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Plant Demographics Studies of Tall Threetip Sagebrush-Grass Vegetation on the Eastern Snake River Plains, Idaho

Kenneth Harold Rea
Utah State University

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PLANT DEMOGRAPHIC STUDIES OF TALL THREETIP SAGEBRUSH-GRASS VEGETATION ON THE EASTERN SNAKE RIVER PLAINS, IDAHO

by

Kenneth Harold Rea

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Range Science
(Ecology)

UTAH STATE UNIVERSITY
Logan, Utah

1976
ACKNOWLEDGEMENTS

This study is the result of the combined efforts of many people and several organizations. The U. S. Forest Service kindly provided these data from the U. S. Sheep Experiment Station, Idaho, and the U.S. I.B.P. furnished partial financial support for data reduction and analysis.

I appreciate the support of my graduate committee, their suggestions, and assistance. Many hours of their time were donated in my behalf.

I would like to thank Dr. Neil West, my major professor, for his critical review of this dissertation, and his help throughout my program. I would also like to thank the following for their assistance and suggestions in various ways: Roy Harniss, Robin Tausch, and Kim Marshall.

Finally, I extend a husband's love and gratitude to my beautiful wife, Cherri, who graciously supported my efforts.

Kenneth H. Rea
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ABSTRACT

Plant Demographic Studies of Tall Threetip Sagebrush-Grass Vegetation on the Eastern Snake River Plains, Idaho

by

Kenneth Harold Rea, Doctor of Philosophy

Utah State University, 1976

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

It has commonly been assumed that grazing decreases the longevity of plants, however, very few studies address this question. Knowledge of mean age, longevity and other aspects of population dynamics would help improve estimates of productivity and nutrient cycling and aid understanding of range condition and trend. These data would also aid in developing a theory of community organization and control.

As a step toward these ends, pantograph records from twelve 1 m² plots established at the U. S. Sheep Station on the Snake River Plains of southeastern Idaho between 1923 and 1935 were examined. The plots were mapped almost yearly until 1956. These records were analyzed for establishment and survival of populations of major vascular, perennial plant species of the tall threetip sagebrush-grass vegetation type.

Average longevities of the grazed plants were significantly different from ungrazed populations for some species. For the pastures grazed by sheep in the fall the average longevities of the dominant grass and two subdominant grasses were increased whereas the average longevity of tall threetip sagebrush was reduced by grazing.
The differences in average longevity due to grazing are thought due to alteration of competitive relationships. The photosynthetically active sagebrush is sensitive to grazing in the fall whereas the grasses are dormant. A slight reduction in the total volume of the sagebrush apparently releases resources to the grasses the following spring.

The greatest mortality was observed during the first year of life for all species. Survivorship curves for the first eleven years of life of most species could be linearized by logarithmic transformations on both axes indicating that the chance for survival improved with age, up to the physiological maximum.

No linear relationships of increasing size to age were found in these plants. This indicates a considerable plasticity in the growth characteristics of these plants, where in poor years negative growth can occur by the reduction of unsupportable biomass. This allows plant size to fluctuate with fluctuating environment, and allows for stands of even sized plants with great age differences.

Labeling recruitment to these plant populations as "pulse" phenomena becomes a matter of definition. If a log-normal distribution is expected, as indicated by some researchers, outliers are not present and "pulse" regeneration does not occur in this system. However, if recruitment is expected to follow a normal distribution then the years with high numbers of seedlings become "pulses," by definition.

From these analyses, it appears that these semi-desert communities are closed (the available resources are totally used) and replacement of individuals is somewhat random following more or less random death.
INTRODUCTION

As human populations increase there is an ever increasing demand on ecosystems by man. Since plant mortality and longevity may be related to various environmental perturbations, a basic knowledge of the demographic responses of plants in unaltered wild populations is becoming a vital need of the working ecologist.

Demographic analyses of perennial plant populations in arid to semi-arid environments are unusual due to lack of easy means to determine age of these plants and limitations of time and money required for collection of data sets over long periods of time. However, as data become available occasional studies do appear in the literature.

Besides the intrinsic interests, the knowledge of plant longevity and mortality has several applications. For example, the use of age-class distribution data to interpret successional trends of plant communities has been common, particularly in temperate regions where age classes are reflected in growth rings of woody plants. This knowledge allows man to more efficiently manage these systems for a higher sustained yield of needed water, foods, fibers, and recreational activities.

Other uses could include enhancement of estimates of the rate of nutrient exchange from living phytomass to non-living components of the ecosystem. By knowing the approximate age, structure, and density of a given species within a community, coupled with its mortality rate (from which the number dying in each age interval can be calculated) a fairly good estimate of detritus input to the system from this taxon becomes available.
Though relatively little work has been done on the demography of perennial plants in non-tree-dominated vegetation, some hypotheses of plant longevity, succession and community organization have been alluded to in the literature by various authors, and indeed have become accepted as "fact" by many ecologists. The thrust of this study was to clearly restate three such hypothesis in testable form and reject or accept them within the confines of the data set available.

Objectives

The three hypotheses chosen were:

1. Livestock grazing has no effect on the average life span of perennial plants; i.e., there is no difference in the survivorship curve between a grazed and ungrazed population.

2. Survivorship curves for perennial range plants can be best fitted by semi-logarithmic regression equations.

3. Regeneration of semi-desert plant communities occurs as a "pulse" or episodic phenomenon more than X percent of the time with irregular thrusts of large numbers of individuals entering the population due to favorable conditions.

The alternates to these hypotheses were then:

A. Livestock grazing has a measurable effect on the average life span of perennial plants; i.e., there is a difference in the survivorship curve between a grazed and ungrazed population.

B. Survivorship curves for perennial plants can be best fitted by other than semi-logarithmic regression equations.
C. Regeneration of semi-desert plant communities does not occur as a "pulse" or episodic phenomenon more than X percent of the time with irregular thrusts of large numbers of individuals entering the population due to favorable conditions.
LITERATURE REVIEW

Harper (1960), and Harper and White (1974) have previously reviewed most of the available literature in the field of plant demography. It can be concluded from these reviews that plant demography has mostly been developed through studies of annual plants in mesic environments. The need for accurate, long term record keeping or reliable age dating techniques has apparently hampered the study of perennial plant populations, except for trees. The harsher environments have less human population, are generally lower in economic value, and therefore have comparatively less of a research history. It is questionable that generalizations developed from earlier work dealing with mesic annuals is applicable to perennials in semi-arid environments.

Grazing effects

Of most relevance to this study are a number of papers dealing with demographic aspects from arid semi-arid grassland and shrubland communities. For instance, the work done by Williams (1966, 1968a, 1968b, 1969, and 1970) on the population dynamics of two perennial grasses in western New South Wales, Australia, is of particular interest. He found that sheep grazing increased the mortality rates of a climax grass while it increased the life span and decreased the mortality rate of the dominant disclimax grass. However, his response index (numbers of plants of a given species per unit area grazed divided by numbers of plants of that species per unit area ungrazed, letting unity be neutral) leaves much to be desired in that it assumes identical population densities in the pastures at the start of the study. A false beneficial effect of grazing can be shown by simply having
twice the density of a given species in the grazed area compared to the ungrazed area at the start of the study.

In southern Arizona, Canfield (1957) utilized pantograph records from the Santa Rita Experimental Range to study longevity of 11 different grasses. He has shown that the primary (climax) grasses live longer without grazing by approximately 2 to 4 years, except for *Trichachne californica* which was 4 years shorter lived when ungrazed. The secondary grasses exhibited a reverse trend living 2 to 4 years longer under grazing, except for *Bouteloua filiformis* which showed no difference. Neither Canfield nor Williams used any statistical analyses to show significant differences.

