separated from the $0-10 \mathrm{~cm}$ increment.

Various attempts were made to determine if grazing had an effect on the roots, however, no significant differences among the four grazing treatments were found. Therefore, further studies to determine root differences among the treatments need not be continued.

Vertical distribution of root biomass was quite pronounced. The $0-10 \mathrm{~cm}$ segment of the soil profile contained $60 \%$ of the roots
and $75 \%$ was found in the upper 20 cm . Significant variations between dates was limited to the upper 10 cm with lower levels remaining quite constant.

Most authors explain root mass fluctuations on the basis of a storage and utilization philosophy. An hypothesis of root decomposition and growth was developed as an alternative which overcomes some of the disadvantages of the storage-utilization view.

In an analysis of the decomposition-growth hypothesis a mathematical model was fitted to the 1969 data. Two logistic equations were added together and fitted to the original data via a non-linear optimization program. The resultant curve was separated into an increasing curve representing growth and a decreasing curve representing decomposition and respiration losses. The fitted curves represented the original data. The various pairs of curves all have merit, however, more experimentation is needed to determine what is happening in the natural system.

## LITERATURE CITED

Andersson, F. 1970. Ecological studies in a Scanian woodland and meadow area, Southern Sweden. II. Plant biomass, primary production and turnover of organic matter. Bot. Notiser 123(1):8-51.

Beard, J. B. 1959. Growth of bentgrass roots as influenced by temperature and management. U.S. Golf Assoc. J. 12 (3):3031. IN: Herb. Abstr. 1960. 30(3):219.

Biswell, H. H. and J. E. Weaver. 1933. Effect of frequency on the development of roots and tops of grasses in prairie sod. Ecol. 14(4):368-390.

Bledsoe, L. J. and D. A. Jameson. 1969. Model structure of a grassland ecosystem, p. 410-437. IN: Dix, R. L. and R. G. Beidleman [ed.] The grassland ecosystem: A preliminary synthesis. Range Sci. Dep., Sci. Ser. No. 2. Colorado State Univ., Fort Collins. 437 p.

Blevins, R. L., G. M. Aubertin, and N. Holowaychuk. 1968. A technique for obtaining undisturbed soil samples by freezing in situ. Soil Sci. Soc. Amer. Proc. 32 (5):741-742.

Blydenstein, J. 1966. Root systems of four desert grassland species on grazed and protected sites. J. Range Manage. 20(2):93-95.

Boehle, J., Jr., W. H. Mitchell, C. B. Kresge, and L. T. Kardos. 1963. Apparatus for taking soil-root cores. Agron. J. 55(2): 208-209.

Bommer, D. 1960. Entwicklung und substanzbildung von glatthaferpflanzen unter der wirkung wechselnder temperatur und tageslange. Proc. Eighth Internat. Grass1. Congr., p. 409-413.

Bray, J. R. 1963. Root production and the estimation of net productivity. Canadian J. Bot. 41(1):65-72.

Burton, G. W., E. H. DeVane and R. L. Carter. 1954. Root penetration, distribution and activity in southern grasses measured by yields, drought symptoms and $\mathrm{P}^{32}$ uptake. Agron. J. 46(4):229-233.

Clark, F.E. 1970. Decomposition of organic materials in grassland soil. U.S. IBP Grassland Biome Tech. Rep. No. 61. Colorado State Univ., Fort Collins. 23 p.

Cook, C. W., L. A. Stoddart, and F. E. Kinsinger. 1958. Responses of crested wheatgrass to various clipping treatments. Ecol. Monog. 28(3):237-272.

Crider, F. J. 1955. Root-growth stoppage resulting from defoliation of grass. U.S.D.A. Tech. Bull. No. 1102. 23 p.

Dahlman, R. C. and C. L. Kucera. 1965. Root productivity and turnover in native prairie. Ecol. 46(1):84-89.

Dahlman, R. C. and C. L. Kucera. 1968. Tagging native grassland vegetation with carbon-14. Ecol. 49(6):1199-1203.

Dittmer, H. J. 1937. A quantitative study of the roots and root hairs of a winter rye plant (Secale cereale). Amer. J. Bot. 24(7):417-420.

Dixon, W. J. [ed.] 1970. BMD Biomedical computer programs. University of California publications in automatic computation. No. 2. University of California Press, Berkeley. p. 495-510.

