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SPATIAL AND TEMPORAL DYNAMICS OF PLANT POPULATIONS IN SALT-DESERT SHRUB VEGETATION GRAZED BY SHEEP

by

Humberto Alzérreca-Angelo

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

of

DOCTOR OF PHILOSOPHY

in

Range Science

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1996

ABSTRACT

Spatial and Temporal Dynamics of Plant Populations in Salt-Desert Shrub Vegetation Grazed by Sheep

by

Humberto Alzérreca-Angelo, Doctor of Philosophy

Utah State University, 1996

Major Professor: Dr. Eugene Schupp
Department: Rangeland Resources

I studied the effect of moderate sheep grazing on a shadscale plant community at the Desert Experimental Range, southwestern Utah, USA, using a 61-yr data set with two grazing treatments (yes vs. no), two seasons (spring vs. winter), and two soil types (loamy-skeletal vs. coarse-loamy). I studied precipitation, total species cover, annuals, shrub survival, seedling recruitment, plant succession, and plant spatial relationships.

Precipitation showed high variability (CV=31%) masking on short-term cycles, resulting in study intervals with average (1935-58), dry (1958-69), driest (1969-75), and wet (1980-94[5]) regimes. Total cover in both grazed and ungrazed pastures increased between 1935 and 1975 before decreasing to 1994. Treatments diverged with time, however, so cover was higher in ungrazed pastures in 1975 and 1994. Individually, *Atriplex confertifolia* decreased from

1958-94 and *Ceratoides lanata* from 1975-94. *Artemisia spinescens* increased in ungrazed pastures from 1935-94, while remaining very low in grazed pastures. Grasses increased from 1935-94 with little grazing effects. Annuals increased from absence in 1935 to 63% frequency in 1994; precipitation may be related to this increase. Grazing and soil type had few long-term or short effects on shrub survival. Similarly, only *C. lanata* showed a microhabitat effect, with greater seedling survival in vegetated than open patches. Seedling recruitment was positively correlated with precipitation. Only *A. confertifolia* recruitment responded to grazing; it was higher in grazed pastures. A fuzzy graph analysis showed a moderate grazing effect on succession. Clumped distributions were common and were unaffected by grazing but increased in wet years. Plant establishment occurred disproportionally in sites occupied or formerly occupied by plants, suggesting facilitation. Negative interference, however, was suggested by new recruitment occurring further from larger existing individuals. Moderate grazing had little effect on spatial relationships.

In conclusion, the multivariate approach yielded broader conclusions than any individual factors. Although some factors showed more grazing effects than others, grazing could not completely explain observed changes; climate and inherent plant attributes must also be considered. Management at moderate grazing levels may only play a limited role in shadscale communities.

(310 pages)

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To my wife, Nelly, my boys, Javier and Fernando, and my parents and relatives back home, I express my deepest love and appreciation.

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CHAPTER 1

STATEMENT OF THE PROBLEM

Introduction

A problem relevant to long-term management of salt-desert rangelands is the poor understanding of plant population and community processes that influence vegetation change under chronic grazing disturbance.

During the last 100 years in the Intermountain West, sheep grazing on salt-desert *Atriplex confertifolia* (shadscale) and *Ceratoides lanata* (winterfat) rangelands is reported to have damaged the natural vegetation and degraded the range (McArdle et al. 1936, Shantz and Piemeisel 1940, Stewart et al. 1940, Whisenant and Wagstaff 1991). There is little concrete evidence of change due to grazing, however, partly because relict or other reference areas for comparison are nonexistent (West 1988). If the range is degraded, accepted principles of range management suggest that controlled grazing or no grazing should eventually lead to range recovery and stabilization of degraded areas. But as with the issue of degradation, the evidence for this precept of recovery of salt-desert shrub vegetation is equivocal.

Not surprising given these views, salt-desert plant communities are managed under the assumption that grazing plays a major role in determining plant community successional trajectories. More specifically, management is based on the assumption that livestock can be manipulated to achieve community stability at or near a climax equilibrium as stated in the Clementsian model of plant succession (Clements 1928, Dyksterhuis 1949). If, however, grazing is not the driving force behind vegetation change in these communities, as suggested in alternative models such as the nonequilibrium (Ellis and Swift 1988) and multiple state models (Westoby et al. 1989), a grazing-centered approach to managing shadscale rangelands may not be appropriate.

Effects of grazing on vegetation change in field experiments are difficult to document for a variety of reasons, including:

1. Spatial variability. Plants are located in relation to the spatial heterogeneity of soils; in response to exposure, altitude, and slope; and in relation to other plants. Such heterogeneity is a source of variability in grazing experiments because it can mask treatment effects.

2. Temporal variability. Precipitation amount, intensity, and distribution are highly variable both annually and seasonally. Drought, defined as periods of more than 1 year with below average precipitation, may affect plant dynamics more severely than grazing. For instance, seedling establishment and seed production may be severely reduced, and plant mortality may significantly increase under drought. Floods, at the other extreme, also occur in this environment and may have cause vegetation change.

3. Other herbivores such as insects, wild mammals, etc. can have large impacts on plant communities regardless of grazing by domestic stock.

As a result, vegetation change is multivariate in nature, with spatial and temporal (climatic) phenomena intermixed with grazing effects. Therefore, the use of a multivariate approach in the search for an understanding of change may be more appropriate than univariate approaches (West 1983, Norton and Michalk 1978).

A unique, long-term data set obtained from permanent plots at the Desert Experimental Range (DER) in southwest Utah allowed me to study aspects of plant community dynamics such as plant replacement, plant survival, and plant spatial interactions from a multivariate perspective.

General Objective

The general objective of my study was to determine long-term plant population and community successional trajectories in salt-desert shrub vegetation under grazed and ungrazed conditions. More specific objectives are presented with each project.

Research Questions

The proposed study intended to address the following general questions:

1. Does grazing affect pasture plant cover through time?
2. Does grazing affect plant survival?
3. Does grazing affect the plant replacement process?
4. Are spatial interactions between plants of different sizes (same or different species) determinants of change in species composition and community structure through time in grazed and ungrazed pastures?

To meet the general objective, my study was divided into four projects: 1) change in plant cover, 2) plant survival, 3) plant replacement, and 4) plant spatial interactions. Each of these projects will be addressed individually and finally integrated in order to develop an improved understanding of the process of vegetation change.

General Literature Review

Vegetation, Environment, and Grazing

Archer and Smeins (1991, p. 109) described the relationship among vegetation, environment, and grazing, which corresponds to the scope of this work. They point out that

> plant species composition and productivity within a region largely reflect the prevailing climate, whereas seasonal and annual variability in rainfall and temperature play a central role in dictating the dynamics of populations over time. However, substantial spatial variability occurs across landscapes, and broad scale, climatic variables cannot account for the spatial patterns which shape vegetation form and function on a local scale. Soils and topography exert a strong influence on patterns of plant distribution, growth and abundance over the landscape through the regulation of the availability of moisture from precipitation, which also affects nutrient availability. Grazing influences are superimposed on this background of topo-edaphic heterogeneity and climatic variability to further influence community level processes.

It is evident from Archer and Smeins (1991) that several uncontrollable variables interact with grazing to potentially affect vegetation status. Grazing, however, is generally the only biotic variable that we manipulate. Interpretations of its effects on vegetation should be carefully balanced against the influences of uncontrollable variables.

Under the conventional hierarchical classification of ecological systems theory (MacMahon et al. 1978), effects of grazing on vegetation can be studied at different levels of ecological organization, including the organismal, population, community, ecosystem, and landscape levels. The approach in this study is not necessarily hierarchical (linear); instead, each level will be visualized as a criterion for observation, permitting all possible combinations among criteria to be examined (Allen and Hoekstra 1992). The criteria pertinent to the proposed study of salt-desert rangeland, and corresponding operating mechanisms, are 1) organismal--grazing resistance; 2) population--plant demography (survival and mortality); and 3) community--competition, plant replacement, and succession. Therefore, the finest level of resolution (grain) is the individual plant. The spatio-temporal limits (extent) of this study are determined by the distribution of the plant community and by the 60-yr data set.

Plant, Population, Community, and Grazing

Native species are presumed to adapt to the prevailing climate and soils. On the other hand, the coevolutionary history of plant/herbivore interactions is also influential in the development of the composition and structure of a plant community (Milchunas et al. 1988). Controversy exists concerning the question of whether grazing is beneficial or detrimental to plants. Grazing may be beneficial to plants directly by increasing heterogeneity and productivity through effects on plant populations and their environment. For example, grazing can stimulate diversity by reducing the capacity of palatable dominants to exclude other less dominant species, thus increasing heterogeneity (Chew 1974). Belsky (1987) noted, however, that plants also benefit indirectly from grazing (litter removal, amelioration of soil fertility, etc.), and that although these benefits are obvious at the community and ecosystem level, they do not occur at the organismal level. In contrast, a negative plant-animal relationship can be described in which animals are viewed as parasites of plants (Ellison 1960); the negative effects of grazing can be expressed at all levels.

Plant adaptation to grazing consists, in general, of two components: avoidance and tolerance. Both components can be integrated in plant mechanisms for resistance to grazing (Briske 1986). Avoidance refers to morphological mechanisms or chemical compounds that a plant may employ to deter herbivores. Tolerance refers to physiological processes at the plant level to enhance survival and growth of replacement tissue after defoliation (Briske 1986). However, according to Briske (1991, p. 106), "the relative magnitude and associated cost of each component are poorly understood." These resistance mechanisms are different for each plant. If grazing is the primary agent of vegetation change, plants with higher resistance to grazing should have a competitive advantage over plants that have less grazing resistance, and they are therefore likely to prevail in the composition of the grazed plant community. In contrast, if resistance has a cost, the more resistant species may be less competitive under conditions of little or no grazing.

The introduction of large numbers of domestic livestock to semiarid salt-desert shrub ecosystems probably resulted in modification of competitive plant interactions. West (1988) suggested that grazing with domestic stock and invasion of alien plants, such as the poisonous *Halogeton glomeratus* in the 1940s, are probably the two major causes of vegetation change in the salt-desert rangelands in the last 100 years. A similar situation involving introduced biota is described by Newsome and Corbett (1977) for rangelands in Australia. As noted before, however, there is little direct evidence supporting this logical view that grazing has been the dominant force.

Through time, direct and indirect grazing effects on plant growth and reproduction are manifested in the dynamics of plant populations. "Herbivores affect the productivity, composition, and stability of plant assemblages through mediation of plant natality, recruitment, and mortality and may cause directional changes in community structure and function" (Archer and Smeins 1991, p. 109). The magnitude of change is dependent mainly on the actual grazing pressure, grazing selectivity of grazers, and the grazing history of the vegetation.

Drought is a common phenomenon in desert shrublands (Pyke and Dobrowolski 1989, Chambers and Norton 1993). Plants from semiarid rangelands have evolved adaptations to drought, and these adaptations also confer some degree of grazing avoidance or tolerance (convergent selection) (Milchunas et al. 1988). As a result, according to Milchunas et al. (1988), grazing-induced changes in plant composition and physiognomy of the plant community are expected to be moderate even in systems with only a short evolutionary history of grazing. Similarly, Platou and Tueller (1985) indicated that grazing may have little effect on shrubland ecosystems unless a high and persistent degree of use occurs. Such conditions could have been met in shadscale rangelands when drought and high stocking rates overlapped.

Vegetation Dynamics and Grazing

The range management profession uses models of vegetation dynamics to predict changes in plant communities grazed by domestic livestock. Good management of rangelands is heavily dependent on the use of appropriate predictive models on which to base management decisions (Friedel 1991). Controversy exists, however, about which model of vegetation dynamics may better predict changes in vegetation in semiarid environments. The traditional Clementsian model (CM) of plant succession, which assumes a stable plant community in equilibrium with its environment as the end point of succession, has been criticized as inadequate to explain vegetation change in such environments (Norton 1978; Ellis and Swift 1988; Hart and Norton 1988; Smith 1988, 1989; Westoby et al. 1989), and a search for alternative models has been recommended (NAS 1994).

The National Academy of Sciences (NAS 1994, p. 11) specifically recommended "a coordinated effort... to develop, test, and employ new models of rangeland change that incorporate the concept of ecological thresholds."

Archer and Smeins (1991, p. 109) stated that "the goal of grazing management for sustained yield is to identify these critical thresholds and manage landscapes so as not to exceed them." The State and Transition Model (STM), which recognizes stable states of a plant community in an relatively uniform environment separated in time by community change triggered by overcoming thresholds, is often mentioned as an alternative to the CM for range condition and trend analysis (Friedel 1990, 1991; Laycock 1991; West et al. 1994). It is advisable, however, to test STM under field conditions and in different ecosystems before generalizing its use (Hosten 1995).

The STM and the CM are, however, not necessarily comparable because, according to Hosten (1995, p. 134), they describe different phenomena. Hosten observed that "the State and Transition Model is able to describe gross changes in plant communities associated with exogenous factors. The Clementsian Model describes species replacement within a community, usually on the bases of autogenic factors." Hosten (1995, p. 134) concluded that "for a full understanding of vegetation dynamics relative to management, both phenomena need to be recognized." The same author pointed out that the best predictor of vegetation change comes from a knowledge of the reaction of individual species to disturbance, and thus he recommended an individualistic approach "as the basis for range condition and trend analysis," (p. 134) to which this dissertation conforms.

Although this study has not been designed to test models of vegetation dynamics, results may be adequate to test some assumptions of both the CM and its popular alternative, the STM. Despite the criticism against the use of CM today, many of the principles of CM are still used in the range profession.

Approaches to the Study of Vegetation Dynamics--a Methodological Justification

Early detection of detrimental change is more important than the detection of range improvement because it permits the land manager to make management decisions in time to control or reverse the undesirable trend. This is a possibility in areas where vegetation change can be manipulated through management. West (1983) stated that predicting trend is more important to range management than assessing what has happened in the past. In desert rangelands, however, reliable methods for detecting long-term changes in range condition are lacking (Gardiner and Norton 1983). The methods currently being used by range managers are based on the CM of plant dynamics which, as mentioned earlier, many authors consider inadequate for semiarid environments. The ecological site approach to monitoring, which compares monitored sites to benchmark sites to measure management impacts, is not always workable. For example, grazed sites sometimes exhibit better condition than ungrazed benchmarks (Norton 1978, Smith 1988, Walker 1988, Hosten 1995). Instead, the use of multiple reference areas (Wilson 1984), approaches that include attributes of plant populations instead of, or in addition to, composition data

(Hosten 1995), or the comparison of plant composition of a site with a well-managed benchmark site (Foran 1980), have been suggested in the assessment of change in vegetation and land condition.

West (1983) and West and Tueller (1972) recommended a multivariate and multifactorial approach as the best way to define range condition, document change, and predict successional trajectories. Information on variables such as horizontal and vertical plant community structure, plant size, age, form, and vigor may contribute to a better interpretation of succession than any single variable alone. The use of graphical aids that integrate more than one variable is also recommended as more illustrative than univariate graphics (Whittaker 1965, West 1983).

Norton and Michalk (1978) emphasized the necessity of using more than one parameter in the assessment of plant community dynamics. They suggested that density, age structure, and dispersion may provide a better understanding of the phenomena. Along this line of thinking, Gardiner and Norton (1983) noted the need for new methods for trend assessment that could identify and separate the causes of change into environmental, climatic, and managerial factors. In an attempt to solve this problem, they proposed the use of demographic information (plant recruitment and survival) and the application of more powerful statistical tools to assess trend and explore possible causes of change.

The selective use of a few vital and manageable plant attributes for analysis of plant succession seems to have considerable potential (West and

Gasto 1978, Noble and Slatyer 1980, Austin 1981). Vital attributes are those attributes of a species that are critical to its role in a vegetation replacement sequence, such as the ability to establish and grow to maturity, the method of propagule dispersal or persistence, and the time taken by the species to reach critical life stages.

Austin (1977) and Austin et al. (1981) pointed out the there are two main approaches to vegetation dynamics: 1) observation of abundance or frequency variables for a quadrat through time and 2) determination of the survival pattern of individual plants, together with the construction of life tables (practical only for a few recognizable species). They also indicated that multivariate techniques and computers expand the possibility of studying community trends using all species at the same time. Austin (1981) remarked, however, that long-term studies of temporal and spatial plant dynamics are scarce and that both phenomena should be studied simultaneously.

Austin et al. (1981) used demographic and multivariate approaches in a 20-year study of the effects of grazing intensity and exclosures on pasture dynamics in arid Australia. The demographic study detected differential responses of perennial grass species to grazing. On the other hand, numeric classification of species through 6 successive observation periods demonstrated that community types were sensitive to differences in winter rainfall during the entire experimental period. Finally, principal component analysis was interpreted to show progressive divergence in the successional trends of grazed and ungrazed plots. Austin et al. (1981) recommended using the "demographic approach to studying plant succession under grazing" because it "allows detailed consideration of the behavior of individual species and speculation about their biology" (Austin et al. 1981, p. 208). The authors recognized the importance of having sufficient observations through time to partition the components and identify episodic events that contribute to vegetation dynamics. This is not always possible, however, because of typical discontinuities in the data, as is the case in this dissertation (see data organization section in this chapter).

The difficulty of separating impacts of various phenomena that operate simultaneously in long-term successional studies is a common feature of such research. This can be readily understood if we consider that vegetation is influenced by primary successional pressures, secondary succession (after grazing), episodic events such as pathogenic outbreaks, plant establishment and senescence, heterogeneity in the abiotic environment, climatic fluctuation, and long-term shifts in climate. In general, the complexity of working with non-homogeneous spatial and temporal factors and the importance of having permanent quadrats for this kind of research is recognized (Austin 1981). This situation applies to this study, where, in addition to grazing, other environmental (especially precipitation) and biological factors are operating simultaneously (Norton 1978, West 1979, Smith 1986, Chambers and Norton 1993).

Materials and Methods

Study Area

The study area has an elevation of 1,600 m.a.s.l. and is located at 38° 36' N and 113° 45' W at the U.S. Forest Service Desert Experimental Range (DER) in southwestern Millard County, Utah, about 75 km west of Milford (Fig. 1). The ecology of the area is representative of the region's 180,000 km^2 of winter grazing lands (Holmgren 1973, Gardiner and Norton 1983, Smith 1986).

Climate

Highly contrasting summer and winter temperatures are typical of the study area, with average monthly temperatures ranging from -3.5 °C in January to 23.3 °C in July. The average annual temperature is 9.4 °C, but wide daily variation is common. In this open country of low vegetation, wind intensity and frequency are high, which, in conjunction with hot summer temperatures, results in high rates of evapotranspiration. The frost-free period is from April to October (125 days); in the remaining months soils are frozen intermittently (Holmgren 1973, Smith 1986).

Rainfall is highly variable among and within years (Fig. 2). Drought is chronic in the area; severe droughts of more than 1 year are reported for the periods 1933-4, 1942-3, 1949-52, 1954-5, 1971-2, and 1975-6 (Smith 1986, Pyke and Dobrowolski 1989, Blaisdell and Holmgren 1984, Chambers and Norton 1993).

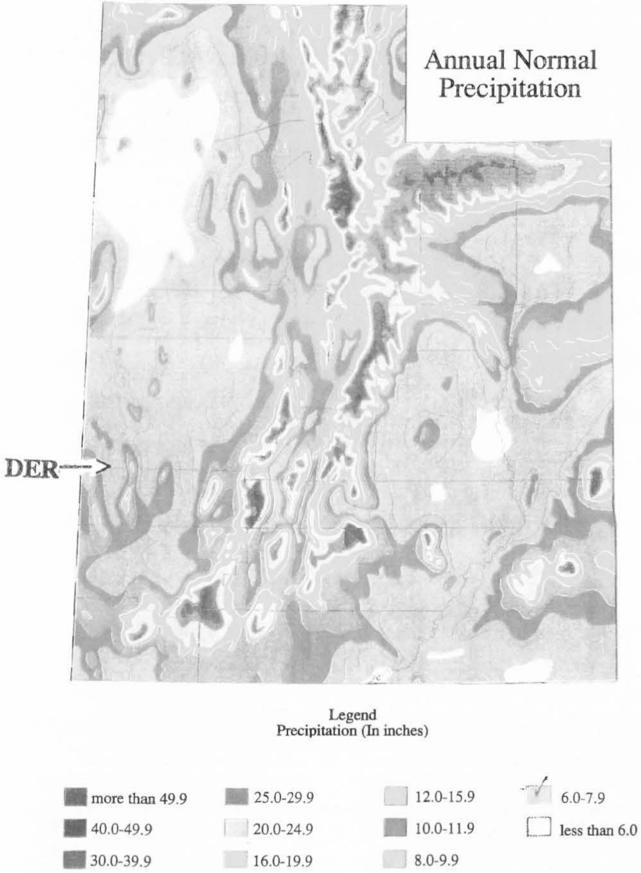


Fig. 1. Location of the Desert Experimental Range in a map of Utah precipitation distribution (Ashcroft et al. 1992).

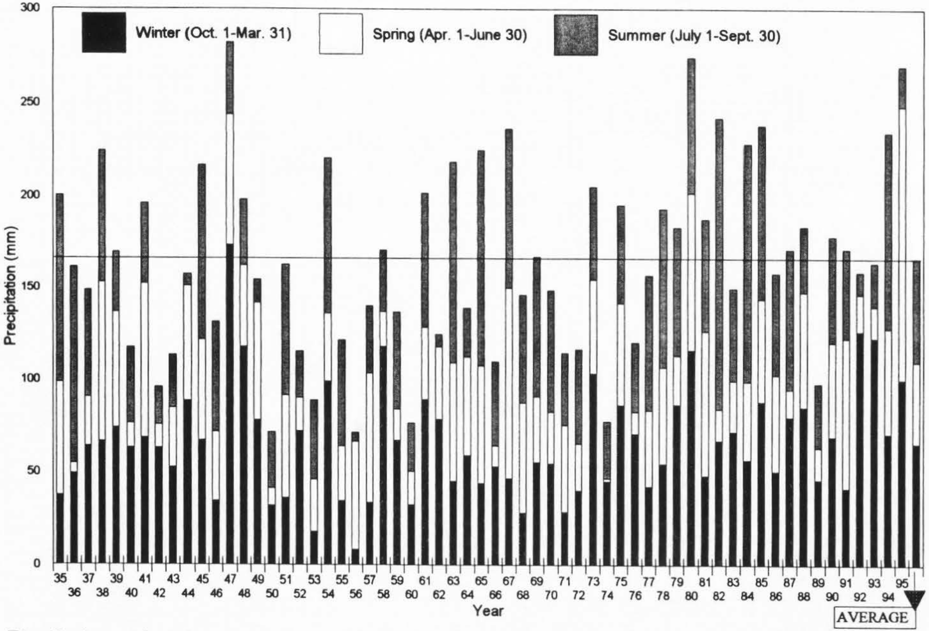


Fig. 2. Annual and seasonal precipitation at the DER headquarters. The hydrologic year is Oct. 1-Sept. 30.

Precipitation for 1935-95 ranged from a low of 71 mm in 1956 to a high of 274 mm in 1980. The average annual precipitation is 165 mm (CV=31%) with approximately 65 mm falling from October through March, mainly as snow (winter), 44 mm from April to June (spring), and 56 mm from July through September (summer). Winter precipitation can be viewed in terms of soil water accumulation for spring growth. The potential evapotranspiration of the area is more than 1,344 mm annually, and up to 2,000 mm has been reported (Brewster 1968, Smith 1986, Chambers and Norton 1993). Under these conditions, the number of days favorable for plant growth during the growing season is probably determined by water balance rather than by temperature or precipitation alone.

Soils and Geomorphology

Geomorphologically, the site is located in a closed-drainage valley on coalescing alluvial fans that extend into the study area from the northwest to the southeast. These fans (or "bajadas") range in elevation from 1,550 to 1,710 m with slopes of up to 15%. At the base of these bajadas is a flood plain of up to 500 m in width draining from west to east throughout the DER. The gradient from the alluvial fans to the lower depositional zones corresponds to a decreasing soil gravel content, increasing composition of fine soil particles, and decreasing calcic horizons.

Soil types of the experimental pastures are Aridisols (haplocambids and haplocalcids--deep, loamy-skeletal, carbonatic group) and Entisols (torrifluvents and torrisamments--deep, coarse-loamy mixed group) (Fig. 3). Mean pH of the soil-D is 8.0 with a range from 7.7 to 8.6 in the upper soil profiles. All soils are saline-sodic at 45 to 55 cm depth. Electrical conductivity is lower in the upper layers (1 mmho/cm) and greatly increases with soil depth (40 mmhos/cm at 45 cm depth) (Brewster 1968, Holmgren 1973, Smith 1986, Tew et al. 1995).

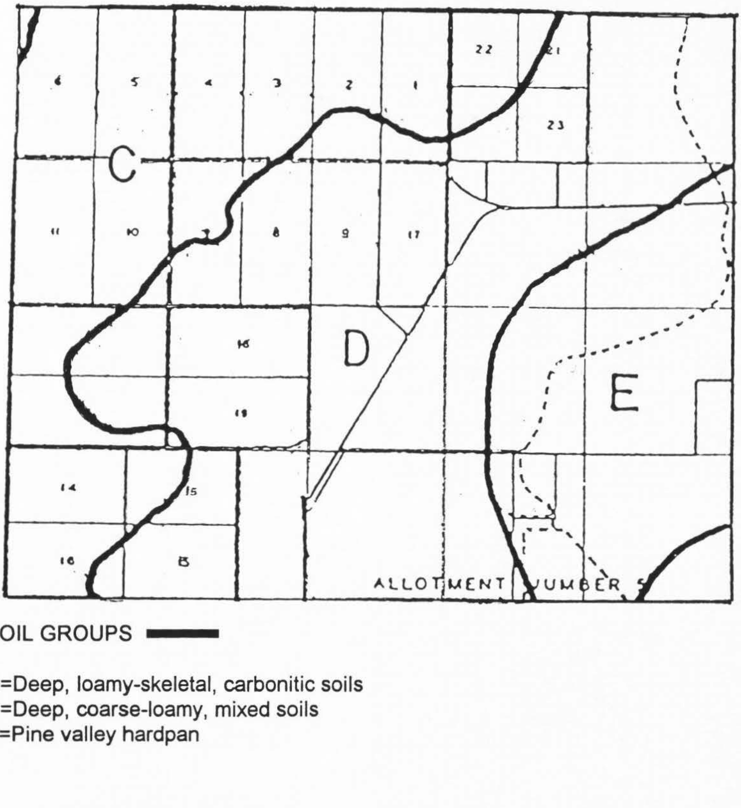
Vegetation

Physiognomically, the study site is a plant community dominated by low-growing shrubs with sporadic inclusion of bunchgrasses and some rhizomatous grasses (Goodrich 1986). Plants have a clumped distribution. Major vascular plants, classified by habitat type, belong to the upland-xerohalophytes group (water table below 1 m) (West 1988). Shadscale-dominated plant communities, common on the site, mainly correlate with halomorphic soils (West 1988).

Important species in this dissertation are referred to with the capitalized 4-letter codes. Codes are derived from the first 2 letters of the genus and the first 2 letters of the species. Less frequently discussed species will be identified by common or scientific name.

Important shrubs in this area include *Atriplex confertifolia* (Torr. & Frem.) Wats. (shadscale, ATCO), *Ceratoides lanata* (Pursh) J. T. Howell (winterfat, CELA), and *Artemisia spinescens* D. C. Eaton in Wats. (budsage, ARSP). ATCO is a forage shrub with spines that limit its consumption by sheep, although seed

DESERT EXPERIMENTAL RANGE
Milford, Utah
1949



SOIL GROUPS ▬

C=Deep, loamy-skeletal, carbonitic soils
D=Deep, coarse-loamy, mixed soils
E=Pine valley hardpan

Fig. 3. Experimental pastures and soil groups in the Desert Experimental Range study area (Tew et al. 1995).

stalks are readily consumed (Holmgren and Hutchings 1972). CELA is a palatable and nutritious browse for both livestock and big game, although its phosphorus content is not as high as budsage (Cook et al. 1954). ARSP is considered a desirable species for winter sheep grazing. Other shrubs of minor importance in the area are *Chrysothamnus* spp. (rabbitbrushes, CHspp.), *Artemisia frigida* Willd. (fringed sagebrush, ARFR), *Kochia americana* Wats. (gray molly, KOAM), and *Ephedra nevadensis* Wats. (Mormon tea, EPNE).

Grasses in general occur more on the shallow alluvial fans in the northern portion of the study area (Smith 1986). Important perennial grasses are *Oryzopsis hymenoides* R. & S. (Indian ricegrass, ORHY), *Hilaria jamesii* (Torr.) Benth. (galleta, HIJA), *Sporobolus cryptandrus* (Torr.) Gray (sand dropseed, SPCR), and *Sporobolus contractus* A.S. Hitch. (spike dropseed, SPCO). The dropseeds and galleta are C_4 warm-season grasses considered to be of lower forage quality and palatability than the C_3 cool-season Indian ricegrass, and may behave as increasers under heavy grazing (Holmgren and Hutchings 1972). Less abundant are the grasses *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. (blue grama, BOGR), *Sitanion hystrix* (Nutt.) Smith. (squirreltail, SIHY), *and Aristida purpurea* Nutt. (purple three-awn, ARPU) (Holmgren 1973, Norton 1978, West 1979, Goodrich 1986, Smith 1986). Common annuals are *Kochia scoparia* (L.) Schard. (KOSC), *Bromus tectorum* L. (cheatgrass, BRTE), *Halogeton glomeratus* (Bieb.) Mey in Ledeb. (halogeton, HAGL), *Salsola* spp. (Russian thistle, SAspp.), and *Chenopodium* spp. (CHspp.), while the most common perennial forb is *Sphaeralcea grossulariifolia* (Hook. & Am.) Rydb. (globemallow, SPGR).

Initial Experimental Design

To study different combinations of intensities and seasons of sheep grazing on the shadscale rangelands, 20 pastures, either 97 or 130 ha in area, were fenced at the Desert Experimental Range in 1934-5 (Table 1 and Fig. 4).

Table 1. Grazing treatments according to paddock numbers established in 1935 at the DER. Grazing intensities were adjusted annually based on preestablished utilization degrees of palatable species*.

	Paddock Number		
	Grazing Intensities		
Seasons	Light	Medium	Heavy
Fall	13	16	8
Fall-Spring	3	20*	15
Fall-Winter	4	5	7
Winter	11	9	12
Winter-Spring	10	6	14
Spring	17**	19**	18**
Winter-Proper	-	1***	-
Winter-Outside	-	-	2****

*Average estimated utilization for palatable ARSP was light 49%, medium 52%, and heavy 68%, and for CELA light 49%, medium 55% and heavy 68% (Smith 1986). In this dissertation grazing intensities were lumped and named "moderate grazing" (see text). **Incomplete data. ***Similar to medium intensity. ****Imitating winter grazing outside the experimental paddocks, similar to heavy grazing intensity.

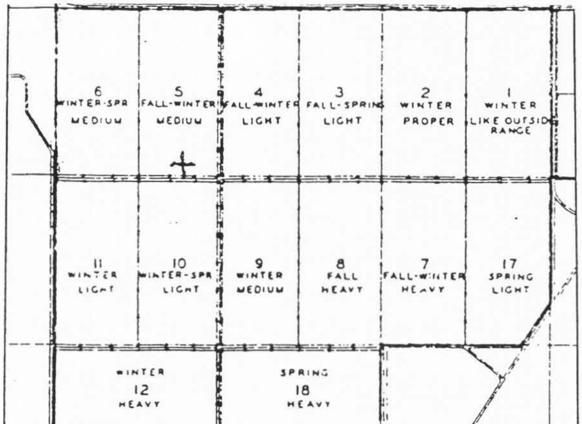


Fig. 4. Experimental pastures and distribution of treatments at the Desert Experimental Range.

In 16 of the 20 experimental pastures, two 0.24-ha exclosures (ungrazed) were randomly selected and fenced, and 2 similar-sized, unfenced (grazed) companion sites with matching vegetation were permanently marked near by (Fig. 5). Within each exclosure, 2 permanent plots of 9.3 m² each were established. These plots were paired with 2 plots in the matching grazed area, and the canopy cover of the vegetation in all plots was mapped. Plots were initially laid out using units of feet (5 × 20 ft), and for consistency these units are retained in my dissertation.