Studies of plant demography on U. S. rangelands have been more recently approached by Dittberner (1971), and Wright (1972). They used records available from the Jornada Experimental Range in southern New Mexico to estimate average longevities of dominant desert grassland plants. Grazing did not appear to have a significant effect on life spans of the species they studied.

A few other demographic studies of western range plants have been made; however, only Wood (1966) considered grazing effects. Pantograph charts from the Desert Experimental Range in western Utah were used to estimate the longevity for *Artemisia spinescens*. Grazing seemed to inhibit plant establishment and was believed to influence the development of even-aged stands with plants of the same size and vigor.

**Shape of survivorship curves**

The second hypothesis to be examined is concerned with the shape of the survivorship curves. Yoda, et al. (1963) suggest that mortal-
ity is a continuous risk throughout the life of a plant, i.e., within year fluctuations in mortality rates occur but between year rates are more or less constant. They conclude that a plant population is being continually adjusted in numbers in response to the increasing size of the plants and a more or less fixed resource.

Harper (1967) favors the log-normal curve for plants. The development of this assumption comes from Harper's (1967) reanalysis of data from Tamm (1956) where changes in plant numbers (log scale) were plotted versus time. This relationship was found to be essentially linear, indicating that the chance of an individual dying remained fairly constant through time. Thus, Harper concluded that plant population changes may be analogous to radioactive decay and characterized by a "half-life."

The assumption of the generality of this relationship was used by Harper and Treshow (1974) in a study of longevity of plants in the foothills of the Wasatch Mountains near Salt Lake City, Utah. They used survival ratios from a set of permanently marked plants over a period of two years, and extrapolated the curves to extinction to estimate longevities for several forbs and one grass.

Another example of how this assumption has been used in the literature comes from Wallace and Romney (1972). In this study, estimates of the average longevity for Artemisia tridentata at the Nevada Test Site are given by assuming a decomposition rate for dead plants and extrapolating this into the density of live plants on the area in a linear fashion. From this technique they estimate average life spans of 30 to 40 years for this species.
The last hypothesis of interest to this study is that alluded to by Went (1955) which deals with a possible mechanism of regeneration of desert plant communities. This idea again appears in Chew and Chew (1965) and was recently re-enforced by Barbour (1969). Barbour points out that germination and survival is rare for Larrea, seeming to occur only in favorable years. He also states that occasional regeneration "pulses" are probably the cause for the few age classes found in many desert plant communities. In these cases, the triggering mechanism is probably favorable weather conditions which are conducive to high seed set, germination and survival of seedlings.

Odum (1969, p. 264) views pulse stability of ecosystems somewhat differently. He refers to the pulse as being a physical perturbation from outside the system and the effect of this exogenous event being a "compromise between youth and maturity" of the system. Thus, the "pulse" observed by the biologist is actually an effect of the true pulsing event.

The pulse idea is again presented by Noy-Meir (1973) when he refers to rainfall as the master input (controlling factor) in desert ecosystems. Effective events occur infrequently and thus, the driving input of the system comes in "pulses" and therefore the production and regeneration of the system follows the same pattern.

From these papers it is evident that "pulse" needs to be defined for the testing of this hypothesis. New plants coming into a population over a period of time will follow some form of frequency distribution which may be skewed to the right or have more individuals in the upper portion than in the lower portion of the distribution. Very infrequent events of large numbers entering a population would not be considered pulses if they were merely the upper portion of some expected frequency distribution.
Thus, for the purposes of this test, an event will only be considered a pulse if it is an obvious outlier from the expected upper portion of the distribution, occurring no more than 25 percent of the time. Furthermore, for a pulse to be the major factor behind regeneration and thus have large ecological impact on community dynamics it must not occur so infrequently as to have little chance of occurrence during the lifetime of a given plant species.

If "pulses" are considered to be infrequent establishment of large numbers of individuals, pulse phenomena then exists by definition. Thus, any point falling above some pre-determined cut-off position in the upper portion of the distribution is a pulse. This definition has been used by some ecologists, and points out how terminology derived from the vernacular or other disciplines, should be handled with care.
METHODS AND PROCEDURES

Study area

The data to be used for this study were collected from a set of grazed paddocks and ungrazed exclosures, of known recent history. They were located no more than 4 km apart, in homogeneous vegetation, at the U. S. Sheep Experiment Station about 10 km north of Dubois, Idaho (Figures 1 and 2). The station is on the Snake River Plains, at an elevation of about 1650 m. This rolling basaltic plateau is characterized by shallow aridosols. The mineral fertility of the soils is generally high, but due to the low level of precipitation (average annual rainfall is 27.8 cm) organic matter is relatively low. The soils involved in this study are typic calcixerolls and lithic calcixerolls. These are typified by dark brown (when moist), slightly calcareous, and loamy A horizons; light brownish-gray, strongly calcareous, and loamy Cca horizons; and lime-covered basalt R horizons.

The climate of this area is characterized by low precipitation, cold winters, and hot summers. The climatic regime shows about 50 percent of the precipitation arriving as snowfall between October to April, and roughly 30 percent as rainfall during May and June (the main growing season). Temperatures range from a maximum of 40° C to -30° C (Blaisdell, 1958). Standard climatic data have been collected at the station from 1925 to present.

Data set

The vegetal data set consists of pantograph charts from 1 m² plots permanently located within the exclosures and paddocks (Figure 3). The
Figure 1. Location of the U.S. Sheep Station on the Upper Snake River Plains, Idaho.
Scale 3 inches = 1 mile or 4.74 cm = 1 kilometer

Figure 2. Map of the U.S. Sheep Station, Dubois, Idaho, showing the location of the paddocks from which samples were taken.
Figure 3. A pantograph being used to map vegetation at the U. S. Experimental Sheep Station, Idaho.
instrument and procedures used are described in Pearse, Pechanec and Pickford (1935). Mapping of the charts was started between 1923 and 1935. Mapping was done by two-man crews (Blaisdell, 1958), with most paddocks involved in this study being first mapped in 1930. Mapping was then done almost annually until 1956. The mapping itself was done in late May to early July, as detailed in table 1.

Maps were not made during 1943, 1944, and 1948 due to lack of personnel. The data set was truncated to have it end in 1950, because of changes in the grazing regimes which occurred at that time (Laycock, 1967). Though six grazed and six ungrazed sets of plot charts have been made available by the U. S. Forest Service for analyses, three of the grazed plots (those under the spring-fall grazing regime) were mapped intermittently and have had to be dropped from the analyses (Table 1).