Dodd, J. D. and G. L. Van Amburg. 1970. Distribution of Cs ${ }^{134}$ in Andropogon scoparius Michx. clones in two native habitats. Ecol. 51(4):685-689.

Dodd, J. D. and H. H. Hopkins. 1958. Yield and carbohydrate content of blue grama grass as affected by clipping. Kansas Acad. Sci., Trans. 61(3):280-287.

Fehrenbacher, J. B. and J. D. Alexander. 1955. A method for studying corn root distribution using a soil-core sampling machine and shaker-type washer. Agron. J. 47(10):468-472.

Frayer, W. E. 1968. SNФФP: A computer program for 2- and 3dimensional plotting. U.S. Forest Service Research Paper NE-91. 24 p .

Fribourg, H. A. 1953. A rapid method for washing roots. Agron. J. $45(7): 334-335$.

Forrester, J. W. 1964. Industrial dynamics. The M.I.T. Press, Cambridge, Mass. p. 49-59.

Garwood, E. A. 1965. Some factors which influence the root growth of herbage species. Thesis for M.Sc., Univ. Reading. 156 p. IN: Herb. Abstr. 1966. $36(1): 48-49$.

Gist, G. R. and R. M. Smith. 1948. Root development of several common forage grasses to a depth of eighteen inches. J. Amer. Soc. Agron. 40(11):1036-1042.

Hall, N. S., W. F. Chandler, C. H. M. van Bavel, P. H. Reid, and J. H. Anderson. 1953. A tracer technique to measure growth and activity of plant root systems. N.C. Agr. Expt. Stn. Tech. Bull. No. 101. 40 p.

Halls, L. K. and T. R. Dell. 1966. Trial of ranked-set sampling for forage yields. Forest Science 12(1):22-26.

Hanson, W. R. and L. A. Stoddart. 1940. Effects of grazing upon bunch wheat grass. J. Amer. Soc. Agron. 32 (4):278-289.

Hopkins, H. H. 1953. Root development of grasses on revegetated land. J. Range Manage. 6:382-392.

Ibbitt, R. P. 1970. Systematic parameter fitting for conceptual models of catchment hydrology. Thesis for Ph. D., Univ. London. 369 p.

Jameson, D. A. and D. L. Huss. 1959. The effect of clipping leaves and stems on number of tillers, herbage weights, root weights and food reserves of litter bluestem. J. Range Manage. 12(3):122-126.

Jameson, D. A. 1963. Responses of individual plants to harvesting. Bot. Rev. 29:532-594.

Jameson, D. A. and R.E. Bement. 1969. General description of the Pawnee Site. U.S. IBP Grassland Biome Téch. Rep. No. 1. Colorado State Univ., Fort Collins. 32 p.

Kelley, J. M., P. A. Opstrup, J. S. Olson, S. I. Auerbach, and G. M. Van Dyne. 1969. Models of seasonal primary productivity in eastern Tennessee Festuca and Andropogon ecosystems. Oak Ridge Nat. Lab. TM-4310. 296 p.

Kelley, O. J., J. A. Hardman, and D. S. Jennings. 1947. A soilsampling machine for obtaining two-, three-, and four-inch diameter cores of undisturbed soil to a depth of six feet. Soil Sci. Soc. Amer. Proc. 12:85-87.

Kotanska, M. 1967. Biomass dynamics of underground plant organs in some grassland communities of the Ojców National Park. Bulletin DE L'Academie Polonaise Des Sciences. CI. II--15(10):625-630.

Kucera, C. L., R. C. Dahlman and M. R. Koelling. 1967. Total net productivity and turnover on an energy basis for tallgrass prairie. Ecol. 48 (4):536-541.

Kumai, S., M. Hirose, and T. Sanada. 1965. Studies on the dry matter production of forage crops. 1. Experiments on the seasonal growth cycle and growth analysis of Ladino Clover. J. Jap. Soc. Grassld. Sci. ll(1):7-13. IN: Herb. Abstr. 1966. $36(3): 194$.

Lang, R. and O. K. Barnes. 1942. Range forage production in relation to time and frequency of harvesting. Wyo. Agr. Exp. Sta., Bull. 253. 32 p.