Canopy cover, defined as the vertical projection of the plant canopy cover over the soil, was measured using the chart technique on a 0.01 ft² grid (0.1 × 0.1 ft) to outline the canopy cover of individual plants (Figs. 6 and 7). These maps also allow the fate of individual plants to be followed through time. A total of 128 100 ft² (9.3 m²) plots was mapped in 1935, and remapped in 1958, 1969, 1975, and 1994. Grazing pressure has been held relatively constant through time by adjusting yearly stocking rates to match fluctuations in total herbage production (Hutchings and Stewart 1953).

Data Organization

The set of 640 plot-maps used in this study corresponds to the sampling years 1935, 1958, 1969, 1975, and 1994. Therefore, experimental intervals are 23 years (1935-58), 11 years (1958-69), 6 years (1969-75), and 19 years (1975-94). The variables considered in this research are total and individual plant

Pasture # 5

Aug. 23, 1935

J.L. Jacobs

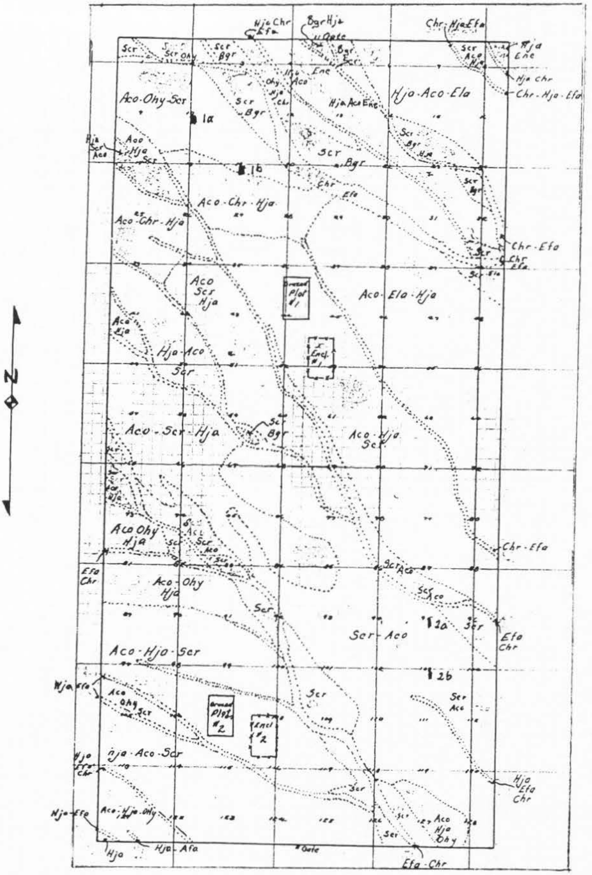


Fig. 5. Example of an experimental pasture showing the location of grazed (Grazed Plot # 1 and Grazed Plot # 2) and ungrazed (Encl. # 1 and Encl.# 2) macroplots.

Pasture # 14

Grazed Plot # 2

Aug. 23, 1935 J.L. Jacobs

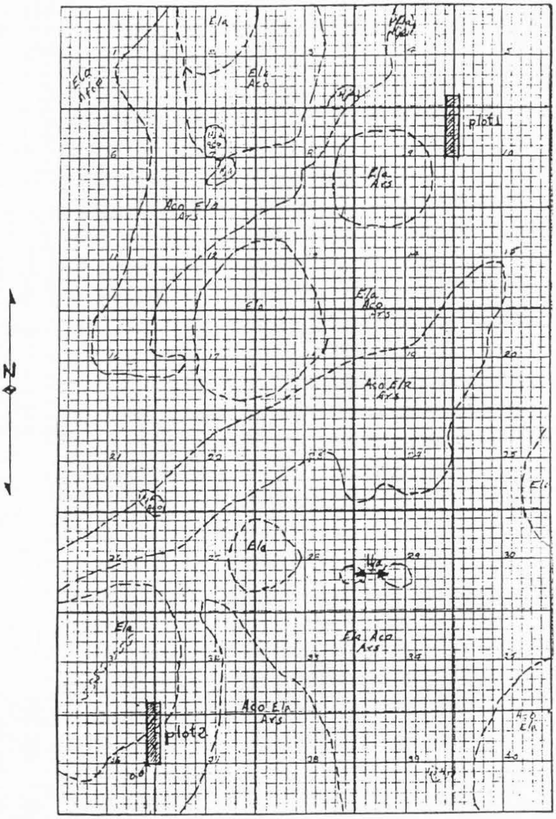
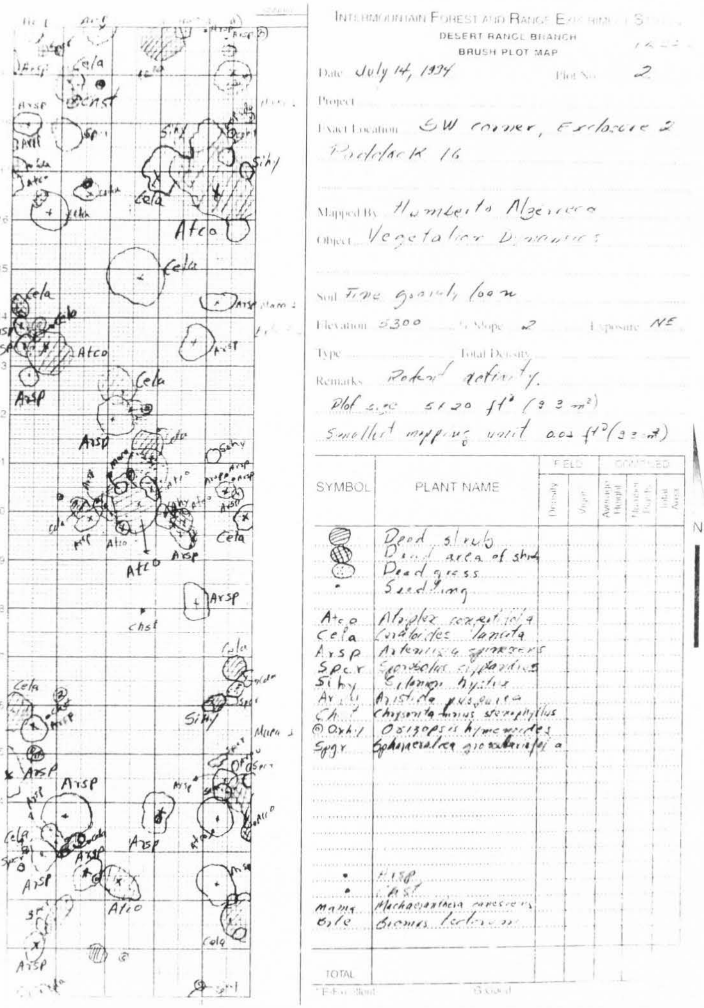


Fig. 6. Example of macroplot showing the location of experimental plots (plot 1 and plot 2).



INTERMOUNTAIN FOREST AND RANGE EXPERIMENT STATION
DESERT RANGE BRANCH
BRUSH PLOT MAP

Date *July 14, 1994* Plot No. *2*

Project

Exact Location *SW corner, Exclosure 2 Paddock 16*

Mapped By *Humberto Alzerreca*

Object *Vegetation Dynamics*

Soil *Fine gravelly loam*

Elevation *5300* % Slope *2* Exposure *NE*

Type Total Density

Remarks *Rodent activity.*
Plot size 5 x 20 ft² (9.3 m²)
Smallest mapping unit 0.01 ft² (9.3 cm²)

SYMBOL	PLANT NAME	FIELD Density	FIELD Vigor*	COMPUTED Average Height	COMPUTED Maximum Height	COMPUTED Total Area
▨	*Dead shrub*					
▦	*Dead area of shrub*					
◌	*Dead grass*					
•	*Seedling*					
Atco	*Atriplex confertifolia*					
Cela	*Ceratoides lanata*					
Arsp	*Artemisia spinescens*					
Spcr	*Sporobolus cryptandrus*					
Sihy	*Sitanion hystrix*					
Arpu	*Aristida purpurea*					
Chst	*Chrysothamnus stenophyllus*					
ⓞ *Orhy*	*Oryzopsis hymenoides*					
Spgr	*Sphaeralcea grossulariifolia*					
•	*Arsp*					
•	*Chst*					
Maca	*Machaeranthera canescens*					
Brte	*Bromus tectorum*					
TOTAL						

*E-Excellent G-Good

Fig. 7. Example of an experimental plot at the DER; paddock 16, exclosure 2 (ungrazed), and Plot No. 2. Plot mapped in 1994 at the DER.

canopy cover, shrub density, interplant distance (closest neighbor), number of plots with annuals, and seedling density and location.

Results from previous studies in the area suggest that differences in grazing season have more impact on the vegetation than differences in intensity of use (Harper 1959, Blaisdell and Holmgren 1984, Smith 1986, Clary and Holmgren 1987, Harper et al. 1990, Marble 1990, Whisenant and Wagstaff 1991, Chambers and Norton 1993). These authors also have noted that there is little difference between the original fall and winter grazing treatments. Based on these considerations, all grazing intensities were lumped as “moderate grazing” and only spring and winter were compared for seasonal effects. The general structure of the study approach (specific approaches are detailed in methods of the corresponding chapters), then, is as diagrammed in Table 2. Note that there are 4 replicated plots in each paddock.

Table 2. General structure of the sample size per year and paddock number for the study of season by grazing and grazing effects on vegetation change in a shadscale plant community grazed by sheep.

	Spring		Winter		Grazing	
	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Number of Plots	20	20	44	44	64	64
Paddock No.	3, 6, 10, 14, and 15.		1, 2, 4, 5, 7, 8, 9, 11, 12, 13, and 16.		1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, and 16.	

CHAPTER 2

PRECIPITATION STUDY

Introduction

In most environments, precipitation and temperature vary among and within years. Because this study was conducted in an area with a desert climate, limited water is one of the most important environmental constraints under which the shadscale plant community evolved. Since water limitation is a function of both precipitation and temperature, the dynamics of these variables are of primary concern in studies of vegetation change of this site. Interpretation of the subsequent analyses will be difficult without first defining the climatic scenario under which changes occurred. This introductory chapter examines annual and seasonal precipitation patterns from 1935 to 1995.

Materials and Methods

The 61 years of precipitation data were summarized by month and year. Most of the data were obtained from the climatic station located at the DER. Missing precipitation records for the period 1983-91 were replaced with information from the closest climatic station, Wah Wah Ranch, located at 38° 29' latitude, 113° 25' longitude, and 1,488 m.a.s.l. This station is approximately 37.5 km from the DER and within the same ecological zone.

In addition to total yearly precipitation, I also considered winter (1 Oct-31

Mar), spring (1 Apr-30 Jun), and summer (1 Jul-30 Sep) precipitation separately. In some cases, the data were further divided into distinct study intervals.

I used simple statistics and graphics to describe the data. In order to determine if an overall trend was present in the 61-year annual precipitation record, a simple linear regression technique was used with precipitation as the dependent variable (Y) and time as the independent variable (X). Later, short-term cyclical movements of total annual and seasonal precipitation trends were described using the moving average technique of order 17 in all cases. This order was selected because it generated more interpretable cyclic trends than other orders. Each number in the 17-year moving average is the mean of 17 values immediately before it. The value for 1980, for example, is the mean of 1963-79. Interannual variability of annual and seasonal precipitation was graphically studied by plotting the residuals. The spatio-temporal behavior of total annual and seasonal precipitation by study intervals was described using variance-mean plots. Depending on the variance-mean relationships, the homogeneity or heterogeneity of the precipitation was assessed; i.e., if the mean increased and the variance decreased, precipitation was becoming more homogeneous; however, if the mean decreased and variance increased, precipitation was becoming more heterogeneous.

Results and Discussion

Mean annual precipitation was 165.9 mm (SD 52 mm), of which 65 mm fell largely as snow in the winter, 45 mm in spring, and 56 mm in summer. The coefficient of variation of the total annual precipitation was 31% (Table 3), and 39 of 61 years fell within one standard deviation of the mean. These statistics define a variable precipitation regime, which, according to Ellis and Swift (1988), is indicative of a nonequilibrium ecosystem. Interestingly, seasonal variation is even greater. Coefficients of variation increased to 46%, 61%, and 57% for winter, spring, and summer precipitation, respectively (Table 3).

In considering individual study intervals, the highest coefficient of variation of total annual precipitation was 35% for the 1970-5 interval, which was also the driest (Table 3). Summer precipitation had the highest CV (61%) during the 1935-58 period, while spring precipitation had the highest CV (69%) during the 1976-95 study interval (Table 3).

Trend and Variability of Annual Precipitation

The 61-year trend line suggested that despite great variability, precipitation generally increased from 1935 to 1995 (Fig. 8). The linear regression was significant (p=0.0500, Table A1), but only explained 6% of the total variance in precipitation. This precipitation increase was not uniform; however, a plot of annual precipitation smoothed with a 17-year moving average reflects the cyclic nature of short-term wet and dry cycles, beginning with a short period of decrease from above-average precipitation to a long period of below-average precipitation, and returning towards above-average precipitation,

Table 3. Annual and seasonal precipitation statistics (mm) by study intervals at the DER.

Period	n(years)	Variable	Annual	Winter	Spring	Summer
1935-95	61	Mean	165	65	44	56
		SD	51	30	27	32
		C.V.(%)	31	46	61	57
		VAR	2679	912	739	1028
1935-58	24	Mean	155	64	43	47
		SD	52	36	24	28
		C.V.(%)	33	56	55	60
		VAR	2768	1340	586	825
1958-69	11	Mean	161	54	45	61
		SD	52	18	26	34
		C.V.(%)	32	34	58	56
		VAR	2714	343	716	1212
1969-75	6	Mean	142	59	34	48
		SD	49	29	20	12
		C.V.(%)	35	48	58	25
		VAR	2489	847	415	148
1975-95	20	Mean	187	74	48	65
		SD	46	26	33	36
		C.V.(%)	24	35	68	56
		VAR	2193	682	1093	1354

within the 61-year period (Fig. 9). To study long-term cycles, however, more than 61 years of data are needed. Despite the clear trend revealed by the moving average, the annual variability of precipitation was large with some extreme and discontinuous years of precipitation values above and below the mean as shown in Figure 10. That is, extreme short-term variability overlays the long-term cyclic trend.

The 61-year study period is only a very small portion of a broader-scale

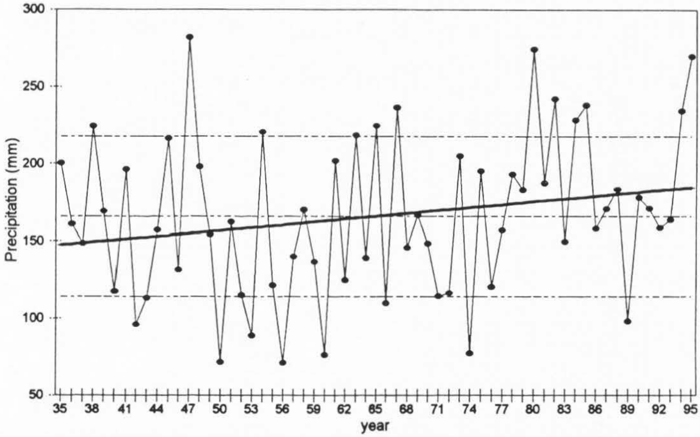


Fig. 8. Trend and annual movements of precipitation from 1935-95 at the DER. Water year (October 1-September 30). The broken lines indicate the mean and ± 1 S.D. of the mean.

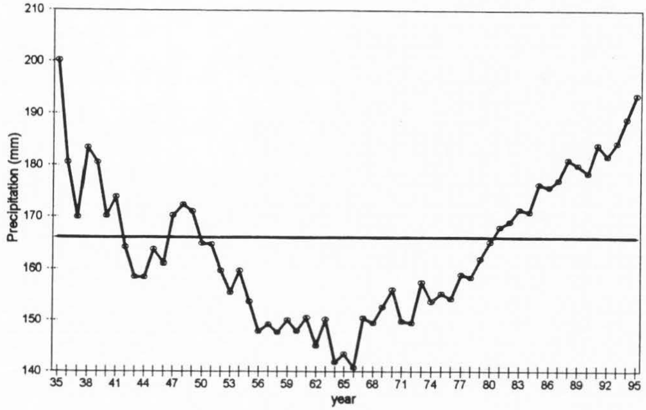


Fig. 9. Seventeen-year moving average and 61-year mean (1935-95) of annual precipitation at the DER. Water year (October 1-September 30).

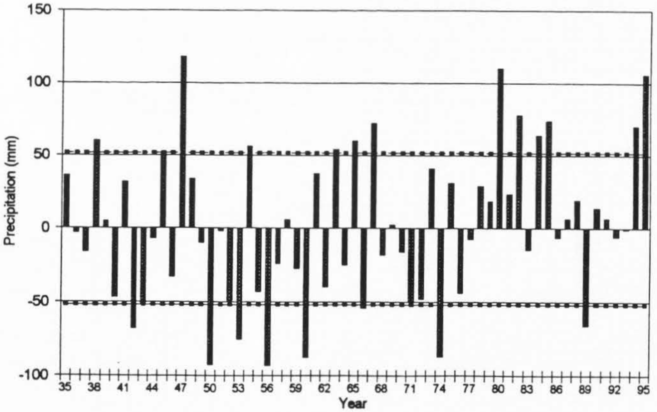


Fig. 10. Deviation from mean annual precipitation at the DER. Water year (October 1-September 30). Mean precipitation is the 61-year average and the broken lines indicate ± S.D. of the mean.

temporal pattern of precipitation. The overall long-term trend of precipitation, and in general of climate, apparently has not been linear, but has shown an alternation of long-term wet and dry cycles (Van Devender and Spaulding 1979). In this context, the 61-year experimental period is part of an overall dry cycle that began in the mid-1930s (Miller et al. 1994). Nevertheless, the DER's precipitation data suggest for this period a wet cycle instead, because mean precipitation increased from 1935 to 1995. This "wet cycle," however, is mostly due to the several influential above-average values between 1978 and 1995 (Fig. 10).

Trend and Variability of Seasonal Precipitation

Winter precipitation followed a trend opposite to that of total precipitation at the beginning of the experiment, with an increase from below-average to above-average precipitation between 1935 and 1949. During most of this period, annual variability was not large (Fig. 11). The steady increase and low variability of precipitation during this period probably led to increasing favorability for the establishment and growth of cool-season plants early in the study. After 1949, precipitation gradually decreased to 1971, and then steadily increased to the end of the study (Fig. 11). Annual variability was generally high during 1949 to 1995 (Fig. 12). Winter precipitation was below average from 1963 until 1984 (Fig. 11). Interestingly, the first 10 years of this dry period presented a continuous deficit of winter precipitation (Fig. 12), suggesting difficult conditions

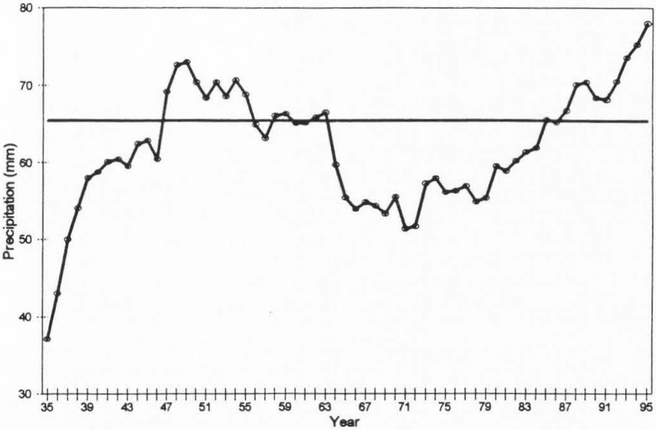


Fig. 11. Seventeen-year moving average and 61-year mean (1935-1995) of winter precipitation at the DER. Water year (October 1-March 31).

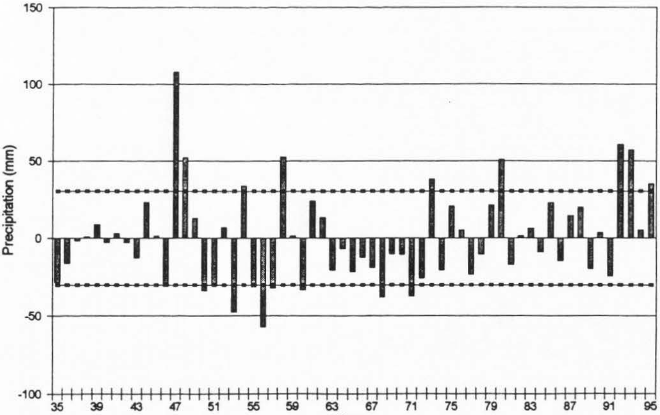


Fig. 12. Deviation from mean winter precipitation at the DER. Water year (October 1-March 31). Mean precipitation is the 61-year average of winter precipitation, and the broken lines indicate ± S.D. of the mean.

for cool-season species. In contrast, the last 4 years of the study (1985-95) were successively above average in precipitation; as with the beginning of the study, this pattern probably favored establishment and growth of cool-season plants.

The moving average of spring precipitation revealed an irregular pattern with short-term fluctuations more evident than in the total or any other seasonal pattern. After especially large fluctuations early, 17-year values remained above the mean from 1944-51, and below the mean from 1958-69, 1973-9, and 1982-90 (Fig. 13). The lack of clear trend of spring precipitation is suggested by the alternating distribution of residuals above and below the mean (Fig. 14); 1958-62 was the longest period with successive years of precipitation below the mean, and no period of more than 3 successive years of precipitation above the mean was found.

Summer precipitation showed a decreasing trend from well above the mean in 1935 to considerably below the mean in 1944. Corresponding to this trend was a switch from 4 successive years above the mean (1935-38) to 6 years below the mean (1939-44) (Figs. 15 and 16). The short period with favorable precipitation may have been important in promoting the establishment and growth of warm-season plants at the beginning of the experiment, although the impact of this favorable period may have been diluted by the long dry period that followed (Fig. 15). During this long dry period, only 8 of 24 years had records above the mean (Fig. 16). This dry period was followed by 2 short-term wet cycles (1965-73) and (1978-91) interrupted by a short dry cycle from 1974-7,

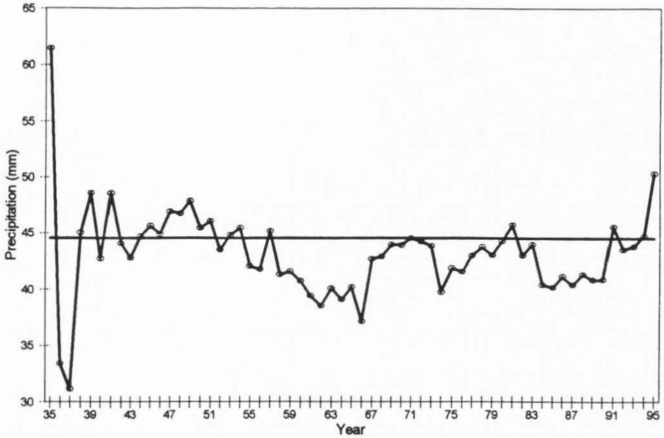


Fig. 13. Seventeen-year moving average and 61-year mean (1935-1995) of spring precipitation at the DER. Water year (April 1-June 30).

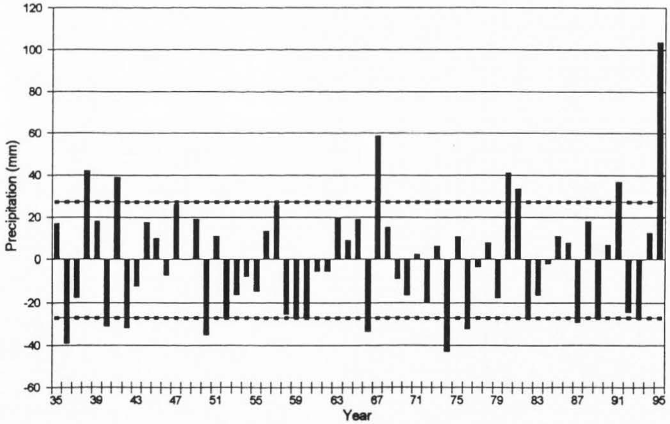


Fig. 14. Deviation from mean spring precipitation at the DER. Water year (April 1-June 30). Mean precipitation is the 61-year average of spring precipitation, and the broken lines indicate ± S.D. of the mean.

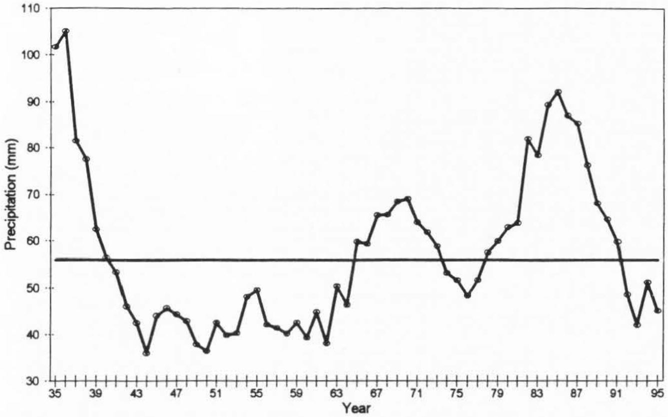


Fig. 15. Seventeen-year moving average and 61-year mean (1935-95) of summer precipitation at the DER. Water year (July 1-September 30).

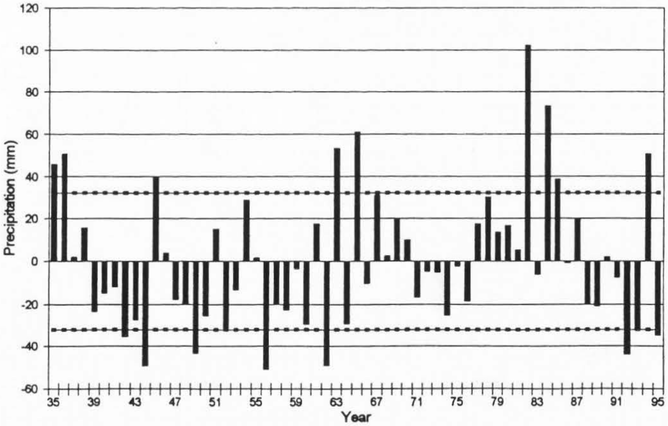


Fig. 16. Deviation from mean summer precipitation at the DER. Water year (July 1-September 30). Mean precipitation is the 61-year average of summer precipitation, and the broken lines indicate ± S.D. of the mean.

and followed by another starting in 1992 (Fig. 15). Among the wet cycles, the 1978-91 period probably lasted long enough to expect a favorable effect for the establishment and growth of warm-season plants (Fig. 15); in this period, exceptionally high summer rainfall occurred in 1982 and 1984 (Fig. 16).

Figure 17 is a summary of the annual and seasonal deviation from mean precipitation by study period. Annual precipitation during the 1935-58 period showed a clear deficit; most of it, however, could be attributed to low summer precipitation for the continuous periods between 1939-44, 1947-50, and 1956-60 (Fig.16). In contrast, the deviations of winter and spring precipitation were very near the 61-year means (Fig. 17). This suggests a period close to the average precipitation regime for cool-season plants, but below average for warm-season plants, except for the short but critical period for plant establishment from 1935-8 (Fig. 16). This interval is climatically defined as average because of the biological importance for plant establishment and growth of near-average winter and spring precipitation, and the above-average summer precipitation from 1935-8.

The second study interval (1958-69) showed a moderate deficit of total annual precipitation (less than 5 mm) (Fig. 17). A major influence for this outcome was the above-average precipitation in summer combined with below-average precipitation in winter (Fig. 17, Table 3). Because evaporation is high in desert environments, it is unlikely that favorable summer precipitation could overcome the winter precipitation deficit (Fig. 14). These circumstances suggest

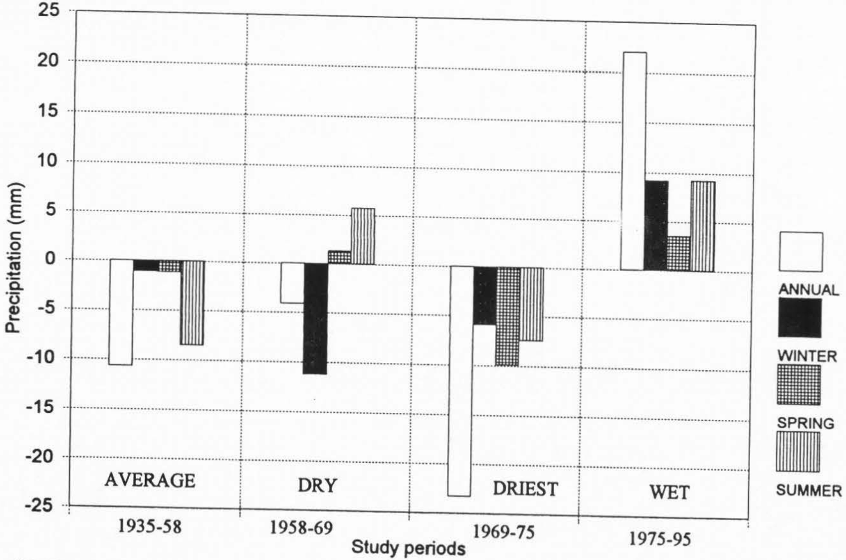


Fig. 17. Deviations from mean annual and seasonal precipitation for the DER-Hydrologic year. The 1935-58 period was defined average because of the relevant biological importance of winter and spring precipitation for plant establishment and growth and because the deviations are nearly average, even though annual and summer precipitation deviations are far below the mean.

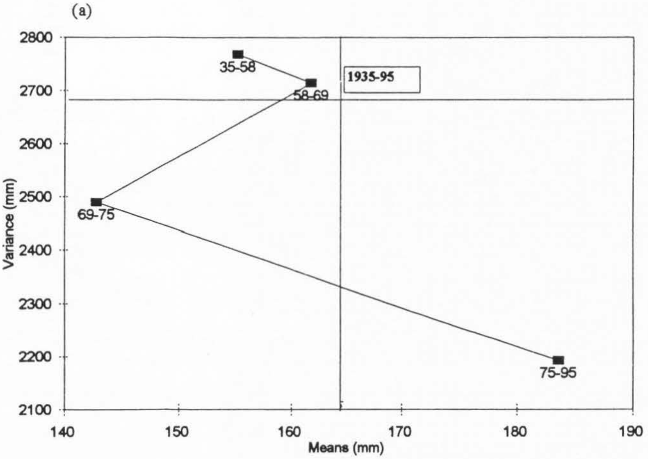
a dry climatic regime for the 1958-69 interval.

The annual precipitation deviation for the 1969-75 period revealed a severe deficit of more than 20 mm resulting from a relatively large deficit each season (Fig. 17). These results indicate a consistent dry precipitation regime unfavorable to both cool- and warm-season species during this study period.

In contrast, the 1975-95 study interval had precipitation values consistently above the mean for all seasons, leading to annual precipitation more than 20 mm above the mean (Fig. 17, Table 3). This clearly suggests a wet climatic regime for this period that probably was favorable for both cool- and warm-season plants.