An examination of the basic data set for the most common species led to the selection of the following taxa: *Artemisia tripartita* Rydb. (tall threetip sagebrush), *Leptodactylon pungens* (Torr.) Nutt. (granite pricklygilia), *Gutierrezia sarothrae* (Pursh) Britton and Rusby (broom snakeweed), *Phlox* species (phlox), *Agropyron spicatum* (Pursh) Scribn. and Smith (bluebunch wheatgrass), *Poa* species (bluegrass), *Koeleria cristata* (L.) Pers. (prairie junegrass), *Oryzopsis hymenoides* (Roem. and Schult.) Ricker (indian ricegrass), *Stipa comata* Trin. and Rupr. (needleandthread). Data on two phlox species *Phlox longifolia* Nutt. (longleaf phlox) and *P. hoodii* Rich. (Hood's phlox) were combined, as were those of *Poa nevadensis*

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Table 1. Summary of quadrats charted from the U. S. Sheep Experiment Station, Dubois, Idaho

<table>
<thead>
<tr>
<th>Plot No.</th>
<th>Quadrat No.</th>
<th>Dates of data collection</th>
<th>Grazing history</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1A</td>
<td>Q4</td>
<td>6/12/30; 6/19/31; 6/21/32; 6/19/33; 5/29/34; 6/6/35; 5/26/36; 7/7/37; 7/15/38; 7/18/39; 6/20/40; 7/21/41; 6/10/42; 6/28/45; 7/12/46; 7/9/47; 7/22/49; 7/14/50</td>
<td>Fall grazed 1923 to 1950, averaging 43 sheep days per acre.</td>
</tr>
<tr>
<td>P1B</td>
<td>Q1</td>
<td>6/11/30; 6/19/31; 6/20/32; 6/17/33; 5/29/35; 5/25/36; 7/7/37; 7/3/38; 7/12/39; 6/19/40; 7/21/41; 6/8/42; 6/19/45; 7/11/46; 7/9/47; 7/22/49</td>
<td></td>
</tr>
<tr>
<td>P1B</td>
<td>Q3</td>
<td>6/12/30; 6/19/31; 6/21/32; 6/19/33; 6/5/34; 6/7/35; 5/25/36; 7/7/37; 7/15/38; 7/13/39; 6/20/40; 7/21/41; 6/9/42; 6/29/45; 7/11/46; 7/9/47; 7/22/49; 7/14/50</td>
<td></td>
</tr>
<tr>
<td>P2A</td>
<td>Q2</td>
<td>6/12/30; 6/22/31; 6/24/32; 5/18/34; 6/4/35</td>
<td>Spring-Fall grazing 1924 to 1950. 19 sheep days per acre in spring increased by 10 in fall.</td>
</tr>
<tr>
<td>P2A</td>
<td>Q3</td>
<td>6/12/30; 6/22/31; 6/24/32; 5/28/34; 6/4/35</td>
<td></td>
</tr>
<tr>
<td>P2B</td>
<td>Q1</td>
<td>6/12/30; 6/22/31; 6/24/32; 5/28/34; 6/4/36</td>
<td></td>
</tr>
<tr>
<td>P7E1</td>
<td>Q1</td>
<td>6/17/30; 6/26/31; 6/21/32; 6/14/33; 6/12/35; 5/21/36; 6/18/37; 7/21/38; 7/11/39; 5/20/40; 7/26/41; 6/23/42; 7/13/45; 7/16/46; 7/29/47; 7/18/49; 7/17/50</td>
<td>Ungrazed since 1923.</td>
</tr>
<tr>
<td>P7E1</td>
<td>Q2</td>
<td>7/31/23; 7/27/26; 7/18/27; 6/18/29; 6/17/30; 7/26/31; 6/21/32; 6/15/33; 6/12/34; 6/13/35; 5/21/36; 6/18/37; 7/20/38; 7/12/39; 7/2/40; 7/27/41; 6/23/42; 7/13/45; 7/16/46; 7/29/47; 7/18/49; 7/17/50</td>
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Table 1. Continued

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<th>Grazing history</th>
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<td>P7E1</td>
<td>Q3</td>
<td>6/17/30; 6/26/31; 6/21/32; 6/15/33; 6/13/34; 5/20/36; 5/12/39; 6/23/42; 7/13/45; 7/29/47; 7/19/49; 7/18/50</td>
<td>Ungrazed since 1923.</td>
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<td>P7E1</td>
<td>Q4</td>
<td>6/17/30; 6/26/31; 6/21/32; 6/15/33; 6/13/34; 6/23/42; 7/13/45; 7/29/47; 7/18/50</td>
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<tr>
<td>P10E1</td>
<td>Q1</td>
<td>6/14/32; 6/13/33; 6/11/34; 6/13/35; 5/25/36; 7/19/38; 7/23/41; 7/12/46; 7/18/50</td>
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<tr>
<td>P10E1</td>
<td>Q2</td>
<td>6/14/32; 6/14/33; 6/12/34; 6/14/35; 4/25/36; 5/26/37; 7/20/38; 6/23/41; 6/13/42; 7/16/46; 7/18/50</td>
<td></td>
</tr>
</tbody>
</table>

Corresponds to paddock numbers given in figure 2.
Vasey (Nevada bluegrass) and *P. sandbergii* Vasey (sandberg bluegrass), due to inability of personnel to reliably distinguish in the vegetative state the exact species of young plant in the field. The nine taxa considered collectively make up about 85 percent of the vegetal cover observed, (Appendix tables I-IV)

Individual plants of these taxa were located on the oldest chart available for each quadrat. If a plant of the same taxon occurred in the same position on the following charts it was considered to be the same plant. A 5 cm leeway on the ground, or a 5 mm leeway from the plant's position on the previous chart was allowed to cover recording errors and plant movements (Lieth, 1950). All plants not appearing on two successive charts were assumed to have lived less than one year. Once all plants were located on the first chart the successive charts were examined for new plants. All new plants were recorded and their successive existence followed. This allowed for the construction of a table showing the number of new individuals (a cohort) found each year, and allowed for following the decline of this cohort through time.

**Analysis of grazing effect**

At this point a decision had to be made concerning those years in which records were not kept. If a given number of plants within a cohort existed both before and after this time period, obviously the same number existed during the unrecorded time period and this number was inserted into the data matrix. However, if individuals died during this period there was no way of knowing exactly how many died at what time. Therefore, the data were analyzed three ways by using: (1) the upper boundary or extreme; i.e., no deaths occurred until the end of the time period, (2) a linear death rate during the time period, and (3) the lower limit; i.e.,
total death occurred at the start of the time period. This was done under the assumption that if the three situations yielded similar results the conclusions should be valid.

These tables (low, linear, and high) were then collapsed in the following manner to eliminate as much climatic variability as possible. The 1931 to 1940 period cohorts were added together across the first eleven age classes; i.e., all age class one's (new plants each year) for the period 1931 to 1940 were added together for a given paddock, the corresponding age class two's (1932 through 1941) were added together, etc. After this summary, all ungrazed paddocks were combined as were the fall grazed paddocks. Thus, three survivorship curves (low, linear, and high) were obtained for each taxon for both the ungrazed and grazed situations. These curves were then subjected to the Kolmogorov-Smirnov test (Tate and Clelland, 1957) to test for differences between their cumulative frequency distributions.

Since the Kolmogorov-Smirnov test is not as well known in the biological sciences as other statistical procedures, the mechanics of this test are presented here. The two distributions to be tested are first ordered by some logical index, i.e., age, size class, etc., and the relative percent of each frequency value in both distributions is calculated. The cumulative percentage values for both distributions are then calculated by adding the relative percentage values together (the cumulative percentage value for the first relative percentage value is the first relative percentage value, the cumulative percentage value for second relative percentage value is first relative percentage value plus the second relative percentage value, etc.).
One of these cumulative frequency distributions is then subtracted from the other and the maximum value obtained becomes the "test statistic". This test statistic is compared to the critical value which is calculated from the total number of observations in each distribution at the alpha level desired. The formula for the critical value is:

\[
\text{Critical Value} = \text{Constant (alpha)} \frac{N_1 + N_2}{N_1 N_2}
\]

If the test statistic exceeds the critical value the two distributions are statistically different from each other at the alpha level chosen.