Lauenroth, W. K. and W. C. Whitman. 1971. A rapid method for washing roots. J. Range Manage. 24(4):308-309.

Lavin, F. 1961. A glass-faced box for field observations on roots. Agron. J. 53 (4):265-268.

Lorenz, R. J. and G. A. Rogler. 1967. Grazing and fertilization affect root development of range grasses. J. Range Manage. 20(3):129-132.

McKell, C. M., A. M. Wilson, and M. B. Jones. 1961. A flotation method for easy separation of roots from soil samples. Agron. J. 53(1):56-57.

Markle, M. S. 1917. Root systems of certain desert plants. Bot. Gaz. 64 (3):177-205.

May, L. H. 1960. The utilization of carbohydrate reserves in pasture plants after defoliation. Herb. Abstr. 30(4):239-245.

Milner, C. and R. E. Hughes. 1968. Methods for the measurement of the primary production of grassland. IBP Handbook No. 6. Blackwell Sci. Publ., Oxford. 70 p.

Moir, W. H. and E. P. Bachelard. 1969. Distribution of fine roots in three Pinus radiata plantations near Canberra, Australia. Ecol. 50(4):658-662.

Muzik, T. J. and J. W. Whitworth. 1962. A technique for the periodic observation of root systems in situ. Agron. J. 54(1): 56.

Nilsson, J. 1970. Notes on the biomass and productivity of belowground organs of a South-Swedish hay-meadow. Bot. Notiser 123:183-194.

Neilson, J. A. 1964. Autoradiography for studying individual root systems in mixed herbaceous stands. Ecol. 45(3):644-646.

Odum, E. P. 1965. Fundamentals of ecology. W. B. Saunders Co., Philadelphia. 546 p.

Ovington, J. D., D. Heitcamp, and D. B. Lawrence. 1963. Plant biomass and productivity of prairie, savanna, oakwood and maize field ecosystems in Central Minnesota. Ecol. 44(1):5263.

Pavlychenko, T. K. 1937a. Quantitative study of the entire root systems of weed and crop plants under field conditions. Ecol. 18(1):62-79.

Pavlychenko, T. K. 1937b. The soil-block washing method in quantitative root study. Canadian J. Research 15(2):33-57.

Pettit, R. D. and C. C. Jaynes. 1971. Use of radiophosphorus and soil-block techniques to measure root development. J. Range Manage. 24(1):63-65.

Pearson, L. C. 1965. Primary production in grazed and ungrazed desert communities of eastern Idaho. Ecol. 46 (3):278-285.

Pielou, E. C. 1969. An introduction to mathematical ecology. John Wiley and Sons, Inc. New York. p. 19-22.

Pilat, A. 1969. Underground dry weight in the grassland communities of Arrhenatheretum elatioris alopecuretosum pratensis R. Tx. 1937 and Mesobrometum erecti stipetosum Vicherek 1960. Folia geobot. and phytotax. 4(3):225-234.

Preston, C. E. 1900. Observations on the root system of certain cactaceae. Bot. Gaz. 30:348-351.

Rodin, L. E. and N. I. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation. [Transl. from Russian by Scripta Technica Ltd. G. E. Fogg [ed.]] Olivir and Boyd, London. 288 p.

Rosenbrock, H. H. 1960. An automatic method of finding the greatest or least value of a function. The Computer Journal 3:175-184.

Schuster, J. L. 1964. Root development of native plants under three grazing intensities. Ecol. 45(1):63-70.

Shantz, H. L. 1911. Natural vegetation as an indicator of the capabilities of land for crop production in the Great Plains area. U.S. Dept. Agr. Bureau Plant Industry Bull. 201.

Smith, F. M. 1971. Growing season precipitation records, Central Plains Experimental Range A.R.S., Nunn, Colorado. U.S. IBP Grassland Biome Tech. Rep. No. 74. Colorado State Univ., Fort Collins. 73 p.

Smith, F. M. and W. D. Striffler. 1969. Pawnee Site microwatersheds: Section description and instrumentation. U.S. IBP Grassland Biome Tech. Rep. No. 5. Colorado State Univ., Fort Collins. 29 p.

Stoddart, L. A. 1935. How long do roots of grasses live? Science 81 (2109):544.