Variance-Mean Plots

Precipitation in desert environments is usually thought to be associated with a high variance and a low mean (Le Houérou 1972, Noy-Meir 1973, Behnke and Scoones 1993, Graetz 1991). Data from DER showed only partial support for this expected pattern. An increase in annual mean precipitation and a decrease in its variance from the first to the second study intervals was interpreted to indicate a decrease in variability, thus a tendency towards homogeneity (Fig. 18a), within a nonequilibrium environment (CV=31%). This increase in quantity and stability of precipitation suggests more favorable conditions for plant growth, although the mean was slightly below the overall mean. From the second to the third interval there was a dramatic decrease in



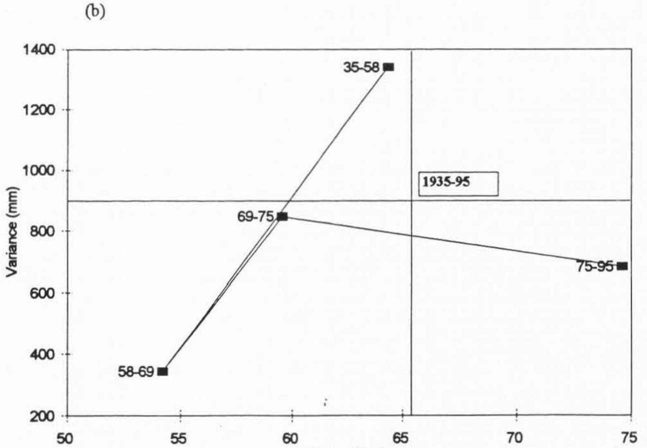


Fig. 18. Variance-mean ratio plots of annual (a) and winter (b) precipitation at the DER. The horizontal line indicates the variance of precipitation from 1935 to 1995, and the vertical line is the mean precipitation for the same period.

both precipitation variance and mean. This period was consistently dry, and precipitation was low enough to define the period as a drought. In contrast to expectations, however, this period was not highly variable. Finally, from the third to the fourth interval (1975-95) precipitation increased to well above average with further decreases in variance (Fig. 18a). This indicates a consistent increase and a relatively even interannual distribution of precipitation, which is unusual for a desert environment. This was the only period with CV less than 30%, reinforcing the notion that amount and distribution of precipitation were more uniform than in other periods. This wet period presumably affected shrubs, which are less tolerant to abundant moisture than grasses (Pyke and Dobrowolski 1989, Archer 1994), potentially leading to long-term shifts in plant community structure.

Considering only winter precipitation, the first period had a slightly below-average mean, but a high variance (Fig. 18b). It is evident from Figure 13, however, that one influential year (1947) contributed greatly to the high variance (1340 mm). By eliminating 1947, the variance was much smaller (839 mm), and in general the precipitation regime appeared favorable for the establishment and development of cool-season woody and herbaceous plants. In the second period, low variance and low mean defined a consistently dry period. From the second to the third period the values of variance and mean increased slightly, suggesting that an increase in winter precipitation is not always followed by a decrease in variance. Finally, in the last period, the mean noticeably increased and the variance slightly decreased, suggesting a less heterogeneous and more favorable winter precipitation regime for cool-season plants.

Mean spring precipitation varied only moderately in the first two stud periods, and variances were close to the 61-year spring average (Fig. 19a). That is, from 1935 to 1969, in general, spring precipitation was favorable for plant growth. During the drought period (1969-75), both variance and mean showed a severe decrease. In the last period (1975-1995), a noticeable increase in both mean and variance again indicate that increasing amounts of rainfall do not necessarily indicate lower variability in desert environments (Fig. 19a).

Summer precipitation showed a low mean and moderate variance in the first study period (Fig. 19b). Both variance and mean increased from the first to the second period. The 1969-75 period revealed a similar variance-mean relationship (low variance and low mean) to the spring and annual patterns already discussed. Finally, both mean and variance for summer precipitation increased noticeably to above average values from the third to the last study interval, suggesting a heterogeneous precipitation regime but with abundant rainfall (Fig. 19b). These conditions are potentially more favorable for grasses than for shrubs. Grasses are more efficient than shrubs in using water that is available for short periods of time and in the upper portion of the soil profile (West 1983, Walker et al. 1981).

Total annual and seasonal precipitation followed mostly the same pattern in drought years (1969-1975) with low variances and low means, while patterns

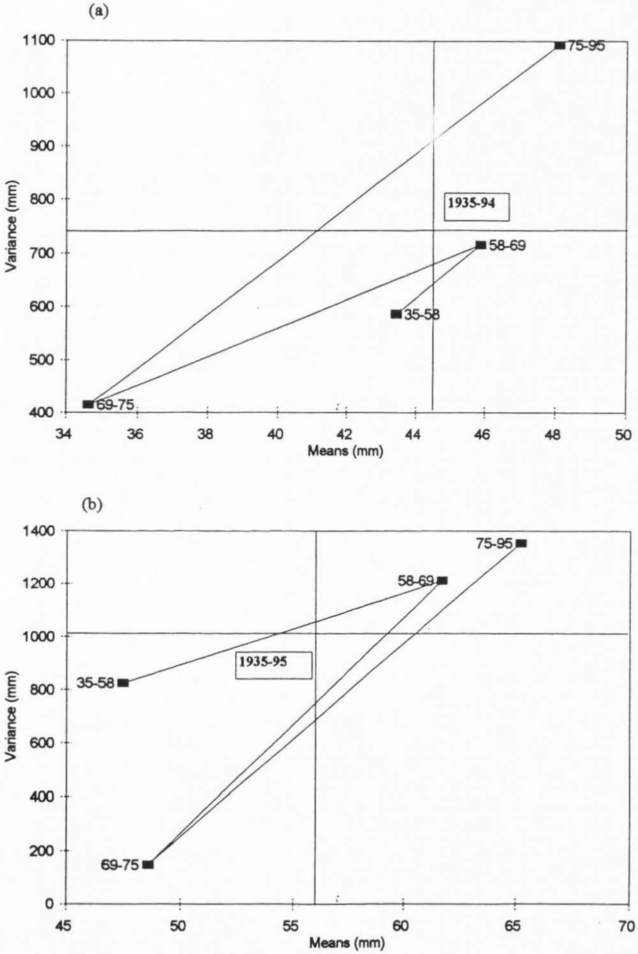


Fig. 19. Variance-mean ratio plots of spring (a) and summer (b) precipitation at the DER.The horizontal line indicates the variance of precipitation from 1935 to 1995, and the vertical line is the mean precipitation for the same period.

in wet years were less consistent. During wet years, winter and total annual precipitation followed a similar pattern (well above-average means and low variances) towards homogeneity in the precipitation regime. This was not the case, however, for spring and summer precipitation, which showed extremely high variances and means above the long-term mean. These results indicate that total and winter precipitation in wet years were relatively more stable than the highly heterogeneous spring and summer precipitation regime. By considering seasonal precipitation for the 1958-69 dry period, spring had a mean above average and smaller variance than summer and winter, implying a favorable spring precipitation regime for plant growth during this dry period.

The extent of favorability may be different depending on the quantitative relationship between variance and mean. A high mean suggests that, on average, a year is expected to have favorable precipitation. But a low variance increases favorability given the mean is already favorable because a good year is less likely to be followed by an extremely low precipitation year that may kill all of the previous year's recruits. On the other hand, the longer-term favorability of precipitation with very low variance (high homogeneity) is questionable if the mean is also very low.

Conclusions and Implications

The understanding of patterns of both total annual and seasonal precipitation in deserts, coupled with the reaction of plant communities to these patterns, can provide a means to predict possible changes in species composition and structure of plant communities. This may be possible in ungrazed and moderately grazed ranges in nonequilibrium ecosystems because vegetation of these areas may respond more to precipitation than to grazing itself (Ellis and Swift 1988). Additionally, understanding climatic variation can help distinguish the role of grazing in vegetation change.

The general trend of an increase in total annual precipitation in the last 61 years at first glance may suggest that the plant community should be steadily moving from a woody to a herbaceous vegetation dominance. This conclusion could be misleading, however, because of the cyclic trend of the precipitation. The observed cyclic precipitation pattern suggests instead that alternating increases and decreases in plant abundances may occur, which are driven by each species' tolerance to the prevalent precipitation regime. Yet the vegetation may not respond to the cyclic pattern of total annual precipitation, but rather to seasonal and short-term cycles in precipitation. Very short-term cycles (2 or 3 years) may produce infrequent establishment of large numbers of individuals of a species favored by such a climatic event (West et al. 1979).

These results indicate that total annual and winter precipitation followed roughly the same cyclic trend, but that these patterns differed from spring and summer trends. Implications of these seasonal differences to vegetation dynamics are expected in a plant community made of different species and ecotypes. These short-term seasonal cycles probably interact with the life history (growth rate, seed production, establishment, plant size, longevity, etc.) of the species involved as well as with other determinants of change such as edaphic or pyric factors. Under these circumstances, frequent sampling (not employed in this study) may increase the possibility of relating precipitation patterns to shifts in vegetation. The longer the intervals between sampling dates, the higher the risk of confounding interpretations because the actual state of vegetation structure may be a result of previous unknown climatic patterns (vegetation inertia). Because of this and because dynamics of nonequilibrium ecosystems are difficult to predict, unexpected climatic events may mask or confound changes attributed to shifts in mean total or seasonal precipitation.

The physiological differences among plant species and the variation among plants within the same species present a range of possible responses to precipitation changes (Plummer 1972). Plants in dry environments "have evolved to exploit different rainfall sequences" (Graetz 1991, p. 66). Consequently, the plant-precipitation interaction may determine a particular successional pathway. For example, cool-season grasses are expected to increase if winter and spring precipitation are high and continuous. If these favorable conditions prevail for a long time, the increase of cool-season grasses may be significant enough to cause changes in plant community structure and composition. Noncontinuous, above-average winter precipitation, however, may favor woody plants instead, because deeply rooted woody species can more efficiently use moisture stored deep in the soil profile (Walker et al. 1981). Conversely, favorable conditions for cool-season grasses probably are not favorable for shrubs that prefer drier conditions, so grasses may still prevail in the plant community. Successive wet years also have implications for promoting the establishment, growth, and reproduction of exotic invaders adapted to continuously wet conditions (shallow root systems) that otherwise would remain, under dry conditions, as minor components of the plant community (Harris 1967). Similarly, long-term dry periods could cause the opposite effect, and drought-tolerant plants, mainly shrubs, may dominate the plant community (Harrington 1991, Archer 1994).

In general, variance-mean plots suggested a strong heterogeneity of the annual and seasonal precipitation regimes in the study area, even under increasing mean rates of precipitation. Overall, an increase in both variance and mean was the most common variance-mean combination detected in this study (6 cases). A decrease in mean precipitation and variance was found in 3 cases, and in 3 cases precipitation variance decreased and mean increased. In not one case was there the expected pattern of increased mean precipitation and variance. This suggests that precipitation may not constrain plant growth in cool deserts nearly as much as in hot deserts. Even if increases of mean precipitation and variance occur in cool deserts, it may have little impact on the vegetation because most of the effective precipitation comes in winter and spring when evapotraspiration is minimal and more water is stored in the soil profile for plant use than in hot deserts (West 1988).

CHAPTER 3

SHEEP GRAZING EFFECTS ON PLANT COVER DYNAMICS OF A SHADSCALE PLANT COMMUNITY

Introduction

A shadscale plant community in the Desert Experimental Range (DER) has been subjected to sheep grazing trials from 1935 to the present. The goal of such long-term studies was to evaluate the impact of grazing intensities and seasons of use to determine appropriate carrying capacities for shadscale communities. Reports of negative impacts of grazing on natural vegetation and of range degradation from uncontrolled grazing of Intermountain salt-desert shrub rangelands prior to 1935 gave impetus for the study (McArdle et al. 1936, Shantz and Piemeisel 1940, Stewart et al. 1940).

Climatic data have been interpreted to indicate that a transition from a drier to a wetter regime was under way by 1935 (Chapter 2 in this dissertation). Therefore, the experimentation at the DER was initiated under unique circumstances. That is, heavy grazing and drought prior to 1935, was followed by both decreased grazing intensity and change to a more favorable climate. These circumstances at the start of the study were reflected in early reports indicating increased plant cover and density in both grazed and ungrazed pastures (Hutchings and Stewart 1953, Harper 1959). These authors suggested that reduction of grazing pressure, and not climate, played the major role in the initial recovery of the vegetation. Because recovery in total plant cover was indistinguishable between grazed and ungrazed pastures, which was interpreted to suggest that changes in precipitation regime may have played the major role. In reality, it could not be unequivocally demonstrated that reduced grazing intensity had an impact on plant community changes at the DER.

More detailed studies about effects of grazing on individual species of the plant community were reported by several authors (Hutchings 1966, Holmgren and Hutchings 1972, Norton and Bermant 1977, Norton and Michalk 1978, Norton 1978, Harper et al. 1990, Whisenant and Wagstaff 1991). Some concluded that grazing was the main driving force for change in relative composition of the plant community (Hutchings 1966, Holmgren and Hutchings 1972, Harper et al. 1990, Whisenant and Wagstaff 1991), while others indicated that grazing did not affect the trend of natural succession and suggested that climate and other factors were probably the major causes of change (Norton and Bermant 1977, Norton and Michack 1978, Norton 1978). More comprehensive analyses that include specific consideration of climatic regimes are necessary to disentangle the impacts of grazing from those of climate; this chapter is a contribution to such analyses.

Since we are interested in long-term effects of sheep grazing on vegetation, long-term data are required. This study helps this effort by adding 19 years to the existing data base, last sampled in 1975. Importantly, this new period had a different precipitation pattern than prior study periods, thus more information is available to better understand the process of vegetation change under climatically variable conditions.

This chapter describes 59 years of vegetation change in the experimental pastures with reference to total plant cover and cover of dominant species. Plant successional patterns in the control pastures (no grazing by large herbivores) are used as indicators of long-term change due primarily to climatic change, while changes in grazed pastures incorporate effects of both continued large herbivore grazing and climate.

The objective of this study was to determine if grazing affects plant cover dynamics in shadscale communities. I addressed this objective at two levels: total plant cover and cover of individual dominant species. The relevant null hypotheses and their logical predictions are:

HO1: Total plant cover has not been affected by 59 years of controlled, moderate levels of sheep grazing.

Prediction: Although total plant cover may change through time, grazed and ungrazed pastures will not differ at any census period.

HO2: Cover of individual species has not been affected by 59 years of controlled moderate levels of sheep grazing.

Prediction: Although cover of individual species may change through time, grazed and ungrazed pastures will not differ at any census period.

Literature Review

The grazing history of this region can be defined by three distinct periods. The first period is the interval prior to the introduction of domestic stock (i.e., until 1870). For this period, little information is available, and what exists is frequently contradictory. Speculation on vegetation characteristics during this period is presented by Hart and Norton (1988) and Miller et al. (1994). The second period began with the introduction of European domestic animals and the subsequent unrestricted use of the public range (i.e., 1870 to 1933). During this period, the grazing value of the desert range was severely reduced (McArdle et al. 1936, Shantz and Piemeisel 1940, Stewart et al. 1940). The first signs of deterioration in this ecosystem were reductions in plant size, vigor, and cover, and reduction in numbers of desirable forage plants linked with an increases in numbers of undesirable forage plants (Holmgren and Hutchings 1972). The third period began with the Taylor Grazing Act in 1934 and extends to the present. During this period, livestock use of the range was reduced and improvements in range condition began (Holmgren 1973, Yorks et al. 1992).

An assumption driving the management changes instituted in the third period was that properly managed grazing would allow the range to recover. To evaluate this assumption, grazing studies were initiated at the DER in 1935. After an initial evaluation of grazing trials at DER, Hutchings and Stewart (1953) reported an overall increase in plant cover and biomass for the 1935-47 period.

They also mentioned increasing trends in production of palatable species under moderate and light grazing, while the opposite happened under heavy grazing. no mention was made of effects of season of grazing on vegetation, however. Hutchings (1966) reinforced his initial report with additional data to 1963. He concluded that, irrespective of grazing, interannual biomass production was highly variable and positively correlated with precipitation, and that, irrespective of precipitation, grazing influenced the vegetation.

Harper (1959) conducted an analysis for the 1935-58 period, and concluded that plant cover of perennial species was much greater in 1958 than in 1935, and that the increase was larger in ungrazed than in grazed plots. At the species level, he found important increases of *Ceratoides lanata* (CELA) and decreases of *Atriplex confertifolia* (ATCO) in winter-grazed pastures, and large increases of *Artemisia spinescens* (ARSP) in ungrazed plots. Among the grasses, *Hilaria jamesii* (HIJA) showed a major increase in all pastures. He attributed these changes to reduced grazing intensities since 1935 rather than favorable climatic changes.

Contrasting species cover of moderately grazed pastures and ungrazed controls for the 1935-67 period, Holmgren and Hutchings (1972) concluded that productivity in terms of total cover increased from 1935 to 1967. Not all species responded the same, however. In grazed pastures, ATCO and CELA increased notably, and ARSP showed a small increase. CELA and ARSP also increased in the ungrazed pastures, but ATCO decreased. Regarding season of grazing, ATCO became dominant under heavy spring grazing while CELA and ARSP declined. In contrast, CELA and ARSP increased on winter grazed pastures. These authors suggested that ATCO dominated the cool-desert ranges because of the overexploitation of the range prior to 1935 and predicted that ATCO would eventually retreat under moderate grazing. However, they indicated "successive cycles of extended drought followed by favorable growth years are needed to undo the vegetal change effected by harmful grazing" (p. 164). In line with this, they speculated that recovery might take longer than expected because, in addition to control of grazing, the coincidence of a good year for seed production followed by a good year for seedling establishment was needed. Such a coincidence, however, is a rare event in these desert environments (Gasto 1969, West and Gasto 1978). Holmgren and Hutchings (1972) concluded that compositional change under grazing is not linear and depends on climatic vagaries (mainly drought) and biological influences (i.e., insect infestation).

Other authors in the early 1970s expressed a similar opinion as to the importance of environmental and other managerial and biological factors that interact and affect plant dynamics and succession in semiarid ecosystems. These factors included among others, climate, soils, topography, allelochemic influences, competition, life history of plants, introduction of alien species, insect outbreaks, and plant mutations (West and Tueller 1972, Tueller 1973). Evidence for the role of environmental factors was found by Norton and Bermant (1977, p. 7), who, after studying plant replacement processes in vegetated patches at

DER, concluded that "the specific trends of increasing total plant cover and establishment of dominance by winterfat with decline in shadscale have been most pronounced on sites originally occupied by plants in 1935. The increase in cover of budsage has also been a spatially heterogeneous change, with preference for sites formerly dominated by shadscale."

Norton (1978), studying plant cover dynamics at DER from 1935 to 1975, reported an increase from 4 to 10% in total plant cover. He remarked that heavy grazing did not affect the general trend in plant cover or species composition. ATCO, a less palatable shrub, increased in the first period and then consistently declined to 1975, but CELA, a palatable shrub, consistently increased in cover during the same period. Norton (1978, p. 610) concluded that "vegetation changes in dominant palatable and unpalatable species were not a function of grazing pressure as mediated by interspecific competition. Inherent plant longevity, opportunity for plant replacement and differential response to climatic pattern may be more influential factors than grazing stress."

Blaisdell and Holmgren (1984) reported that grasses increased in pastures grazed heavily in early and late winter. They related the season-of-grazing response to plant development stages; CELA and ARSP are vulnerable to grazing when grazed in March and April. Thus, phenological differences among palatable species are probably responsible for increases or decreases related to timing of grazing. They also related production trends in CELA to grazing intensity, reporting increases with light grazing but no change with heavy grazing.

West (1988, p. 221) summarized the status of research done in the shadscale community before 1988, stating:

> Not much research was done on this vegetation type until after the scare provided by the *Halogeton* (a poisonous annual from Eurasia) invasion beginning in the 1940s. Thus, our perspective is short, and the data are inadequate to decipher retrogression. We do know that the most palatable shrubs-*Artemisia spinescens*, *Ceratoides lanata* and *Kochia americana*-declined substantially, especially when grazing use extended into the spring (Blaisdell and Holmgren 1984). Unfortunately these shrubs also had the least reproductive capacity. The less palatable species-*Atriplex confertifolia, Atriplex gardneri, A. falcata, A. tridentata, A. cuneata,* [and] *A. corrugata*-have come back more rapidly after control of livestock grazing. These trends, however, are difficult to distinguish from annual fluctuations and the effects of longer-term climatic influences (Norton 1978).

More recently, Marble (1990) reported for 1987 no difference in cover between plots grazed in early or midwinter (19.7%) and mid or late winter (20.1%), but significant differences between grazed (19.9%) and ungrazed (23.7%) plots regardless of grazing season. He reported, however, significantly higher non-vascular cover in lightly than heavily grazed pastures.

Some seasonal treatment differences were detected when biomass (Smith 1986) or cover (square foot density method) were measured (Whisenant and Wagstaff 1991). Combined grazing and climatic factors are mentioned as the possible cause of differential effects on plant populations in dry years (Chambers and Norton 1993). Despite apparently conflicting results, there is overall agreement that spring grazing has had the greatest effect on vegetation and that impacts of fall and winter grazing treatments are indistinguishable.

In summary, from the previous studies it is clear that plant cover and biomass increased after 1935 after 1975. It is also clear that plant composition has been changing at different rates; faster in pastures grazed during the growing season than in those without grazing or grazed during the dormant season. In general, however, all treatments appear to be following a similar trend toward a more herbaceous plant community. Explanations other than grazing for this change have been limited to sporadic inclusion of climate in the analyses. As a result, there is still no agreement as to whether climate, grazing, or the combination has been most important as agents of change. If we want a better management of this ecosystem, we must develop a more thorough understanding of grazing and climate interactions without overlooking other possible determinants of change.

Materials and Methods

Total Plant Cover Dynamics

Total cover was determined by summing the canopy cover of all perennial plants in the plot. In hopes of reducing the number of factors to analyze and to facilitate further interpretation without losing critical information, a preliminary statistical comparison was made between winter and spring grazing. There were no significant differences between winter and spring grazing treatments for any year ($p \geq 0.05$). Similarly, total plant cover means of light ($\bar{x}=22.7 \pm 1.3$), moderate

($\bar{x}$=19.4±1.6), and heavy ($\bar{x}$=19.5±1.9) treatments showed values with only negligible differences (Marble 1990). Because of this lack of differences, we combined data across spring and winter grazing treatments and across grazing intensities. The two resulting treatments, grazed and ungrazed, were studied across the four study intervals identified in chapter 2: 1935-58, 1958-69, 1969-75, and 1975-94.

The experimental design was a factorial ANOVA with repeated-measures factors and between-group factors. Repeated measures factors were the five sampling dates: 1935, 1958, 1969, 1975, and 1994. Between group factors were the two grazing treatments: grazed and ungrazed. The resulting sample size was 64 grazed and 64 ungrazed plots/year for a total of 640 observations in 5 sampling years.

The data were analyzed with the SAS PROC MIXED procedure (Bonferroni test), which allowed multiple comparison with control for an overall experiment-wise error rate (Hatcher and Stepanski 1994). The accepted significance level was 0.05.

Individual Species Cover Dynamics

The accumulated canopy cover values by species and plot were organized for analysis in season × treatment × time × species matrices. About 20 perennial species were recorded in each of the 5 sampling years, but most were of little importance in the botanical composition of the plant community and were not analyzed.

Because the dynamics of the plant community largely relied on three shrub species and three grass species, these six species were selected for this study. Dominant shrubs in 1935 were *Atriplex confertifolia* (ATCO) (65%), *Ceratoides lanata* (CELA) (15%), and *Artemisia spinescens* (ARSP) (4%). Dominant grasses were *Sporobolus cryptandrus* (SPCR) (6%), *Hilaria jamesii* (HIJA) (6%),and *Oryzopsis hymenoides* (ORHY) (1%). These six species together contributed 97%, 98%, 94%, 94%, and 87% of the total cover for 1935, 1958, 1969, 1975, and 1994, respectively.

In contrast to total plant cover, season was believed to be important for individual species analysis. Therefore, the experimental design for this portion of the study consisted of two seasons (winter and spring), 2 grazing treatments (with and without), and 5 sampling years (replicated through time). The variables used in the multivariate analysis were the six species. An example of the data matrix is included in Table A2.

Prior to analysis, descriptive statistics were calculated for each variable (species) across grazing treatment, season, and time using the SAS statistical package (PROC UNIVARIATE). Data were highly skewed to the right (positively skewed), indicating a lack of symmetry of the data. That is, values above the mean were more variable than values below the mean. With log transformations, symmetry improved and the problem of outliers was corrected. Assumptions of normality and equality of variances were not totally met for the majority of species, however. This is not surprising since multivariates rarely satisfy these assumptions. Nevertheless, the analysis was continued because: 1) multivariate analysis of variance (MANOVA) is relatively robust in cases of moderate violation of these assumptions (Stevens 1966); 2) transformation improved the symmetry of the distribution, and 3) sample sizes were relatively large (20 or more plots for any given treatment).

The model used was:

$$Yijk=\mu + \alpha i^{TIME} + \beta j^{GRAZE} + \tau k^{SEASON} + \alpha\beta_{ij} + \alpha\tau_{ik} + \beta\tau_{jk} + \alpha\beta\tau_{ijk} + \epsilon_{ijk}$$

In a more general equation (e.g., considering observations, number of dependent variables, etc.), the model can be written as: $Y=X\beta + \epsilon$, where Y is a matrix of n (nₒ observations) × p (nₒ variables), X is a matrix of n × t (nₒ parameters), $\underline{\beta}$ is a matrix of t × p, and ϵ is n × p. The model was entered in SAS as: latco lcela larsp lorhy lhija=time|graze|season, where l refers to the natural log.

A similar approach was used to analyze the data reduced to 2 variables: grasses and shrubs. This was done to better understand the shrub-grass interface through time, independent of species.

Annuals

Mapped-plots were analyzed for the presence of *Bromus tectorum* (BRTE), *Salsola* spp (SAspp.), and *Halogeton glomeratus* (HAGL) across the 5 years (1935, 1958, 1969, 1975, and 1994). Contingency tables were constructed to test for differences in the presence of exotic annuals by year and by grazing treatment. The χ^2 statistic was used in the tests with a Bonferroni correction to adjust the probability level according to the number of independent tests performed. With this conservative correction an overall p=0.05 is maintained by using p=0.05/K for each comparison, where K=the total number of comparisons made (Zar 1984).

In 1994, the intensity of invasion by annuals was also analyzed. Subjectively scored heavy and light invasion categories were compared for grazed and ungrazed pastures. Heavy invasion corresponded to more than a 90% cover by one or a combination of the 3 species under evaluation, while light invasion was defined as all other plots; virtually all of these had none or only widely dispersed populations of these annuals. A 2-way table was constructed, and the χ^2 statistic used to evaluate significance.

Results

Total Plant Cover Dynamics

The treatment by time interaction was significant (F=2.62, df=4, p=0.0345, Table A3). This finding is consistent with the hypothesis that the relationship between the time variable and cover values differs for the 2 grazing treatments, as seen in Figure 20. After a moderate separation of the treatments from 1935 to 1958, the two treatments were nearly parallel until 1969, after which, the separation continued to increase to 1970 and 1994. Post-hoc contrasts for each

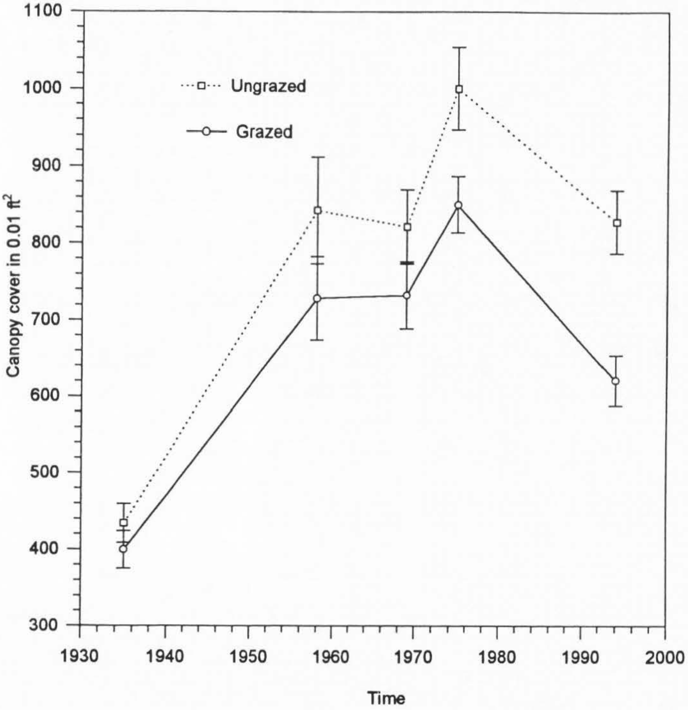


Fig. 20. Total plant cover dynamics in grazed and ungrazed pastures at the DER. Vertical bars are standard errors of the means. Canopy cover was measured on a 0.01 ft^2 (9.3 cm^2) grid. The area of each plot was 100 ft^2 (9.3 m^2).

time period reveal no difference among grazing treatments for any of the first three sample dates. Cover means in 1975 and 1994, however, differed significantly between grazing treatments (p=0.0330, and p=0.0002, respectively) with ungrazed plots having greater cover (Table A3).

Time, the repeated measures factor, was also significant (F=88.3, df=4, p=0.001). Post-hoc contrasts revealed that cover scores for the years 1958, 1969, 1975, and 1994 were all significantly higher than cover scores observed in the baseline year of 1935 (p=0.0001). From 1959 to 1969, however, total cover did not change significantly (p=1.000). In the next period, from 1970 to 1975 mean cover scores increased significantly (p=0.0001, Fig. 20). The difference, however, was only significant for the ungrazed treatment (p=0.0040), not for the grazed treatment (p=0.1497). During 1975-1994, cover decreased significantly in both grazed (p=0.0001) and ungrazed (p=0.0009) treatments (Fig. 20, Table A3).

Individual Species Cover Dynamics

Results of Multivariate Analysis

The purpose of this trend study was to determine whether the 6 species differed in plant cover with season of grazing, intensity of grazing, and time. Results were analyzed using a MANOVA between groups design.

The overall time grazing interaction effect was significant (Wilks' lambda=0.91, p=0.0001, Table A4), as was the overall grazing × season interaction (Wilks' lambda=0.94, p=0.0001). In contrast, neither the overall time-by-season (Wilks' lambda=0.96, p=0.3219) nor the overall time × grazing × season effect was significant (Wilks' lambda=0.98, p=0.9398). The analysis of main factors revealed significant multivariate effects for time (Wilks' lambda=0.51, F=19.04, df=24, p=0.0001), grazing (Wilks' lambda=0.79, F=27.13, df=6, p=0.0001), and season (Wilks' lambda=0.89, F=12.17, df=6, p=0.0001, Appendix D1).

Results of Univariate Analysis

To determine the nature of the main effects, contrasts were performed to study trend and treatment effects for each of the dependent variables.

Atriplex confertifolia (ATCO). ATCO responded significantly to the main factors of time (p=0.0001) and grazing (P=0.0001), but not to season (p=0.6226), or any interaction (Tables 4, 5, and 6; Table A5).

Between 1935 and 1958 cover of ATCO did not change, but after 1958 it decreased significantly for each census until 1994 when cover was only 41.1% of the 1935 value (Table 4, Fig. 21; Table A6). The rate of decrease depended on grazing, however (Table 6). Cover was greater in grazed plots in 1958 (p=0.0450), 1969 (p=0.0003), and 1975 (p=0.0083, Fig. 22; Table A6). By 1994, however, the grazing treatments again did not differ (p=0.3501). Thus, although the overall decrease through the study was equivalent, the rate of decrease of ATCO depended on grazing treatment. ATCO cover means did not differ

Table 4. Contrast to evaluate the hypothesis of no overall time effect for study species at the DER.

Contrast	F value	Wilks'l. statistic	Pr>F	Variable	Estimate	Pr>F
T1 vs T2	8.9666	0.9195	0.0001			
				ATCO	-0.2121	0.3113
				CELA	-0.6149	0.0436
				ARSP	-0.7979	0.0025
				SPCR	-0.6207	0.0165
				ORHY	-0.5985	0.0034
				HIJA	-0.7864	0.0154
T2 vs T3	4.9600	0.9538	0.0001			
				ATCO	0.8308	0.0001
				CELA	-0.1519	0.6176
				ARSP	-0.1187	0.6513
				SPCR	-0.6114	0.0181
				ORHY	-0.3023	0.1378
				HIJA	-0.3717	0.2513
T3 vs T4	1.9671	0.9811	0.0683			
				ATCO	0.6253	0.0029
				CELA	-0.2356	0.4388
				ARSP	-0.0073	0.9776
				SPCR	-0.1510	0.5586
				ORHY	-0.2258	0.2674
				HIJA	-0.1247	0.7001
T4 vs T5	15.2843	0.8702	0.0001			
				ATCO	0.4865	0.0205
				CELA	1.4636	0.0001
				ARSP	-0.0181	0.9448
				SPCR	-0.5208	0.0440
				ORHY	-1.7094	0.0001
				HIJA	0.0423	0.8960
T1 vs T5	60.1525	0.6301	0.0001			
				ATCO	1.7306	0.0001
				CELA	0.4611	0.1300
				ARSP	-0.9423	0.0004
				SPCR	-1.9041	0.0001
				ORHY	-2.8562	0.0001
				HIJA	-1.2403	0.0001

The order of contrast means is: T1G T1U T2G T2U T3G T3U T4G T4U T5G T5U

Table 5. Contrast to evaluate the hypothesis of no overall season effect for study species at the DER.

