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The Influence of Climate on Biomass and Mineralomass of a Crested Wheatgrass Community in Northern Utah

Randall S. Shinn

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THE INFLUENCE OF CLIMATE ON BIOMASS AND MINERALOMASS OF A
CRESTED WHEATGRASS COMMUNITY IN NORTHERN UTAH

by

Randall S. Shinn

A thesis submitted in partial fulfillment of the requirements for the degree of
MASTER OF SCIENCE
in
Range Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah
1975
ACKNOWLEDGMENTS

I wish to thank both Dr. West and Dr. Balph for their help in the preparation of this thesis manuscript.

I thank Mary Jean Perlemutter who carefully processed my samples and did the graphics for this paper.

I want to thank my wife, Vicki, who not only helped me collect the samples but also typed manuscript drafts and gave me constant encouragement.

Finally, I acknowledge the financial support of the US/IBP Desert Biome and thank all the friends and technicians who have helped me during the last three years.

Randall S. Shinn
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ABSTRACT

The Influence of Climate on Biomass and Mineralomass of a
Crested Wheatgrass Community in Northern Utah

by

Randall S. Shinn, Master of Science

Utah State University, 1975

Major Professor: Dr. Neil E. West
Department: Range Science

Aboveground biomass, litter biomass and root biomass of a crested
wheatgrass (Agropyron desertorum [Fisch.] Schult.) dominated community
were inventoried in the fall of 1971, 1972, and 1973. In addition,
energy, nitrogen, fats and ash determinations were made on the materials

The sampling methods used generated data sufficiently precise to
detect significant differences ($\alpha = .10$) among biomass components
among years. The chemical contents of the components were similar
in the fall of 1972 and the fall of 1973 despite the large differences
in growing season precipitation.

A simple linear regression formula was generated from which
aboveground biomass was predicted using individual plant volume as
the independent variable. Regression techniques were tried in an
effort to use aboveground biomass to predict root and litter biomass.
This approach proved unsuccessful because of high variability within
the data.
Changes in the biomass of the components were analyzed with respect to differing precipitation regimes. Aboveground biomass responded positively and linearly to increasing growing season precipitation. Litter biomass decreased as current growing season precipitation increased. However, litter increased as a function of increasing previous-growing-season precipitation. Root biomass decreased with increasing previous-growing-season precipitation. It was found that both litter:shoot and root:shoot ratios decreased as a function of increasing growing season precipitation.
INTRODUCTION

The Desert Biome Program began in 1968 as a part of the United States Analysis of Ecosystems Program. An objective of the desert project was to develop predictive models capable of forecasting changes in desert ecosystems resulting from climatic changes upon human perturbations to the desert. The goal was to predict the consequences of such modifications in terms of changing sizes of plant and animal populations, changing community composition and changing soil and water characteristics (Goodall, 1970).

The research design of the Desert Biome Program was developed primarily by David Goodall at Utah State University. The design divided the research effort into three integrated parts: 1) the process studies, 2) the modelling effort, and 3) the validation studies (Goodall, 1968).

The process studies were particular research projects designed to investigate the mechanisms responsible for annual variation in key components of the ecosystem (Norton, 1974).

Early planning sessions were attended by ecologists familiar with the arid lands of Western America. They collectively defined the key components and key processes to be investigated (Bowns, 1969, 1970a, 1970b, 1970c). The ecosystem was conceptualized as a mover of energy and materials. Components of the system were defined as the energy and chemical contents bound up in living organisms, dead material, and abiotic parts of the ecosystem. Processes were defined
as the means by which the components move through the system and alter form. Factors were defined as the biotic and abiotic forces which determine the rates at which the processes move the components (Wagner, 1970). The objective of each process study was to generate mathematical functions expressing the rates of changes in the key components as each responds to a reasonable range of factors (Goodall, 1969).

The modelling effort was to be based on the results of the process studies. The modellers were to fit together the mathematical functions generated by the process studies into integrated computer models (Wagner, 1971). Nine main processes were considered important: carbon fixation, deployment of photosynthate, growth and senescence, herbivory, granivory, detritivory, decomposition, the water and nitrogen cycles. Models of these ecosystem processes were to be integrated into whole ecosystem models to track the movement of carbon, nitrogen, ash elements and energy through the ecosystem in response to factors of temperature, soil-water and nutrient availability (Norton, 1974). The ecosystems models were divided into three modules: plant, animal and soils (Goodall, 1972). The models were intended to be sufficiently general for application to each of the four North American desert types (Norton, 1974).

Validation studies were designed to test the predictions made by the models (Goodall, 1969). The North American desert ecosystems were represented by the selection of four validation sites considered typical of the four North American regional deserts: Great Basin, Mohave, Sonoran and Chihuahuan. On each validation site an initial
inventory was made of the biomass and chemical contents of the biota. Meteorological events were recorded continuously on each site. Annual estimates of biomass and chemical contents were made on selected components of each ecosystem (Balph, 1973; Turner, 1973; Thames, 1973; Whitford, 1973). The models were first tested by using the data from the initial validation site inventories. The models were driven by factors derived from validation site meteorological data. As a measure of accuracy the models' predictions were compared with the annual biomass and chemical contents estimates from the validation sites (Goodall, 1969).

The combined models, representing in the computer the behavior of the whole ecosystem, constitute a focal point of the Desert Biome Program (Goodall, 1969). If the accuracy of the models is considered a function of how well the models' predictions compare with the validation site data, then the validation data are critical to the success of the program. Validation data provide a means by which some assumptions underlying the Desert Biome Program will be herein tested, and by which process functions can be developed independent of the process studies and modeling effort.