Striffler, W. D. 1971. Hydrologic data, 1970, Pawnee Grasslands. U.S. IBP Grassland Biome Tech. Rep. No. 75. Colorado State Univ., Fort Collins. 23 p.

Stuckey, I. H. 1941. Seasonal growth of grass roots. Amer. J. Bot. $28(6): 486-491$.

Takeda, T. and W. Agata. 1966. Analysis of the growth in forage crops. 5. Effect of the repeated treatment of "cut and regrowth" on the growth responses of Ladino clover under various temperatures. Proc. Crop Sci. Soc. Japan. 34(3):281-286. IN: Herb. Abstr. 1967. 37 (1):54.

Tajima, K. 1965. Studies on the physiology of crop plants in response to the effect of high temperature. 1. Effect of high temperature on growth and respiration of crop plants. 2. Inhibition by high temperature of cytochrome coxidase activity and its restoration by phospholipid. Proc. Crop Sci. Soc. Japan. $33(4): 371-378$. IN: Herb. Abstr. 1967. 37 (1):54.

Troughton, A. 1957. The underground organs of herbage grasses. Commenwealth Bureau of Pastures and Field Crops, Hurley, Berkshire. Bull. No. 44.

Uresk, D. 1971. Dynamics of Bouteloua gracilis in a shortgrass ecosystem. Ph.D. thesis, Colorado State Univ., Fort Collins.

Van Dyne, G. M. 1969. Implementing the ecosystem concept in training in the natural resources sciences. p. 327-367. IN: Van Dyne, G. M. (ed.) The ecosystem concept in natural resource management. Academic Press, New York. 383 p.

Watt, K. E. F. 1968. Ecology and resource management-A quantitative approach. McGraw-Hill Book Co. New York. 450 p.

Weaver, J. E. 1920. Root development in the grassland formation (A correlation of the root systems of native vegetation and crop plants). Carnegie Institution of Washington. Publ. No. 292.

Weaver, J. E., F. C. Jean, and J. W. Crist. 1922. Development and activity of roots of crop plants (A study in crop ecology). Carnegie Institution of Washington. Publ. No. 316.

Weaver, J. E. and J. Crist. 1922. Relation of hardpan to root penetration in the Great Plains. Ecol. 3(3):237-249.

Weaver, J. E. 1926. Root development of field crops. McGrawHill Book Co., Inc. New York. 291 p.

Weaver, J. E. and F. W. Albertson. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. Ecol. Monog. 13(1):63-117.

Weaver, J. E. and E. Zink. 1946b. Length of life of roots of 10 species of perennial range and pasture grasses. Plant Physiol 21:201-217.

Weaver, J. E. and E. Zink. 1946a. Annual increase of underground materials in three range grasses. Ecol. 27 (2):115-127.

Weaver, J. E. 1947. Rate of decomposition of roots and rhizomes of certain range grasses in undisturbed prairie soil. Ecol. 28(3):221-240.

Weaver, J. E. 1954. North American prairie. Johnsen Publishing Co., Lincoln, Nebraska. 348 p.

Weaver, J. E. 1958. Summary and interpretation of underground development in natural grassland communities. Ecol. Monog. 28:55-78.

Weaver, J. E. 1961. The living network in prairie soils. Bot. Gaz. 123(1):16-28.

Williams, E. J. 1959. Regression analysis. John Wiley and Sons, Inc. New York. p. 62-64.

## APPENDICES

## APPENDIX 1

## Soils map of sections 15 and 23, Pawnee Site



APPENDIX 2
Listing of program RøФTAS



ROOTAS FORTRAN EXTENDED VFRSION $2.0 \quad 11 / 19 / 71$
15.11 .40.

GO ro 11
$15 W T(K)=W T(K)-A S H$
107
60
108
C ----CHECK TO SEE THAT THIS SECTION CONTAINS ONLY NUMBER 2*S.

C -----REAO NIJMBEG THREF (3) CARDS.
16 IF (NCARD.NE.3) WRITE $(6,85)$ NCARD:K NCART $=10 \mathrm{UM}$
$\mathrm{N}=1$
$1 C T=0$
 115

C -----CHECK TO SFE ALL NUMBEO 3 CARDS --"--CHECK TO SFE ALL NUMBER 3 CARDS BELONG TO THIS 9ATCH.