Contrast	F value	Wilks'l. statistic	Pr>F	Variable	Estimate	Pr>F
Spr.*Win.	12.1684	0.8938	0.0001			
				ATCO	-0.0652	0.6226
				CELA	-0.4443	0.0212
				ARSP	-0.9546	0.0001
				SPCR	-0.4088	0.0125
				ORHY	0.1843	0.1524
				HIJA	0.9908	0.0001

Table 6. Contrast to evaluate the hypothesis of no overall grazing effect for study species at the DER.

Contrast	F value	Wilks'l. statistic	Pr>F	Variable	Estimate	Pr>F
Gra.* Ung.	27.1270	0.7907	0.0001			
				ATCO	0.5401	0.0001
				CELA	-0.4670	0.0155
				ARSP	-1.7874	0.0001
				SPCR	0.3337	0.0413
				ORHY	0.0586	0.6489
				HIJA	0.1512	0.4605

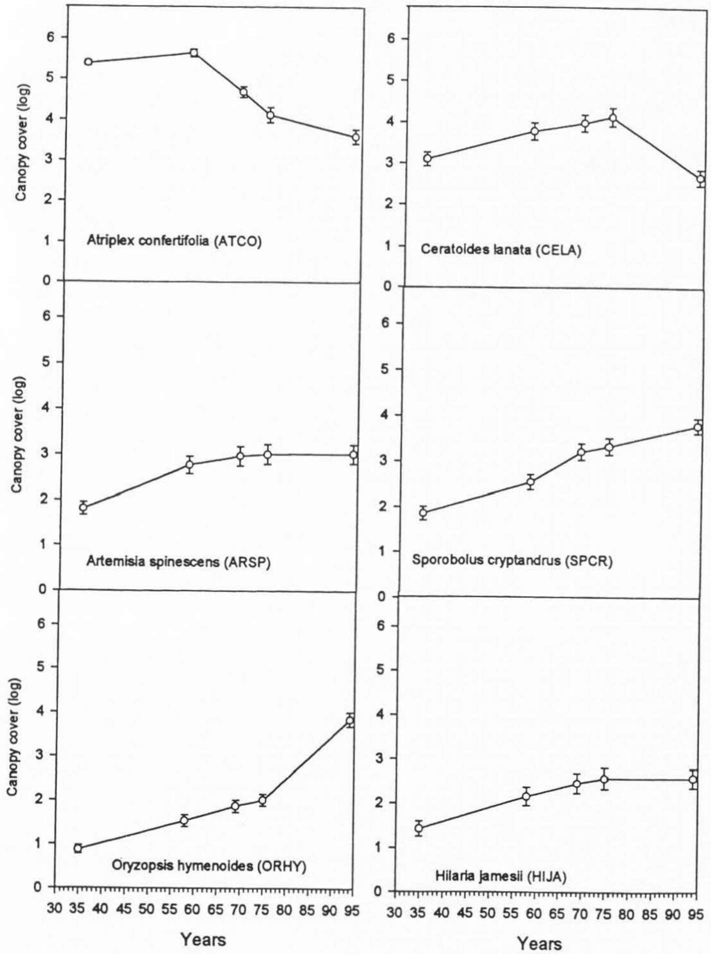


Fig. 21. Main effects of time on cover of six species at the DER. Vertical bars are standard errors of the means.

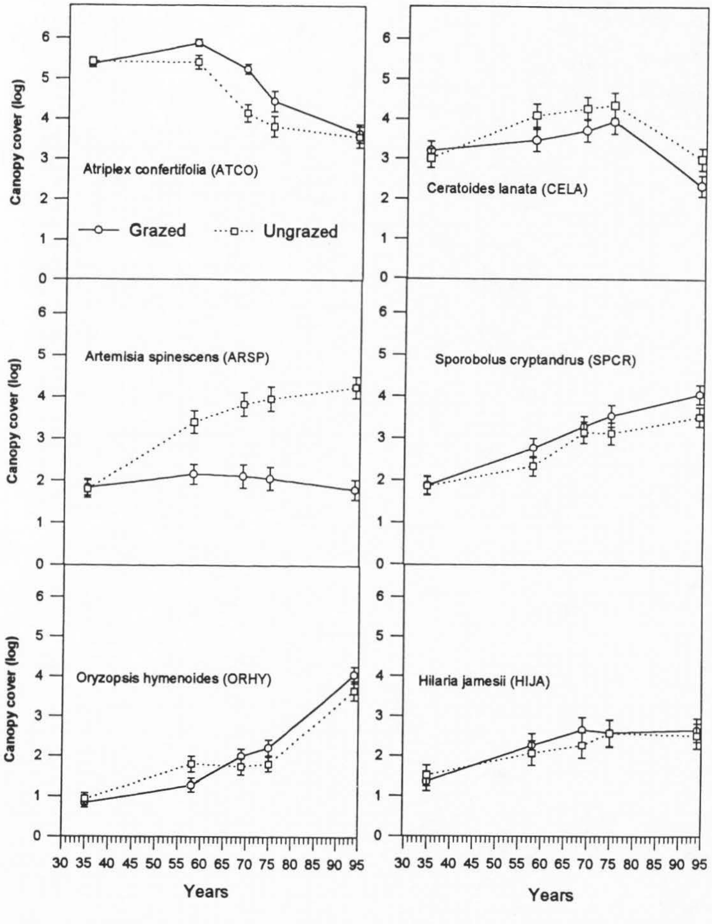


Fig. 22. Time by grazing analysis in six species at the DER. Vertical bars are standard errors of the means.

between seasons for any of the five sampling dates (all p≥0.2295), Fig. 23; Table A7). Nevertheless, within seasons, spring-grazed showed a higher mean than spring-ungrazed treatments (p=0.0003), while grazing treatments did not differ in winter (p=0.0523, Fig. 24; Table A8).

Ceratoides lanata (CELA). This palatable shrub responded significantly to time (p=0.0001, Table 4; Table A5), season (p=0.0212, Table 5), and grazing (p=0.0155, Table 6), but did not exhibit an interaction. The strongest effect appears to be that of time, with season and grazing treatments being marginal. The contrast for time indicates a small but significant increase from 1935 to 1958 (p=0.0436, Fig. 21). From 1958 to 1969 and from 1969 to 1975, cover did not increase significantly. Between 1975 and 1994, however, cover significantly decreased (p=0.0001) to a value that did not differ from that found in 1935 (p=0.1300, Table 4).

Despite the overall greater cover for ungrazed pastures shown by the significance of the grazing main effect (see above), grazed and ungrazed treatments did not differ for any single year (all p≥0.1103, Fig. 22; Table A6). In contrast, cover means did differ between seasons in 1969 with higher cover in winter than in spring (p=0.0484, Fig. 23; Table A7). Between seasons, the winter grazing treatment had a higher cover than spring grazing treatment (p=0.0330, Fig 24; Table A8).

Artemisia spinescens (ARSP). ARSP was the most dynamic species in the plant community. In addition to the main effects (all p≤0.0009), the time ×

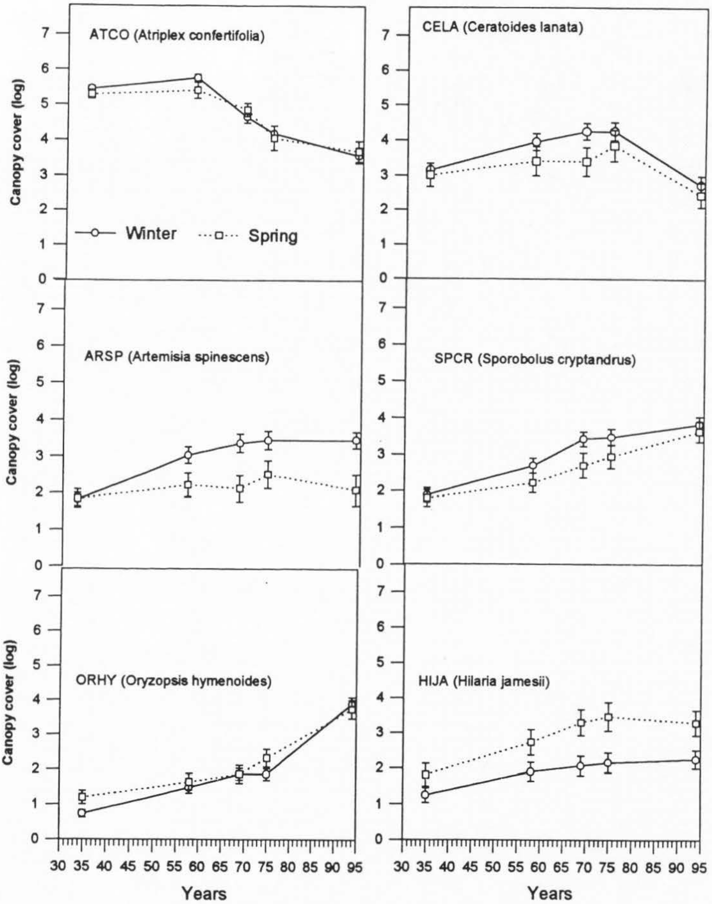


Fig. 23. Time by season analysis in six species at the DER. Vertical bars are stantard errors of the means.

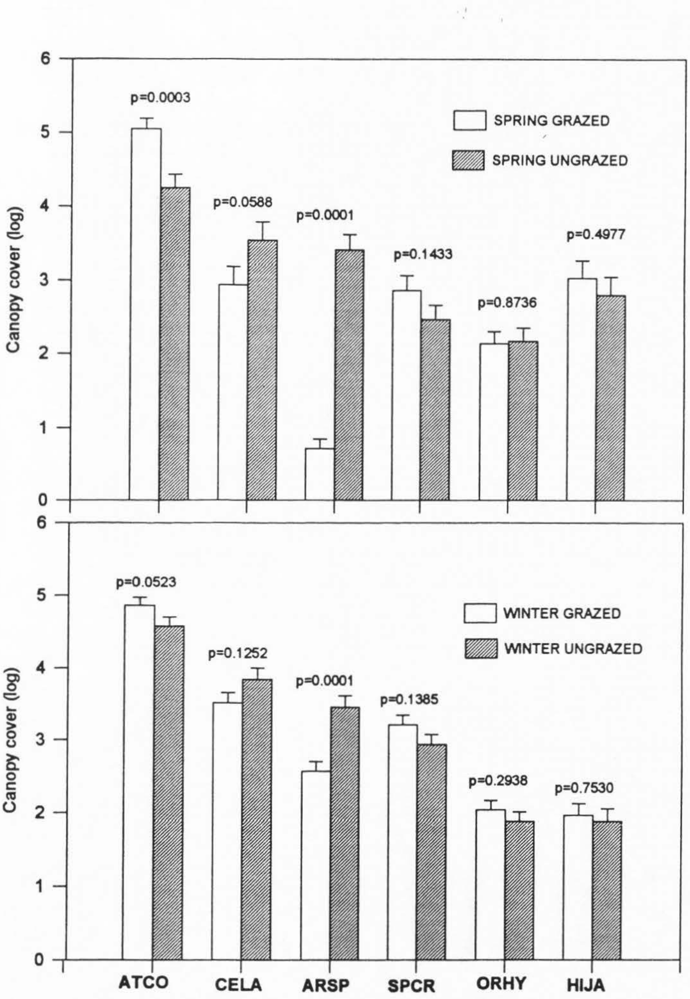


Fig. 24. Effect of species and season of grazing on canopy cover at the DER. Vertical bars are standard errors of the means.

grazing (p=0.0001), grazing-by-season (p=0.0001), and time × season (p=0.0366) interactions were significant (Table A5). For individual contrasts, the time main effect was only significant from 1935 to 1958 when cover increased (p=0.0025, Table 4, Fig. 21). Considering grazing effects, cover in the ungrazed treatment increased significantly (p=0.0001; Table A6) from 1935 to 1958, after which there were no further increases across sequential intervals; however, a cumulative significant increase was detected for the 1959 to 1994 interval (p=0.0289; Table A6). In contrast, the grazed population did not change in cover throughout the experiment (p=0.9564, Fig. 22). Consequently, from 1958 to the present, ungrazed pastures had significantly greater cover than grazed pastures (all p=0.0001), and the time-by-grazing interaction was significant only for the first interval (p=0.0029, Fig. 22, Table 7).

Cover was higher in the winter than spring for 1958 (p=0.0284, Fig. 23), 1969 (p=0.0009), 1975 (p=0.0002), and 1994 (p=0.0003) when season of grazing was compared (Fig. 23; Table A7). Additionally, although ungrazed pastures had greater cover than grazed pastures in all seasons (p=0.0001), the difference was greater in spring than winter pastures (Fig. 24; Table A8).

Sporobolus cryptandrus (SPCR). SPCR significantly responded to time (p=0.0001; Table A5) and to a lesser extent to season (p=0.0125) and grazing treatment (p=0.0413), but not to any interaction. Cover significantly increased through time (all p≤0.0440) except for the short, dry 1970-5 period (p=0.5586, Fig. 21).

Table 7. Contrast of interest responsible for evaluating the hypothesis of no time × grazing interactions for study species at the DER.

Contrast	F val.	Wilks'l. statist.	Pr>F	Variable	Estimate	Pr>F
[T1*T2]*[G*U]	3.1198	0.9704	0.0051			
				ATCO	-0.6188	0.1400
				CELA	-0.8118	0.1825
				ARSP	-0.7979	0.0025
				SPCR	-0.3403	0.5100
				ORHY	0.4751	0.2434
				HIJA	-0.1830	0.6529
[T2*T3]*[G*U]	1.2721	0.9877	0.2681			
				ATCO	-0.4731	0.2590
				CELA	-0.0771	0.8991
				ARSP	0.6108	0.2453
				SPCR	0.1825	0.7238
				ORHY	-0.8314	0.0415
				HIJA	-0.1508	0.8159
[T3*T4]*[G*U]	0.2359	0.9977	0.9657			
				ATCO	0.2832	0.4991
				CELA	-0.0336	0.9564
				ARSP	0.1632	0.7560
				SPCR	-0.3160	0.5406
				ORHY	-0.1830	0.6529
				HIJA	0.2934	0.6505
[T4*T5]*[G*U]	0.4984	0.9951	0.8097			
				ATCO	0.5078	0.2258
				CELA	0.1364	0.8226
				ARSP	0.5638	0.2834
				SPCR	-0.1056	0.8379
				ORHY	0.1582	0.6975
				HIJA	-0.0617	0.9241
[T1*T5]*[G*U]	6.3202	0.9419	0.0001			
				ATCO	-0.3009	0.4727
				CELA	0.8378	0.1689
				ARSP	2.9091	0.0001
				SPCR	-0.5755	0.2620
				ORHY	-0.3810	0.3494
				HIJA	-0.3535	0.5852

The order of contrast means is: T1G T1U T2G T2U T3G T3U T4G T4U T5G T5U

Considering grazing effects, cover in the grazed treatment increased significantly (p=0.0306, Fig. 22; Table A6) from 1935 to 1958, after which there were no further increases. Cover was higher for winter than spring treatments for the year 1969 (p=0.0441, Fig. 23; Table A7).

SPCR also showed a higher winter- than spring-grazed cover (p=0.0441, Table A7). However, this comparison is not valid. Although spring and winter ungrazed treatments did not differ in 1935 (p=0.9419; Table A5), by 1994 spring-ungrazed controls had significantly greater cover than winter-ungrazed controls (p=0.0414, Fig. 24; Table A8), making the comparison between spring- and winter-ungrazed controls inappropriate. Within a season, grazed and ungrazed treatments did not differ in cover in either winter (p=1385) or spring (p=0.1433, Fig. 24; Table A8).

Orysopzis hymenoides (ORHY). This C_3 warm-season grass had significant effects for time (p=0.0001), but not for any other main factor or interaction (Table A5). ORHY mean cover increased from 1935 to 1958 (p=0.00034, Fig. 21), and again from 1975 to 1994 (p=0.0001; Table A5).

Hilaria jamesii (HIJA). This warm-season grass had significant effects for time (p<0.0002) and season (p<0.0001). Similar to the other species, HIJA mean cover increased from 1935 to 1958 (p=0.0154), but cover did not change throughout the rest of the study (Fig. 21; Table A5).

Spring cover was significantly higher than winter cover in 1969 (p=0.0076, Fig. 23; Table A7), 1975 (p=0.0045), and 1994 (p=0.0243). HIJA also had higher mean cover for spring-grazed than for winter-grazed pastures in the analysis of grazing by season (p=0.0002, Fig. 24; Table A8). As with SPCR, this comparison is not valid, because spring- and winter-ungrazed controls did not differ in 1935 (p=0.9876, Appendix D2); however, after 59 years of the experiment spring controls had significantly greater cover than winter controls (p=0.0017, Table A7), the same shift seen with grazing. This suggests that the spring- and winter-ungrazed pastures followed different successional pathways, and the season of grazing effect may not be biologically meaningful.

Shrub-Grass Interface

The analysis revealed significant multivariate effects for time (all p=0.0001, Fig 25; Table A9). Shrubs, a major component of the plant community in 1935 (84%), responded significantly to the time main factor (p=0.0001, Fig. 25; Table A9). Cover increased significantly from 1935 to 1958 (Fig. 25, p=0.0001), remained unchanged through 1975, and then declined during 1975 to 1994 (p=0.0001). Grasses, a minor component of the plant community in 1935 (16%), also responded significantly to the time main factor (p=0.0001, Fig. 25; Table A9) with cover increasing from 1935 to 1958 (p=0.0001), 1959 to 1969 (p=0.0038), and 1975 to 1995 (p=0.0001). The shrubs considered in this study decreased in absolute cover from 84 to 50%, while grass cover increased from 16% to 51% during the 59-year experimental period. Considering all plants inventoried in the pastures, cover in 1935 was 85% for woody and 15% for

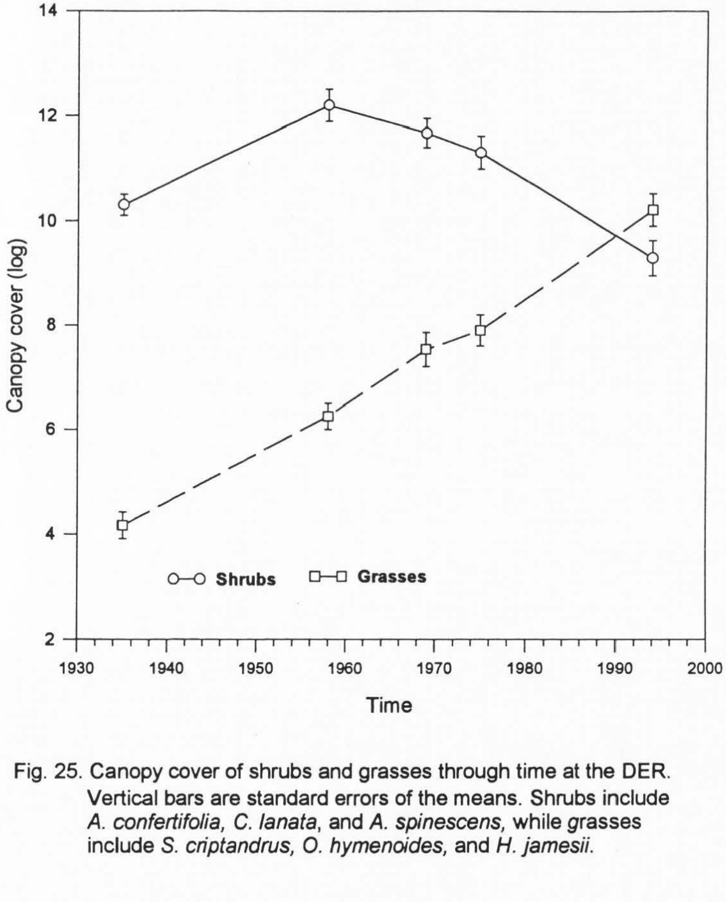


Fig. 25. Canopy cover of shrubs and grasses through time at the DER. Vertical bars are standard errors of the means. Shrubs include *A. confertifolia, C. lanata*, and *A. spinescens,* while grasses include *S. criptandrus, O. hymenoides,* and *H. jamesii.*

herbaceous species. In 1994, cover was 51% for woody and 49% for herbaceous species.

Annuals

Variability among years in the presence of annual plants in response to variability in precipitation makes this vegetation class difficult to study definitively without continuous data. Available data, however, were interpreted to show a steady increase in exotic annuals since 1935 (Fig. 26), although individual species differed in their dynamics (Fig. 27). *Salsola* spp. was not present in the plots in 1935, and *Halogeton glomeratus* was not present in 1935 and 1958. *Salsola spp.* increased from about 8% in 1958 to 28% in 1975 and decreased to 13% in 1994, while *Halogeton glomeratus* increased from about 12% in 1969 to 33 and 27% in 1975 and 1994, respectively (Fig. 27). *Bromus tectorum*, except for a 2% presence in the plots in 1958, was absent until 1994 when it appeared at an extraordinarily high frequency of 54% of all plots (Fig. 27). Harper et al. (1996) reported that *Bromus tectorum* was already common in 1989 in the experimental pastures at the DER.

A grazing effect was evident for the annuals only in 1994, when grazed plots had a significantly greater frequency of annuals than ungrazed plots (P=0.0001, Fig. 28; Table A10). Intensity of invasion by annuals for 1994 showed no significant interaction between intensity of invasion and grazing (P=0.402, Fig. 29; Table A11). That is, heavy annual invasion was not

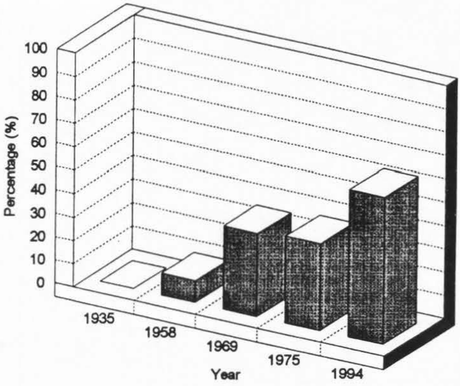


Fig. 26. Percentage of plots with exotic annuals at the DER (*B. tectorum, Salsola spp.*, and *H. glomeratus)* (n=128 plots/year).

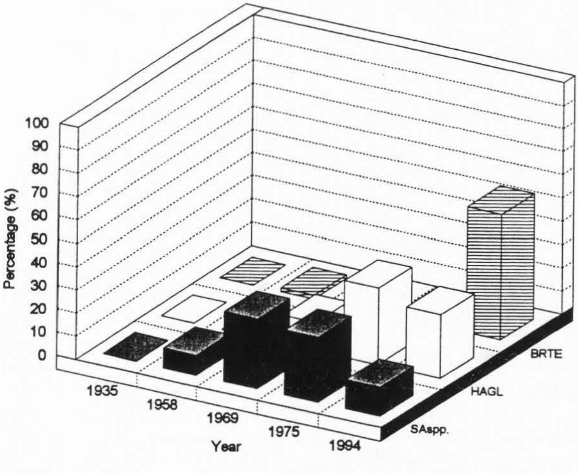


Fig. 27. Percentage of plots with *B. tectorum, Salsola spp.*, and *H. glomeratus* at the DER (n=128 plots/year).

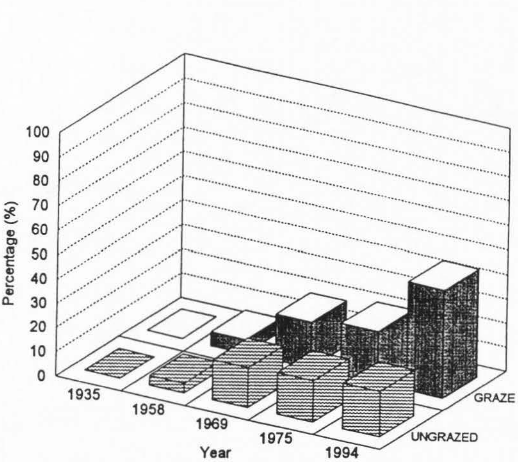


Fig. 28. Percentage of plots with annuals in grazed and ungrazed plots at the DER (*B. tectorum*, *Salsola spp.*, and *H. glomeratus*) (n=128 plots/year).

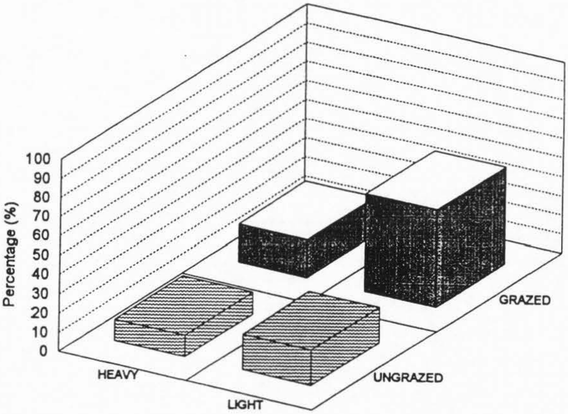


Fig. 29. Heavy and light presence of annuals in grazed and ungrazed plots at the DER (*B. tectorum*, *Salsola spp.*, and *H. glomeratus*) (n=128 plots/year).

disproportionally observed in grazed compared to ungrazed plots.

Discussion and Conclusions

Total Plant Cover Dynamics

The significant cover differences between 1935 and the 4 other sampling years suggest that vegetation prior to 1935 was markedly affected by management and climatic factors, as suggested by McArdle et al. (1936), Stewart et al. (1940), and Shantz and Piemeisel (1940), after management and climatic factors changed. This pattern of increasing cover was constant even after a series of drought years occurred during the late 1950s (Chapter 2) and grazing was maintained at moderate levels. The increase in total plant cover reported by Hutchings and Stewart (1953), Harper (1959), Holmgren and Hutchings (1972), Norton (1978), and Norton and Bermant (1977) for the experimental pastures was still evident in 1994.

The dramatic increase in total cover from 1935 to 1958 occurred with near-average winter and spring precipitation regimes (Chapter 2). Although summer precipitation was far below average for the period, at the beginning of the recovery period from 1935-8 it showed above-average values. These conditions apparently favored plant recovery. In contrast, recovery may be slow or nonexistent under drought conditions during the season when most plant populations, especially shrubs, are in the process of establishment. Therefore, it seems that the increase in total plant cover in exclosures and moderately grazed pastures was due more to changes in climate than to treatment effects.

The lack of a time effect from 1959 to 1969 and of a treatment effect in 1969 suggests that plant cover may have reached a level limited by environmental constraints of the desert ecosystem (nutrients, water, etc.). In particular, this period was characterized by a transition from an average to a dry precipitation regime, especially during winter, suggesting low water availability for cool-season plants. It is likely that long-lived species tolerant to dry conditions (West and Tueller 1972) probably consolidated their position in the plant community, and few new plants became established.

From 1969 to 1975, however, mean cover scores increased significantly only in the ungrazed treatment. Interestingly, this increase occurred during the driest period and may be due to increases in cover of shrubs such as CELA and ARSP, which are known to be tolerant to dry conditions (West and Tueller, 1972). Because this increase was lower in the grazed plots, grazing may have a greater effect in dry compared to wet years. A consequence of the increased cover in the ungrazed treatment coupled with no change in cover for the grazed treatment is that after 40 years total plant cover was now significantly less in grazed than ungrazed pastures. Chronic grazing disturbance, perhaps interacting with drought, has probably begun to differentially affect the vegetation, and this effect is reflected in total plant cover.

The significant downward shift in plant cover in both grazed and ungrazed treatments from 1975 to 1994 overlapped with a notable increase in precipitation from the driest to very wet conditions (Chapter 2). The unusually high winter precipitation of the last study period (1975-94) may have favored an increase in cover of C_3 plants (mainly grasses) in contrast to a probably large decrease in cover of C_4 plants (mainly shrubs), which are less tolerant to wet conditions than grasses (Pyke and Dobrowolski 1989). In addition, the cumulative effects of grazing on palatable components of the plant community probably became more apparent in 1994 than in 1975. Grazing created more open spaces than found in the ungrazed plots. The ungrazed pastures were probably changing in response to competition, climate, and small animal activity rather than to release from intense grazing pressure decades before. The lack of large herbivore activity for 59 years in the exclosures has perhaps influenced plant succession to a kind of plant community that is not necessarily the appropriate one to compare with pastures changing under grazing pressure. Some degree of vertebrate grazing is a natural component of the plant community in any rangeland.

Individual Species Cover Dynamics

Atriplex confertifolia (ATCO)

ATCO, the least palatable shrub in the area (Chambers and Norton 1993), was the main component of the plant community in 1935 (65% of the plant composition by cover), and did not significantly change from 1935 to 1958. The increased density reported by Norton (1978) during this period did not significantly contribute to increased in cover. This is interpreted to suggest little

ATCO recovery following release from heavy grazing, probably because ATCO was directly affected by heavy grazing prior to 1935. Holmgren and Hutchings (1972) suggested that ATCO dominated the cool desert ranges because of the overexploitation of the range prior to 1935, and they predicted that ATCO would eventually retreat under moderate grazing. This may explain the higher cover values in the grazed than ungrazed pastures in 1958, 1968, and 1975, although cover did not differ between grazing treatments by 1994. Thus, ATCO cover retreated both with and without grazing; only the rate of cover decrease depended on grazing.

The period when grazed plots had greater cover than ungrazed plots overlapped with the driest climatic conditions. This suggests that ATCO is more successful in pastures where palatable vegetation has been severely defoliated, which probably occurs more in dry than wet years. Severe defoliation of associated species should decrease competition for water and nutrients incorporated into the system through manuring and urination from grazing animals (Archer and Smeins 1991). Such a scenario may be beneficial for plants of low palatability in general. Similarly, the low availability of palatable plants in dry years probably resulted in some degree of ATCO grazing (mainly in spring), and this may have induced higher rates of physiological activity resulting in slower decreases in plant cover. In turn, higher physiological rates may decrease the life span of the shrubs (Walker 1988), permitting a faster turnover of grazed stands and consequently an increasing probability of plant replacement. This did not change the overall decreasing trend of ATCO, however, but only the rate.

In 1994, ATCO turnover apparently increased, and available gaps were readily occupied by mesophytic plants such that ATCO cover in grazed and ungrazed pastures was indistinguishable in 1994. Mortality may have been higher due to competition in nongrazed than grazed plots. ATCO was reduced under moderate or no grazing, as predicted by Holmgren and Hutchings (1972).

Ceratoides lanata (CELA)

This palatable C_3 shrub increased in cover from 1935 to 1958, after which CELA cover remained relatively constant until collapsing after 1975. In previous studies, increases of CELA cover in ungrazed and winter-grazed pastures were reported (Harper 1959, Norton and Bermant 1977, Norton 1978, Holmgren and Hutchings 1972), while decreases in cover were observed in pastures heavily grazed in spring (Holmgren and Hutchings 1972, Blaisdell and Holmgren 1984).

Despite a significant overall grazing effect, the dramatic changes observed at DER occurred regardless of grazing. Major factors in CELA dynamics appear to be demography, climatic change, and competition from herbaceous plants. Plant size increased significantly from 30 to 217 cm^2 in the 1935-1975 interval (Norton 1978). By 1975, more than half of the CELA population was at least 40 years old (Norton 1978). These results suggest a predominantly young population in 1935 with many of these individuals still alive and dominating the population in 1975. With an estimated 50-year life expectancy (Chambers and Norton 1993), however, an increase in mortality rate for this initial population was expected, probably exacerbated by stress. CELA is drought tolerant and has an extensive fibrous root system and a taproot that penetrates deep into the soil (6-7 m) (Stevens et al. 1977). However, these morphological adaptations to drought may make CELA susceptible to relatively high amounts of water observed in the wet 1975-94 interval. Finally, increases in perennial and annual herbaceous plants (Harper et al. 1996), possibly favored by the wet climate, were actively competing with weakened CELA plants. As a result, the combination of aging, wetness, and competition apparently led to the collapse of CELA by 1994.