It is the purpose of this thesis to use some validation site data to test four assumptions underlying the validation of the Desert Biome ecosystem models. These assumptions are:

1) that the validation studies envisioned can adequately measure annual changes in the biomass of important biotic components of the ecosystem;
2) that the validation studies can adequately measure annual changes in chemical content of the important biotic components per unit area;

3) that the validation studies can develop regression models which accurately predict states of hard-to-sample components;

4) that annual changes in biotic components are logically correlated with changes in meteorological factors.
THE STUDY AREA

The study was conducted on a six-year-old crested wheatgrass (Agropyron desertorum [Fisch.] Schult.) seeding in northern Utah. The study area was in one of four vegetation types investigated by the Desert Biome Curlew Valley validation program. The site was located about 25 km southwest of Snowville, Utah, in Sections 5-8, T. 13 N. R. 9 W. at 1320 m elevation (Balph, 1973). Growing season precipitation on the site averaged 332 mm from 1970 through 1974. Precipitation occurs primarily as winter snow and spring rain (Shinn, 1973). The soils on the site are uniformly Thiokol silt loams. Root-inhibiting salt concentrations of greater than one percent occur below 40 cm (Southard, 1973).

Before the seeding treatment, the dominant native plants were big sagebrush (Artemisia tridentata Nutt.) and shadscale (Atriplex confertifolia [Torr.] Wats.). In the fall of 1965 the area was plowed with a flex-type wheatland plow. Ninety-five percent of the shrubs were killed. Immediately thereafter about eight kg of A. desertorum seeds were broadcast per ha. Grazing on the seeding was deferred for three years until January 1968. The seeding has since been grazed moderately by cattle each winter (Anonymous, 1965).

The seeded area is now a homogeneous stand of crested wheatgrass with a mean grass density of 12 plants per square meter. Only traces of other species, largely annuals and exotic weeds, occur (Shinn, 1973).
METHODS AND MATERIALS

Two objectives of the validation studies were to estimate the biomass and chemical content of the important components of the ecosystem. The primary plant components of the crested wheatgrass study area were the aboveground portions of the grass plants, the grass roots and the grass litter on the soil surface. The sampling techniques for making estimates of aboveground grass biomass on the Curlew Valley validation sites were developed by Holte (1972). The techniques used to estimate root and litter biomass were developed by Bjerregaard (1971). It is assumed that the methods used were the best available with respect to constraints imposed by the budget.

Throughout this paper biomass is defined as the weight of organic material which can be sampled at any given time.

Data on *A. desertorum* aboveground phytomass, roots and litter were collected the third week of August 1971 and 1972 and the third week of September in 1973.

All grass, root, and litter materials were collected each year from individually numbered list-count quadrats (Oosting, 1948). The quadrats were rectangular as recommended by Pechanec and Stewart (1940) for vegetation sampling in sagebrush-grassland communities. Quadrat dimensions were 1 x 2 m. All the sample plots were selected randomly from within a single ha. Ten plots were sampled in 1971, 40 in 1972, and 10 in 1973.

Each plant within a list-count quadrat was individually numbered, measured for height and basal area, harvested, bagged, dried at 41 C
for 72 hours and then weighed. This part of the overall sampling program provided data on annual aboveground grass biomass.

Plants collected on the list-count quadrates were subsampled to provide data on the current year's new growth-old growth ratios. These plants were hand sorted. New growth was separated from old growth on the basis of color. Separated materials were dried at 41°C for 72 hours and then weighed. This procedure provided data on annual aboveground new growth:old growth ratios.

Litter was sampled following removal of the plants from the list-count quadrats. Litter was defined as all plant-derived organic material lying on the soil surface (Medwecka-Kornas, 1971; West, 1975). The litter samples were of the type defined by Medwecka-Kornas (1971) as accumulated ground litter samples. Each list-count quadrat was randomly subsampled eight times using a 10 x 50 cm sampling frame to define the sample area. All litter material was collected from within the frame. Water flotation techniques were used to separate the litter materials from the soil. Further separation was achieved by passing the materials through a 2 mm mesh shaker sieve. Litter was then dried at 41°C for 72 hours and weighed. Weights were recorded by plot number in categories larger or smaller than 2 mm. Litter materials larger than 2 mm generally consisted primarily of fresh organic and partly decomposed materials. Litter smaller than 2 mm consisted primarily of decomposed and amorphous matter. These litter samples provided data on the annual mass of plant litter.

Root samples were taken from the list-count quadrats following the removal of the plants and litter by using the soil core method.
(National Academy of Sciences, 1962; Bjerregaard, 1971). One root core was taken from the center of each litter plot with an 8 cm diameter orchard auger in 20 cm increments to a depth of 40 cm. Preliminary studies during the summer of 1971 showed that root biomass in the seeded area was much reduced below 40 cm. Root samples taken down to 60 cm deep showed that 83 percent of the roots were distributed through the upper 40 cm (Shinn, 1973b). Where a random root core location encountered the root crown of a grass plant, the crowns were sampled in the same manner as all other root core samples. Sampled material was processed by water flotation using the method described by Bjerregaard (1971). Further hand sorting removed obviously woody root materials. Root materials were dried at 41 C for 72 hours and weighed to provide data on annual root biomass.

In 1972 and 1973 subsamples of aboveground grass, root and litter materials were randomly selected for analysis of chemical content. All materials were dried at 41 C for 72 hours and ground in a Wiley mill with a 60 mesh screen in preparation for caloric, ash, nitrogen and fat analysis. Caloric determinations were made using a Phillipson microbomb calorimeter (Phillipson, 1964). Crude protein determinations were made using the microkjeldahl technique. The Soxhlet method was used for fat content determinations. These protein, fat and ash analyses were those specified by the Association of Official Agricultural Chemists (1970).