117 IF (ISATCH, EG.KRATCH) GO TO 18

18 IF (NCARD.NF. 3) क0 1024 IF (NCART.GT.O) GO TO 19 WRITE (6.83) NCARD GO TO 17
$19 \mathrm{~N}=\mathrm{N}+1$
$20 \mathrm{JA}(\mathrm{N})=\mathrm{N}$ $J F L A G=2$ $L=3$
CALL STAK INCART*K•JFLAGOL.IPTR.ICTI
IF (JFLAG.NF.0) GO TO 22
IDEN(1) $=4 \mathrm{HZZZ2}$
NOIA(K) $=$ NDM
NTMICK $(K)=$ NTM
$0021 \quad 1=1.6$
21 IDENT $(K, I)=1$ DEN(I) GO TO 17
22 NOIA $(K)=$ NOM
NTHICK(K) =NTM
DO $23 \quad I=1.6$
$23 \operatorname{IDENT}(K, 1)=I D E N(1)$
IF (WT (K) -LE.O.) IOENT $(K .1)=4 \mathrm{HZZ22}$
607017
119

- 120
- 121

122

- 123
- 124
125
    - 126
127
128
$\begin{array}{r}128 \\ \hline\end{array}$

24 WRITE $(6,86)$
DO $25 \mathrm{~K}=1$. N
IF (WT(K).EQ.WX(K)) WRITE 16.87 )K A 148
25 CONTINUE

A.

THIS SORT ROUTINE ARRANGES THE DATA BY THE FIRST THREE IOENTIFIER FIELDS(IDENT). THIS SECTION CAN BE CHANGED TO SORT ON AS MANY IDENTIFIERS AS NEEDED. ONI.Y TWO CHANGES NEEDED, $1=1,(1-7), K=$ (2-8) - 1 .
(...

| PROGRAM | ROOTAS | AS FORTRAN EXTENDEO VERSION 2.0 11/19/71 | 15.11.40. |  |
| :---: | :---: | :---: | :---: | :---: |
| 160 | C $\quad$ |  | A | 160 |
|  |  | DO $311=1.3$ | 4 | 161 |
|  |  | $K=4-1$ | A | 162 |
|  |  | 0026 Lal , N | , | 163 |
|  |  | $J=J A(L)$ | A | 164 |
| 165 | 261 | IA (L) = IDENT (J,K) | A | 165 |
|  |  | INDEX=N-1 | A | 166 |
|  |  | IND=0 | A | 167 |
|  | 27 | D0 $29 \mathrm{M}=1$. INDEX | 4 | 168 |
|  |  | IF (IA M - -1A M - 1) 29.29.2A | A | 169 |
| 170 | 281 | ISAVE=14(M+1) | A | 170 |
|  |  | JSAVE $=J 4(M+1)$ | A | 171 |
|  |  | $\underline{I A}(\mathrm{M}+1)=1 \mathrm{~A}(\mathrm{M})$ | A | 172 |
|  |  | $J A(M+1)=J A(M)$ | A | 173 |
|  |  | IA $(M)=15 A V E$ | A | 174 |
| 175 |  | $J A(M)=J S A V E$ | A | 175 |
|  |  | IHOLO FM | A | 176 |
|  |  | $1 \mathrm{ND}=1$ | A | 177 |
|  | 29 | CONTINUF. | 4 | 178 |
|  |  | IF (IND) 30.31 .30 | ${ }^{\text {a }}$ | 179 |
| 180 | 30 | INOEX $=1$ HOLD | A | 180 |
|  |  | IND $=0$ | * | 181 |
|  |  | G0 1027 | 4 | 182 |
|  | c 31 | CONTINUE | , | 183 |
|  | C | ----THIS SECTION WRITES THE RESULTS OF THE GROUPING PROCESS. | A | 184 |
| 185 |  | $K=0$ | , | 185 |
|  |  | $10 \mathrm{~N}=4 \mathrm{H}$ | 1 | 186 |
|  |  | 00 $32 \mathrm{~L}=1 . \mathrm{N}$ | 4 | 187 |
|  |  | J=JA(L) | A | 188 |
|  |  | IF (IDENT (J.1).EQ.IDN) KmK+1 | A | 189 |
| 190 |  |  | A | 190 |
|  | c 32 | CONTINUE | 4 | 191 |
|  |  | $\text { IF }(K, E O . O) \quad G 0 \quad T 0 \quad 33$ $\text { WRITE }(6.89) K$ | 4 | 192 193 |
|  |  | ----CHECK FOR 7ERO DEVISORS. | A | 194 |
| 195 | 330 | $0034 \mathrm{Lmi+5}$ | 4 | 195 |
|  |  | IF (KTHICK(L).EQ.0) WRITE (6,90) (KTHICK(1). $=1=5$ ) | 1 | 196 |
|  | 34 | CONTINUE. | 1 | 197 |
|  |  |  RE, NPLOT | $\stackrel{4}{4}$ | 198 199 |
| 200 |  | IF ITHICK.NE.O.OR. NCORE.NE.O.OR.NPLOT.NE, 0 ) GO TO 35 | $\lambda$ | 200 |
|  |  | 60 TO 71 | 4 | 201 |
|  | C |  | 4 | 202 |
|  | C |  | A | 203 |
|  | c | B. | A | 204 |
| 205 | $c$ |  | A | 205 |
|  | c | THIS SECTION CONVERTS THE RAW data into a more readarle form. the | 4 | 206 |
|  | C | OATA IS PRESENTED BY VARIOUS WATERSHEOS AND BY PLOT, CORE, AND | $A$ | 207 |
|  | C | SECTION. MEANS AND STANDARD ERRORS ARE CALCULATED ANO INCLUDED ON | 4 | 208 |
|  | c | ThE TAgLES. A SUmmary table is calculated for each date. | 4 | 209 |
| 210 | C |  | 4 | 210 |
|  | C |  | A | 211 |
|  | C |  | 4 | 212 |