Artemisia spinescens (ARSP)

The overall cover increase for ARSP from 1935 to 1958, as in other species, appears to be related to the combination of relaxation from heavy grazing prior to 1935 and favorable climatic patterns during this period.

The response of this C_3 shrub (Caldwell 1984) depended heavily on whether it was grazed or not, and on season of grazing. Cover increased dramatically in the ungrazed treatment from 1935 to 1958 and again from 1958 to 1994, but remained unchanged in the grazed pastures. This clearly suggests that this highly palatable shrub (Chambers and Norton 1993) was under heavy grazing pressure prior to 1935 and responded markedly to release from grazing pressure. Interestingly, even moderate levels of grazing kept ARSP cover at 1935 levels. Additionally, the difference between grazed and ungrazed treatments was clearly greater in spring-grazed than winter-grazed pastures. Comparable results until 1975 were reported by Hutchings and Stewart (1953), Harper (1959), Holmgren and Hutchings (1972), Norton and Bermant (1977), and Norton (1978).

The seasonal differences of grazing in ARSP are understandable; ARSP is highly palatable to sheep, which prefer fresh forage in spring when this species is physiologically more active (Wood 1966, Chambers and Norton 1993). In winter, plants are dormant, and thus grazing is less harmful. In fact, Holmgren and Hutchings (1972) reported that ARSP increased from 1935 to 1967 in winter-grazed pastures and disappeared in pastures grazed heavily in spring.

In contrast to results with other species, climate apparently played only a minor role in the observed changes of ARSP. This increase without grazing corresponds to wetter periods, suggesting a role for climate in the absence of grazing. ARSP, however, tolerated the drought of 1970-75 very well. An extensive deep root system may provide some degree of drought tolerance (Wood 1966).

Sporobolus cryptandrus (SPCR)

Because of the strong response of SPCR to time, cover changes for this warm-season grass (Waller and Lewis 1979) probably responded mainly to climatic changes, especially summer precipitation. SPCR significantly increased during intervals with average summer precipitation (1959-69 and 1976-94), but not in the period with below average (1970-75). From 1935 to 1958, however, the increased cover of SPCR may be due to a combination of relaxation from heavy grazing and a favorable summer precipitation from 1935 to 1938. After 1938, summer precipitation was below average, and we do not know how SPCR responded to this deficit during the rest of the period. Other factors partially determining increased SPCR cover may be the reduced competition and consequent availability of gaps due to the decrease of ATCO after 1958 and CELA after 1975. Additionally, competition from ARSP was probably severely reduced by grazing in grazed plots. This may explain the more abundant increase of grasses of low palatability (such as SPCR) (Holmgren and Hutchings 1972, Smith 1986) in grazed compared to ungrazed pastures.

Oryzopsis hymenoides (ORHY)

The lack of response to all study factors except time for ORHY suggests that the significant increase of this cool-season grass was probably due mainly to precipitation changes and only indirectly to grazing. ORHY behavior through time appears typical for a C_3 species; it reacted positively to favorable winter precipitation during the 1935-58 and 1976-94 intervals, and remained with little change during the 1959-69 and, especially, 1970-75 intervals when winter precipitation was far below average (see Chapter 2). The sharp increase in ORHY cover from 1976 to 1994 appears mainly dependent upon the exceptionally high and consistent winter precipitation during this period, although, as with SPCR, reduced competition from decreasing shrub populations probably helped. Chambers and Norton (1993) reported higher rates of ORHY mortality in shrub-dominated than grass-dominated pastures.

In general, changes in ORHY cover have been attributed to the combination of heavy grazing with winter or early spring use. In winter, grasses are dormant and comprise lower proportions of the sheep's diet than do shrubs, and in early spring initial grass defoliation will be compensated by a long period without grazing until the next winter (Cook et al. 1954, Holmgren and Hutchings 1972). This study did not have a heavy grazing treatment to make the appropriate comparison. We conclude that at least under no-grazing or moderate grazing conditions, ORHY cover changed primarily in response to winter precipitation and only indirectly to grazing.

Hilaria jamesii (HIJA)

This warm-season sod-forming grass (Waller and Lewis 1979) increased in cover from 1935 to 1958, but did not change through the rest of the study. The discussion presented for SPCR for the 1935-58 period is probably applicable to HIJA. The lack of an increase in cover from 1975 to 1994 despite favorable summer precipitation suggests that under moderate and no-grazing conditions

HIJA did not successfully compete with other herbaceous vegetation during this period. In contrast, increased cover for HIJA was reported under heavy grazing by Harper (1959) and Gutierrez-Garza (1978).

Shrub-Grass Interface

Grasses increased in cover significantly through all but the driest 1970-5 interval. Shrub cover increased from 1935-58, showed little change from 1959 to 1975, and decreased from 1976-94. The significant changes mostly corresponded to periods with average and above-average precipitation, while little change occurred in the dry and driest intervals. This suggests a strong vegetation-precipitation relationship in which significant cover changes occur during average or wet years and with little or no changes during dry years. The strong influence of climatic fluctuations on plant community dynamics was also reported in other studies (Pyke and Dobrowolski 1989; Nelson et al. 1989, 1990; Dobrowolski and Ewing 1990).

In general, as discussed previously, these patterns of change are related to various factors such as shrub die-off due to a combination of aging and increased precipitation, and grazing in some cases, and an increase of grasses with increasing precipitation.

Annuals

Harper at al. (1996), indicated that exotic annuals were not widespread on DER prior to the 1940s, but by 1989 they were very common. Therefore, the importance of annual species as factors in the overall process of vegetation change can no longer be ignored. Severe invasion of *B. tectorum* and other exotic plants in the Intermountain West (Young et al. 1973, Mack 1981, Young et al. 1987, Harper et al. 1990) and competition with perennial plants (Harris 1967, Johnson and Aguirre 1991, Melgoza and Nowack 1991, Nasri and Doescher 1995) is reported elsewhere. The invasion of *B. tectorum* and other alien annuals into cold deserts may be related to the development of new genomes better adapted to the environmental conditions of the cold desert than those of the same species 30 years ago (Harper et al. 1990).

Seedlings of *B. tectorum* grow faster at cold temperatures and produce larger, heavier, and deeper roots than native perennial grass species (Harris 1977, Svejcar 1990). These morphological characteristics confer a competitive advantage on *B. tectorum* relative to native perennial grasses and shrubs. Successive favorable years for plant growth, seed production, and seedling establishment appear to favor invasion by *B. tectorum*. Given the above-average winter precipitation during the last study period (1976-1994), it is not surprising that *B. tectorum* went from absent in 1975 to a frequency of 54% in 1994. At the same time, the competitive ability of cheatgrass may be influential in reducing cover of native shrubs and perennial grasses by limiting recruitment of new individuals. In addition, accumulation of annual plant biomass creates conditions for fires, which can be a catastrophic disturbance in a plant community not naturally prone to frequent fires (West 1988, Harper et al. 1996).

Grazed and ungrazed plots heavily invaded by annuals usually showed evidence of soil surface disturbance. In extreme cases, the soil surface was completely removed by rodent activity. Therefore, favorable climatic conditions coupled with soil disturbance promoted heavy invasion by annuals. Apparently, rodent activity increases mortality of perennial plants and provides at the same time a favorable seed bed for establishment of annual plants by removing the soil. The significantly higher frequency of annuals in grazed compared to ungrazed plots in 1994 was probably related to sheep-grazing activities such as trampling, urination, manuring, and seed distribution.

Harper et al. (1996) indicated that another cause for the successful invasion of alien annuals, especially into stands where CELA was dominant, was the infection and mortality of CELA seedlings by microfungal saprophages associated with exotic chenopods. This and other probable causes are linked to the increasing precipitation received during the last study period.

General Discussion and Conclusions

The interval from 1935 to 1958 can be characterized as a period of range recovery. Evidence suggests that climate change was the major factor for this recovery, as suggested by Norton and Bermant (1977), Norton (1978), and Norton and Michalk (1978). Nevertheless, a differential response of ARSP to intensity and season of grazing suggests that even moderate grazing affects this palatable component of the plant community, and supports the hypothesis that relaxation of heavy grazing played a role in recovery of this species (McArdle et al. 1936, Shantz and Piemeisel 1940, Stewart et al. 1940).

From 1958 to 1994, total cover dynamics fluctuated, suggesting that the plant community probably reached a ceiling of recovery around 1958, and thereafter changes were restricted by upper and lower limits imposed by a non-equilibrial desert ecosystem and moderate grazing. Vegetation dynamics in the pastures were related to climatic fluctuations. Dry years showed little change for all species except ATCO and higher precipitation intervals, especially from 1975-1994, showed significant increases of the grasses ORHY and HIJA and significant decreases of the shrubs CELA and ATCO. This suggests the importance of climate and related causes (i.e., change of water balance in the soil) in combination with inherent plant characteristics (i.e., low tolerance to wetness of shrubs, aging, etc.) in altering plant composition and directing succession. From 1975 to 1994, changes in plant cover were uniform in grazed and ungrazed pastures and this suggests again that plants were responding mainly to climate. It appears that in wet years the impact of moderate grazing is additionally reduced because, with the exception of ARSP, treatments did not differ in cover for CELA, ATCO, ORHY, and SPCR, but were different for CELA, ATCO, and ARSP in dry years.

The significant decrease in ATCO cover from 1958 to 1994 coincides with the increased cover for several species. The decrease of ATCO as a major component of the plant community, augmented by the severe reduction of the second important shrub (CELA), may have played a major role in increased grass cover by 1994.

One of the climatically related causes for the changes observed from 1976-94 was the increase in exotic annuals, notably BRTE. The importance of such annuals in influencing the process of change must be considered. The detrimental effects of alien annuals on indigenous vegetation are widely documented (Harris 1967, Young et al. 1973, Mack 1981, Young et al. 1987, West 1988, Harper et al. 1990, Young and Tipton 1990, Johnson and Aguirre 1991, Melgoza and Nowack 1991, Nasri and Doescher 1995, Harper et al. 1996).

In general, the dynamics of plant community after the 59-year experiment appear to partially confirm the prediction of Holmgren and Hutchings (1972) that ATCO will decrease in cover under moderate grazing and under successive years of extended drought. Both conditions, moderate grazing and drought, were met, and ATCO is retreating. Holmgren and Hutchings did not predict, however, that the ATCO cover would continue to decrease during wet years, that CELA cover would decrease, that perennial grass cover would increase, or that annuals would increase during wet years. My results indicated that under far above-average precipitation, perennial and annual grasses increased in cover, while palatable and unpalatable shrubs decreased in cover, all of this mostly independent of grazing.

The role of grazing in this long-term experiment after the recovery period from 1935 to 1958 appears to be overshadowed by other determinants of change such as climate and its indirect effects (increase of annuals and perennials), and by characteristics inherent to the plant populations (i.e., aging and different degree of tolerance of plants to wetness or drought). Grazing, however, had some significant seasonal effects in cover of shrubs and grasses during the dry periods. Therefore, moderate grazing had a relatively important role in short-term changes. However, overall grazing had a limited role, probably influencing the rate more than the direction of the plant community change.

CHAPTER 4

SURVIVAL AND RECRUITMENT OF *ATRIPLEX CONFERTIFOLIA*, *CERATOIDES LANATA*, AND *ARTEMISIA SPINESCENS* POPULATIONS GRAZED BY SHEEP

Introduction

Detection of trend in grazed shadscale vegetation in desert environments has relied upon traditional cover, density, and biomass measures (Holmgren and Hutchings 1972; Norton 1978; Gutierrez-Garza 1978; Smith 1986, Harper 1959, 1990). In contrast, few studies have addressed the population dynamics of this plant community (Norton 1986, West 1979, Harper 1990, Chambers and Norton 1993). Detection of change is important, but for management purposes, identification of the cause of change is critical (Gardiner 1984). While some authors have related change mainly to grazing by domestic livestock (Holmgren and Hutchings 1972; West 1979; Harper 1959, 1990), others have speculated that change may be due to climatic influences (Hutchings and Stewart 1953, Norton 1978, Chambers and Norton 1993) or inherent characteristics of plant species and populations (Norton and Bermant 1977, Norton and Michalk 1983, Chambers and Norton 1993). Analyzing plant population dynamics of a 60-year old grazing experiment appears to offer considerable promise for identification of underlying causes of change in the shadscale plant community. The development of this autoecological understanding is important as a contribution to the development of appropriate management strategies that will allow sustainable utilization of shadscale communities.

Demographic approaches such as analyses of plant recruitment and survival, as well as the application of more powerful statistical tools, have been recommended for the assessment of trend and the explanation of possible causes of change (Norton and Michalk 1978, Austin 1981, Gardiner and Norton 1983, Gardiner 1984, 1986). Survival and recruitment, unlike density and cover, are not derived variables. Thus the processes of change are not obscured by partial or complete modification of an index, as, for example, in the case of frequency (Gardiner 1984).

The plant survival approach applied to contrasting grazed and ungrazed communities may yield concrete evidence of the effects of destocking on vegetation. Isolation of grazing effects, however, is difficult in field experiments because of the lack of control of other variables such as soil differences, climatic fluctuations, changes in populations of other herbivores, past grazing history differences, etc. Under such circumstances it is particularly important to consider as many study variables as possible, particularly historical information. Fortunately, in this study historic vegetation maps, although unevenly recorded, permitted identification of individuals and their reexamination on sequential recording dates. The isolation of ungrazed areas and the consistent use of equal grazing intensities by sheep during 60 years allowed a robust testing of hypotheses concerning the recovery of rangeland vegetation and the effects of known intensities of livestock grazing on that recovery. Additionally, soils information was available in this study. Finally, precipitation data were used intensively in the interpretation of the plant survival analysis and in relating precipitation to soil and grazing variables.

Data concerning recruitment of new individuals are also critical for plant population dynamics and were extracted from the vegetation maps. Although the spacing between census dates was not equal, this information provides additional insight when related to climate. Additionally, in two cases, data from 2 sequential years were available, providing an opportunity to analyze seedling survival during wet periods.

The specific goal of this research was to identify factors influencing shrub plant survival, and to a lesser degree recruitment, in grazed and ungrazed paddocks at DER. Factors examined included time interval (climatic regime), cohort, age, soil type, and grazing. Particular emphasis was placed on the effects of grazing by sheep. The analysis was restricted to the dominant shrubs *Atriplex confertifolia* (ATCO), *Ceratoides lanata* (CELA), and *Artemisia spinescens* (ARSP).

The objective of this study was to determine if time, soil differences, and grazing have affected plant survival dynamics of ATCO, CELA, and ARSP. For each aspect of survival, except for the general plant survival study, two models were evaluated.

Long-Term Plant Survival (1935-94)

The aspects studied in the long-term plant survival section and the models evaluated are:

1. General plant survival

HO: For a given species, survival rates of all cohorts are equal during any time interval.

This model tests for equality in survival rates during each time interval (Fig. 30), that is, whether or not during any given interval all cohorts of a species had equal survival. This model suggests that the time interval (climatic regime) is a more important determinant of survival than is cohort age. The structure of the model is:

$S_1(C_1, 58\text{-}69) = S_5(C_2, 58\text{-}69)$;

$S_3(C_1, 69\text{-}75) = S_6(C_2, 69\text{-}75) = S_8(C_3, 69\text{-}75)$;

$S_4(C_1, 75\text{-}94) = S_7(C_2, 75\text{-}94) = S_9(C_3, 75\text{-}94) = S_{10}(C_4, 75\text{-}94)$;

where S_i are survival rates by combination of cohort and interval classes, C_i are the cohort identifications, and 1935-58, 1958-69, etc. are time intervals.

2. Plant survival by soil types

HO1: For a given species, survival rates are equal across two soil types (Model 1).

Model 1 tests for equality of survival rates across soil types for a given cohort during a given time interval. The structure of model 1 is:

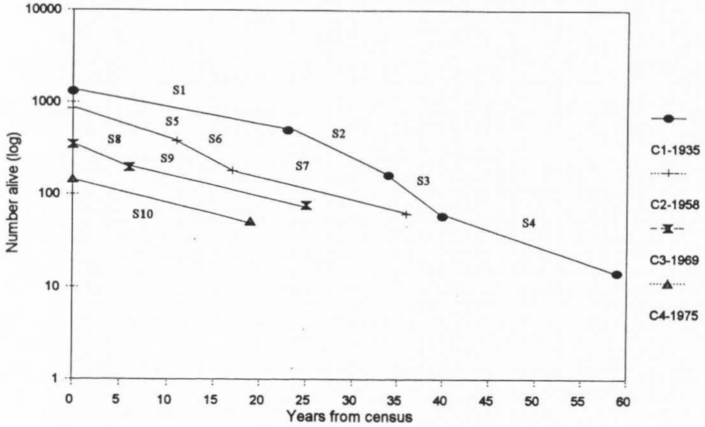


Fig. 30. Survivorship curves for ATCO cohorts to illustrate hypothesis 1 of the general survival analysis. Each sequential point from left to right represents the number of plants that were still present at the start of each census interval. S=survival rate, C=cohort.

$S_1(C_1c, 35\text{-}58)=S_{11}(C_1d, 35\text{-}58)$;

$S_2(C_1c, 58\text{-}69)=S_{12}(C_1d, 58\text{-}69)$;

$S_3(C_1c, 69\text{-}75)=S_{13}(C_1d, 69\text{-}75)$;

$S_4(C_1c, 75\text{-}94)=S_{14}(C_1d, 75\text{-}94)$;

$S_5(C_2c, 58\text{-}69)=S_{15}(C_2d, 58\text{-}69)$;

$S_6(C_2c, 69\text{-}75)=S_{16}(C_2d, 69\text{-}75)$;

$S_7(C_2c, 75\text{-}94)=S_{17}(C_2d, 75\text{-}94)$;

$S_8(C_2c, 69\text{-}75)=S_{18}(C_3d, 69\text{-}75)$;

$S_9(C_2c, 75\text{-}94)=S_{19}(C_3d, 75\text{-}94)$;

$S_{10}(C_4c, 75\text{-}94)=S_{20}(C_4d, 75\text{-}94)$;

where c=soil type-C, and d=soil type-D (see methods for description of soils). For example, survival for cohort 1 from 1935-58 was set equal on soil C and soil D ($S_1=S_{11}$ in Fig. 31).

HO2: For a given species, survival rates are equal across two soil types and across cohorts (Model 2).

Model 2 is a more restrictive model than Model 1 and tests for a given time interval whether or not survival rates are equal across both soils and across all cohorts. That is, it tests for a soil type × cohort interaction. The structure of model 2 is:

$S_1(C_1c, 35\text{-}58)=S_{11}(C_1d, 35\text{-}58)$;

$S_2(C_1c, 58\text{-}69)=S_5(C_2c, 58\text{-}69)=S_{12}(C_1d, 58\text{-}69)=S_{15}(C_2d, 58\text{-}69)$;

$S_3(C_1c, 69\text{-}75)=S_6(C_2c, 69\text{-}75)=S_8(C_3c, 69\text{-}75)=S_{13}(C_1d, 69\text{-}75)=S_{16}(C_2d, 69\text{-}75)$

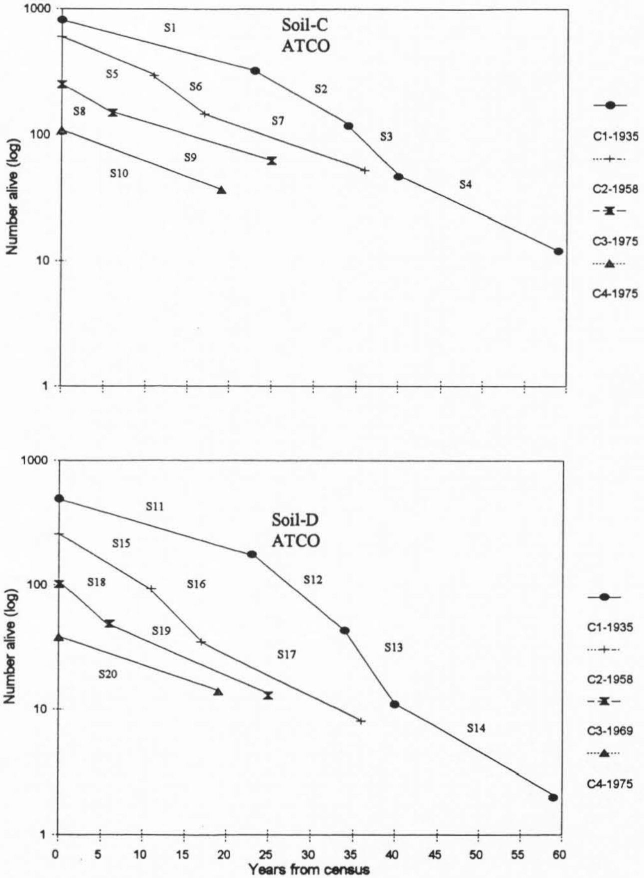


Fig. 31. Survivorship curves for ATCO cohorts to illustrate hypothesis 1 and 2 of the survival analysis including soil factors. S=survival rate, C=cohort.

$=S_{18}(C_3d, 69\text{-}75)$;

$S_4(C_1c, 75\text{-}94)=S7(C_2c, 75\text{-}94)=S_9(C_3c, 75\text{-}94)=S_{10}(C_4c, 75\text{-}94)=S_{14}(C_1d, 75\text{-}94)=S_{17}(C2d, 75\text{-}94)=S_{19}(C_3d, 75\text{-}94) = S_{20}(C_4d, 75\text{-}94)$;

For example, we set $S_2=S_5=S_{12}=S_{15}$ (Fig. 31), which means that all survival rates were equal during the period 1958-69 independent of soil type or cohort.

3. Plant survival by grazing treatments

HO1: For a given species, survival rates are equal across grazing treatments (Model 1).

Model 1 tests for equality of survival rates between the grazed and ungrazed populations for a given cohort during a given time interval.

HO2: For a given species, survival is equal across grazing treatments and across cohorts (Model 2).

Model 2 is a more restrictive model than Model 1 and tests for a given time interval whether or not survival rates are equal across both grazing treatment and across all cohorts. That is, it tests for a grazing × cohort interaction.

The structures of the two models dealing with grazing are equivalent to those used for soils with the exception of changing c to g (g=grazed) and d to u (u=ungrazed).

Seedling Recruitment

HO1: For a given species, seedling recruitment is equal across grazing treatments. That is, grazing is not a factor in seedling recruitment.

HO2: For a given species, seedling recruitment is equal across years. That is, recruitment is independent of the climatic regime of the year of sampling.

Short-term Seedling and Adult Plant Survival (1994-5)

HO1: For a given species, seedling survival during a wet climatic regime (1994-1995) is equivalent under grazed and ungrazed conditions and is equivalent in vegetated and bare ground patches.

HO2: For a given species, adult plant survival during a wet climatic regime (1994-1995) is equivalent under grazed and ungrazed conditions.

Literature Review

Wood (1966) used pantograph charts from the experimental area at DER to estimate the longevity of *Artemisia spinescens*. He concluded that sheep grazing and trampling inhibited plant establishment and promoted development of *Artemisia spinescens* stands that are uniform in terms of age, size, and vigor.

West (1979), studying seedling survival patterns of major perennials in salt desert shrub communities at DER (1938-68), found few significant differences between the survival of plants in grazed compared to ungrazed plots, but significant differences between sampling periods. Thus, seedling survival and establishment may be strongly related to climatic factors rather than to grazing. West (1979) indicated that the low numbers of CELA, ATCO, and ARSP seedlings in 1937 were probably due to insufficient water in the spring of 1936 and 1937.

Norton (1986) analyzed plant survival for ARSP, ATCO, and CELA under grazed and ungrazed conditions at DER. Significant differences between grazing treatments in plant survival were reported for all 3 species in the 1935-58 experimental interval, for CELA in the period 1958-69, and for no species in the 1969-75 experimental period. As a result, grazing apparently affected plant survival only early in the experiment; grazing enhanced the net population growth rate of ATCO but depressed growth rates for the palatable ARSP and CELA. Norton (1986) attributed these survival patterns to lag effects of past grazing under higher grazing pressure.

Harper et al. (1990) studied shrub mortality over a 54-year period with data from 46 plots at DER. They found no significant grazing effects on mortality rates for ATCO and CELA, while late winter and spring grazing often significantly increased ARSP mortality. Grazing in late winter increased recruitment rates for ATCO, but reduced those rates for ARSP. They concluded that late winter/early spring grazing favored ATCO at the expense of CELA and ARSP.

Owens and Norton (1989) studied seedling survival of *Artemisia tridentata* under ungrazed conditions at the Tintic research area in west-central Utah during 1984-86. Their results show that survival patterns across each growing season clearly followed precipitation patterns with higher survival associated with higher precipitation regimes. In another study, Owens and Norton (1990) investigated survival of juvenile big sagebrush plants under different grazing regimes. Invasion rates of big sagebrush were higher under a short-duration grazing treatment compared to season-long grazing, but neither size nor independent plant density affected plant survival. Owens and Norton (1992) found that the interaction between grazing and seedling location resulted in both highest survival for sheltered seedlings and the lowest survival for unprotected seedlings in grazed pastures. They related this higher seedling survival of seedlings under shelter to the clumped distribution of plants in this sagebrush-grass ecosystem and suggested that these areas are centers of interspecific competition that may play a role in later stages of plant succession.

Adult and seedling survival during the 1975-8 drought period was studied by Chambers and Norton (1993). They registered extremely low numbers of seedlings for all three shrubs, especially for CELA. Within these limited numbers of seedlings, more ATCO seedlings were found in the spring-grazed pastures. Gasto (1969) and Harper (1959) also reported a higher number of ATCO seedlings in grazed than in ungrazed pastures. They reported that light and winter grazing increased survival and natality of CELA. Natality of shrubs, in general, has been higher in grazed than in ungrazed pastures. They found that heavy and spring grazing increased adult mortality of ARSP, a decreaser under grazing, and ATCO, a typical increaser under grazing, but had no effect on

CELA. In general, seedling mortality was higher than adult mortality.

Holmgren and Hutchings (1972) suggested that in desert environments erratic precipitation results in infrequent years for abundant seed production and successful establishment. Statler (1967) studied seeding trials with CELA in Wyoming and reported, in general, a 12.7% seedling emergence and about 6.5% establishment from 2400 seeds. This poor performance, despite the mechanically prepared soil bed, was attributed to low precipitation during the growing season. Ferguson (1972) conducted seeding trials with *Purshia tridentata* and found that soil moisture significantly influenced the vigor and growth of bitterbrush seedlings. Annual precipitation was related to the success of initiation and establishment of seedlings and sprouts of *Artemisia cana* in southeastern Montana (Wambolt et al. 1990). Many authors have noted that the appropriate combination of soil moisture and temperature is critical for the successful establishment of salt-desert shrubs (Gasto 1969, Holmgren and Hutchings 1972, West and Tueller 1972).

Most of the results concerning adult and seedling survival in the shadscale plant community reviewed above originated from studies under average or dry climatic conditions. These studies suggested, in general, that spring and heavy grazing treatments effects on the survival of CELA, ATCO, and ARSP adults and that seedling emergence and survival are probably related to climatic variables. Comparing results of such studies with a new set of data that covers the wet climatic period from 1975 to 1995 will be very informative. Finally, because the study of long-lived shrubs requires long-term data, the additional census will add much to our understanding of population dynamics in this system.

Methods and Materials

Traditional approaches to the study of plant population dynamics demand regular data acquisition and known age structure of the population under study. Problems in developing age-size relationships for desert plants (West et al. 1979, West 1979) and lack of regularity in data collection prevent the use of standard techniques for this kind of study, such as life tables and regression. Therefore, alternative approaches were used. The individual plant approach, as recommended by Austin (1981), Austin et al. (1981), and Gardiner and Norton (1983), was used in this study.

Long-Term Survival

Data sets

All individual plants extracted from the vegetation maps for each studied shrub were labeled with a unique identification number and classified as either having survived or died within the sampling periods (1935-58, 1958-69, 1969-75, and 1975-94). These data for each species were organized in three sets (Tables A12, A13, A14):

1. A general plant survival analysis set that includes for each species all

surviving individuals of each cohort at each census.

2. A soil effects analysis set that is the same as above except individuals were further divided into those present on soil type-C or soil type-D. Soil type-C is described as deep loamy-skeletal carbonitic, with a calcic horizon weakly cemented and deeper than soil-D, while soil type-D is described as deep coarse-loamy mixed, sandy and silty, with a calcic horizon more compact and indurated than in soil type-C (Tew et al. 1995). Because of the fine soil particles in the texture, soil-D has higher water-holding capacity when enough precipitation is present to saturate the soil. However, soil-C is more efficient at capturing small amounts of water before it is lost to evaporation. Although finer soil classification information is available for DER, adequate sample sizes were not possible for inferential statistics when smaller soil units were considered.

3. A grazing effects analysis set that is also the same as in 1 except individuals were further divided into those present on grazed versus ungrazed plots.

Survival Analysis

The pattern of survival across the study period was tested using a maximum likelihood analysis and multinomial distribution (White 1983). This analytical technique estimates survival rates across finite periods of time and then tests hypotheses setting survival rates equal for different time periods. For example, to test for soil effects, survival rates from populations were set equal across soil types for the particular time period while survival rates for other periods are allowed to vary. This process is repeated interactively for all parameters.

Testing hypotheses using this approach depends on the correct formulation of the models (mathematical representation of the assumptions underlying each hypothesis). The hypotheses and models for this study were discussed in the hypotheses presentation section. Survival rates were estimated for the models including a general model in which all the survival rates were permitted to vary. Survival rates were tested for χ^2 goodness of fit to the data with a probability level of 0.05. It should be noted that this test is valid only if the reduced model forms a more constrained model within the general model. To select the best model, likelihood ratio tests were used as described in detail elsewhere (White 1983; Gardiner 1984, 1986; Brownie et al. 1985).

Assumptions in survival analysis are that all success/failure events are independent, all individuals assigned to a cohort must be identifiable at any time, and the fate of an individual is a multinomial random variable (Gardiner 1984, 1986; Owens 1987). The number of dead plants within each time interval and treatment constitutes a multinomial sample.

Survival rates and associated standard errors were estimated for the study periods by the FORTRAN program SURVIV (White 1983; Table A15). This technique, originally used to study animal populations, has been successfully used in plant population studies by Gardiner and Norton (1983), Gardiner

(1984, 1986), Salihi and Norton (1987), Owens and Norton (1989, 1990, 1992), and Fox (1993).

Study Intervals

The sampling years were 1935, 1958, 1969, 1975, and 1994, which gave intervals of 23, 11, 6, and 19 years, respectively. Ideally, the interval between sequential sampling dates should be equal. Unequal time intervals may result in a biased estimate of finite survival rates. To allow valid estimations of survival rates in such cases, the use of a correction factor is recommended which is made by estimating survival rates to the appropriate power (White 1983). For example, Owens (1987, p. 13) explained this procedure as follows: "If 100 plants are marked initially and 50 survive to ten days the survival rate is different than if 50 plants survived to five days" then "estimates would be S for the ten day interval and $S^{.5}$ for the five day interval where

S=1-(number of observed deaths/total number of plants),

and the exponent of 0.5 represents one-half of the ten day period." For comparisons between periods, a 10-year interval was used for this study. Therefore, the exponent for the 1958 sampling date was 2.3 since there were 23 years between observations. The other exponents were 1.1, 0.6, and 1.9, respectively (Table A15). Given 128 plots/year and 5 years, the total sample size for plots in this study was 640.

Seedling Recruitment

The mapped plots from this study provided seedling (new individuals originated from seeds) recruitment data for the perennial vegetation at the time of sampling. The lack of continuous years of sampling precluded the systematic study of seedling dynamics. However, the data on successful recruitment during each discrete census could be related to actual climatic conditions. This information can provide insight into overall plant dynamics and trend processes in the plant community.

The sampling years for this study were 1935, 1937, 1969, 1958, 1975, 1994, and 1995. For each sampling year 128 plots were investigated for the presence of ATCO, ARSP, and CELA seedlings.