**Analysis of survivorship curve shape**

The test of the second hypothesis involved regression analyses of the survivorship curves for the three situations (low, linear, and high) and cross comparing the co-efficients of determination (R²'s) due to regression after adjusting these for the effects of the data transformations (Draper and Smith, 1966). The regression analyses were of the form \( Y_i = b_0 + b_1 X_i \), where \( Y_i \) was the number of individuals per age class, and \( X_i \) was the age class. Two forms of the above equation were used to estimate numbers of individuals per age class. The first was of the form \( \ln Y_i = b_0 + b_1 X_i \) and the second was of the form \( \ln Y_i = b_0 + b_1 \ln X_i \). In this case, where the \( Y \) values were subjected to logarithmic transformation, the expected values from the regression analysis were retransformed back to the original scale so that the sum of squares for deviations could be recalculated and used to calculate the adjusted co-efficient of determination. The adjusted co-efficient of determination is much more meaningful as it is the true indicator of the predictive capability of the two models in the original scale.
The binomial distribution was used to compare the sets of coefficient of determination values, as it is a non-parametric statistic which allows for comparison between two sets of events without the restrictions of knowing the parent distributions. By assuming that either model has the same probability (.5) of yielding the higher $R^2$ value, the probability of either model having $S$ successes from $N$ trials is:

$$P(S/N) = \binom{N}{S} (.5)^S (.5)^{N-S}$$

The probability value obtained from this equation is the alpha level at which one model may be rejected in favor of the other.

### Pulse phenomena

In testing the last hypothesis, some examination of the frequency distribution was needed so that the upper portion of the distribution could be examined to determine if outliers were present causing some loading of this tail of the distribution. Less than zero individuals cannot enter the population, whereas events of large entries do infrequently occur. These facts, coupled with the abundance of literature dealing with log-normal phenomena showing up in biological situations (Williams, 1964) prompted an examination of the number of new individuals entering the population from a log-normal standpoint.

The data were standardized for each paddock by subtracting the mean for each age class from each observation of that age class and dividing the result by the standard deviation. The data were then subjected to logarithmic transformation. This gave each paddock a mean of 0 and a standard deviation of 1, and effectively eliminated differences between paddocks without alteration of the frequency distributions of the new individuals of the paddocks.
The data for each taxon were then combined across paddocks and chi-square goodness-of-fit tests to normal were performed on the age class one individuals. The upper portion of the frequency distributions were then examined to determine if pulse events had occurred. Pulses showing up at this point could probably be attributed to weather phenomena.

The age class one data were ranked from low to high across all paddocks for each species so that good and poor years for plant input could be determined and examined in relation to the climatic pattern of the locality. Good correlations at this point between moisture fluctuations and species numbers would have allowed for extraction of moisture from the data set and a re-examination of the data for pulse phenomena.

Serial correlations were run between the first year occurrence of a set of individuals to the number surviving in that set five years later to determine if the input events of large numbers of individuals have great impact on community structure.
RESULTS AND CONCLUSIONS

Grazing effects

The results of the Kolmogorov-Smirnov tests for the effects of grazing on plant longevity are shown in tables 2a, 2b, 2c and 2d. The results of this analysis were consistent across the three situations examined (low, linear, and high) in table 2a, except for Stipa comata, in which the data set adjusted for the high extreme was non-significant, and Phlox species which was barely significant under the low extreme. Due to the small amount of Phlox present within the data set and the great variability within this small sample this test was not considered positive. Stipa comata, however, is one of the major species within this area and its test would lend itself to greater creditability as to a true difference. Tables 2b, 2c, and 2d show that the young age classes provide the major area of difference between the fall grazed and ungrazed populations. When the age class one individuals were dropped from the analysis, the difference between Artemisia tripartita populations was non-significant and the difference between Oryzopsis hymenoides populations was almost non-significant. When age classes one and two were dropped, the difference between Stipa comata populations showed a decline in significance, and when age classes one, two, and three were dropped, the only taxon left with significant differences between grazed and ungrazed populations was Agropyron spicatum.

Therefore, of the nine taxa examined, four appear to exhibit in varying degrees an effect of grazing upon their longevity; these being Agropyron spicatum, Artemisia tripartita, Oryzopsis hymenoides, and Stipa comata.
Table 2a. Critical values and test statistics for the Kolmogorov-Smirnov tests on the survivorship curves for fall grazed versus ungrazed plants with all age classes considered.

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<th>High Assumption</th>
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<td></td>
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<td>3.03</td>
<td>3.01</td>
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<td>3.35</td>
<td>3.32</td>
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<td>(3)^a 6.22 **</td>
<td>(3) 5.93 **</td>
<td>(3) 5.69 **</td>
</tr>
<tr>
<td>Artemisia tripartita</td>
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<td></td>
<td></td>
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<tr>
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<td>11.02</td>
<td>10.99</td>
<td>10.98</td>
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<td>12.16</td>
<td>12.14</td>
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<td>(3) 17.68 **</td>
<td>(2) 17.76 **</td>
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<td>46.91</td>
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<td>51.52</td>
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<td>13.18</td>
<td>13.18</td>
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<td>14.57</td>
<td>14.57</td>
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<td>5.71</td>
<td>5.71</td>
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<td>Oryzopsis hymenoides</td>
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<td>(2) 19.60 **</td>
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Table 2a. Continued

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<th>High Assumption</th>
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<td>(4) 6.08 **</td>
<td>4.95</td>
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* Significant at the .10 level
** Significant at the .05 level

aThe age class at which the maximum difference in the two cumulative frequency distributions occurred.
Table 2b. Critical values and test statistics with age class one individuals omitted from the analysis.

<table>
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<th>Plant Type</th>
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<td>4.11</td>
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<td>Test statistic</td>
<td>(4) 8.41 **</td>
<td>(4) 7.82 **</td>
<td>(4) 7.23 **</td>
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<td>(5) 19.78 *</td>
<td>(5) 19.02 *</td>
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* Significant at the .10 level
** Significant at the .05 level

\(^a\)The age class at which the maximum difference in the two cumulative frequency distributions occurred.
Table 2c. Critical values and test statistics with age classes one and two omitted from the analysis.

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<td>High Assumption</td>
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<td>----------------</td>
<td>-------------------</td>
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<td>(5) 8.29 *</td>
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</table>

* Significant at the .10 level
** Significant at the .05 level

*The age class at which the maximum difference in the two cumulative frequency distributions occurred.*
Table 2d. Critical values and test statistics with age classes one, two, and three omitted from the analysis.

<table>
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<tr>
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<td>(6) *5.58</td>
<td>(6) *5.66</td>
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<td><strong>Gutierrezia sarothrae</strong></td>
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Table 2d. Continued

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* Significant at the .10 level  
** Significant at the .05 level  
\(^a\) The age class at which the maximum difference in the two cumulative frequency distributions occurred.
Of those plants showing an effect of grazing on longevity, *Artemisia tripartita* and *Ory sospis hymenoides* exhibited the least difference. This effect was primarily located in the youngest age classes as evidenced by the lack of significance shown by these species when the younger age classes were successively deleted from the analyses (Tables 2b, 2c, and 2d).

*Agropyron spicatum*, the dominant grass, showed the greatest response to fall grazing. The effect in this case appears to be more evenly distributed across the age classes, as significant differences remained in the tests of this species even when the first three age classes were removed.

The effect of fall grazing upon the grasses was to lengthen their average life spans as shown by the life table analysis of these plants (Table 3). In all cases the ungrazed grass plants have a lower expectation of life than the grazed plants for the first eight years of the eleven years examined.

The effect of grazing on the one shrub showing significance, *Artemisia tripartita*, is exactly the opposite of the effect of grazing on the grasses. In the shrub's case grazing appears to shorten the average life span as the expectation of life for grazed *Artemisia* plants was lower than that for ungrazed plants for all years under the fall grazing regime.