ENTRY POINTS

| 020237 ROOTAS | 000000 TAPESE | 002022 COPY1E |
| :--- | :--- | :--- |
| 004044 | TAPE1E | 006066 FORT1E |
| 012132 PLOTSIE | 012132 TAPE3E | 006066 TAPE2E |
| 016176 TREATIE | 016176 TAPETE |  |


| EXTERNALS |  |  |  |
| :--- | :--- | :--- | :--- | :--- |
| OBNTRY. IPUTCI. INPUTC, OPUTCI. OUTPTC. STAK |  |  |  |
| OUTPTB. STOEV | IPUTRI. INPUTB. TREAT | STOP. |  |






## APPENDIX 3

Samples of various tables of individual root mass weights
 SITF PAW NATF 690524 WATFPSHFN UN


|  |  | ----r.2AMS | DED MSO PEF C. | CM WF円TH |  | G/MS0 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $7 \quad 1$ | 85.686 | 24.401 | 12.?11 | 12.690 | 1.638 | 2039.551 |
| 72 | 53.544 | 18.612 | 13.690 | 6.769 | 1.717 | 1456.349 |
| MEAN | 64.515 | 21.507 | 12.950 | 9.770 | 1.677 | 1747.95n |
| $10 \quad 1$ | 66. 455 | 14.779 | 11.642 | 4.743 | 4.322 | 1633.089 |
| $10 \quad 2$ | 87.431 | 14.141 | 9.992 | 7.855 | 4.855 | 1834.689 |
| MEAN | 76.943 | 14.450 | 10.767 | 4.299 | 4.588 | 1733.889 |
| MFAN | 73.279 | 17.934 | 11.852 | 9.014 | 3.133 | 1740.919 |
| STO FRROP | ?.591 | 2.491 | . 772 | . 506 | 1.029 | 4.971 |