In order to relate seedling density to climate, the data were organized by the following climatic categories: yearly, winter, spring, and winter+spring precipitation. Previous year's precipitation data were not used because seedling germination and establishment were more related to other year's rather than to previous precipitation regimes. Because of the small number of sampling points along the 60-year time period (n=7), Spearman correlation coefficients rather than inferential statistics were used as referential measures of association between variables. Because correlation coefficients based on a relatively small sample size can be quite misleading (for example, a single pair of [X, Y] values may contribute excessively to the value of the correlation coefficient), I plotted the values, as recommended in this type of case, to check for influential values.

No extreme pairs of (X, Y) values were found in any of the plots (Figure A1).

To study grazing effects on recruitment, seedlings were divided into grazed and ungrazed categories across years of census and analyzed using the Wilcoxon Signed-Rank Test with a probability level of 0.05. All census years except 1935 were included in the analysis because no grazing effects were expected on seedling recruitment at the beginning of the experiment. A separate test that evaluated grazing effects on total cumulative seedling recruitment conducted out using the χ^2 statistic.

Because the location of emerged seedlings was recorded in 1994, we also tested if there was an association between the location of emerged seedlings and soil cover categories (bare ground versus vegetated patches) with the χ^2 statistic.

Short-Term Seedling and Adult Plant Survival

Data for short-term seedling and adult plant survival analyses were collected in 1994 and 1995. These data were used to compare plant survival in a wet climatic regime with results from a dry climatic regime (Gasto 1969, Holmgren and Hutchings 1972, Owens and Norton 1992, Chambers and Norton 1992), and as complementary information to aid interpretation of the plant survival results and to support trend assessment. Contingency tables were constructed, and the chi-square statistic was used to test for differences. In the resulting matrices, only cells with expected frequencies of at least 5 individuals, as recommended in this type of analysis (Hatcher and Stepanski 1994), were included. The Fisher's exact test statistic was used to evaluate significance when cells with less than 5 expected individuals were present.

The following factors in the analysis of seedling survival were considered:

1. seedling location with two levels, either vegetated patches or bare ground; and

2. grazing treatments with two levels, either grazed or ungrazed.

Results

Model Comparisons

The selection of models used to describe the data for the soil and grazing treatments was based on likelihood ratio test analyses as indicated in the methods section. In each case, a more general model, Model 1 (i.e., survival rates are equal across grazing treatments) with 10 constraints, was compared with a less general Model 2 (i.e., survival rates are equal across both grazing treatments and across all cohorts) that had 16 constraints. The results of the tests for all species suggested that Model 2 with 16 constraints did not fit the data better than Model 1 because p=0.0000 in all tests (Table A16). Consequently, Model 1 is more appropriate to consider than Model 2.

***Atriplex confertifolia* (ATCO)**

General survival

We reject the null hypothesis that plant survival during any one period is equal across all cohorts (χ^2=41.078, df=6, Fig. 32; Table A17). Responsible for this rejection were cohort 1 (1935) (χ^2=23.075), cohort 2 (1958) (χ^2=8.357), and cohort 3 (1969) (χ^2=9.642).

Considering individual cells in Table A17, mortality in cohort 1 was higher than expected in the 1958-69 interval (χ^2=5.360). During the driest interval (1969-75), cohort 2 had higher mortality rates than expected (χ^2=4.202), while the younger cohort 3 showed lower mortality values than expected (χ^2=3.968). During 1975-94, the old plants of cohort 1 showed lower mortality than expected (χ^2=6.038). At the end of the study, cohort 1 had fewer survivors than expected while cohort 3 had more than expected. Cohorts frequently respond to the same climatic regime differently. Additionally, data in Figure 32 are interpreted to suggest influence of climatic regime. Given that survival functions on a log scale give a straight line when mortality rate is constant, the survival curves indicate greater mortality rates in dry periods than in wetter periods.

Soil Effects

Although soil effects on ATCO survival were significant (χ^2=35.772, df=10, Fig. 31, Table A18), the significance appears to be due to only a single cell

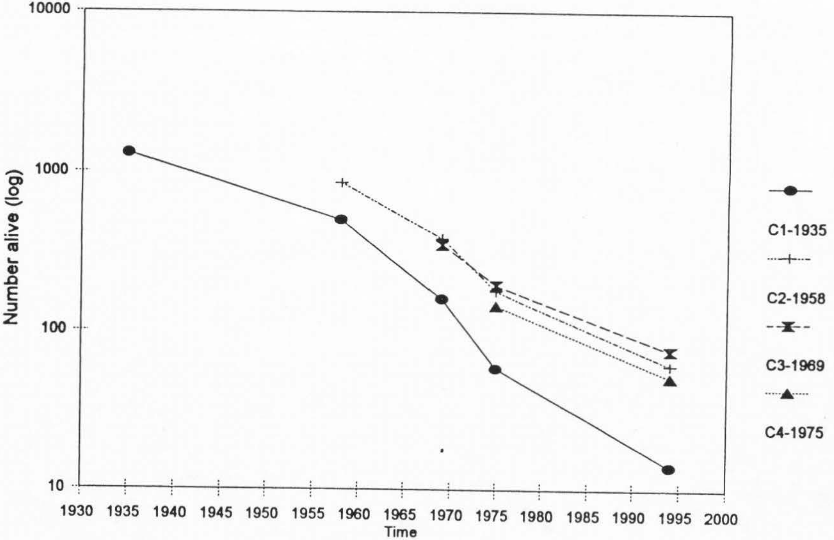


Fig. 32. General survivorship curves for ATCO plants from 1935 to 1994 without discriminating between grazing treatments or soil types . Although the patterns of survival on unequal interval basis appear similar, significant differences were found for C1 for the 1958-69 and 1975-94 periods, and for C2 and C3 in the 1969-75 period.

(C2-94, χ^2=5.832, df=1) of cohort 2 (1958) (χ^2=11.848, df=3) in 1994. In this case, fewer individuals were surviving at the end of the study on coarse loamy soil type-D.

Grazing Effects

Model 1 did not fit the data (χ^2=39.172, df=10, Fig. 33; Table A19), so we reject the null hypothesis and conclude there was a grazing effect. This lack of fit, however, was due only to the 1935 cohort in the 1969-75 interval when ungrazed pastures had lower than expected mortality (χ^2=7.468) and grazed pastures had higher than expected mortality (χ^2=7.156). Despite these differences, the numbers surviving to the end of the study did not differ from expected; grazing had little impact on mortality rates or final survival.

***Ceratoides lanata* (CELA)**

General Survival

As with ATCO, the hypothesis of equal survival rates among cohorts for each time interval is rejected for CELA (χ^2=73.576, df=6, Fig. 34; Table A20). All cohorts contributed to this rejection. For individual cells during 1958-69, mortality was lower than expected (χ^2=5.414) for cohort 1, while it was higher than expected (χ^2=11.033) for cohort 2. In the next period (1969-75), mortality was again lower than expected for cohort 1 (χ^2=4.023); in contrast, cohort 3 had higher mortality rates than expected (χ^2=8.874). During the last wet period (1975-94), mortality was higher than expected in cohort 4 (χ^2=7.560). Thus,

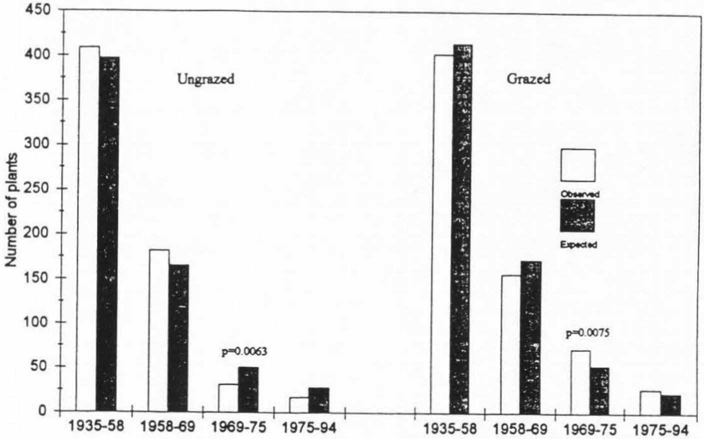


Fig. 33. Pairwise comparisons of observed and expected values for the ungrazed and grazed 1935 ATCO cohort. The only significant combination was due to the lower than expected mortality rate in the ungrazed treatment and the higher than expected mortality rate in the grazed treatment in the 1969-75 climatically driest interval.

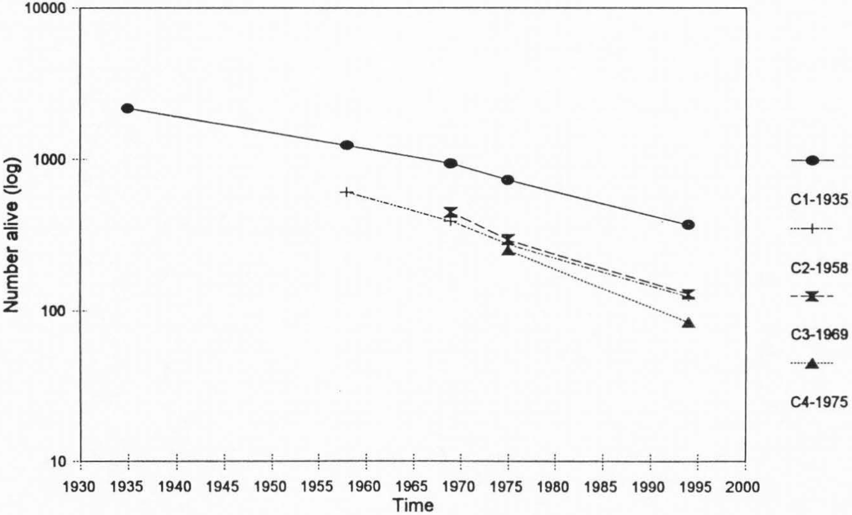


Fig. 34. General survivorship curves for CELA plants from 1935 to 1994 without discriminating between grazing treatments on soil types. Although the patterns of survival appear similar, significant differences were found for C1 and C2 from 1958-69, for C1 and C3 from 1969-75, and for C4 from 1975-94.

there was a clear tendency for younger cohorts, independent of the interval, to have higher mortality rates than older cohorts. In 1994 there were significantly more survivors than expected for cohort 1 (χ^2=18.446, p=0.0000) and significantly fewer than expected for cohort 4.

Soil Effects

There were also significant differences in survival based on soil types (χ^2=39.155, df=10; Table A21). This significance is apparently due to cohort 1 (1935) on soil type-D (χ^2=14.083) and C (χ^2=15.072). Survival was lower than expected during 1975-1994 for this cohort on soil D (χ^2=8.189), and it was higher than expected on soil C (χ^2=8.764). This led to significantly fewer survivors than expected on soil type-D and significantly more survivors than expected on soil type-C at the end of the study.

Grazing Effects

The first model did not fit (χ^2=47.699, df=10, Fig. 35; Table A22) so we reject the null hypothesis and conclude that there was a grazing effect. This lack of fit, however, was due only to the 1935 cohort in the 1935-58 interval when ungrazed expected mortality. These differences were apparently strong enough for ungrazed pastures to have more (χ^2=9.707, p=0.0018) and grazed pastures to have fewer (χ^2=9.037, p=0.0026) survivors than expected at the end of the study. Even so, there is little evidence that grazing had a major impact on mortality.

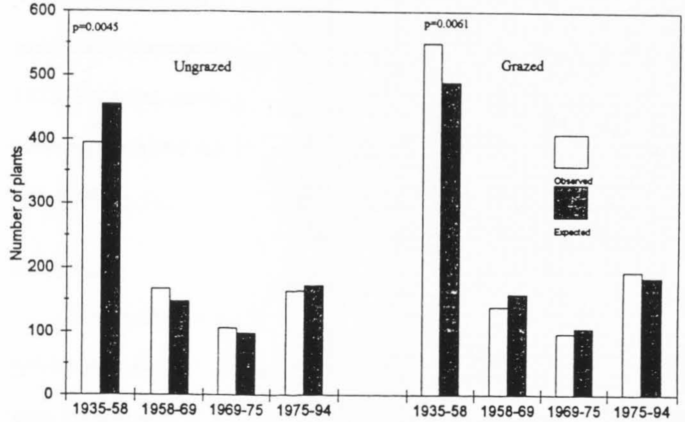


Fig. 35. Pairwise comparisons of observed and expected values for the ungrazed and grazed 1935 CELA cohort. The only significant combination was due to the lower than expected mortality rate in the ungrazed treatment and the higher than expected mortality rate in the grazed treatment in the 1935-58 interval.

***Artemisia spinescens* (ARSP)**

General Survival

As with other species, ARSP cohorts did not have equal survival rates during a given time interval (χ^2=53.486, df=6, Fig. 36; Table A23). The significance was due to the 1958 and 1969 cohorts. ARSP mortality was lower than expected in the 1969-75 period for C2 (χ^2=11.982), and higher than expected in the same period for C3 (χ^2=14.476). In contrast, during the wet 1975-94 period, mortality was lower than expected in cohort 3 (χ^2=7.049). By 1994 cohort 2 had significantly more survivors than expected (χ^2=11.685, p=0.0006).

Soil Effects

No significant soil effects in survival rates of ARSP were found (χ^2=15.950, df=10; Table A24), and thus we conclude that ARSP survival rates were independent of soil type.

Grazing Effects

Survival differed significantly among grazing treatments (χ^2=50.195, df=10, Fig. 37; Table A25). Similar to CELA, however, the significance in ARSP was due only to cohort 1 in both ungrazed (χ^2=17.707, df=4) and grazed (χ^2=16.674, df=4) treatments. Cohort 1 in the ungrazed treatment had lower mortality than expected in 1935-58 (χ^2=5.459), and higher mortality than expected in the 1975-94 periods (χ^2=4.480, Table A25. In contrast, in the

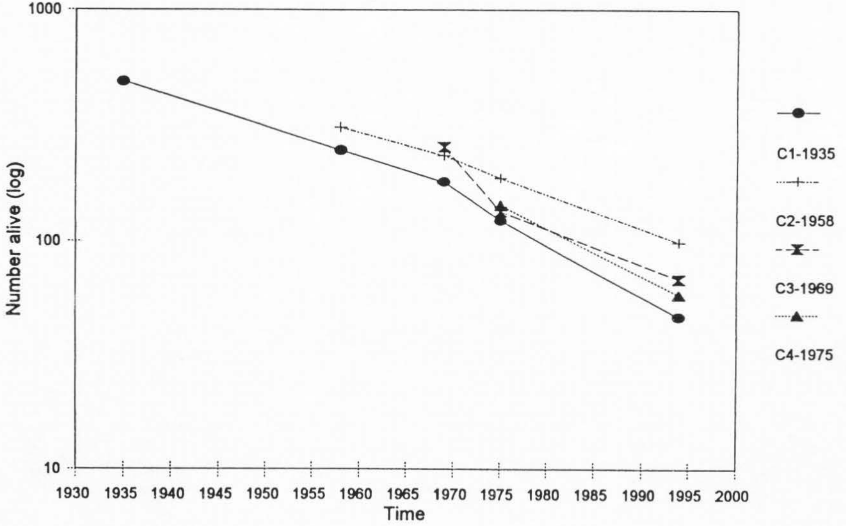


Fig. 36. General survivorship curves for ARSP plants from 1935 to 1994 without discriminating between grazing treatments or soil types. The patterns of survival show significant differences for C2 and C3 from 1969-75, and for C3 from 1975-94.

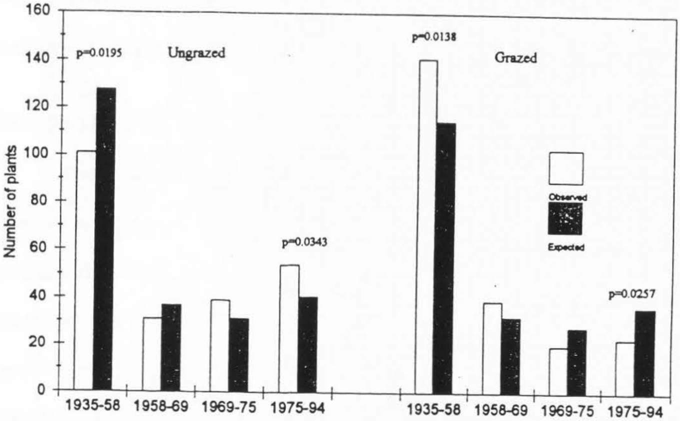


Fig. 37. Pairwise comparisons of observed and expected values for the ungrazed and grazed 1935 ARSP cohort. The significant combinations in the ungrazed treatment were due to lower than expected mortality rates in the 1935-58 and higher than expected mortality rates in the 1975-94 periods. In the grazed treatment significance was due to higher than expected mortality rates in 1935-58 and lower than expected mortality rates in the 1975-94 periods.

grazed treatment mortality was higher than expected (χ^2=6.065) during 1935-58 and lower than expected during the 1975-94 (χ^2=4.977). These differences were apparently strong enough for ungrazed pastures to have more (χ^2=17.707) (despite the higher mortality during 1975-94 period and grazed pastures to have fewer (χ^2=4.808) survivors than expected (despite the lower mortality during 1975-94) at the end of the study. Nevertheless, there is not much evidence that indicates a major grazing effect on mortality.

Seedling Recruitment

The number of seedlings encountered on each of the sample dates, by species and by grazing treatments, and important precipitation data are presented in Table 8. The data are highly variable. For example, coefficients of variation as high as 117 and 99% were estimated for seedling numbers of ARSP and ATCO, respectively. For the climatic variables, spring precipitation showed the highest CV with 72%, and yearly precipitation the lowest with a CV of 31%.

The lowest recorded number of seedlings for all species occurred in 1937 (2.8%) and 1969 (2.0%), which also corresponded to the lowest total precipitation records (148 mm in 1937, and 161 mm in 1969). In contrast, the highest values occurred in 1994 (33.5%) and 1995 (30.9%) with precipitation levels of 234 and 270 mm, respectively. Considering seedling recruitment and precipitation, ATCO (r=0.82), ARSP (r=0.81), and total seedling numbers (r=0.79) were significantly correlated with total precipitation, and CELA (r=0.86)

Table 8. Number of shrub seedlings recruited by year and treatment, precipitation variables, coefficients of variation (CV%), percentages of recruits by species, years and treatments, and percentage of all total recruits.

Species	Treatment	1935	1937	1958	1969	1975	1994	1995	Total	CV%
ATCO	Grazed	8.0	0.0	71.0	8.0	44.0	178.0	153.0	462.0	---
	% by year	36.4	0.0	61.7	88.9	71.0	82.0	80.1	74.5	---
	Ungrazed	14.0	4.0	44.0	1.0	18.0	39.0	38.0	158.0	---
	% by year	63.6	100.0	38.3	11.1	29.0	18.0	19.9	25.5	---
Total ATCO		22.0	4.0	115.0	9.0	62.0	217.0	191.0	620.0	99.2
CELA	Grazed	6.0	4.0	22.0	5.0	9.0	24.0	22.0	92.0	---
	% by year	66.7	14.8	59.5	41.7	39.1	68.6	45.8	48.2	---
	Ungrazed	3.0	23.0	15.0	7.0	14.0	11.0	26.0	99.0	---
	% by year	33.3	85.2	40.5	58.3	60.9	31.4	54.2	51.8	---
Total CELA		9.0	27.0	37.0	12.0	23.0	35.0	48.0	191.0	51.2
ARSP	Grazed	1.0	0.0	13.0	0.0	14.0	44.0	53.0	125.0	---
	% by year	100.0	0.0	38.2	0.0	35.9	37.0	51.0	41.9	---
	Ungrazed	0.0	0.0	21.0	1.0	25.0	75.0	51.0	173.0	---
	% by year	0.0	0.0	61.8	100.0	64.1	63.0	49.0	58.1	---
Total ARSP		1.0	0.0	34.0	1.0	39.0	119.0	104.0	298.0	117.3
TOTAL ALL SPECIES		32.0	31.0	186.0	22.0	124.0	371.0	343.0	1109.0	93.6
	% of total	2.9	2.8	16.8	2.0	11.2	33.5	30.9	100.0	
Annual precipitation (mm)		200.0	148.0	166.0	161.0	195.0	234.0	270.0		22.2
Winter precipitation (mm)		37.0	64.0	112.0	47.0	86.0	71.0	100.0		37.0
Spring precipitation (mm)		62.0	27.0	19.0	43.0	55.0	57.0	148.0		72.4
Winter-spring precip. (mm)		99.0	91.0	131.0	90.0	141.0	128.0	248.0		41.4

with winter precipitation (Figs. 38 and 39; Table A26).

Wilcoxon Signed-Tests showed no significant grazing effects on seedling recruitment for all seedlings or for individual species, except for ATCO ($p=0.0464$, all other $p \geq 0.1158$; Table A27). The large differences in numbers of recruited seedlings in grazed (178 in 1994 and 153 in 1995) versus ungrazed pastures (39 in 1994 and 38 in 1995) probably were responsible for this result (Table 8). Considering total seedling recruitment by species, ATCO showed significantly more seedlings in grazed than in ungrazed pastures ($\chi^2=149.06$, df=1, $p=0.0001$). In contrast, ARSP had more seedlings in ungrazed than in grazed pastures ($\chi^2=7.7315$, df=1, $p=0.0054$). Grazing did not affect CELA seedling recruitment ($\chi^2=0.2525$, df=1, $p=0.6125$). These results suggest that grazing favored the recruitment of ATCO seedlings, the least palatable plant in the area, and negatively affected the recruitment of ARSP seedlings, the most palatable species for sheep.

Using data from 1994, we tested if seedling recruitment was proportional to the area available by soil cover categories (Table 9). The result ($\chi^2=887$, df=1, $p<0.0001$) showed that seedling recruitment was not proportional to available area. About 47% of seedlings emerged in vegetated patches even though these patches covered only 7% of the area. Data are not available for further tests, but this result is interpreted to suggest that changes in vegetation cover through time may affect recruitment.

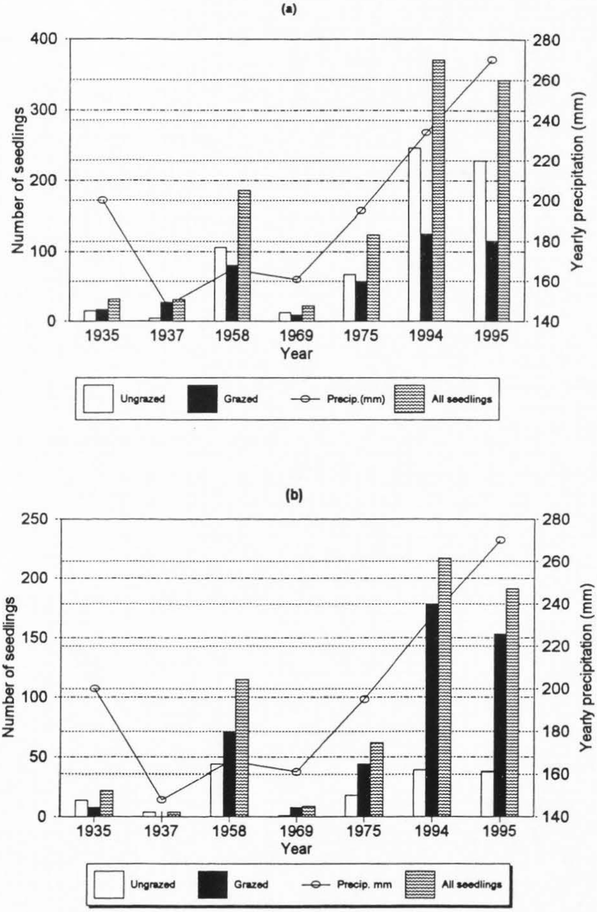


Fig. 38. Seedling recruitment for (a) total seedlings and (b) ATCO across 7 sampling dates at the DER (n=128 9.3 m² plots).

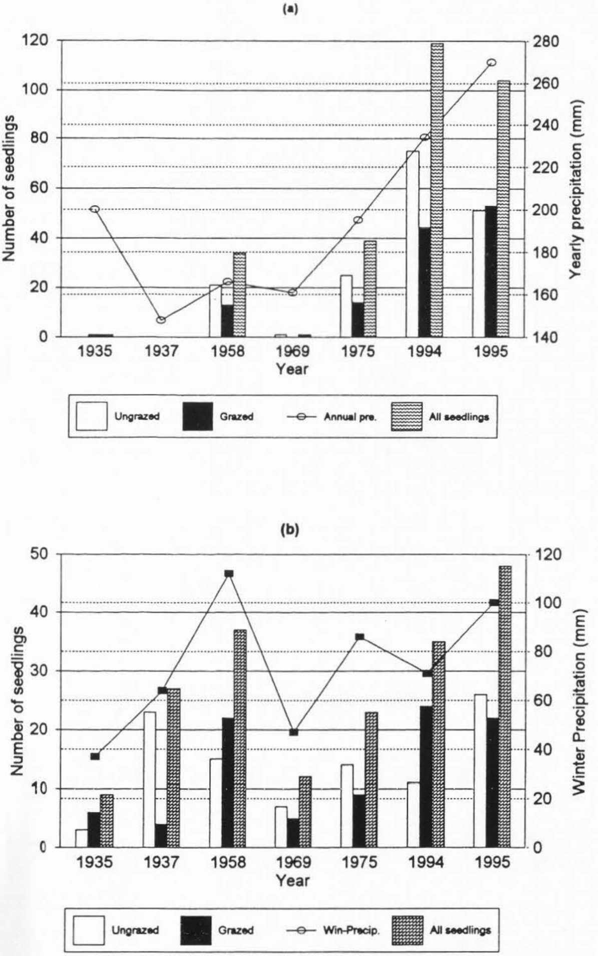


Fig. 39. Seedling recruitment for (a) ARSP and (b) CELA across 7 sampling dates at the DER (n=128 9.3 m² plots).

Table 9. Number of recruited seedlings and soil cover categories (bare ground and vegetated patches).

Soil cover categories	% cover	1994 seedlings
1. Bare ground	83	196
2. Vegetated patch	7	175

Short-Term Seedling and Adult Survival (1994-5)

The results of seedling and adult survival analyses from 1994 to 1995 (2 successive wet years) are presented in Table 10 and Tables A28-A30 (seedling survival by grazing treatments), Tables A31-A33 (seedling survival by location), and Tables A34-36 (adult survival).

According to Fisher's Exact Test, the proportion of surviving CELA seedlings was significantly greater in vegetated patches (94.4%) than on bare ground (64.7%). Neither location nor grazing effects were significant for seedling survival of ATCO or ARSP. The proportion of surviving adult CELA plants was significantly greater in ungrazed (92.3%) than grazed plots (88.6%) ($p=0.045$). No significant differences were found for ATCO and ARSP.

Discussion and Conclusions

Atriplex confertifolia (ATCO)

Evidence suggests that age, possibly interacting with climate, influences ATCO survival. The higher than expected mortality rate of cohort 1 in 1969

Table 10. Seedlings and adult survival in 2 successive years, 1994-95. Locations are bare ground or vegetated patches, and treatments are grazed and ungrazed.

Species	χ^2	df	p	Treatment
ATCO	1.408	1	0.235	Seedling survival by treatment
CELA			0.171*	Seedling survival by treatment
ARSP	0.616	1	0.433	Seedling survival by treatment
ATCO	0.167	1	0.683	Seedling survival by location
CELA			0.041*	Seedling survival by location
ARSP	1.680	1	0.195	Seedling survival by location
ATCO	2.576	1	0.108	Adult plant survival by treatment
CELA	4.006	1	0.045	Adult plant survival by treatment
ARSP	2.086	1	0.149	Adult plant survival by treatment

***p values estimated with Fisher's Exact Test statistic.**

suggests that plants that had already survived 34 years were more affected by the dry 1958-69 period than were other cohorts. Thirty-four years is a significant age for short-lived shrubs such as ATCO whose estimated average life span is only 20 years (Norton and Michalk 1978). Further evidence of an age effect is seen in the next interval, when cohort 2 and cohort 3 showed opposite survival patterns, with higher than expected mortality in the former and lower than expected mortality in the latter. Plants of cohort 2 that already survived 17 years did not tolerate the 1969-75 drought as well as the younger plants of cohort 3 (at least 6 years old). Although these results are interpreted to suggest older plants are more susceptible to drought than younger plants, we cannot rule out genetic variability among cohorts in susceptibility. Interestingly, mortality rates during the 1975-94 period were lower than expected for plants of cohort 1 that had already survived 59 years. Above-average precipitation may have favored survival of old ATCO plants. This is contrary to the thesis that the epidemic of shrub mortality in the mid-1980's, especially of ATCO, was possibly caused by unusually high precipitation received during that period (Pyke and Dobrowolski 1989). However, Pyke and Dobrowolski (1989) suggested that shrub die-off tended to occur in areas more susceptible to flooding than on slopes or areas with better drainage. The experimental pastures at DER are mainly located in areas with sufficient slope to avoid extensive flooding. Consequently, topographic location is important for clarifying the issue of ATCO mortality during wet years. In general, my results were interpreted to suggest that drought is probably likely to be more important in explaining higher ATCO mortality in DER than above-average precipitation.

There was only minimal evidence that soil type influenced survival. Survival of cohort 2 was lower than expected at the end of the experiment in soil type-D. No period had greater mortality than expected, so this was really a cumulative effect through the 59 years of the experiment.

Lastly, there was only minimal evidence for grazing effects as well. The higher than expected mortality in the grazed paddocks may be due to reduced maximum life span of the short-lived, fast-maturing ATCO plants. According to Tilman (1988), herbivory lowers mean plant age. In addition, as seen above, ATCO is apparently susceptible to drought. The combined effects of grazing and drought resulted in accentuated mortality of cohort 1 in the driest study period (1969-75). Significant mortality in ATCO stands grazed in a dry period were also reported by Chambers and Norton (1986) and for pastures grazed in late winter by Harper et al. (1990).

***Ceratoides lanata* (CELA)**

Differences in mortality rates among were observed for all study intervals. These results suggest that age is, as with ATCO, a major factor in determining CELA mortality. In contrast to ATCO, however, most evidence suggests that older plants have greater survival. Older cohorts tend to have lower mortality rates than expected while younger cohorts tend to have higher mortality rates than expected.

The higher than expected mortality rates of younger cohorts overlapped with the dry and driest climatic regimes. This suggests that younger plants are less tolerant of drought than older plants, or, probably that older, deep-rooted plants successfully competed for moisture with new recruits and they prevailed in the community. CELA persistence lasting 59 years is related to the long life-span (> 50 years) of this shrub (Chambers and Norton 1993). Other field observations also suggested that CELA is highly tolerant to drought (Holmgren and Hutchings 1972, Chambers and Norton 1993).

The very high mortality of cohort 4 occurred despite the favorable climatic conditions during the 1975-94 period, and may be explained by severe competition with herbaceous annual and perennial plants faced by the 1975 CELA recruits.

Only cohort 1 in the last interval revealed a soil effect, with higher mortality rates than expected on the coarse-loamy mixed soil type-D and lower mortality rates than expected on the loamy-skeletal soil. This suggests that old CELA plants may have differential responses to wetness depending upon soil type. Perhaps coarse-loamy mixed soil type-D, which has a higher water retention capacity and is located mainly in lower areas than soil type-C, became saturated during the above-average precipitation reported of the fourth period and caused the mortality of these older plants. Prolonged soil saturation may increase the risk of plant death by anoxia, especially for deep-rooted shrubs such as CELA. An average of 186 cm (n=170) of root penetration was measured for CELA plants in DER in islands dominated by this species (DER 1952). In addition, CELA presence is more abundant in the depressions and lower areas of the experimental pastures. Harper et al. (1996) attributed the die-off of CELA stands to excessive moisture at DER in 1969.

Grazing apparently has had only a minimal effect on plant survival. Only the first cohort during the first interval responded differentially to grazing. As would be predicted, mortality was higher than expected in grazed and lower than expected in ungrazed stands. This difference was large enough to translate into significantly greater numbers of individuals than expected surviving 59 years to the end of the study in ungrazed pastures and significantly fewer than expected individuals surviving in grazed pastures. Apparently the 1935 CELA cohort (at least 23-year old plants) did not tolerate grazing during the recovery period.