The fact, that grazing has opposite effects upon the longevities of plants with different growth form, could have great ecological impact. If the competitive balance between grasses and the shrub is shifted by
Table 3. Expectations of life (years) for plants showing an effect of grazing on longevity (linear assumption)

<table>
<thead>
<tr>
<th>Age class (Years)</th>
<th>Agropyron spicatum</th>
<th>Artemisia tripartita</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fall grazed</td>
<td>Ungrazed</td>
</tr>
<tr>
<td>1</td>
<td>1.71</td>
<td>1.53</td>
</tr>
<tr>
<td>2</td>
<td>3.86</td>
<td>3.01</td>
</tr>
<tr>
<td>3</td>
<td>4.31</td>
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<td>2.56</td>
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<td>9</td>
<td>2.28</td>
<td>2.08</td>
</tr>
<tr>
<td>10</td>
<td>1.43</td>
<td>1.38</td>
</tr>
<tr>
<td>11</td>
<td>.50</td>
<td>.50</td>
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</table>

<table>
<thead>
<tr>
<th>Oryzopsis hymenoides</th>
<th>Stipa comata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age class (Years)</td>
<td>Fall grazed</td>
</tr>
<tr>
<td>1</td>
<td>3.10</td>
</tr>
<tr>
<td>2</td>
<td>5.05</td>
</tr>
<tr>
<td>3</td>
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<td>4</td>
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<td>10</td>
<td>1.42</td>
</tr>
<tr>
<td>11</td>
<td>.50</td>
</tr>
</tbody>
</table>
grazing far enough in favor of the grasses, there would be a gradual elimination of the *Artemisia* by simply maintaining the grazing pressure over an extended period of time. However, if the balance between the *Artemisia* and the grasses is maintained by grazing, the subsequent removal of grazing from the system could shift the advantage to the shrub, allowing *Artemisia* to increase at the expense of the grasses.

The effect of grazing shown here is opposite to that generally observed. This can possibly be explained from the autecology and ecophysiology of the species involved. The usual grazing and active growing season for these grasses is in the spring. At this time these plants are replenishing their depleted winter reserves, and generating photosynthetic material for new growth. Spring grazing has a profound impact on these grasses by removing this new growth from plants with depleted reserves, causing a reduction in their vigor (Stoddart, 1946, Cook, 1971). In the fall, grasses have already become dormant with only sun-bleached dry foliage showing. Thus, they can withstand grazing without significant damage (Blaisdell and Pechanec, 1949). In fact, grazing at this point will remove dead foliage which could interfere with growth the following spring. Mueggler (1950) has shown that fall snow cover is common in this area. This further reduces the impact of grazing upon the grasses by covering their sensitive crown areas.

*Artemisia*, however, reacts differently. *Artemisia tridentata* is not dormant in the fall as shown in gas exchange studies by DePuit and Caldwell (1973, 1975a, 1975b) and Pearson (1975). If *Artemisia tridentata* behaves similarly then Wright's (1969) observations of its fall grazing intolerance could be explained. Although grazing of sagebrush varies considerably from year to year, usually about 10 percent of the
current year's growth is removed (Laycock, 1967). Extremely heavy use of the shrubs, which have high energy and protein content (Cook and Harris, 1950), is seen some years due to early snow cover. The impact on the shrubs due to fall grazing is thought to result in a decline in interspecific competition and opening of the community. Therefore, it is understandable that subsequent increases in the grasses are seen.

Shape of survivorship curves

From a superficial examination of the semi-logarithmic plots of the survivorship curves for the various plant populations (Figures 4a, 4b, 4c, 4d, 4e, 4f, 4g, 4h, 4i), it is obvious that linear regression equations (after logarithmic transformations of the Y axis) do not best describe the survival patterns for these plant populations for their first eleven years of life. Table 4 shows the co-efficients of determination (R^2's) of regression adjusted for data transformations for the two models used (logarithmic transformations of the Y axis) "semi-log" versus (logarithmic transformations of both axes) "log-log" and shows the results of the binomial tests for the two models.

From all the species tested only ungrazed Phlox yielded higher co-efficient of determination values for the "semi-log" model. The binomial test, for all ungrazed plants, gives a probability of .018 or rejects the "semi-log" model as being better more than 98 percent of the time. Thus, the "log-log" model is superior to the "semi-log" model in describing the survivorship curves for these species. Therefore, for these taxa and environments, the generalization that survivorship curves of perennial plants can be linearlized by logarithmic transformations of the Y axis
Figure 4a. Survivorship curves for grazed and ungrazed Agropyron spicatum populations.
Figure 4b. Survivorship curves for grazed and ungrazed *Artemisia tripartita* populations.
Figure 4c. Survivorship curves for grazed and ungrazed Gutierrezia sarothrae populations.
Figure 4d. Survivorship curves for grazed and ungrazed Koelaria cristata populations.
Figure 4e. Survivorship curves for grazed and ungrazed *Leptodactylon pungens* populations.
Figure 4f. Survivorship curves for grazed and ungrazed *Oryzopsis hymenoides* populations.
Figure 4g. Survivorship curves for grazed and ungrazed Phlox species populations.
Ungrazed ○
Grazed △

Figure 4h. Survivorship curves for grazed and ungrazed Poa species populations.
Figure 4i. Survivorship curves for grazed and ungrazed *Stipa comata* populations.
Table 4. Regression co-efficients of determination ($R^2$'s) for "semi-log" and "log-log" models of survivorship curves for the nine taxa adjusted for data transformations.

<table>
<thead>
<tr>
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<tbody>
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<td>.579</td>
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<td>.433</td>
<td>.419</td>
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<td>.802</td>
<td>.790</td>
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<tr>
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<td>.615</td>
<td>.631</td>
<td>.899</td>
<td>.909</td>
<td>.900</td>
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<td>.553</td>
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<td>.704</td>
<td>.702</td>
<td>.991</td>
<td>.990</td>
<td>.988</td>
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<td>.594</td>
<td>.973</td>
<td>.974</td>
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</table>

Binomial test

$$P(x) = 9!/(1!8!)(.5)^1(.5)^8 = .018$$

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<th>Semi - Log Linear</th>
<th>Semi - Log High</th>
<th>Log - Log Low</th>
<th>Log - Log Linear</th>
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<td>.887</td>
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</tbody>
</table>

Binomial test

$$P(x) = 9!/(0!9!)(.5)^0(.5)^9 = .002$$
which was presented by Harper (1967), and applied by Treshow and Harper (1974) and Wallace and Romney (1972) is rejected.

These results once again emphasize that plant responses cannot be described by an overly simplistic and general model. From this analysis it is obvious that "log-log" regression equations closely describe the survivorship curves for the first eleven years of data for these plants. Yet, plants do not live forever as the "log-log" model indicates; so, to adequately describe the survivorship curves of these plants, at least two equations would need to be used: one to describe the first portion of the curve as done here, and another to describe the physiological age limits of the plants, their senescence, and subsequent death. However, determining trends in this portion of the curve was beyond the scope of the data set available for this study.

The 0 to 1 age class portion of this curve has also been neglected in this study due to lack of sufficient data. This portion of the curve would probably be very steep due to the high proportion of deaths experienced from the time of germination to the development of age class 1.

The shape of the survivorship curves mentioned in this study agree with work done by Wright (1972). He concluded that as grasses in a semiarid environment in southern New Mexico get older their chance of survival increased, up to some physiological limit.

**Pulse phenomena**

The chi-square goodness-of-fit tests to normal for the frequency distributions of the logarithmically transformed year one increment data for eight species are given in table 5. From this analysis it is apparent that most of the perennial plants enter the population in a log-normal
Table 5. Chi-square goodness-of-fit tests to normal of the frequency distributions of the first year recruitment after logarithmic transformation.