| $\begin{gathered} \text { SITF DAW } \\ \text { DLOT } \end{gathered}$ | CODF | $\begin{array}{ll} \text { OATE } & 700474 \\ & 0-10 \mathrm{CM} \end{array}$ | $\begin{aligned} & \text { WATFRSHFO NO. } 1 \\ & \text { TOTAI. } \end{aligned}$ |
| :---: | :---: | :---: | :---: |
|  |  |  |  |
|  |  | r.AnSu/CM OFPTH | ra/mes |
| 77 | 1 | 115.427 | 2721.052 |
| 73 | 2 | 44.344 | $7 \cap 5 ? .513$ |
| 77 | 3 | 97.705 | 1969.526 |
| 73 | 4 | 3R.994 | 1359.341 |
| 73 | 5 | 57.14R | 1117.558 |
| MFAN |  | R0. 784 | 198.3 .004 |
| 71 | 1 | 104.299 | 7176.950 |
| 77 | $?$ | 90.335 | 2002.404 |
| 77 | 3 | 131.176 | 2512.915 |
| 72 | 4 | 97.749 | 2n95.32? |
| 77 | 5 | 193.517 | 216A.96? |
| WFAM |  | 195.41 h | 2190.910 |
| 90 | 1 | 41.913 | 2020.440 |
| 99 | $?$ | 144.24 | 76P3.743 |
| 97 | 7 | 127.770 | 2470.732 |
| 90 | 4 | 11?.355 | 2277.644 |
| 90 | 9 | 120.316 | 7377.150 |
| MFAN: |  | 119.420 | 2365.461 |
| 74 | 1 | 13n.ala | 2454.07? |
| 35 | 7 | ¢7.0.36 | 1721.160 |
| 75 | 3 | 234.250 | 3ん74.342 |
| pe | 4 | 153.725 | 7799.773 |
| 25 | 5 | 105.177 | 2197.929 |
| MFAN1 |  | 135.443 | 2566. 255 |
| AO | $!$ | 145.740 | 2695.073 |
| 40 | , | 122.271 | 2401.605 |
| 40 | 7 | 114.180 | 7375.577 |
| -1) | 4 | 174.440 | 2579.321 |
| 67 | 5 | 171.741 | 7019.074 |
| 454a! |  | 174.448 | 2An4. 311 |
| 77 | 1 | 49.337 | 1734.914 |
| 77 | $?$ | 59.741 | 1617.601 |
| 27 | 3 | 97.774 | 2044.760 |
| 77 | 4 | 39.734 | 1361.202 |
| 77 | 5 | 147.01. | 2710.946 |
| MEAN |  | 41.734 | 1994.886 |
| 11 | 1 | 55.0.44 | 1551.89? |
| 11 | $?$ | +2.6MS | 1406.741 |
| 11 | 7 | 10n.145 | 2125.030 |
| 11 | 4 | $41.02 \hat{}$ | 2011.062 |
| 11 | 5 | 43.324 | 1414.76? |
| MFPAN |  | 74.455 | 190.3 .89 H |
| 69 | 1 | 95.345 | 2065.160 |
| 49 | $?$ | 4?.8? | 190R.467 |
| 6R | 7 | 120.6an | 2381.460 |
| 69 | 4 | 104.117 | 2174.630 |
| A9 | 5 | 69.156 | 1774.523 |
| MFAR? |  | $74.4{ }^{\prime} 3$ | 2053.24N |
| MFAM |  | 107.7n9 | 2170.310 |
| STI EROR |  | $3.14 n$ | 39. 251 |




## APPENDIX 4

Graphs of exponential fits to 1969 root data





## APPENDIX 5

Complete set of ANOV tables run on various depth increments

Key to the abbreviations used in Appendix 5

```
        D = Dates
        T = Treatments
        W(T) = Watersheds within treatments
        DT = Date-treatment interaction
DW(T) = Error term
N.S. = Non-significant
    * = Significant at 5% level
        ** = Significant at l% level
```

| Source | D.F. | S.S. | M.S. | F |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
| D | 7 | 590.6 | 84.4 | $.873(7,28)$ | N.S. |
| T | 3 | 105.1 | 35.0 | $1.258(3,4)$ | N.S. |
| W(T) | 4 | 111.3 | 27.8 | $.288(4,28)$ | N.S. |
| DT | 21 | 1246.0 | 59.3 | $.614(21,28)$ | N.S. |
| DW(T) | 28 | 2704.5 | 96.6 |  |  |

ANOV run on crown mass using 1969 watershed means.

| Source | D.F. | S.S. | M.S. | F |  |
| :--- | :---: | ---: | :--- | :--- | :--- |
| D | 7 | 5733.5 | 819.1 | $2.975(7,28)$ | $*$ |
| T | 3 | 455.3 | 151.8 | $.549(3,4)$ | N.S. |
| W(T) | 4 | 1105.7 | 276.4 | $1.004(4,28)$ | N.S. |
| DT | 21 | 5306.8 | 252.7 | $.918(21,28)$ | N.S. |
| DW(T) | 28 | 7709.0 | 275.3 |  |  |