Probably sheep grazed on the numerous young recruits because availability of forage was limited to a only few palatable species during this period.

Artemisia spinescens (ARSP)

As with CELA, there is evidence that under at least some circumstances younger plants suffer greater mortality than older plants. In the very dry 1969-75 period, mortality was lower than expected for cohort 2 and higher than expected for the younger cohort 3. Perhaps the combination of severe drought and competition with established plants was more detrimental to the younger ARSP population of 1969. Interestingly, this younger C3 cohort showed lower than expected mortality in the wet period from 1975-94; I do not have an explanation why this cohort would survive better than other cohorts.

As with other species, only minimal evidence for grazing impacts was found; in 1958 the 1935 cohort had mortality rates that were higher than expected in grazed pastures and lower than expected in ungrazed pastures. Sheep preference for this highly palatable species may explain this result. Even though cover of the initial ARSP population was low (12%), selective grazing on this species (Norton 1986, Goodrich 1986, Harper et at. 1990) apparently resulted in greater susceptibility to grazing. This situation, however, was reversed during the fourth study period, with mortality higher than expected in ungrazed pastures and lower than expected in grazed paddocks. Perhaps these results represent an age-related collapse of the ungrazed population that had not been thinned earlier by grazing. Additionally, the unusually large number of ARSP recruits added to the ungrazed paddocks (1037; Table A14) may have strongly competed with the older ungrazed ARSP, increasing mortality. In contrast, the 224 new ARSP individuals recruited into the grazed paddocks probably exerted little intraspecific competition on the old ARSP stand.

From the general plant survival results, it is clear that under some conditions, ATCO, CELA, and ARSP cohorts have different survival rates regardless of soils and grazing. These differences, in general, are apparently more important during dry periods for ATCO and ARSP than during the wet period and less important for CELA in dry periods than in climatically average or wet periods. The CELA survival pattern was more constant than that of the other two shrub species, suggesting that CELA tolerated grazing and climatic stress very well, and that changes were mainly related to age and probably competition. In contrast, dry precipitation regimes apparently affect ATCO and ARSP more than CELA.

Grazing did not affect shrub survival in many cases, while the effects of soil type were even less than grazing. Grazing effects were primarily found in dry periods.

Seedling Recruitment

The results in general suggested a strong association between precipitation and seedling recruitment; lows and highs in precipitation corresponded to lows and highs in seedling recruitment. Seedling recruitment apparently is responding mainly to climate rather than other factors such as the availability of viable seed in the seed bank. Ferguson (1972) conducted seeding trials with *Purshia tridentata* and found that soil moisture had a significant effect on seedling vigor and growth. Other authors have also reported the importance of precipitation for seedling recruitment and survival in arid shrublands (West 1979, Owens and Norton 1989, Chambers and Norton 1993).

Further evidence that recruitment is not limited by seed availability comes from patterns of individual species. ATCO, for example, produced more seedlings in the wet years of 1994 and 1995 than in other years (Table 8) despite the greatly reduced number of adult plants (Tables A12, A13, and A14), and presumably seeds, in the community. Gasto (1969) also reported that ATCO and CELA seedlings emerged irrespective of the abundance of mature plants in the community. Other species also produced the most seedlings in 1994 and 1995, although the lack of relationship with adult abundance is less clear. Seedling recruitment was apparently independent of grazing for CELA and ARSP. This supports the idea that seedling emergence is more dependent on the climate than on grazing for these palatable shrubs. Seedling recruitment was dependent on grazing for the unpalatable ATCO, however, with more seedlings recruited in grazed than ungrazed pastures. Grazing activity, then, appears to favor ATCO seedling recruitment.

To better visualize the context in which recruitment of seedlings by location is discussed, vegetated patches constitute, on average, only 7% of total soil cover. Higher numbers of seedlings than expected emerged in vegetated patches in 1994, suggesting that in the shadscale plant community seedling emergence occurs mainly in sheltered places despite the abundance of bare ground. These sheltered patches probably offer better nutrient and moisture conditions in the soil and humidity in the surrounding environment and provide a more favorable micro-environment for seedling emergence than open areas. Desiccation precludes the successful recruitment of seedlings in open areas (Gasto 1969, Owens and Norton 1992). Additionally, the other plants and litter in the vegetated patches may provide a natural barrier against wind and water, which are important dispersion vehicles for seeds, whereas patches may impede the spread of seed that fall from nurse plants in the patch (Chambers and MacMahon 1994).

Short-Term Seedling and Adult Survival (1994-5)

More CELA seedlings survived in vegetated patches than in open areas. In contrast, ATCO and ARSP survival did not differ between locations; apparently, above-average precipitation favored seedling establishment in open areas where competition was probably less severe than in vegetated patches. However, under drier conditions the benefits of an ameliorated abiotic environment in these patches may be outweighed by the negative effects of competition in vegetated patches, and desiccation will be extreme in open areas and may severely reduce the probability of survival. Gasto (1969) reported high survival of seedlings located adjacent to large individual plants. Owens and Norton (1992) found that the interaction between grazing and seedling location resulted in both the highest survival for sheltered seedlings and the lowest survival for unprotected seedlings of *Artemisia tridentata* in grazed pastures. They related this higher seedling survival under shelter to the clumped distribution of plants in this sagebrush-grass ecosystem. In another study, Owens and Norton (1989) reported that survival rates were higher after 30 days of emergence for seedlings with more than 300 mm^2 of resource area as compared with medium (50-300 mm^2) and small (<50 mm^2) resource areas. They pointed out that the interaction of shelter with 300 mm^2 available area increased the probability of *Artemisia tridentata* seedling survival.

Overall, seedlings of all species established successfully. Seedling survival to 1995 was >73% in all cases (Tables A28-A33). Chambers and Norton (1992) studied seedling survival during the dry period from 1975 to 1978 and concluded that, overall, seedling mortality was low for CELA and ARSP and high for ATCO. Based on this, they suggested that CELA and ARSP were more tolerant to drought than ATCO. Holmgren and Hutchings (1972) indicated that in desert environments, erratic precipitation results in infrequent years for good seed production and good establishment of plants and that a simultaneous occurrence of these two events is rare. Our results support the hypothesis that good seedling emergence and establishment are positively correlated with successive years of good precipitation. We suggest, however, that emergence need not be linked to years of good seed production if a viable seed bank is produced.

Grazing did not significantly affect ATCO adult survival from 1994-95. In contrast, Chambers and Norton (1993) reported that grazing during the 1975-78 drought period increased ATCO mortality. They concluded that ATCO is susceptible to effects of below-average precipitation and that these effects are exacerbated by grazing. Chambers and Norton (1993) also found a negative population growth for ATCO during dry years compared to a positive growth in my study during wet years.

Adult CELA plants did die in higher numbers in grazed than ungrazed pastures from 1994 to 1995 despite the favorable precipitation regime. Chambers and Norton (1993) reported no grazing effects on CELA in dry years, suggesting that grazing during the drought had little effect on CELA. However, they also indicated a positive growth of CELA in winter-grazed and a negative growth in winter-ungrazed pastures. Our results showed negative population growth for CELA in grazed and ungrazed plots, regardless of season of grazing. This negative growth appears to be a continuation of the general declining trend in density from 1958 and in cover and density from 1975 for CELA populations. Perhaps CELA plants already weakened by excessive water in the soil environment could not tolerate grazing.

The lack of significant differences between grazed and ungrazed adult

ARSP populations suggests that moderate grazing may not affect survival of highly palatable ARSP plants under favorable climatic conditions. Interestingly, a similar conclusion was reported by Chambers and Norton (1993) for dry years. They suggested that harmful effects of grazing may actually be occurring during years with above-average precipitation, which results of this study are interpreted to indicate is not the case. The lack of grazing effects in wet years may be related to the large increase of recruits observed in the 1975-94 study interval (Table A14). Perhaps ARSP plants were so abundant and grazing levels moderate so that no grazing effects were apparent. However, I cannot explain why grazing effects were not evident for ARSP populations in dry years. The increase of ARSP recruits was even greater in ungrazed than grazed pastures. Apparently the more numerous adult population in ungrazed pastures produced abundant seeds, many of which successfully emerged and established when exposed to favorable climatic conditions.

In general, seedling survival was lower than adult survival for CELA (80 vs 90%) and ARSP (73 vs 82%), and higher for ATCO (93 vs 82%). For the dry period from 1975 to 1978, Chambers and Norton (1992) concluded that seedling survival was lower than adult survival for all three species. West (1979) arrived at similar conclusion after studying plant populations at the DER.

CHAPTER 5

ANALYSIS OF RANGELAND SUCCESSION IN SPRING-GRAZED PASTURES WITH FUZZY GRAPH THEORY

Introduction

In range science, succession refers to a positive development of the vegetation as opposed to retrogression, which identifies a negative change. The succession concept lies at the core of the range management profession (Clements 1928, Stoddart and Smith 1955, Smith 1989). Range science deals with directing plant succession toward states deemed desirable by society. By describing successional patterns, then, we can determine if the objectives of management are being reached.

Rangeland succession in salt desert plant communities has been the subject of several studies (Hutchings and Stewart 1953, Harper 1959, Holmgren and Hutchings 1972, Norton 1978, West 1979, Blaisdell and Holmgren 1984, West and Goodall 1986, Yorks et al. 1992, Whisenant and Wagstaff 1991, Harper et al. 1996). These studies produced valuable information to quantitatively describe succession of the shadscale vegetation type under sheep grazing.

Such fragile ecosystems are especially susceptible to anthropogenic interventions and natural disturbances, and recovery of such systems may be slow. Some authors have indicated that community dynamics in desert environments are extremely slow and may be almost static. Plants replace themselves and no obvious changes occur (West 1988, Norton and Michalk 1978, Norton 1978, Yorks et al. 1992). Rice and Westoby (1978) studied vegetation change in 12 protected and unprotected salt-desert vegetation types (6- to 15-year exclosures) in the Great Basin, and concluded that plant succession is not meaningful in these plant communities.

There are examples from the shadscale vegetation type, however, in which natural disturbances and anthropogenic interventions resulted in severe changes in the direction of succession. Droughts (Pyke and Dobrowolski 1989, Chambers and Norton 1993), floods (Harper et al. 1996), pathogen outbreaks (Holmgren and Hutchings 1972, West and Tueller 1972, Tueller 1973), climatic shifts (Norton 1978, Nelson et al. 1989), and invasion by alien annual plants (Young et at. 1987, West 1988, Harper et al. 1996) are reported as important factors determining particular successional pathways (previous chapters). Similarly, managerial interventions are constantly influencing natural succession. For example, prior to 1935, the study area of this investigation was believed to be in severe retrogression due to heavy and uncontrolled winter and spring grazing (McArdle et al. 1936, Stewart et al. 1940, Hutchings and Stewart 1953).

Palatable plants in the area are believed to have evolved under light grazing pressure. High intensities of grazing in the late 19th century caused deterioration of these plants and resulted in an increase in unpalatable shrubs (Young et al. 1976, 1979). Laycock (1991) indicated that this change is an example of crossing a threshold into a new steady state. Such generalized deterioration on western rangelands was the main reason for the passage of the Taylor Grazing Act in 1934 and the initiation of the grazing trials at the Desert Experimental Range (DER). The main objective of the research at the DER was to determine whether timing and intensity of grazing can be controlled to reverse retrogression of the degraded shadscale rangelands. It was anticipated that this factor could be controlled to alter the competitive relationships among the species and plant populations. The cumulative effects of these interventions were expected to eventually change the structure and composition of the plant community to a new, desirable combination.

Because of the historic degradation of this system, any contribution to improve our understanding of plant succession in fragile ecosystems under sheep grazing is justified. The need for faster and easier ways to detect and interpret succession has been pointed out by West and Tueller (1972) and Norton (1978). To follow this line of thinking, the frequent use of new tools to study succession is required. That is, the objective of this study was to employ the fuzzy graph technique in describing successional changes in spring-grazed pastures at the DER.

Fuzzy set theory is one of several methods developed for studying forest dynamics (Botkin et al. 1972, Horn 1975). Fuzzy graph theory was introduced by Roberts (1989) as a flexible method for study and mapping forest dynamics. This method, however, also may be useful for mapping the dynamics of shrublands.

Data at two sampling dates are all that are needed to describe changes in relative abundance of the plant community.

Literature Review

Norton and Michalk (1978) and Norton (1978) evaluated demography of *Artemisia spinescens*, *Ceratoides lanata*, and *Atriplex confertifolia* using data from permanent plots at the DER. One of their propositions was that "rate of change in vegetation composition is a function of population turnover, or inversely related to longevity of major species" (Norton and Michalk 1978, p. 4). They reported an average increase in crown area from 30 to 220 cm² for *Ceratoides lanata* during 40 years, and then related the size and age of the plant to plant succession in communities in which this species is dominant. Norton and Michalk (1978) suggested that total plant density in the community is relatively homeostatic, which automatically confers a competitive advantage on long-lived species in the salt-desert shrub vegetation.

Norton and Michalk (1978) and Norton and Bermant (1977) conducted pilot studies of species/plant site fidelity for winterfat (*Ceratoides lanata*) and shadscale (*Atriplex confertifolia*) with data from exclosures at DER. They reported a probability of self-replacement of 0.7 for *Ceratoides lanata* (high persistence, permitting little replacement by other plants) and only 0.1 for *Atriplex confertifolia* (low persistence, permitting the establishment of other species). The total shrub density remained more or less stable in both grazed and ungrazed treatments. Data from 1989 showed that *Ceratoides lanata* was still highly persistent (Harper et al. 1990).

Through time, plants can develop avoidance (protection) and tolerance mechanisms in response to grazing and climatic factors (Milchunas et al. 1988). Grazing directly affects competitive interactions by differential utilization of populations within the community, each of which displays tolerance and protection mechanisms to different degrees (Briske 1991). *Atriplex confertifolia*, for example, has spines that give this species an advantage under grazing compared to other plants of similar palatability but without such protection. Similarly, perennial grasses such as *Hilaria jamesii* or *Sporobolus cryptandrus* have the ability to grow rapidly after defoliation compared to shrubs. This tolerance mechanism should increase the relative competitive ability of these grass species under grazing, because vigorous regrowth enables these species to intercept greater amounts of solar energy and assimilate greater amounts of carbon.

The plant replacement dynamics described, however, are dependent on the kind of grazer and on its grazing management. Shadscale plant communities are mostly grazed by sheep during winter and spring. Therefore, species preferred by sheep, such as *Artemisia spinescens* and *Ceratoides lanata,* are expected to decrease, and the rate of decrease should be higher under spring grazing when plants are physiologically active than under winter grazing when plants are dormant.

Norton (1978) studied successional trends of plant populations under sheep grazing at the DER (40-years data) and reported a high correlation between trends of grazed and ungrazed plots. He concluded that the grazing treatments did not affect the general trend of species composition as measured by relative cover. Other factors such as interspecific competition, plant longevity, plant replacement, and climatic effects were offered more influential than grazing in promoting vegetation change (Norton 1978). Species composition outside (moderately grazed) and inside exclosures showed parallel changes across 36 years in an *Artemisia-Agropyron* rangeland in eastern Oregon (Sneva et al. 1984). Whisenant and Wagstaff (1991), working at the DER, concluded, however, that grazing affected vegetation trend, and that season of grazing had a more pronounced effect on species composition than did grazing intensity.

Friedel (1990) discussed the importance of biomass as an indicator of trend when plants are long-lived and respond slowly to disturbances (e.g., in the case of chenopod shrublands in Australia). Yields of short-lived species, however, can be used to separate temporal climatic fluctuations from the general trend.

Smith (1986) studied the dynamics of phytomass production at the DER and pointed out that trends in plant production through time showed no treatment differences at the ecosystem level, and few differences at the community or species level. For example, the palatable shrub *Artemisia spinescens* declined in phytomass production with late-winter/spring use and increased under dormant season grazing. Conversely, a decline in phytomass production of *Atriplex confertifolia* under dormant-season grazing was observed. *Ceratoides lanata* showed no consistent long-term trend with any treatment.

Grasses, on the other hand, showed little difference in phytomass production among treatments, or increased with heavy use and in communities dominated by shrubs (Smith 1986). Drought and timing of precipitation are mentioned as factors that, combined with grazing, influenced changes in production and vegetation composition. Smith (1986) suggested that community composition is returning toward that which existed prior to the introduction of domestic stock. However, condition and stability of DER range before the introduction of domestic livestock are not understood well enough to make a valid comparison.

Nevertheless, the conclusion that amount and distribution of precipitation strongly influence the dynamics of the system is consistent with reports that indicate strong precipitation-production correlations in the shadscale ecosystem (Blaisdell and Holmgren 1984, Cleary and Holmgren 1987, Tew et al. 1995).

West (1988, p. 220) pointed out that "the harsh environments of salt deserts slow down community dynamics, but because the same species or species similar in appearance and stature often succeed each other after disturbance, auto-succession probably best describes what occurs over the shorter run."

Materials and Methods

Study Area

The history of the grazing trials as well as the physical and climatic characteristics of the study area is detailed in Chapters 1, 2, and 3 in this dissertation.

Study Paddocks

Spring grazing is frequently mentioned as an important factor influencing vegetation change in the shadscale community (Harper 1959, Holmgren and Hutchings 1972, West 1988), and was selected as a factor for this study. Data on relative abundances of plants were extracted by grazing treatment for 5 experimental paddocks. Twenty plots/year for each treatment were used in the analysis. The species included in the study were the shrubs *Atriplex confertifolia* (ATCO), *Ceratoides lanata* (CELA), and *Artemisia spinescens* (ARSP), and the perennial grasses *Sporobolus cryptandrus* (SPCR), *Oryzopsis hymenoides* (ORHY), and *Hilaria jamessii* (HIJA). These species were the most important components of the plant community throughout the 59-year study period.

Data Structure

In order to study time-variance dynamics, fuzzy graphs were constructed for 4 consecutive experimental intervals: 1935-58, 1958-69, 1969-75, and 1975-94. In addition, the 59-year interval between 1935 and 1994 was analyzed separately. The same procedure was followed for both spring-grazed and spring-ungrazed pastures.

Abundance values (based on canopy cover) and changes in abundance are the basic data employed in this analysis. A map of system dynamics for each of the study intervals using fuzzy graph theory was produced from an analysis of repeated measurements of the relative cover variables.

According to Roberts (1989, p. 262) :

> Fuzzy graph theory is derived from fuzzy set theory, a generalization of classical set theory (Zadeh 1965).... In fuzzy set theory elements of the universe have grades of membership in a set.... Specifically, in fuzzy set theory, elements have membership values in the interval [0, 1], rather than in the set {0, 1} as for classical set theory.... Similarly, fuzzy relations are generalizations of classical set relations. A relation can be thought of as a rule applied to sets of ordered pairs.... In practice, the values assigned to the relation are typically determined by a membership function with a domain of [0, 1].... From fuzzy relations it is possible to define directed graphs by employing a simple algorithm....

Defining the Relations

There are three fuzzy relations for "succession," each of which reflects a different definition of succession. The definitions of succession increase in rigor from one to three. "These fuzzy relations express the degree to which species x is 'succeeding to' species y by assigning the relation $R_{x,y}$, a number in the interval [0,1]" (Roberts 1989, p. 263).

The first definition of succession requires that for species x to succeed to species *y*:

1.1) species *x* must be present at time 0

1.2) species *y* must increase in the interval from time 0 (t_0) to time 1 (t_1).

The succession relation can be symmetric, meaning that species within the same tier can succeed to any other species within that tier.

In the second definition of succession, for species *x* to succeed to species *y* requires that:

2.1) species *y* must increase faster than species *x*, or

2.2) species *x* must decline faster than species *y*.

This definition is not symmetric; that is, species x and species *y* cannot succeed each other. It is possible, however, for one species to succeed to the other even if both species decline in abundance across the time interval (Roberts 1989).

The third definition of succession is the most rigorous and requires that for species *x* to succeed to species *y*:

3.1) species *x* must decrease in the interval t_0 to t_1

3.2) species *y* must increase in the interval t_0 to t_1.

This definition is antisymmetrical because species cannot be succeeding to each other within the same tier. It essentially separates the species into increaser and decreaser categories.

The selected relation was examined for transitive closure (i.e., if species *x* is succeeding to species *y*, and species *y* is succeeding to species *z*, then species *x* is necessarily succeeding to species *z)*. To ensure transitive closure, the abundance of a species relative to the total of all six species in this study will be used.

All three definitions were used to study succession during 1935-94. Because we wanted to study plant dynamics under the most rigorous definition of succession and separate increaser and decreaser plants, only the third definition of succession was used for the analysis of system time-variance for the 1935-58, 1958-69, 1969-75, and 1975-94 study periods (an example of the analysis is included in Table A37).

Alpha-cuts (specified thresholds) are employed to isolate dominant trends and suppress inconsequential values. They can be of three intensities: 1) 0.005 is used to suppress inconsequential values; 2) 0.025 suppresses changes in relative abundance of less than 2.5%; and 3) 0.05 suppresses changes of less than 5% and emphasizes dominant trends (Roberts 1989). Because we were working with important preselected species and the focus was on identification of dominant trends, the alpha-cut of 0.05 was used in all cases.

Finally, a rank correlation analysis was conducted to determine if significant differences existed between the relative botanical compositions of grazed and ungrazed treatments in 1935 and 1994.

Results and Discussion

Table 11 shows the differences in relative abundances by study intervals

Table 11. Differences in relative abundances (canopy cover) of principal species by study intervals in pastures grazed in spring at the DER (n=20 9.3 m^2 plots).

Species	1958-1935	1969-1958	1975-1969	1994-1975	1994-1935
1. ATCO	1.8	-24.2	-13.2	-3.5	-39.1
2. ARSP	-3.5	-0.7	0.0	-0.3	-4.5
3. CELA	-2.2	3.5	10.5	-21.2	-9.4
4. SPCR	-0.3	7.2	1.1	9.6	17.6
5. ORHY	0.1	2.0	1.6	13.5	17.1
6. HIJA	4.1	12.3	-0.2	2.0	18.9

ATCO = *Atriplex confertifolia*; ARSP = *Artemisia spinescens*; CELA = *Ceratoides lanata*; SPCR = *Sporobolus cryptandrus*; ORHY = *Oryzopsis hymenoides*; HIJA = *Hilaria jamesii.*

of the 6 dominant species in the spring-grazed pastures and the difference between 1994 and 1935. All 3 shrubs decreased under grazing, with ARSP almost disappearing from the pastures by 1969 and CELA decreasing by more than half from 1975 to 1994 (Fig. 40a, Table 11). Clearly, grazing had a selective impact on palatable ARSP which was used year after year in a critical initial state of development. ATCO, the least palatable shrub, slightly increased in the first interval and then steadily decreased in all other intervals with high negative values during the dry and driest intervals; ATCO decreased by half from 1935 to 1994 (Fig. 40a, Table 11). All grasses were successional increasers (Table 11). Selective grazing on palatable shrubs in the spring and the decrease of ATCO probably gave competitive advantage to the grasses. This is consistent with trends reported in the study of the grass-shrub interface

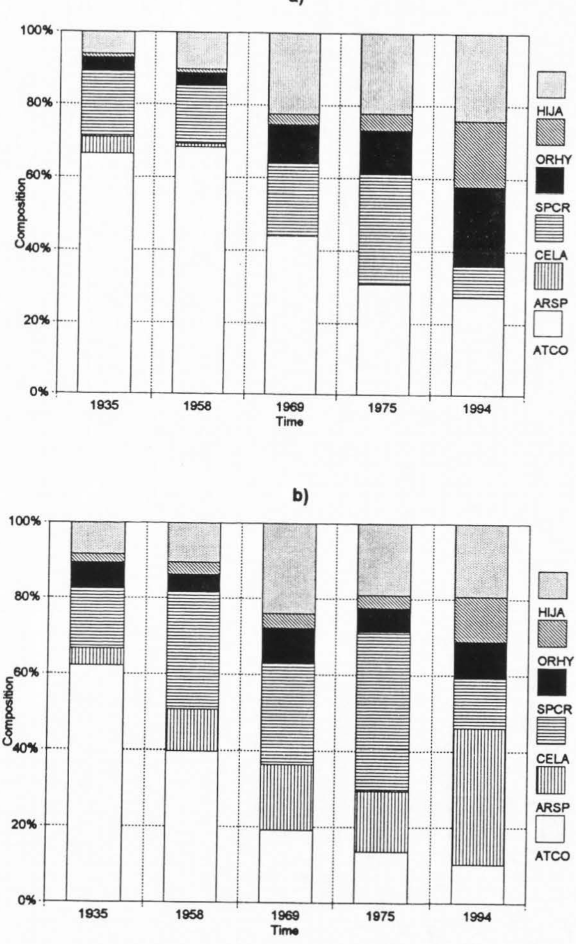


Fig. 40. Dynamics of relative species composition in a) spring-grazed and b) spring-ungrazed pastures at the DER (n=20 9.3 m² plots).

in Chapter 3. The increase of grasses, however, was not uniform. SPCR and ORHY, after little change in the first interval, increased in all other intervals with the lowest increases during the driest 1969-75 interval. HIJA increased in the first, second, and fourth interval but decreased during the driest period.

Table 12 shows the differences in relative abundances of the six dominant species in ungrazed spring pastures for four intervals as well as the difference between 1994 and 1935. In the 59-year interval, two shrubs, ATCO and CELA, decreased, with ATCO showing the greatest decrease (Fig. 40b, Table 12). ATCO is the least palatable plant for sheep in the study site; the ATCO decrease may be linked to the increase in highly palatable ARSP and the grasses ORHY and HIJA (Fig. 41b, Table 12) as suggested by the preference of plants to establish in vegetated areas rather than in open areas in the seedling recruitment section. CELA is a palatable shrub for sheep and was expected to increase with the removal of grazing. It showed erratic behavior under ungrazed conditions, however, with the greatest increase from 1935 to 1958 and a severe decrease below the 1935 level in 1994. Note that CELA is the only plant that shows an increase in canopy cover during the driest study period from 1969 to 1975. Plant cover of CELA, however, collapsed in the wet period (1975-94). ARSP showed positive values for all intervals except the driest 1969-75 period with the greatest value in the wet interval (1975-94).

All 3 grasses increased to 1994. However, the increase was not constant across study periods because all decreased during the driest 1969-75 interval

Table 12. Differences in relative abundances (canopy cover) of principal species by study intervals in ungrazed spring pastures at the DER (n=20 9.3 m² plots).

Species	1958-1935	1969-1958	1975-1969	1994-1975	1994-1935
1. ATCO	-22.6	-20.6	-5.6	-3.3	-52.1
2. ARSP	6.5	6.5	-1.3	19.7	31.4
3. CELA	15.1	-4.4	15.1	-28.6	-2.7
4. SPCR	-2.2	4.5	-2.9	3.5	2.9
5. ORHY	1.0	0.6	-0.3	8.2	9.5
6. HIJA	2.1	13.5	-5.0	0.4	10.9

ATCO = *Atriplex confertifolia*; ARSP = *Artemisia spinescens*; CELA = *Ceratoides lanata*; SPCR = *Sporobolus cryptandrus*; ORHY = *Oryzopsis hymenoides*; HIJA = *Hilaria jamesii*.

(Fig. 41b, Table 12). This decrease suggests that grasses were intolerant to drought conditions.

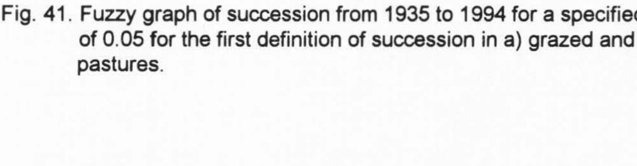
ATCO decreased less in grazed than ungrazed pastures (Table 11 and 12). ARSP increased in ungrazed and consistently decreased in grazed pastures, suggesting a strong grazing effect on this palatable shrub. CELA showed important increases in ungrazed pastures in the first and third study periods, compared to decreases in the grazed pastures in the first period. CELA, however, decreased in both grazed and ungrazed pastures during the last and wet study period.

Grasses were successional increasers in both grazed and ungrazed pastures but increased more under grazing than under nongrazing conditions (Table 11 and 12). Little change occurred in either grazed or ungrazed pastures during the driest interval (1969-75).

1935-94 Comparisons

In considering the first definition of succession for the spring-grazed and spring-ungrazed controls, the fuzzy graph is a map of the species as shown in Fig. 41. Fig. 41a presents two tiers with equal numbers of species. The increasers were the grasses SPCR, ORHY, and HIJA, and the decreasers were the shrubs ATCO, CELA, and ARSP. Clearly, we have a separation of plant dynamics by growth form. Cumulative sheep grazing on ARSP, a palatable species, apparently caused this shrub to decrease. ATCO, the least palatable species, also decreased, but at a slower rate than in ungrazed pastures (Tables 11, 12, Fig. 40).

Fig. 41b presents the fuzzy graph for the first definition of succession for the spring-ungrazed pasture. The graph also has two tiers, but differs from the



a) Grazed

b) Ungrazed

Fig. 41. Fuzzy graph of succession from 1935 to 1994 for a specified alpha-cut of 0.05 for the first definition of succession in a) grazed and b) ungrazed pastures.

grazed pastures in the location of ARSP, which was a decreaser in grazed and an increaser in ungrazed pastures.

In considering definition two, Fig. 42 shows the fuzzy graphs for the second definition of succession for the spring-grazed and spring-ungrazed pastures. In the grazed pastures (Fig. 42a), the grasses HIJA, SPCR, and ORHY increased in magnitude in the order in which they are listed and the shrubs ARSP, CELA, and ATCO decreased. ATCO showed greatest decrease, which is likely due to factors such as competition from the increaser grasses rather than to grazing. In the ungrazed pastures (Fig. 42b), ARSP, HIJA, ORHY, and SPCR are increasers in that order. CELA and ATCO decreased, with ATCO again showing the greatest decrease.

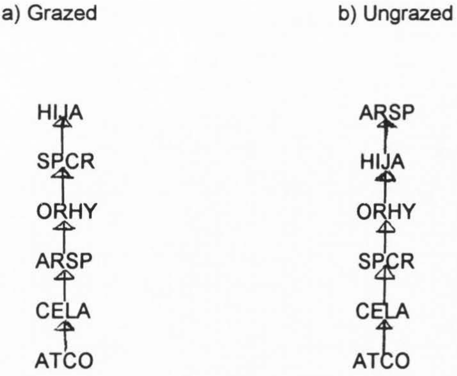


Fig. 42. Fuzzy graph of succession from 1935 to 1994 for a specified alpha-cut of 0.05 for the second definition of succession in a) grazed and b) ungrazed pastures.

Finally, the third definition of succession for the spring-grazed and ungrazed pastures (Fig. 43a, b) presents maps similar to those of the first definition (Fig 41a, b). The difference is that the third definition of succession is not symmetric. Consequently, in contrast to definition one, the species within the same tier are not succeeding to each other. The third definition of succession essentially separates the species into two classes, increasers and decreasers. Increasers in the grazed pastures were the grasses SPCR, ORHY, and HIJA, and decreasers were the shrubs ATCO, CELA, and ARSP (Fig. 43a). In ungrazed pastures (Fig. 43b), ARSP and all the grasses were increasers. The other two shrubs, CELA and ATCO, were decreasers. Thus, as with the first definition of succession, ARSP is the only species responding to grazing by this definition.


a) Grazed

b) Ungrazed

Fig. 43. Fuzzy graph of succession from 1935 to 1994 for a specified alpha-cut of 0.05 for the third definition of succession in a) grazed and b) ungrazed pastures.

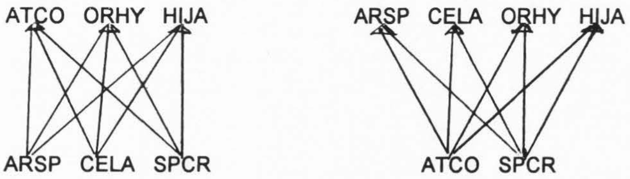
In 1935, the rankings of relative abundances of the 6 species in grazed pastures were correlated with rankings in the ungrazed pastures (r_s=0.94, p=0.0048; Table A38), suggesting the botanical composition of the 2 grazing treatments was the same. After 59 years, however, the correlation between grazing treatments was not significant (r_s= -0.54, p=0.2657), suggesting that the botanical composition of grazed and ungrazed spring pastures had diverged by 1994. This is consistent with the changes observed in Fig. 40.