Precipitation on the study area was measured continuously with one weighing, recording rain gauge located 1000 m from the study ha.
It was assumed that the impact of herbivory was constant during the three year study. Effects on the vegetation due to grazing cattle were judged to be constant. Lagomorph density in nearby native shrub vegetation fell from three per ha in 1971 to .6 per ha in 1972 (Anderson, 1973). However, the grass sampling area was more than 300 m from native shrub vegetation and therefore effects of foraging rabbits (Lepus californicus) were probably insignificant even in years of high densities (Westoby and Wagner, 1973). There were no obvious invertebrate population outbreaks on the grass site. Therefore changes in annual standing crops, biomass and chemical contents of the components of vegetation were assumed to be unrelated to herbivore activities.
RESULTS AND DISCUSSION

In this section four assumptions of the Desert Biome research design are tested. Each assumption is presented and tested under a separate heading.

The structure of the crested wheatgrass community was quantitatively documented each year with the data collected on aboveground plant, root and litter biomass and their respective chemical content. Collection of these data over a three year period provided an opportunity to investigate and quantify the interrelationships among the components with respect to time and changing precipitation regimes.

Assumption 1: The validation studies envisioned can adequately measure annual changes in the biomass of important biotic components of the ecosystem.

The research design assumed that the important biomass components of the ecosystem were dynamically changing through time. It was the purpose of the models to predict the states of the system. Similarly it was assumed that the biomass of the components could be measured in the field. If the models are validated with validation site data, changes which cannot be detected on the validation sites must be either ignored or treated as static components in the models. Therefore, it is important to determine what components can be accurately and precisely measured on the sites.

Data on the vegetation components of the Curlew Valley crested wheatgrass site were collected in the fall of each sample year. In Curlew Valley, *A. desertorum* begins its spring green-up in early
April. Green leaves develop and grow through June. Leaf growth then declines as the growth of reproductive parts begins. By early July seed heads are formed. The seeds grow and mature through July and August. Seeds fall in September. In late August the stand was considered to be at a relatively steady state, having used all available soil moisture. Aboveground grass biomass of *A. desertorum* reached a maximum in late August (Table 1) with the development of mature seed heads. These findings are consistent with those reported by Currie and Peterson (1966). They found that Fall yields of *A. desertorum* in south central Colorado were greater than Spring yields in five out of eight years and that the eight year mean Fall yield was about 20 percent greater than the eight year mean Spring yield. In contrast, Sneva and Hyder (1960) have reported that Spring standing crops are generally greater than Fall standing crops in eastern Oregon.

Biomass of the three components of the plant subsystem fluctuated appreciably over the three years (Tables 2, 3, and 4). Aboveground biomass of *A. desertorum* was about 2400 kg per ha in 1971, 700 kg per ha in 1972 and 2200 kg per ha in 1973. Sixty percent of the aboveground biomass was new growth in 1972. Seventy-nine percent of the aboveground biomass was new growth in 1973. Therefore, aboveground *A. desertorum* new growth was 400 kg per ha in 1972 and 1740 kg per ha in 1973. New growth on the Curlew Valley site exceeded that reported for similarly treated seedings near Benmore and Eureka, Utah, where the range of new growth production reported by Cook (1966) over the nine year period was 52 kg per ha. The great fluctuations in biomass among years were due largely to differing annual precipitation regimes.
Table 1. Changes in the estimated aboveground biomass of *Agropyron desertorum* through the 1972 growing season, assuming a constant density of 12 plants per m$^2$

<table>
<thead>
<tr>
<th>Date</th>
<th>Weight per individual (grams)</th>
<th>90% confidence interval</th>
<th>Kg per ha</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 1972</td>
<td>5 grams</td>
<td>$\pm 1.0$ grams</td>
<td>600</td>
</tr>
<tr>
<td>July 1972</td>
<td>4 grams</td>
<td>$\pm 1.0$ grams</td>
<td>480</td>
</tr>
<tr>
<td>August 1972</td>
<td>6 grams</td>
<td>$\pm .5$ grams</td>
<td>720</td>
</tr>
</tbody>
</table>

Table 2. Biomass of plant components of the Curlew Valley crested wheatgrass site, August, 1971

<table>
<thead>
<tr>
<th>Component</th>
<th>Weight per individual (grams)</th>
<th>90% confidence interval</th>
<th>Biomass (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground <em>Agropyron desertorum</em></td>
<td>21</td>
<td>$\pm 3$</td>
<td>2,400</td>
</tr>
<tr>
<td>Litter Total</td>
<td>25.79</td>
<td>$\pm 3.49$</td>
<td>5,200</td>
</tr>
<tr>
<td>Roots 0-20 cm</td>
<td>4.29</td>
<td>$\pm .57$</td>
<td>8,500</td>
</tr>
<tr>
<td>Roots 20-40 cm</td>
<td>5.05</td>
<td>$\pm .51$</td>
<td>10,000</td>
</tr>
<tr>
<td>Roots Total</td>
<td>9.34</td>
<td></td>
<td>18,600</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>26,100</td>
</tr>
</tbody>
</table>
Table 3. Biomass of plant components of the Curlew Valley crested wheatgrass site, August, 1972