ANOV run on $0-10 \mathrm{~cm}$ increment using 1969 watershed means with crowns.

| Source | D.F. | S.S. | M.S. | F |  |
| :--- | :---: | ---: | :---: | :---: | :---: |
| D | 7 | 3585.2 | 512.2 | $4.242(7,28)$ | $*$ |
| T | 3 | 128.5 | 42.8 | $.311(3,4)$ | N.S. |
| W(T) | 4 | 551.5 | 137.8 | $1.142(4,28)$ | N.S. |
| DT | 21 | 2599.6 | 123.8 | $1.025(21,28)$ | N.S. |
| DW(T) | 28 | 3380.5 | 120.7 |  |  |

ANOV run on $0-10 \mathrm{~cm}$ increment using 1969 watershed means with crowns deleted.

| Source | D.F. | S.S. | M.S. | $F$ |  |
| :--- | :---: | ---: | :---: | :---: | :---: |
| D | 7 | 209.6 | 29.9 | $1.951(7,28)$ | N.S. |
| T | 3 | 29.8 | 9.9 | $.304(3,4)$ | N.S. |
| W(T) | 4 | 130.9 | 32.7 | $2.132(4,28)$ | N.S. |
| DT | 21 | 249.1 | 11.9 | $.773(21,28)$ | N.S. |
| DW (T) | 28 | 429.8 | 15.4 |  |  |

ANOV run on $10-20 \mathrm{~cm}$ increment using 1969 watershed means.

| Source | D.F. | S.S. | M.S. | F |  |
| :--- | :---: | ---: | :---: | :---: | :---: |
| D | 7 | 105.5 | 15.1 | $2.879(7,28)$ | $*$ |
| T | 3 | 4.8 | 1.6 | $.514(3,4)$ | N.S. |
| W (T) | 4 | 12.5 | 3.1 | $.596(4,28)$ | N.S. |
| DT | 21 | 85.4 | 4.1 | $.776(21,28)$ | N.S. |
| DW(T) | 28 | 146.6 | 5.2 |  |  |

ANOV run on $20-40 \mathrm{~cm}$ increment using 1969 watershed means.

| Source | D.F. | S.S. | M.S. | F |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
| D | 7 | 76.7 | 11.0 | $2.560(7,28)$ | $*$ |
| T | 3 | 30.9 | 10.3 | $.990(3,4)$ | N.S. |
| W(T) | 4 | 41.6 | 10.4 | $2.429(4,28)$ | N.S. |
| DT | 21 | 120.3 | 5.7 | $1.338(21,28)$ | N.S. |
| DW(T) | 28 | 119.9 | 4.3 |  |  |

ANOV run on $40-60 \mathrm{~cm}$ increment using 1969 watershed means.

| Source | D.F. | S.S. | M.S. | F |  |
| :--- | ---: | ---: | ---: | :--- | :--- |
| D | 7 | 24.7 | 3.5 | $.945(7,28)$ | N.S. |
| T | 3 | 8.5 | 2.8 | $.578(3,4)$ | N.S. |
| W (T) | 4 | 19.5 | 4.9 | $1.305(4,28)$ | N.S. |
| DT | 21 | 70.4 | 3.4 | $.897(21,28)$ | N.S. |
| DW (T) | 28 | 104.6 | 3.7 |  |  |

ANOV run on $60-80 \mathrm{~cm}$ increment using 1969 watershed means.

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[^0]:    ${ }^{2}$ Soil profiles were examined by James Crabb, Soil Conservation Service, USDA.

[^1]:    ${ }^{3}$ A Cobra model which is manufactured by the Atlas Copco Company in Belgium and can be purchased from Atlas Copco, Inc., Denver, Colorado.

[^2]:    Figure 11. Three data sheets used for recording various values during the 1970 growing season.

[^3]:    ${ }^{4}$ TAYLN was written by Donald Jameson, Range Science Department, Colorado State University, Fort Collins.

[^4]:    * = Significant at 5\% level
    ** $=$ Significant at $1 \%$ level
    Degrees of Freedom $=7,28$

[^5]:    NUMAFR of ATIEMDIES WHICH DANGE