<table>
<thead>
<tr>
<th></th>
<th>Agropyron spicatum</th>
<th>Artemisia tripartita</th>
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<th>Leptodactylon pungens</th>
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<tbody>
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<td>Observed</td>
<td>Expected</td>
<td>Observed</td>
<td>Expected</td>
</tr>
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</tr>
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<td>1</td>
<td>1.8</td>
<td>1.0</td>
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Chi-square values

4.6  25.9 *  22.9 *  7.6

*Significant at .05 level
Table 5. Continued

<table>
<thead>
<tr>
<th>Oryzopsis hymenoides</th>
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<th>Poa species</th>
<th>Stipa comata</th>
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<td>Observed</td>
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<td>Observed</td>
<td>Expected</td>
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</tr>
<tr>
<td>8</td>
<td>7.8</td>
<td>16</td>
<td>14.2</td>
</tr>
<tr>
<td>3</td>
<td>3.6</td>
<td>5</td>
<td>6.9</td>
</tr>
<tr>
<td>2</td>
<td>1.7</td>
<td>3</td>
<td>2.9</td>
</tr>
</tbody>
</table>

Chi-square values

<table>
<thead>
<tr>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>11.4</td>
<td>11.7</td>
</tr>
</tbody>
</table>

Critical chi-square value 12.6

*Significant at .05 level*
fashion as expected from Preston (1969). Only two species deviate far enough from log-normal to be statistically significant. The area of their deviation is in the center of their distributions rather than in the upper portions. Thus, it can be concluded that the phenomenon of large first year increments entering the population at odd intervals at Dubois, Idaho are not pulses but rather the upper portion of an expected distribution.

However, if recruitment of first year individuals to the population was expected to follow a normal distribution, the above test would then support pulse phenomenon by definition. For the purposes of this research, however, Preston (1969) was used as the authority.

Since pulse events did not occur in the first year increments of this data, a check was made to see if recruitment to the population was dependent upon the fluctuations seen within first year increments; i.e., do high numbers the first year carry through the population.

Serial correlations between years (1,2), (1,3), (1,4), and (1,5) are presented in table 6a. Some of these correlations are fairly high indicating that a fairly predictable decrease in numbers is occurring in some species starting with age class one; however, this effect is not present in all species and so further investigation was warranted.

Correlations were then run between age classes (2,3), (3,4), and (4,5) (Table 6b). From these correlations it is apparent that by the third age class all species have become more or less stabilized, in that relatively large increments appearing in this age class will generally carry on through the successive age classes.
Table 6a. Correlation co-efficients for abundances of age classes 1 to 2, 1 to 3, 1 to 4, and 1 to 5.

<table>
<thead>
<tr>
<th>Species</th>
<th>1 to 2</th>
<th>1 to 3</th>
<th>1 to 4</th>
<th>1 to 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agropyron spicatum</td>
<td>.33</td>
<td>.20</td>
<td>.27</td>
<td>.20</td>
</tr>
<tr>
<td>Artemisia tripartita</td>
<td>.65</td>
<td>.24</td>
<td>.20</td>
<td>.21</td>
</tr>
<tr>
<td>Koelaria cristata</td>
<td>.46</td>
<td>.29</td>
<td>.26</td>
<td>.30</td>
</tr>
<tr>
<td>Leptodactylon pungens</td>
<td>.43</td>
<td>.41</td>
<td>.25</td>
<td>.27</td>
</tr>
<tr>
<td>Oryzopsis hymenoides</td>
<td>.80</td>
<td>.72</td>
<td>.56</td>
<td>.62</td>
</tr>
<tr>
<td>Phlox species</td>
<td>.93</td>
<td>.92</td>
<td>.86</td>
<td>.80</td>
</tr>
<tr>
<td>Poa species</td>
<td>.80</td>
<td>.78</td>
<td>.68</td>
<td>.71</td>
</tr>
<tr>
<td>Stipa comata</td>
<td>.88</td>
<td>.87</td>
<td>.77</td>
<td>.68</td>
</tr>
</tbody>
</table>

Table 6b. Correlation co-efficients for abundances of age classes 1 to 2, 2 to 3, 3 to 4, 4 to 5.

<table>
<thead>
<tr>
<th>Species</th>
<th>1 to 2</th>
<th>2 to 3</th>
<th>3 to 4</th>
<th>4 to 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agropyron spicatum</td>
<td>.33</td>
<td>.79</td>
<td>.83</td>
<td>.85</td>
</tr>
<tr>
<td>Artemisia tripartita</td>
<td>.65</td>
<td>.68</td>
<td>.86</td>
<td>.97</td>
</tr>
<tr>
<td>Koelaria cristata</td>
<td>.46</td>
<td>.86</td>
<td>.90</td>
<td>.85</td>
</tr>
<tr>
<td>Leptodactylon pungens</td>
<td>.43</td>
<td>.65</td>
<td>.90</td>
<td>.95</td>
</tr>
<tr>
<td>Oryzopsis hymenoides</td>
<td>.80</td>
<td>.92</td>
<td>.80</td>
<td>.86</td>
</tr>
<tr>
<td>Phlox species</td>
<td>.93</td>
<td>.98</td>
<td>.92</td>
<td>.96</td>
</tr>
<tr>
<td>Poa species</td>
<td>.80</td>
<td>.94</td>
<td>.87</td>
<td>.85</td>
</tr>
<tr>
<td>Stipa comata</td>
<td>.88</td>
<td>.88</td>
<td>.90</td>
<td>.95</td>
</tr>
</tbody>
</table>
IMPLICATIONS

The results of this research are of interest to the synecologist in that implications as to community organization and dynamics can be drawn and applied to grazing management.

Mueggler (1950) has shown that an ungrazed exclosure and the fall grazed paddock have remained in approximately the same condition throughout his study period. Yet, it has been demonstrated here that there is a measurable effect of grazing upon the average longevity of some grasses and the shrub. Even though the shrub's average longevity has declined, the annual recruitment rate is still high enough to sufficiently offset the drop in average longevity, i.e., there is greater turnover in the grazed than ungrazed population. Thus, the abundance of this species is not drastically changed within the system and the apparent contradiction explained.

Anything which greatly changes the balance between average longevity and recruitment rates, however, will have a dynamic impact upon the vegetation of the system. This is probably the case for the depleted spring grazed ranges which when switched to spring deferment and heavy fall grazing show such a remarkable improvement (Laycock, 1967). In this case grazing pressure was lifted from the grasses during their critical stages of growth and shifted to the shrubs. The Artemisia is somewhat vulnerable to fall grazing (Wright, 1969) and resulting shifts in recruitment and average longevities are evidenced by the changes in the relative cover of these species rather than densities.
It has been shown by Craddock and Forsling (1938) that forage production is highly correlated with winter-spring moisture in the study area (Figure 5). Furthermore, if these semi-arid areas are open communities with a stable size-age relationship in the plants, as assumed by Wright (1972) in the construction of his simulation model, a fairly high correlation between total density and winter-spring moisture would be expected. Such a correlation does not exist (Table 7).

Moisture does not appear to have a high correlation between either basal area or density. This would indicate that the plants of the community are highly plastic with regards to size, and simply fluctuate in volume with the environmental perturbations. Such episodic growth in plants is mentioned by Slatyer (1968), and unlike animals plants can actually show negative growth under adverse conditions by losing unsupportable biomass. This is further supported by Table 8, in which the basal area by age classes are listed for the species studied. An examination of these data show that there is not a stable size-age relationship. Thus, it can be concluded that this is a closed community.