<table>
<thead>
<tr>
<th>Component</th>
<th>Weight per individual (grams)</th>
<th>90% confidence interval</th>
<th>Biomass (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agropyron desertorum</td>
<td>6</td>
<td>± .5</td>
<td>700</td>
</tr>
<tr>
<td>Litter &gt; 2 mm</td>
<td>13.71</td>
<td>± .53</td>
<td>2,700</td>
</tr>
<tr>
<td>Litter &lt; 2 mm</td>
<td>16.33</td>
<td>± .57</td>
<td>3,300</td>
</tr>
<tr>
<td>Litter Total</td>
<td>30.04</td>
<td>± .57</td>
<td>6,000</td>
</tr>
<tr>
<td>Roots 0-20 cm</td>
<td>6.55</td>
<td>± .37</td>
<td>13,000</td>
</tr>
<tr>
<td>Roots 20-40 cm</td>
<td>3.58</td>
<td>± .36</td>
<td>7,100</td>
</tr>
<tr>
<td>Roots Total</td>
<td>10.13</td>
<td></td>
<td>20,200</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
<td>27,800</td>
</tr>
</tbody>
</table>

Table 4. Biomass of plant components of the Curlew Valley crested wheatgrass site, September, 1973

<table>
<thead>
<tr>
<th>Component</th>
<th>Weight per individual (grams)</th>
<th>90% confidence interval</th>
<th>Biomass (kg/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agropyron desertorum</td>
<td>19</td>
<td>±2</td>
<td>2,200</td>
</tr>
<tr>
<td>Litter &gt; 2 mm</td>
<td>8.19</td>
<td>± .63</td>
<td>1,600</td>
</tr>
<tr>
<td>Litter &lt; 2 mm</td>
<td>15.46</td>
<td>± .85</td>
<td>3,100</td>
</tr>
<tr>
<td>Litter Total</td>
<td>23.65</td>
<td>± .85</td>
<td>4,700</td>
</tr>
<tr>
<td>Roots 0-20 cm</td>
<td>8.97</td>
<td>± .63</td>
<td>17,900</td>
</tr>
<tr>
<td>Roots 20-40 cm</td>
<td>4.77</td>
<td>± .26</td>
<td>9,500</td>
</tr>
<tr>
<td>Roots Total</td>
<td>13.74</td>
<td></td>
<td>27,300</td>
</tr>
<tr>
<td>TOTAL</td>
<td></td>
<td></td>
<td>34,300</td>
</tr>
</tbody>
</table>
Primary production in arid and semi-arid environments increases linearly as a function of increasing rainfall (Walter, 1964). Weaver and Albertson (1956) reported that grasslands yields may vary by a factor of eight between wet and dry years.

The litter mass was estimated to be 5200 kg per ha in 1971, 6000 kg per ha in 1972, and 4700 kg per ha in 1973. Over the three years there averaged about four times as much grass litter as aboveground grass biomass. About 40 percent of the grass litter occurred in particle sizes greater than 2 mm.

Total root biomass estimates increased progressively over the three years. Root biomass from the soil surface to 40 cm deep was 18500 kg per ha in 1971, 20200 kg per ha in 1972, and 27300 kg per ha in 1973. About 60 percent of the roots occurred in the 0-20 cm zone and 40 percent in the 20-40 cm zone. Root biomass averaged 16.5 times that of the aboveground standing crop. During the three year study it was estimated that root components comprised about 90 percent of the combined aboveground and belowground biomass. One could expect the root to top biomass proportion to increase with increasing aridity (Bray, 1963). Therefore, the Curlew Valley data are consistent with the findings of Rodin and Bazilevich (1968), who reported that root materials comprised 85 percent of the oven dry peak biomass of dry steppe and temperate dry steppes of Eurasia. The problem of separating root biomass from underground litter will be discussed later.

Examination of Tables 2, 3, and 4 show that the precision of the validation data is good for all three vegetation components. Precision
increased in 1972 and 1973 when the number of samples was doubled. If an arbitrary minimum resolution requirement for validating the models is established so that means have 90 percent confidence intervals no greater than plus or minus 10 percent of themselves, then the majority of these data approach or surpass minimum resolution. Significant differences (\( \alpha = .10 \)) can be detected with respect to the year that biomass of some of the components was harvested. Thus, the assumption made in the research design is valid. Field measurements adequately detected changes in the biomass of the three important plant components.

Until the advent of the International Biological Program, the precise documentation of aboveground, belowground and litter biomass of any plant community was rare. In isolation, these data are of small importance. However, they will take on greater value when similar data from other plant communities are reported. They will provide a base of comparative information which can be used to document the structure of communities, estimate productivity and turnover rates, and thereby guide management policy.

Assumption 2: Validation studies can adequately measure annual changes in chemical content of the important biotic components per unit area.

This assumption is basic to the model-validation concept. The models were to predict changing chemical contents of the biotic components as they responded to factors and processes. Validation studies tested the models by making chemical content analysis on biomass samples from the validation sites. If the validation site measurements are not precise enough to detect changes in chemical
contents, then the validation concepts of the research design are in error.

The chemical content of biotic components is potentially a function of two factors: 1) the chemical concentration of the component, and 2) the weight of the component per unit area. Table 5 shows the chemical concentrations of ash elements, nitrogen and fats as well as the caloric contents of the vegetation components of the crested wheatgrass site in the fall of 1972 and 1973.

Holt and Hilst (1969) reported that the chemical composition of plants change from day to day. Malone (1968) further reported that chemical changes occur in plants from season to season. In Curlew Valley chemical concentrations of energy and nutrients of each component were remarkably similar in the fall of 1972 and 1973 (Table 5). This is notable as 1972 was a dry year and 1973 a relatively wet year. The validation studies detected two exceptions; nitrogen decreased from 1.09 g to .57 g per 100 g of new A. desertorum shoot growth and ash elements increased from 11.96 g to 22150 g per 100 g of old A. desertorum shoot growth. However, chemical concentrations remained relatively constant from one Fall to the next.