These findings are consistent with some recent work done by Werner (1975). She investigated the relative importance of chronological age versus size-state of rosettes in predicting the fate of *Dipsacus fullonum* L., a biennial plant. Her results indicate that until some critical size is reached, flowering will not occur. Furthermore, many populations of "biennial" plants have a life cycle of more than two years.

This plasticity in size-age relationships could present the ecologist with stands of individuals which are approximately the same size giving the appearance of being even-aged, where indeed, the ages vary considerably.
Forage production and winter-spring precipitation on two experimental paddocks, 1924-1932 (Craddock and Forsling, 1938).

Correlation coefficient 0.944
Table 7. Correlation matrix between winter-spring precipitation, total community basal area, total community density, total *Agropyron spicatum* density, total *Agropyron spicatum* basal area, and total *Agropyron spicatum* age class one individuals.

<table>
<thead>
<tr>
<th>Precipitation October to June</th>
<th>Total basal area</th>
<th>Total density</th>
<th>Total <em>Agropyron spicatum</em> density</th>
<th>Total <em>Agropyron spicatum</em> basal area</th>
<th>Total <em>Agropyron spicatum</em> age class ones</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.00</td>
<td>0.01</td>
<td>0.38</td>
<td>0.19</td>
<td>0.53</td>
<td>0.02</td>
</tr>
<tr>
<td>1.00</td>
<td>0.26</td>
<td>0.24</td>
<td>0.23</td>
<td>0.33</td>
<td>0.33</td>
</tr>
<tr>
<td>1.00</td>
<td>0.85</td>
<td>0.85</td>
<td>0.53</td>
<td>0.53</td>
<td>0.53</td>
</tr>
<tr>
<td>1.00</td>
<td>1.00</td>
<td>0.07</td>
<td>0.21</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Table 8. Mean size (cm²) by age class for ungrazed plants

<table>
<thead>
<tr>
<th>Age (Years)</th>
<th>Agropyron spicatum</th>
<th>Artemisia tripartita</th>
<th>Koelaria cristata</th>
<th>Orhyzopsis hymenoides</th>
<th>Phlox species</th>
<th>Poa species</th>
<th>Stipa comata</th>
<th>Gutierrezia sarothrae</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.8</td>
<td>11.0</td>
<td>2.4</td>
<td>.1</td>
<td>.2</td>
<td>2.5</td>
<td>.3</td>
<td>44.0</td>
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<tr>
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<td>5.5</td>
<td>17.0</td>
<td>2.6</td>
<td>.5</td>
<td>.2</td>
<td>2.8</td>
<td>6.6</td>
<td>17.0</td>
</tr>
<tr>
<td>3</td>
<td>10.1</td>
<td>45.7</td>
<td>4.3</td>
<td>1.0</td>
<td>.3</td>
<td>3.8</td>
<td>1.5</td>
<td>54.0</td>
</tr>
<tr>
<td>4</td>
<td>6.3</td>
<td>56.7</td>
<td>7.5</td>
<td>3.0</td>
<td>.3</td>
<td>4.6</td>
<td>7.3</td>
<td>41.0</td>
</tr>
<tr>
<td>5</td>
<td>7.1</td>
<td>74.8</td>
<td>10.4</td>
<td>2.0</td>
<td>.4</td>
<td>4.9</td>
<td>3.7</td>
<td>46.0</td>
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<td>6</td>
<td>8.3</td>
<td>62.5</td>
<td>13.3</td>
<td>15.0</td>
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<td>5.1</td>
<td>2.6</td>
<td>.1</td>
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<td>5.1</td>
<td>57.6</td>
<td>10.3</td>
<td>14.0</td>
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<td>5.0</td>
<td>10.0</td>
<td>.1</td>
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<tr>
<td>8</td>
<td>7.1</td>
<td>47.0</td>
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<td>57.0</td>
<td>22.7</td>
<td>35.0</td>
<td>.1</td>
<td>4.0</td>
<td>3.0</td>
<td>.1</td>
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<tr>
<td>10</td>
<td>5.4</td>
<td>88.5</td>
<td>27.3</td>
<td>25.0</td>
<td>.1</td>
<td>9.5</td>
<td>2.0</td>
<td>.1</td>
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<tr>
<td>11</td>
<td>6.4</td>
<td>82.0</td>
<td>19.3</td>
<td>18.0</td>
<td>.1</td>
<td>5.0</td>
<td>2.0</td>
<td>.1</td>
</tr>
<tr>
<td>12</td>
<td>2.5</td>
<td>59.0</td>
<td>11.7</td>
<td>34.0</td>
<td>.1</td>
<td>1.0</td>
<td>2.0</td>
<td>.1</td>
</tr>
<tr>
<td>13</td>
<td>10.6</td>
<td>62.6</td>
<td>10.3</td>
<td>8.0</td>
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<td>7.0</td>
<td>3.0</td>
<td>.1</td>
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<tr>
<td>14</td>
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<td>8.0</td>
<td>7.0</td>
<td>.1</td>
<td>3.0</td>
<td>2.0</td>
<td>.1</td>
</tr>
<tr>
<td>15</td>
<td>5.6</td>
<td>74.0</td>
<td>11.0</td>
<td>3.0</td>
<td>.1</td>
<td>1.0</td>
<td>2.0</td>
<td>.1</td>
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<tr>
<td>16</td>
<td>3.0</td>
<td>54.0</td>
<td>24.0</td>
<td>.1</td>
<td>.1</td>
<td>1.0</td>
<td>2.0</td>
<td>.1</td>
</tr>
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<td>17</td>
<td>3.0</td>
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<td>.1</td>
<td>.1</td>
<td>1.0</td>
<td>2.0</td>
<td>.1</td>
</tr>
</tbody>
</table>
One additional interesting point which appeared in these analyses is that years which have the highest densities of new individuals, are years which have lower cover values (Figures 6a and 6b). This would further indicate a closed community, in that space must be available for germinating individuals to grow into seedlings. In a closed community space would be at a premium except during years of lower cover.

If it can be assumed that death is a random event in these communities, then true recruitment into these communities must also be a more or less random event. Recruitment is buffered by the approximately log-normal appearance of age class one individuals, and further altered by the fact that the death of large plants will open up much more space for recruitment than the death of smaller plants within the community.

It should be mentioned that the above discussion has singled out specific mechanisms and how they might work, as indicated from this data set. Any ecosystem is a complex of many mechanisms working simultaneously. These interlinked mechanisms work together, and any response seen within the ecosystem can rarely be attributed to a single mechanism. Thus, no single answer exists to explain community structure or dynamics; however, it is hoped that the insights presented by this study have furthered the understanding of how semi-arid plant communities may function.
Figure 6a. Graph of total density of all plants from 1931 to 1950.

Figure 6b. Graph of total basal area of all plants from 1931 to 1950.
SUMMARY

Studies in plant demography have been mostly confined to work on woody species where growth-ring analysis allows a somewhat accurate indication of age, and to short-lived, annual plants. Even though there is a dearth of information on perennial non-tree species, especially in the semi-arid regions, several hypotheses of plant longevity, succession and community organization have appeared in the literature. Three such hypotheses have been examined in this study: first, does grazing have an effect on the average longevity of perennial plants; second, are the survivorship curves of these perennial plants log-normal indicating a constant death rate; and third, are the infrequent years with high seedling numbers pulse phenomena or are they the upper portion of an expected frequency distribution?

Pantograph charts from twelve permanent plots located at the U. S. Sheep Experiment Station near Dubois, Idaho, were examined. The data extracted from these records covered the years 1930 to 1950 with the exceptions of 1943, 1944, and 1948. Three sets of charts, the spring-fall grazed paddock, were eliminated due to an excessive number of years in which charts were not recorded.