Golley (1961) reported some general energy values for plant materials. He found that aboveground parts averaged about 4 kcal per g, root materials 4.7 kcal per g and litter 4.3 kcal per g. The Curlew Valley A. desertorum averaged about 4 kcal per g for aboveground plant parts, 2.9 kcal per g for root materials and 3 kcal per g for litter. The discrepancies between Golley's estimates and the Curlew Valley data are not surprising. Golley (1961) stated at the conclusion of
Table 5. Concentrations of chemical contents in plant components collected in August 1972 and September 1973a

<table>
<thead>
<tr>
<th>Component</th>
<th>Calories/gram</th>
<th>% Ash by wt</th>
<th>% Nitrogen by wt</th>
<th>% Fats by wt</th>
</tr>
</thead>
<tbody>
<tr>
<td>New Growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agropyron desertorum</em></td>
<td>4214±.71</td>
<td>4234±1.07</td>
<td>6.00±.73</td>
<td>6.27±1.85</td>
</tr>
<tr>
<td>Old Growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agropyron desertorum</em></td>
<td>3934±.82</td>
<td>3561±1.78</td>
<td>11.96±1.32</td>
<td>22.50±.21</td>
</tr>
<tr>
<td>Litter &gt; 2 mm</td>
<td>3270±.17</td>
<td>3644±.50</td>
<td>26.88</td>
<td>22.33±.35</td>
</tr>
<tr>
<td>Litter &lt; 2 mm</td>
<td>2391±.19</td>
<td>2754±.10</td>
<td>46.03</td>
<td>40.12±.08</td>
</tr>
<tr>
<td>Total Grass Litter</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Roots 0-20 cm</td>
<td>2985±.10</td>
<td>2848±1.50</td>
<td>32.81±.18</td>
<td>37.16±.15</td>
</tr>
<tr>
<td>Roots 20-40 cm</td>
<td>2981±1.75</td>
<td>2957±.70</td>
<td>32.10±.36</td>
<td>31.82±.03</td>
</tr>
</tbody>
</table>

aDeviations about the means are all less than plus or minus two percent of the mean unless otherwise specified. Deviations were calculated by dividing the range of output by two and expressing it as a plus or minus percentage of the mean.
his paper that seasonal and annual variations in energy contents of plant materials were sufficiently great to discourage researchers from using general published averages. Regardless, the Curlew Valley *A. desertorum* did have a higher energy content than the generally published values for these components. In addition, the aboveground portions had a higher energy and nitrogen content than those reported for *A. desertorum* by Cook and Harris (1968). They reported digestable energy to be about 2 kcal per g and nitrogen about .65 percent of oven dry weight late in the growing season. The Curlew Valley aboveground *A. desertorum* had a nitrogen content of about .85 percent.

Chemical concentrations changed little from fall to fall (Table 5). Tables 2, 3, and 4 show that biomass fluctuated measurably from year to year. Thus, the chemical contents per ha fluctuated primarily as a function of changing biomass. This is shown in Table 6 which gives estimates in kg per ha of nitrogen, ash elements, calories, and fats.

Additivity of variances is an important factor to consider in interpreting data conversions, data synthesis and model validation. Additivity of variance is defined by the formula

$$S_p = \sqrt{\frac{S_1^2N_1 + S_2^2N_2}{(N_1-1)+(N_2-2)}}$$

where $S_p$ is the pooled variance (Ostle, 1965). This equation assumes that both data sets are drawn from independent populations with equal variability. Data interpretation is difficult if the data are imprecise and then manipulated so that the pooled variance of the final result is very great. Table 6 was generated by multiplying the biomass
Table 6. Chemical contents in kg per ha of the plant components collected August, 1972, and September, 1973

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>New Growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agropyron desertorum</em></td>
<td>5</td>
<td>10</td>
<td>29</td>
<td>108</td>
<td>1.77x10^6</td>
<td>7.36x10^6</td>
<td>31</td>
<td>74</td>
</tr>
<tr>
<td>Old Growth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agropyron desertorum</em></td>
<td>2</td>
<td>4</td>
<td>25</td>
<td>103</td>
<td>1.10x10^6</td>
<td>1.65x10^6</td>
<td>6</td>
<td>13</td>
</tr>
<tr>
<td>Total aboveground phytomass</td>
<td>7</td>
<td>14</td>
<td>54</td>
<td>211</td>
<td>2.87x10^6</td>
<td>9.01x10^6</td>
<td>37</td>
<td>87</td>
</tr>
<tr>
<td>Litter &gt; 2 mm</td>
<td>29</td>
<td>17</td>
<td>737</td>
<td>366</td>
<td>8.83x10^6</td>
<td>5.83x10^6</td>
<td>46</td>
<td>23</td>
</tr>
<tr>
<td>Litter &lt; 2 mm</td>
<td>47</td>
<td>46</td>
<td>1503</td>
<td>1241</td>
<td>7.89x10^6</td>
<td>8.54x10^6</td>
<td>49</td>
<td>40</td>
</tr>
<tr>
<td>Total Grass Litter</td>
<td>76</td>
<td>63</td>
<td>2240</td>
<td>1607</td>
<td>16.7 x10^6</td>
<td>14.4 x10^6</td>
<td>95</td>
<td>63</td>
</tr>
<tr>
<td>Roots 0-20 cm</td>
<td>208</td>
<td>273</td>
<td>4277</td>
<td>6635</td>
<td>38.8 x10^6</td>
<td>50.9 x10^6</td>
<td>120</td>
<td>106</td>
</tr>
<tr>
<td>Roots 20-40 cm</td>
<td>109</td>
<td>134</td>
<td>2304</td>
<td>3021</td>
<td>21.2 x10^6</td>
<td>28.1 x10^6</td>
<td>77</td>
<td>77</td>
</tr>
<tr>
<td>Total Roots</td>
<td>317</td>
<td>407</td>
<td>6581</td>
<td>9656</td>
<td>60.0 x10^6</td>
<td>79.0 x10^6</td>
<td>197</td>
<td>183</td>
</tr>
<tr>
<td>Overall Total</td>
<td>400</td>
<td>484</td>
<td>8875</td>
<td>11474</td>
<td>79.8 x10^6</td>
<td>99.2 x10^6</td>
<td>329</td>
<td>333</td>
</tr>
</tbody>
</table>
figures from Tables 3 and 4 times the chemical concentration figures from Table 5. The variability of the data in Tables 3, 4, and 5 is low, and only one multiplication was made in creating Table 6, therefore the additivity of variance was ignored.

Table 6 shows that aboveground phytomass averaged about 10 kg per ha of nitrogen and 130 kg per ha of nitrogen and 8000 kg per ha of ash. Litter materials contributed about 70 kg per ha of nitrogen and 1900 kg per ha of ash. Rodin and Bazilevich (1968) estimated that combined aboveground and belowground phytomass would yield 1060 kg per ha of nitrogen and 340 kg per ha of ash on the dry steppes and temperate dry steppes of Russia. They estimated the litter to contain about 8 kg per ha of nitrogen and 24 kg per ha of ash. West (1972), working in southeastern Idaho, reported that A. desertorum leaves, roots, and litter contained 1.23, .70, and .65 percent nitrogen, respectively. These figures demonstrate the variability in the chemical makeup of apparently similar plant communities.

It has been pointed out that changes in biomass components account for most of the chemical differences of the A. desertorum plant community between years. It was seen from Tables 2, 3, 4, 5, and 6 that the field and laboratory techniques employed in the validation studies are sensitive enough to measure the annual changes in the chemical makeup of the community. These data verify that chemical concentrations in biotic components are dynamically quantifiable. The second assumption of the research design is valid.

Assumption 3: Validation studies can develop regression models which accurately predict states of hard-to-sample components. The
modellers assumed that there were quantifiable relationships among the biomass components of the ecosystem. It was assumed that data collected on the validation sites could generate regression equations to predict root and litter biomass given aboveground biomass (MacMahon, 1972). This would eliminate the expense of continually harvesting all three vegetation components on the validation sites. The relative success or failure of generating adequate regression equations may comment on the probable success of the modelers to quantify similar relationships in their models.

To test the assumption three hypotheses were made: It was hypothesized 1) that regression models could be developed to predict aboveground phytomass from simple aboveground plant measurements, 2) that litter biomass could be predicted from parameters of aboveground biomass, and 3) that root biomass could be predicted from parameters of aboveground biomass.

The first hypothesis was that aboveground biomass of *A. desertorum* could be predicted from simple measurements of plant stature. Simple linear regression equations predicting aboveground plant yields from simple plant measurements have been developed and reported for *A. desertorum* by Cook (1960) in Curlew Valley and Hickey (1961) in New Mexico. Hickey worked with a sample size of 923 plants and reported an $r^2$ of .85. His plant measurements included basal diameter, compressed crown diameter and compressed leaf length. On the Curlew Valley site, cylindrical volumes were calculated from the basal area and height data on 225 *A. desertorum* and regressed on their individual dry weights. The graph of this relationship is shown in Figure 1.
Figure 1. The relationship between volume and biomass of *A. desertorum*. \( y = 1.33 + 0.01x, \ r^2 = 0.85 \)
The simple linear regression formula, WT=1.33+.01V accounts for 85 percent of the variability within the data ($r^2=.85$). If adequate regression resolution is arbitrarily defined as $r^2=.80$ then *A. desertorum* volume was an adequate predictor of aboveground grass biomass.

A second hypothesis was made that there is a precise relationship between parameters of aboveground biomass per unit area and the root biomass below that area. To test this hypothesis the relationship between the sum of the *A. desertorum* basal areas per square meter and the estimated root biomass below that square meter was plotted (Figure 2). This relationship yielded an imprecise $r^2=.04$. The relationship between *A. desertorum* biomass per square meter was also imprecise (Figure 3, $r^2=.09$). These analyses show that neither *A. desertorum* basal nor aboveground biomass per unit area was a good predictor of belowground biomass per unit area.

A third hypothesis was put forth that there is a precise relationship between parameters of aboveground phytomass per plot and the litter mass on that plot. To test this hypothesis a graph was generated of the relationship between the sum of the *A. desertorum* basal areas per square meter and the sum of the litter mass on those plots (Figure 4, $r^2=.01$). A graph was also made of the relationship between the phytomass of the *A. desertorum* per square meter and the mass of litter on those square meters (Figure 5, $r^2=.01$). Neither basal area of *A. desertorum* nor aboveground biomass of *A. desertorum* per square meter was a good predictor of litter mass.

The relationships among aboveground biomass, root biomass and litter mass were found to be imprecise. These relationships must be
Figure 2. The relationship between basal area of *A. desertorum* per m² and estimated root biomass per m².
Figure 3. The relationship between aboveground standing crop of *A. desertorum* per $m^2$ and estimated root biomass.
Figure 4. The relationship between the total basal area of *A. desertorum* per m$^2$ and the estimated total litter biomass per m$^2$. 
Figure 5. The relationship between the aboveground biomass of *A. desertorum* per m$^2$ and estimated litter biomass per m$^2$. 
considered functions of at least two dynamic processes: aboveground grass, root and litter production and aboveground grass, root and litter disappearance (Medwecka-Kornas, 1971). In deserts, production is primarily a function of total annual precipitation (Walter, 1964). Disappearance is a function of rates of decay, mineralization, animal consumption, transport and harvest (West, 1975). It is not possible to determine the product of these processes by making only one state measurement per year. The relationships might be determined by monitoring rates of grass, root and litter production and rates of grass, root and litter disappearance as they occur through the seasons. The research design was wrong in assuming that the product of several dynamic processes could be predicted from simple infrequent state measurements.