To study the effect of grazing on average longevity of perennial plants, the survivorship curves for nine taxa were subjected to the Kolmogorov-Smirnov test. Fall grazing was found to have an effect on four plants in these communities. Three grasses (Agropyron spicatum, Oryzopsis hymenoides, and Stipa comata) have higher average longevities under fall grazing whereas the shrub (Artemisia tripartita) has a lower average longevity.
Comparisons between the adjusted co-efficients of determination (R²'s) due to linear regression, in which "semi-log" and "log-log" transformations were performed, to describe the shape of the aforementioned survivorship curves, for the first eleven years of life, show that the "log-log" descriptions are best. This indicates that there is an increasing chance of survival up to some physiological limit for these species.

The investigation of pulse phenomenon was accomplished by combining the age one individuals from all paddocks (after normalization to a mean of 0 and a standard deviation of 1), logging these values, and running chi-square goodness-of-fit tests. The fluctuations observed in the first five age classes were examined to determine when true recruitment occurred. These analyses led to the conclusion that the infrequent occurrences of large numbers of seedlings are not pulse phenomena, but rather, the upper portion of a log-normal distribution. Recruitment itself appears to be a somewhat random event following the more or less random pattern of death within the community.

By combining these results with the obvious lack of a size-age relationship, it can be concluded that these semi-arid communities are closed, i.e., the resources available are being totally used by the existing plants. Individuals within the communities are highly plastic with respect to size, and merely fluctuate with changes in environmental conditions.
LITERATURE CITED


Cook, C. Wayne and Lorin E. Harris. 1950. The nutritive content of the grazing sheep's diet on summer and winter ranges of Utah. Utah Agricultural Experiment Station Bulletin 342. 66 p.


VITA
Kenneth Harold Rea
Candidate for the Degree of
Doctor of Philosophy

Dissertation: Plant Demographic Studies of Tall Threetip Sagebrush-Grass Vegetation on the Eastern Snake River Plains, Idaho

Major Field: Ecology (Range Science)

Biographical Information:


APPENDIX
APPENDIX A.

Tables I through IV
Table I. Restricted relative density (percent of total plants of the nine taxa) for all plots.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>P7E1-Q1</th>
<th>P7E1-Q2</th>
<th>P7E1-Q3</th>
<th>P7E1-Q4</th>
<th>P10-Q1</th>
<th>P10-Q2</th>
<th>P1A-Q4</th>
<th>P1B-Q1</th>
<th>P1B-Q3</th>
<th>Overall mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agropyron spicatum</td>
<td>63.90</td>
<td>57.87</td>
<td>64.74</td>
<td>41.65</td>
<td>32.12</td>
<td>60.18</td>
<td>64.67</td>
<td>22.84</td>
<td>81.60</td>
<td>54.40</td>
</tr>
<tr>
<td>Artemisia tripartita</td>
<td>4.74</td>
<td>4.92</td>
<td>4.07</td>
<td>3.64</td>
<td>3.08</td>
<td>0.98</td>
<td>5.68</td>
<td>0.52</td>
<td>0.87</td>
<td>3.17</td>
</tr>
<tr>
<td>Gutierrezia sarothrae</td>
<td>0.56</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.84</td>
<td>0.00</td>
<td>0.31</td>
<td>0.06</td>
<td>0.00</td>
<td>0.20</td>
</tr>
<tr>
<td>Koelaria cristata</td>
<td>6.96</td>
<td>6.53</td>
<td>3.44</td>
<td>5.86</td>
<td>5.57</td>
<td>1.87</td>
<td>4.80</td>
<td>3.66</td>
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<tr>
<td>Leptodactylon pungens</td>
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<td>0.07</td>
<td>0.00</td>
<td>3.24</td>
<td>0.00</td>
<td>6.15</td>
<td>6.14</td>
<td>0.17</td>
<td>0.08</td>
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<tr>
<td>Oryzopsis hymenoides</td>
<td>0.78</td>
<td>2.90</td>
<td>0.25</td>
<td>0.57</td>
<td>1.15</td>
<td>4.08</td>
<td>1.43</td>
<td>14.03</td>
<td>0.18</td>
<td>2.82</td>
</tr>
<tr>
<td>Phlox species</td>
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<td>0.31</td>
<td>0.00</td>
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<td>0.09</td>
<td>0.00</td>
<td>0.53</td>
<td>0.03</td>
<td>0.26</td>
<td>0.29</td>
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<tr>
<td>Poa species</td>
<td>18.89</td>
<td>14.17</td>
<td>17.73</td>
<td>10.93</td>
<td>34.98</td>
<td>3.10</td>
<td>16.18</td>
<td>27.82</td>
<td>13.22</td>
<td>17.45</td>
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<tr>
<td>Stipa comata</td>
<td>3.18</td>
<td>13.23</td>
<td>9.76</td>
<td>33.14</td>
<td>22.16</td>
<td>23.65</td>
<td>0.25</td>
<td>30.82</td>
<td>2.47</td>
<td>15.41</td>
</tr>
</tbody>
</table>
Table II. Relative density (percent of total plants in the total community) for all plots.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>P7E1-Q1</th>
<th>P7E1-Q2</th>
<th>P7E1-Q3</th>
<th>P7E1-Q4</th>
<th>P10-Q1</th>
<th>P10-Q2</th>
<th>P1A-Q4</th>
<th>P1B-Q1</th>
<th>P1B-Q3</th>
<th>Overall mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Agropyron spicatum</td>
<td>27.83</td>
<td>36.91</td>
<td>57.43</td>
<td>36.27</td>
<td>16.20</td>
<td>51.45</td>
<td>45.40</td>
<td>16.37</td>
<td>70.57</td>
<td>29.83</td>
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<tr>
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<td>2.06</td>
<td>3.15</td>
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<td>3.17</td>
<td>1.55</td>
<td>0.84</td>
<td>3.98</td>
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<td>0.42</td>
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<td>0.37</td>
<td>0.75</td>
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<td>3.05</td>
<td>5.11</td>
<td>2.81</td>
<td>1.60</td>
<td>3.37</td>
<td>2.62</td>
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<td>2.82</td>
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<td>4.31</td>
<td>0.36</td>
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<td>0.23</td>
<td>0.50</td>
<td>0.58</td>
<td>3.49</td>
<td>1.01</td>
<td>10.05</td>
<td>0.16</td>
<td>2.02</td>
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<td>0.37</td>
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</tr>
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<td>15.73</td>
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<td>11.36</td>
<td>19.94</td>
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<td>11.73</td>
</tr>
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<td>8.66</td>
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</tbody>
</table>
Table III. Restricted relative basal area (percent of the total cover from the nine taxa) for all plots.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Quadrat Number</th>
<th>Overall mean</th>
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<tbody>
<tr>
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<td>P7E1-Q1</td>
<td>P7E1-Q2</td>
</tr>
<tr>
<td>Agropyron spicatum</td>
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</tr>
<tr>
<td>Artemisia tripartita</td>
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</tr>
<tr>
<td>Gutierrezia sarothrae</td>
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<tr>
<td>Koelaria cristata</td>
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Table IV. Relative basal area (percent of total cover of all species in the total community) for all plots.

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<th>P7E1-Q3</th>
<th>P7E1-Q4</th>
<th>P10-Q1</th>
<th>P10-Q2</th>
<th>P1A-Q4</th>
<th>P1B-Q1</th>
<th>P1B-Q3</th>
<th>Overall mean</th>
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<td>36.17</td>
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<td>1.90</td>
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<tr>
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