Assumption 4: Annual changes in the biotic components of the ecosystem are logically correlated with changes in meteorological factors.

The Desert Biome ecosystem models are founded on the concept that meteorological events drive the components of the system. It must be assumed that the components of the system respond in a quantitatively predictable fashion to the meteorological factors impinging upon them. If this were not true, prediction would be impossible. To test this assumption, data from three years of validation studies were used to determine whether the three primary vegetation components on the crested wheatgrass site responded precisely to different regimes of annual growing season precipitation.
The components of biomass were graphed as dependent variables. The three different precipitation regimes were graphed as the independent variables. Regression equations and coefficients of determination were calculated for each relationship. Each graph has only three points, one for each year of the study. Therefore they have questionable statistical value. However, the graphs are important for the trends they display and the regression equations provide computable functions for the relationships.

The most basic relationships to examine were the effects of precipitation on the vegetation components of the ecosystem. Table 7 gives the growing season precipitation from 1970 through 1973. Growing season precipitation was defined as the total precipitation falling on the site from September 1 to August 31 the following year. Growing season precipitation ranged from 180 mm to 420 mm per year during the three years of the study. This represented 75 percent of the range of precipitation recorded in Snowville, Utah, during the last 24 years.

<table>
<thead>
<tr>
<th>Growing Season</th>
<th>Precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>September 1969 - August 1970</td>
<td>350 mm</td>
</tr>
<tr>
<td>September 1970 - August 1971</td>
<td>420 mm</td>
</tr>
<tr>
<td>September 1971 - August 1972</td>
<td>180 mm</td>
</tr>
<tr>
<td>September 1972 - August 1973</td>
<td>380 mm</td>
</tr>
</tbody>
</table>
The hypothesis was made that increases in annual growing season precipitation generated increases in annual aboveground standing crops of *A. desertorum*. Several researchers have reported linear relationships between precipitation and aboveground phytomass production in semi-arid areas of America (Craddock and Forsling, 1938; Hutchings and Stewart, 1953; Blaisdell, 1958; Sneva and Hyder, 1962; Currie and Peterson, 1966). Figure 6 shows the relationship between annual growing season precipitation and annual aboveground standing crops of *A. desertorum* on the Curlew Valley site. The rate of increase in aboveground standing crop is linear with respect to increasing precipitation. The precision is good over the range of conditions encountered. This adds further support to the theory that primary productivity in arid to semi-arid areas increases proportionately with increasing rainfall (Walter, 1964).

A second hypothesis was made that increases in annual growing season precipitation decrease rates of grass litter production and increase rates of litter decomposition, causing a net decrease in the mass of soil surface litter. Figure 7 shows the graph of the relationship substantiating the hypothesis. This is an inverse relationship. Further analysis shows that litter mass correlates directly with previous growing season precipitation (Figure 8). This was expected as *A. desertorum* litter falls primarily in the winter and early spring as leaf and stem parts produced the previous summer. Additionally, litter:aboveground grass ratios and growing season precipitation have an inverse relationship (Figure 9). This supports the concept that when precipitation is high, aboveground biomass is high and
Figure 6. The relationship between growing season precipitation and the resultant August aboveground biomass of *A. desertorum*. 
Figure 7. The trend of the relationship between current growing season precipitation and the current year's mass of *A. desertorum* soil surface litter.
Figure 8. The trend of the relationship between preceding growing season precipitation and the current year's mass of *A. desertorum* soil surface litter.
Figure 9. The trend of the relationship between growing season precipitation and annual litter mass:aboveground biomass ratios.
litter mass relatively low. When precipitation is low, aboveground biomass is low and litter mass relatively high. This relationship appears more precise than that developed between aboveground phytomass and litter under assumption 3 because of the introduction of the precipitation factor. Precipitation heavily influences both production and decomposition rates in the desert.

A third hypothesis was made that increases in growing season precipitation would generate increases in root biomass. Figure 10 shows the graph of this relationship. The scatter diagram lends no credence to the hypothesis. There are two factors which complicate the interpretation of root core data: 1) there are no generally accepted methods to distinguish live root material from dead material in the cores and 2) there are no generally accepted methods to determine the longevity of root materials. However, Dahlman and Kucera (1965) estimated that the root turnover rate is once every four years in native tall grass prairie vegetation in Missouri. Also, Kucera et al. (1967) estimated that only 25 percent of the belowground standing crop was living root material in the same vegetation type.

Further analysis of the Curlew Valley data shows that if root biomass is regressed on previous growing season precipitation the relationship is inverted (Figure 11). This implies that the material collected in the root samples is more a function of the previous season's production and decomposition than of events of the current season.

When root biomass:aboveground biomass ratios are plotted against growing season precipitation an inverse relationship emerges (Figure 12). This shows that the root and shoot portions of *A. desertorum* operate
Figure 10. The trend of the relationship between current growing season precipitation and the current year's root biomass.
Figure 11. The trend of the relationship between previous growing season precipitation and the current year's root biomass.
Figure 12. The trend of the relationship between current growing season precipitation and annual root biomass:aboveground biomass ratios.
in a compensatory manner in response to precipitation input. When
growing season precipitation is high, aboveground biomass is high and
root biomass relatively low. When growing season precipitation is
low, shoot biomass is low and root biomass relatively high.

Shoot:root ratios ranged from 1:7.7 to 1:12.5 during the three
year study. For perennial grasses in arid and semi-arid regions,
ratios between 1 and 20 have been reported (Noy-Meir, 1973). Shoot:
root ratios are high in arid lands for three reasons. The proportion
of roots to tops increases with increasing aridity (Bray, 1963). The
proportion of dead to live roots can be expected to increase in arid
areas where cooler, dryer conditions reduce decomposition rates
(Lewis, 1970). Shoot/root fractions include not only active roots
and shoots but also reserve organs and underground litter. There may
be an unusual amount of dead root material on the Curlew Valley grass
site remaining from the shrub eradication program carried out in 1965.

The relationships between precipitation and root response were
the least precise of the three components studied. Better methods
and more frequent sampling will be required to gain better insights
into the dynamics of underground plant components.

The research design calls for an understanding of how chemical
contents per ha vary as a function of different precipitation regimes.
Concentrations of chemical contents in plant components have been shown
to change little from Fall to Fall. Annual changes in chemical contents
per ha can be expected to vary closely as a function of annual changes
in component biomass. Therefore, it is expected that fairly precise
relationships will also be found between the chemical contents per ha
of the components and changing precipitation regimes.
Vegetal biomass and its chemical content were studied for three years on the Curlew Valley crested wheatgrass IBP validation site. These data were used to test four assumptions underlying the construction and validation of the Desert Biome ecosystem models.

The Desert Biome research design assumed that aboveground biomass, litter and root biomass were dynamic components and would show measurable changes from year to year. The validation site data showed that this assumption was correct.

The Desert Biome research design made the assumption that the content of vital elements of the three primary vegetation components were dynamic and changed from year to year. The validation data showed that chemical concentrations within plant components were remarkably static from Fall to Fall and that changes in chemical contents were primarily a function of annual changes in biomass.

The Desert Biome validation design assumed that aboveground plant biomass could be used as the independent variable from which litter and root biomass could be predicted. The validation data showed that this assumption was incorrect. Aboveground biomass may well account for the production of litter and roots but does not provide any accounting for decomposition of roots and litter on and under the soil surface. A measure of production alone cannot be used to estimate both production and decomposition. Aboveground biomass data alone cannot be used to predict root and litter mass.
The Desert Biome research design made the assumption that annual changes in the vegetation components of biomass could be logically and precisely correlated to annual precipitation regimes. The validation data showed this to be true. Precipitation data provided an index to both production and decomposition rates. Regression equations were generated from which the biotic responses of the grass tops, roots and litter were predicted from annual growing season precipitation.

The objective of the Desert Biome was to develop sophisticated computer models to simulate the behavior of desert ecosystems. The models were intended for use in land and resource management. However, the Desert Biome models are presently too general to be used for this purpose (Goodall, 1972). In this respect the modelling effort has not met expectations.

It has been shown herein that the validation studies provide a firm data base from which regression models can be developed. Given the mean A. desertorum plant volume and density one can predict the aboveground standing crop of A. desertorum per unit area (Figure 2). Given the Fall aboveground standing crop of A. desertorum and the annual growing season precipitation one can predict the mass of the litter (Figure 10) and root (Figure 13) components of the stand. This shows that validation data can be integrated into a valuable body of ecological knowledge independent of the findings of the rest of the Desert Biome Program. The value of the validation studies will increase as a function of their duration. In several years the validation data may be viewed as one of the major contributions of the Desert Biome Program.
LITERATURE CITED


VITA

Biographical Information: Born at Salem, Oregon, April 6, 1948, son of Darwin W. and Shirley R. Shinn; married, Vicki Anne Fox, October 12, 1968, no children.

Education: Attended elementary school in Tigard, Oregon; graduated from Tigard Senior High School, June, 1966; received the Bachelor of Arts degree from Lewis and Clark College, Portland, Oregon, with a major in Natural Sciences, June, 1970; completed the requirements for the Master of Science degree, specializing in Range Ecology, at Utah State University in December, 1974; began work towards a Ph.D. with the Range Science Department at Utah State University January, 1975.

Occupational Experience:
June 1966-December 1969; Warehouseman and sprinkler fitter's helper for Viking Automatic Sprinkler Company, Portland, Oregon; worked on the fabrication and installation of fire preventive sprinkler systems full-time during the summers and part-time during the remainder of the year in 1968 and 1969.

June 1970-October 1970; Research technician, Utah State University Ecology Center; primarily did gas-liquid chromatography and pheremone isolation in the laboratory on an ungulate pheremone and behavior research project under Dr. Dietland Muller-Schwarze; collected deer glands from hunter check stations and aided in the care and management of captive research animals.

October 1970-December 1970; Laboratory teaching assistant, Department of Wildlife Science, Utah State University; helped Dr. Allan Stokes set up and carry out teaching laboratories for the students in the Animal Behavior class.

March 1971-December 1974; US/IBP Desert Biome Validation research technician, Utah State University Ecology Center; carried out broad ranging ecological research on a Great Basin desert site in Curlew Valley, Utah, following the general design of the Desert Biome Validation program. A co-worker and I were respon­sible for much of the research design, sampling, laboratory work, data analysis and written reports on the Curlew Valley program. This included work in the fields of abiotics, meteorology, plant and animal ecology, entomological sampling and soil-water relationships.

September 1974; Ecological consultant for VTN Corporation, working through the Utah State University Foundation; worked for 6 days designing and employing plant sampling techniques on oil
shale lease tracts UA and UB near Vernal, Utah. The data were collected as part of the two year baseline study required of Phillips Petroleum, Sun Oil and White River Oil prior to oil shale development.

December 1974; Ecological consultant for Dr. Mike Wolfe, Utah State University Ecology Center, and Mike Kochert, Raptor Specialist, Snake River Birds of Prey Natural Area, BLM, Boise, Idaho; consisted of three days on-site reconnaissance and discussion of long and short term approaches, research designs and methods of assessing the relationships among land use patterns and vegetation types, raptor prey base and raptor prey preferences.


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