Analysis of System Time-Variance

The analysis of time-variance consisted of analyzing the fuzzy graphs constructed for 4 consecutive time periods within the 59-year overall period.

The first period, 1935-58, was the longest (23 years) and represented the recovery period from heavy grazing prior to 1935. During this period, the grazed pastures experienced an increase in ATCO, ORHY, and HIJA, and a decrease in ARSP, CELA, and SPCR (Fig. 44a). In ungrazed pastures (Fig. 44b) ARSP, CELA, ORHY, and HIJA increased and ATCO and SPCR decreased. CELA and ARSP were located differently in the 2 grazing treatments, as decreasers in the grazed and increasers in the ungrazed pastures. This suggests that grazing at the beginning of the experiment had an effect on the palatable CELA and ARSP. The least palatable ATCO, however, was an increaser under grazing and a decreaser when ungrazed. The results suggest that suppression of grazing had a negative impact on ATCO, probably because competition from ungrazed palatable plants increased in ungrazed pastures (Fig. 44b). The grasses ORHY and HIJA increased in both grazed and ungrazed pastures, and SPCR decreased also in both pastures, suggesting that grazing was not a determinant of the behavior of grasses.

The second period spanned 1958 to 1969, and system dynamics for this period were different from the previous period. In grazed pastures (Fig. 45a), CELA and SPCR moved from decreaser to increaser status, and ATCO moved from an increaser to a decreaser category. Thus, even under grazed conditions, the unpalatable ATCO began to decrease. Previous results (Chapters 3 and 4) indicated that grazing was moderate and only affected the highly palatable ARSP, suggesting that plants remained competitive enough to affect ATCO (Fig. 45a). The fuzzy graph of system dynamics for the second period also shows different behavior than the previous period for ungrazed pastures (Fig. 45b).



a) Grazed

b) Ungrazed

Fig. 44. Fuzzy graph of succession from 1935 to 1958 for a specified alpha-cut of 0.05 for the third definition of succession in a) grazed and b) ungrazed pastures.

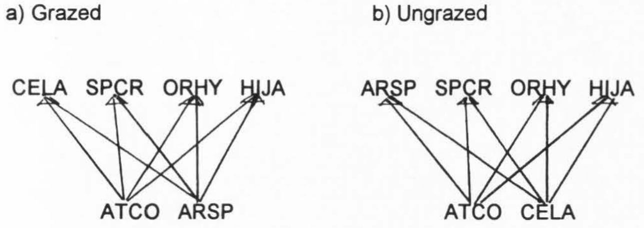


Fig. 45. Fuzzy graph of succession from 1958 to 1969 for a specified alpha-cut of 0.05 for the first definition of succession in a) grazed and b) ungrazed pastures.

SPCR moved from decreaser to increaser status, and CELA moved from increaser to decreaser status. As a result, all grasses and the highly palatable ARSP were located in the group of increasers, and ATCO and CELA in the group of decreasers. CELA is a palatable plant and was expected to increase under ungrazed conditions, but instead it increased under grazing, suggesting that it was not directly affected by grazing during this period.

The third study period, which was shortest and driest, covered 1969 to 1975. In the grazed pastures (Fig. 46a), HIJA moved from increaser to decreaser category, and ARSP was not included in the mapping, while all other species remained the same. Probably ARSP could not tolerate grazing under drought and fell below the 0.05 alpha-cut threshold used in the study and therefore was excluded in the mapping. On the other hand, it appears that SPCR and ORHY tolerate drought better than HIJA under grazed conditions. The palatable CELA remained an increaser, which suggests that grazing had no

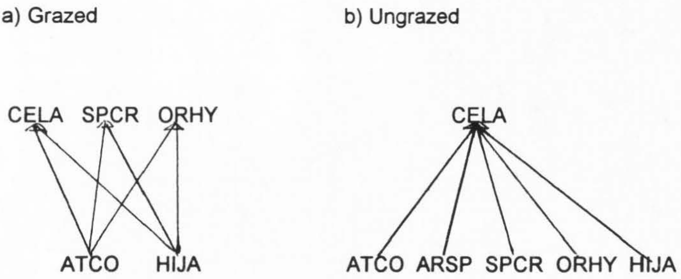


Fig. 46. Fuzzy graph of succession from 1969 to 1975 for a specified alpha-cut of 0.05 for the third definition of succession in a) grazed and b) ungrazed pastures.

effect on this species even under drought conditions, while ATCO was still a decreaser in the grazed pastures. In the ungrazed pastures (46b), however, a very dynamic scenario was present. CELA moved from a decreaser in the previous period to an increaser and all previous increasers became decreasers. This suggests, again, that CELA is highly tolerant of dry conditions and under these conditions may be able to outcompete other plants.

In the last and wet study period (1975-94), under grazed conditions (Fig. 47a) a clear separation of species by life form into two tiers was observed, with grasses in the increaser group and shrubs in the decreaser group. In comparison with the previous period, CELA moved to the decreaser category and HIJA became an increaser, while ARSP recovered from the previous period but remained in the group of decreasers as in the 1935-58 and 1958-69

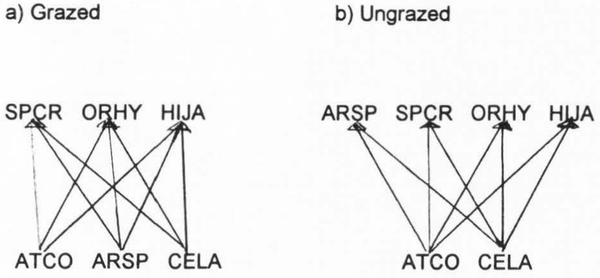


Fig. 47. Fuzzy graph of succession from 1975 to 1994 for a specified alpha-cut of 0.05 for the third definition of succession intervals in a) grazed and b) ungrazed pastures.

intervals. In ungrazed pastures (Fig. 47b), the situation reversed to the same pattern as found in the 1959-69 interval; CELA become a decreaser while all other species but ATCO returned to the increaser category. This suggests that CELA may be intolerant of wet conditions. The general trend toward grass dominance during this wet interval is clear in both grazed and ungrazed pastures (Fig. 47b).

Although grasses became a dominant life form in grazed pastures, and grasses and ARSP in the ungrazed pastures, grasses may not necessarily remain a dominant growth form in the community. Shifts in precipitation or chance events may alter the successional pathway at any time. So far, however, succession, especially in the grazed pastures, is towards a grass-dominated plant community. Even if sheep are removed from the system, the community apparently will continue to move, although perhaps at a slower rate, towards one that is dominated by grasses.

We do not conclusively know what the dominant species were before the introduction of livestock in the area around 1870, and thus can only speculate whether or not succession is proceeding toward that original plant community. Early explorers commented on the abundance of grasses before the arrival of European livestock in the area (Cottam 1961). However, no concrete evidence is available to allow quantitative comparisons and it is difficult to separate climatic influences from the grazing effects. During the wet study period from 1975-94, precipitation apparently heavily favored the grasses and not the shrubs (see previous chapters) (Pyke and Dobrowolski 1989, Archer 1994). Therefore, high rainfall could have had a confounding impact on vegetation response to grazing treatments through time and is probably causing the plant community to cross a threshold into a state dominated with a relative grazing influence depending on the species and interacting with climate. From this point of view, sheep grazing can be visualized as an additional factor affecting the rate, rather than the direction, of change in the shadscale vegetation type.

In every period, differences between grazing and ungrazed pastures occurred. In addition to ARSP, CELA also showed consecutive changes. CELA changes, however, showed a strong interaction with precipitation. In ungrazed pastures, CELA increased under very dry conditions; in grazed pastures, CELA increased under dry and very dry conditions. ATCO and grasses mainly changed regardless of grazing.

Grazing, thus, did partially influence the observed pathways of succession in the spring pastures at the DER. Overall plant community dynamics, however, mainly followed climatic fluctuations. In general, plant response to climatic factors was apparently more important in determining plant community changes than plant response to grazing.

CHAPTER 6

SPATIAL RELATIONSHIPS BETWEEN DIFFERENT PLANT COMBINATIONS IN GRAZED AND UNGRAZED SALT-DESERT PLANTS

Introduction

Ecologists have long been interested in the important relationship between grazing and plant competition in the western United States (Jameson 1963; Ferguson and Basile 1967; Mueggler 1970, 1972; Heady 1975; Mack and Harper 1977; West et al. 1979; Caldwell 1984; Archer and Tiezen 1986; Pendery and Provenza 1987; Archer and Smeins 1991). Even if the structure of natural communities in nonequilibrium ecosystems such as the shadscale plant community are not necessarily determined by competitive interactions, as proposed by several ecologists (Ellis and Swift 1988, Westoby et al. 1989), competition is probably still an important process in nearly all plant communities. Because range science deals with the manipulation of vegetation through grazing management, it is important to consider grazing-induced plant community changes from the perspective of potential competitive relationships.

The shadscale plant community of this grazing experiment is composed of an aggregation of various plant populations arranged in various patterns of abundance and space. The study of spatial interactions between plants of different sizes under grazed and ungrazed conditions may provide insights for understanding competitive interactions among plants and how they relate to plant community dynamics. The study of spatial arrangements can be used to answer questions such as, are size-distance interactions between plants of the same or different species important in changing species composition and structure? This question is important because it may allow separation of grazing effects from inherent competitive phenomena in the plant community.

In sessile organisms with plastic growth, spatial pattern and size of individual plants can be useful in determining past interactions (Welden et al. 1988). For example, Pielou (1960, 1961) used the correlation between distance separating a pair of neighboring plants and the sum of their sizes as an indicator of their interactions, with a significant positive correlation indicating competition. Later, Gutierrez and Fuentes (1979) pointed out that relationships between inter-plant distance and sum of sizes of the plant fit a straight line, and they used the slope of this regression as a measure of competition intensity. In contrast, Yeaton and Cody (1976) used the correlation coefficient as an indicator of competition.

Competition may not be the only interaction involved, however. Accumulating evidence suggests that plants growing in proximity may also be in beneficial relationships, especially in extreme environments such as the arid shadscale plant community (Bertness and Callaway 1994). Long-lived shrubs, the primary space holders in vegetated patches, can positively modify the micro-habitat by decreasing temperature and evaporation and increasing soil resource availability, organic content, etc. (West 1983, Hunter and Aarssen 1988). These ameliorating effects on the microenvironment can favor the establishment of other plants (Bertness and Callaway 1994). Consequently, both negative and positive interactions may occur simultaneously, with the net effect depending on the temporal and spatial availability of resources and stresses. Under some conditions the negative effects of competition may dominate while under other conditions the positive effects of facilitation may dominate. This is apparently a common phenomenon in desert environments (Garcia-Moya and McKell 1970, Hunter and Aarssen 1988, Franco and Nobel 1989, Tongway and Ludwig 1990).

Importantly, this balance between competition and facilitation may be altered by grazing, probably in interaction with climate. Of particular interest for this study are the roles of defoliation and trampling. Heavy grazing and trampling, especially in dry years, may open up vegetated patches and impede establishment of palatable plants. In contrast, light grazing may not cause any change.

The basic assumption in our study is, if plant competition is the dominant interaction, new plant establishment should be negatively affected by the near proximity and size of the closest established plant. That is, as the sizes of established plants increase, distance to newly established plants should also increase. In contrast, if facilitation is the dominant interaction, new plant establishment should be positively associated with existing plants.

Both the type and strength of the relationship between existing focal plant size and newly established plants are probably not constant through time and between grazing treatments. For example, in dry periods, competition may increase because of decreased water availability, but, at the same time, facilitation may increase because an ameliorated microclimate may be even more critical during drought. Under this scenario, recruitment during dry periods may be more likely to be associated with vegetated patches than during wet periods, but these recruits that do establish in the open may be spaced farther from existing patches. In this study, we sought to determine whether potential competition or facilitation is the dominant interaction, and whether or not grazing and climate influence the balance between the two.

Overall, our objectives were to determine: 1) the degree to which plant distribution is clumped, or positively associated (evidence for facilitation), 2) whether or not a distance-size relationship exists between new plants and established focal plants (evidence for competition), 3) whether or not evidence for competition and/or facilitation varies across a temporal gradient of water stress, and 4) whether or not variation in competition and/or facilitation is related to grazing disturbance.

HO1: Recruitment of new plants in the shadscale community is independent of existing plants.

Predictions: If the hypothesis is true, 1) plants will be distributed at random and 2) plant size-distance relationships will not be detectable.

HO2: Plant interactions are constant across years.

Prediction: If the hypothesis is true, plant relationships will be independent of existing plants.

HO3: Plant interactions are constant for similar plant combinations across grazed and ungrazed pastures.

Prediction: If the hypothesis is true, plant relationships will be independent of sheep grazing.

Literature Review

Although negative plant interactions such as competition have been widely studied in ecology, the importance of positive plant interactions in the dynamics of plant communities has only recently been recognized in desert and other harsh environments (West and Tueller 1972, Hunter and Aarssen 1988, Franco and Nobel 1989, Bertness and Callaway 1994). Both positive and negative interactions appear to be common in these communities, and both must be considered.

Negative spatial associations may result from competition for resources. For instance, Gurevitch (1986) found that size and growth of the C_3 grass *Stipa mexicana* was significantly limited by competition from the perennial C_4 grass *Aristida glauca*. Studies of intraspecific nearest-neighbor companions in the Sonora Desert showed that competition was occurring among *Larrea tridentata*, *Franseria deltoidea,* and other desert plants, while interspecific competition was less common. The authors suggested that vertical separation of root systems was the mechanism through which interspecific competition is reduced (Yeaton et al. 1977). Fonteyn and Mahall (1981) discussed results from a controlled removal experiment using the co-dominant species *Larrea tridentata* and *Ambrosia dumosa* in the Mojave Desert and reported, however, that interference between species was usually more intense than within species, and that interference occurs when water availability is low.

Competition also may interact with other stresses such as herbivory, too. Caldwell (1984) indicated that when competition from associated vegetation was removed by tilling within a 90-cm radius, defoliated plants produced 3 times the biomass of nondefoliated plants growing with full competition. These results clearly demonstrate that the ability of plants to respond to defoliation is not only determined by an inherent set of morpho-physiological characteristics, but also by competitive pressure from associated plants of the same or different species.

In contrast, Hunter and Aarssen (1988) and Bertness and Callaway (1994) pointed out that facilitation in desert environments may be common and related to habitat amelioration of consumer pressures and, especially, physical stresses by neighbors.

These interactions between plants in arid environments are related to the spatial distribution of resources. In dry areas, shrubs and associated vascular vegetation are usually located on hummocks of elevated microrelief called "islands of fertility" (Garcia-Moya and McKell 1970, West 1983). These shrub-dominated patches are thought to be essential to the delicate balance of the soil-plant system in desert environments. They are critically important for the availability of soil nutrients such as nitrates. Removal of shrubs from the patches is believed to trigger the loss of nutrients by leaching and eventually result in little chance of plant establishment in the spot (Garcia-Moya and McKell 1970). On the other hand, recruitment is thought to occur more frequently in vegetated or formerly vegetated clusters than in open spaces (West and Goodall 1986). For example, Gasto (1969) found higher seedling survival of *Atriplex confertifolia* and *Ceratoides lanata* when located adjacent to large individuals. Similar results are reported by Owens and Norton (1989, 1992) for *Artemisia tridentata*. According to West (1988), several factors, such as soil moisture, soil organic matter, microclimate, nutrients, etc., are more favorable for plant regeneration in vegetated spots in saltbush-dominated plant communities. He thinks that "these advantages ostensibly outweigh any competitive interactions" (West 1988, p. 220). Apparently, both negative biological activities (competition) and positive activities (elevated rates of nutrient cycling, germination, and establishment) are concentrated in these vegetated patches. Thus, they are the likely places to look for early signs of degradation (Tongway and Ludwig 1990).

In contrast, bare patches between clumps of vegetation in desert environments frequently constitute more than 30% of the total area and provide abundant space for plant establishment and growth with less competition. However, higher temperatures and wind lead to high rates of evaporation and, consequently, to a decrease in soil moisture and an increase in soil salinity. Similarly, wind and water erosion result in lower soil nutrient concentrations in open than in vegetated patches (Garcia-Moya and McKell 1970). However, mycrophytic crusts of the interspaces may alleviate some soil property problems (Loope and Gifford 1972, West and Skujins 1977, Marble 1990). These non-vascular organisms reduce soil erosion, contribute to the nitrogen input in the soil, increase infiltration, and may reduce sedimentation in bare patches when not disturbed by trampling or other disturbance.

Norton and Michalk (1978) did a preliminary study of bare patch dynamics to help explain the overall increase in plant cover from 4 to 11% after 40 years of sheep grazing at the DER. They found that only 5% of this increase in cover could be explained by occupancy of bare patches by new plants; the remaining 95% increase occurred in vegetated patches. It is likely that the few plants that established in the bare patches initiated the formation of new patches through the process of facilitated succession by ameliorating the initial harsh environment of the open ground and providing better conditions for later introductions. This result reinforces the thesis that spatial heterogeneity, particularly in the form of vegetated patches, plays an important role in plant establishment and function in desert ecosystems.

The balance between competition and facilitation interactions is probably altered by herbivore activity. Destruction or damage of adult plants and especially seedlings by small herbivores constitutes an important natural disturbance in desert ecosystems. For instance, small mammals, particularly rodents and rabbits, destroy seeds and seedlings (Brown and Heske 1990). For the DER, vegetation was estimated to support a population of rodents weighing about 1.12 kg/ha (Blaisdell and Holmgren 1984). The impact of rodents can be seen in exclosure studies. For example, a 12-year removal of kangaroo rats in the Chihuahua desert yielded significantly higher cover of tall grasses than with the exclusion of livestock (Brown and Heske 1990). Similarly, mouse and pocket gopher activities are frequently related to root injury (Holmgren and Basile 1959, Ferguson 1968, Anderson and Shumar 1986). Insects, lagomorphs, etc. pose an additional biotic threat to desert vegetation. For example, destruction or injury of bitterbrush seedlings is frequently related to grasshoppers (Acridae), caterpillars (Lepidoptera), Cicadidae, and other insect activity (Holmgren 1954, Ferguson et al. 1963, Anderson 1987). Because of the abundance of smaller herbivores, Miller et al. (1994) suggested that in presettlement times they may have had a larger impact on the population dynamics of the Intermountain sagebrush steppe than large herbivores. In general, small animals can inflict high adult and seedling mortality in localized areas, leading to the creation of open areas favorable for colonization by annuals. Thus, small herbivores can completely alter the competition-facilitation balance.

On the other hand, large herbivore grazing by domestic stock has played a major role in changing these communities, although the lack of relict areas impedes precise quantification (West 1988). Grazing can influence plant composition in a number of ways. Of interest here are effects on spatial patterns and the balance between competition and facilitation.

Although grazing is a complicated process varying in subtle ways among both grazer and grazed species (Briske 1991), plants under competition generally show greater decreases in biomass production and slower rates of recovery after defoliation than do plants without competition (Archer and Detling 1984, Mueggler 1972, Caldwell 1984). Through time, direct and indirect effects of grazing on plant growth and reproduction are reflected in plant population dynamics and on the spatial arrangement of the vegetation, and may cause directional changes in community structure and function (Archer and Smeins 1991), as well as in the spatial heterogeneity of the landscape.

Heavy grazing by livestock is also involved in the expansion or creation of patches. Trampling by livestock can lead to reduction of infiltration, and an increase in runoff resulting in erosion and loss of nutrients, potentially increasing spatial heterogeneity of the landscape. In contrast, moderate or light grazing may have very little effect, or none at all on the spatial patterns of plants, mainly because recruits beneath vegetation are less likely to be eaten and trampled as may happen to recruits established in open areas.

Materials and Methods

Plant Spatial Patterns

Eighteen grazed and their ungrazed companion plots were randomly selected from the total of 64 grazed and 64 ungrazed plots (27% of the population) for a total of 36 plots for each of 5 sampling dates.

The equivalent of a 1 × 1 ft (0.093 m^2) quadrat was placed 62 times along a continuous transect through each map, and the total number of plants present within each sample unit was counted. Because plots were only 5×20 ft (1.5×6.1 m), a straight line 62-ft transect could not be used. Instead, the transect was created by combining adjacent 1-ft^2 quadrats up the length of the plot, over 2 ft to the center, down the length, over 2 ft to the opposite edge, and then up the length. This left a 1-ft buffer between loops of the transect. Data were analyzed on a plot-by-plot basis for presence of clumped distributions using the variance/mean ratio as an index of dispersion (Ludwig and Reynolds 1988). If the index of dispersion is greater than 1 (the variance is greater than the mean), a clumped pattern is suspected (Ludwing and Reynolds 1988). In this study, we determined the degree of aggregation by testing for agreement between the number of plants per sample unit in the transect with a negative binomial distribution using the 5% probability level and χ^2 statistics (Ludwing and Reynolds 1988). With this test, values more than 1.1356 indicated a significantly clumped distribution.

To test for differences in plant spatial patterns across years, the Wilcoxon Scores (Rank Sums) with the NPAR1WAY SAS procedure were used. Later, to evaluate differences in spatial patterns by year, χ^2 tests were performed. In these tests, I assumed that clumped and unclumped plant distributions split equally in all sampling years. Continuous and discontinuous plant distributions were compared using χ^2 statistics.

As a measure of the tendency for plant replacement to preferentially occur in currently or formerly occupied sites (site fidelity), individual plants present on each census date in the same 1-ft^2 quadrat across the 5 sampling dates were summed and the variance/mean ratio was calculated for the summed abundances. An increase in the index of the accumulated total relative to any individual sampling year indicates that plant establishment tends to repeatedly occur in the same sites rather than in bare ground patches.

Considering only significantly clumped plots, we evaluated the effects of grazing treatments and time on the degree of clumping with a repeated measures design with the variance/mean ratio as the response variable. The Proc Mixed Procedure of the SAS statistical package was used for this analysis.

Plant Relationships

Because we are primarily interested in establishment, I modified previous methods for size-distance relationships of neighbors (Pielou 1960, 1961; Yeaton and Cody 1976; Gutierrez and Fuentes 1979) by assessing the relationship between the distance of a newly established plant and the size of the nearest established focal plant. In this study, I closely followed the methodology detailed by Welden et al. (1988).

Focal plants considered were the shrubs *Atriplex confertifolia* (ATCO), *Ceratoides lanata (CELA),* and *Artemisia spinescens* (ARSP). Recruit species considered were the same shrub species as well as the grasses *Sporobolus* *cryptandrus* (SPCR), *Oryzopsis hymenoides* (ORHY), and *Hilaria jamesii* (HIJA), as well as the combined category of "grass." This grass category in addition to the above grasses included the perennials *Sitanion hystrix* and *Aristida purpurea*. The actual plant combinations of recruit and existing individuals analyzed across grazing treatment and time were limited by the availability of a sufficiently large sample size extracted from the 128 plots mapped at each of the 5 sampling dates. All combinations with less than 28 observations were discarded from the analysis. Table 13 shows the sample sizes for all potential interspecific and intraspecific combinations extracted from the mapped plots for this study. The variables used in the analysis were:

1. Size of the focal plant, obtained by adding the 1/100 ft^2 (9.3 cm^2) cells on the grid paper of the plot map corresponding to the canopy area of each individual plant.

2. Distance between the centers of the canopy areas of the focal plant and of the newly established plant measured with a dividcus and using the grid of the map for scale. The unit of measurement was 0.1 ft.

Plants located nearer to a plot boundary than to an appropriate neighbor individual were not included. Additionally, no measurements were made when other plant species not considered in this study were found between a potential existing plant-recruit combination. In grass species that reproduce vegetatively, such as HIJA, it was difficult to identify individual plants. In these cases,

Table 13. Sample size for the study of plant relationships. The first species of the column plant combinations is the recruit and the second is the existing focal plant. Bolded numbers indicate sample sizes sufficient to be included in the analysis.

Plant combinations	1958 grazed	1958 ungra.	1969+ 1975 grazed	1969+ 1975 ungra.	1994 grazed	1994 ungra.
1. ATCO-ATCO	**59**	**53**	**30**	21	16	15
2. ARSP-ATCO	19	25	22	**38**	**29**	**31**
3. CELA-ATCO	**36**	24	**28**	23	13	3
4. GRASS-ATCO	**51**	**36**	**99**	**70**	**93**	**49**
4.1 HIJA-ATCO	18	9	11	16	13	2
4.2 SPCR-ATCO	18	12	**60**	**35**	23	11
4.3 ORHY-ATCO	14	9	22	18	**44**	**31**
5. ARSP-ARSP	6	15	20	25	15	**38**
6. ATCO-ARSP	16	7	5	15	2	6
7. CELA-ARSP	5	3	7	10	0	18
8. GRASS-ARSP	12	18	27	**94**	**39**	**77**
8.1 HIJA-ARSP	5	2	19	8	4	13
8.2 SPCR-ARSP	7	5	2	**58**	**30**	9
8.3 ORHY-ARSP	0	6	5	23	16	**30**
9. CELA-CELA	**45**	**48**	**50**	**37**	**28**	26
10. ATCO-CELA	**57**	**45**	23	10	20	5
11. ARSP-CELA	4	**33**	16	27	17	**101**
12. GRASS-CELA	**35**	**59**	**120**	**146**	**131**	**89**
12.1 HIJA-CELA	12	**28**	18	25	17	18
12.2 SPCR-CELA	13	18	**69**	**81**	**31**	17
12.3 ORHY-CELA	7	11	27	26	**75**	**47**

measurements were determined for the centroid of the grass clump closest (single shoots or seedlings were not considered) to the focal plant.

In CELA, individual plants were identified by following the plant units mapped through time across the census dates. Nonetheless, because of the multi-stemmed growth habit of CELA, I could not always be sure if a mapped plant was one genetic individual or a clump of different individuals, or if an individual identified as new was in fact the remnant of an old CELA plant. I am confident that such errors were rare, however.

Because of constraints on suitable samples combined with the small number of new plants recruited in the 1969 and 1975 sampling dates, sample sizes for those years were seriously limited. Therefore, we combined the 1969 and 1975 samples. This was justified because: 1) these have the shortest study intervals of all the study periods (11 and 6 years) and together make a shorter interval than some others, and 2) they both had a below-average precipitation regime.

Because normal probability plots showed non-normality for the dependent and independent variables, log transformations were used to improve normality. Outliers were investigated by checking the spreadsheets for errors and by consulting the vegetation charts if necessary.

I calculated regressions according to the model:

$\text{distance}=a+b(\text{plant size})+\epsilon$

where distance is the distance separating the neighbors, a is the y-intercept, b is the slope of the regression line, plant size is the canopy area of the focal plant, and ϵ is the residual error.

Although in most size-distance relationships either variable can be viewed as the biological cause of the other, I used distance as the dependent variable and size of the focal plant as the independent variable. I believe this is a more likely cause-and-effect relationship when considering the recruitment of new individuals around existing adults. This yields a regression line that provides an estimate of the intensity of competition (Welden et al. 1988). For example, relative to a shallow line, a steeper line indicates that an equivalent increase in size yields a greater increase in spacing. Although a significant size-distance regression with a positive slope indicates competition, this significance does not indicate the mechanism by which plants suppress their neighbors or whether or not competition is actually occurring (Harper 1961). This approach adds insight, but additional experiments are necessary to address mechanisms of spacing. Similarly, the coefficient of determination and /or correlation coefficient represent the importance of competition (Yeaton and Cody 1976, Welden et al. 1988). The larger the coefficients, the more variance in distance is explained by plant size alone and, thus, presumably by competition.

When significant relationships were found for both grazed and ungrazed treatments, an analysis of covariance by interval with plant size as the covariate was used to test if significant differences existed between the slopes of the regression lines corresponding to the grazed and ungrazed treatments. The

Proc Mixed Procedure of the SAS statistical package was used in this analysis. Similarly, to detect differences in the importance of competition, a χ^2 test was applied to the correlation coefficients for a given significant species combination (Welden et al. 1988, Edwards 1984).

Results

Plant Spatial Patterns

Comparing the proportions of clumped and unclumped plots across years, the Wilcoxon Scores (Rank Sums) test showed significance, suggesting that clumped and unclumped patterns are not equally distributed across years (p=0.0119; Table A39). Overall, 59% of the total plots showed clumped distributions and the remaining 41% had random or, possibly in some cases, regular distributions (Table 14). At the beginning of the experiment in 1935, 61% (22/36) of plots showed clumped distributions. From that point they steadily decreased to a low of 50% (18/36) for the dry period in 1975, and then rose to a high of 75% (27/36) in 1994 during the wet period (Table 14, Fig. 48). Comparisons by sampling dates between clumped and unclumped distributions only showed significant results for the 1994 wet year, with more clumped than unclumped plots (χ^2=9.0000, df=1, p=0.0027, Fig 48, Table 14). This suggests wet periods tend to promote clumping more than dry years. Although other years are not significant, the general trend is the drier the interval, the fewer clumped distributions.

The χ^2 statistic used to test grazing effects on plant distributions yielded no significant results for any individual sampling date. We conclude that grazing was not important in determining plant distributions (all $p>0.317$; Table A40).

Additionally, no significant difference was found between grazed and ungrazed plots in the proportion of continuous and discontinuous plant distributions across years ($\chi^2=0.148$, $p\geq0.700$, df=1, Table 15; Table A41). On the other hand, only 25% of the plots presented a constant aggregated distribution through time (Table 15). This result suggests grazing did not affect the temporal dynamics of clumping. In contrast to individual sampling dates, the sum of all plants found in a plot across all 5 dates yielded 97% clumped distributions, suggesting that plant replacement is occurring consistently in the same area.

In a second stage of analysis, after determining which plots were clumped, we analyzed the clumped plots to see if the degree of clumping (i.e., the variance/mean ratio) changed across years or by grazing treatment. The results of the repeated measures ANOVA support the major conclusions above. Only the main effect of time ($p=0.0290$, df=4, Fig. 49; Table A42) was significant. Significance was due to the comparison between 1975 and 1994 ($p=0.0362$), which corresponds to the change from the driest to the wettest study periods.

Table 14. Precipitation class and number of plots with clumped (C) and unclumped (U) distributions by grazing treatment and by total (n=36 by year).

Precip. Year	Average 1935		Average 1958		Dry 1969		Driest 1975		Wet 1994		Totals	
	C	U	C	U	C	U	C	U	C	U	C	U
Grazed	10	8	9	9	8	10	9	9	13	5	49	41
Ungrazed	12	6	11	7	11	7	9	9	14	4	57	33
Total	22	14	20	16	19	17	18	18	27	9	106	74

Total sample size 180

% Clumped 59 (106/180)

% Unclumped 41 (74/180)

Table 15. Frequency of continuous and discontinuous plant distributions across 5 sampling dates. Continuous means all 5 years had clumped distributions, while discontinuous means at least one period had a distribution other than clumped.

Treatments	Continuous		Discontinuous	
	n	%	n	%
Grazed	5	28	13	72
Ungrazed	4	22	14	78
Total	9		27	
%	25		75	

Grazed and ungrazed treatments do not differ in the frequency of continuous and discontinuous plant distributions across years ($p \geq 0.700$).

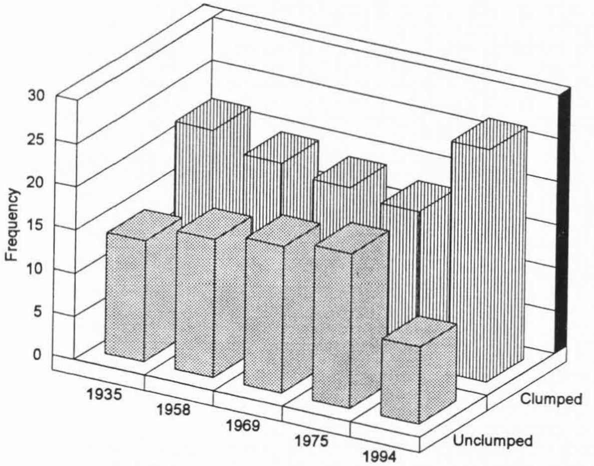


Fig. 48. Frequency of clumped and unclumped plots across years at the DER.

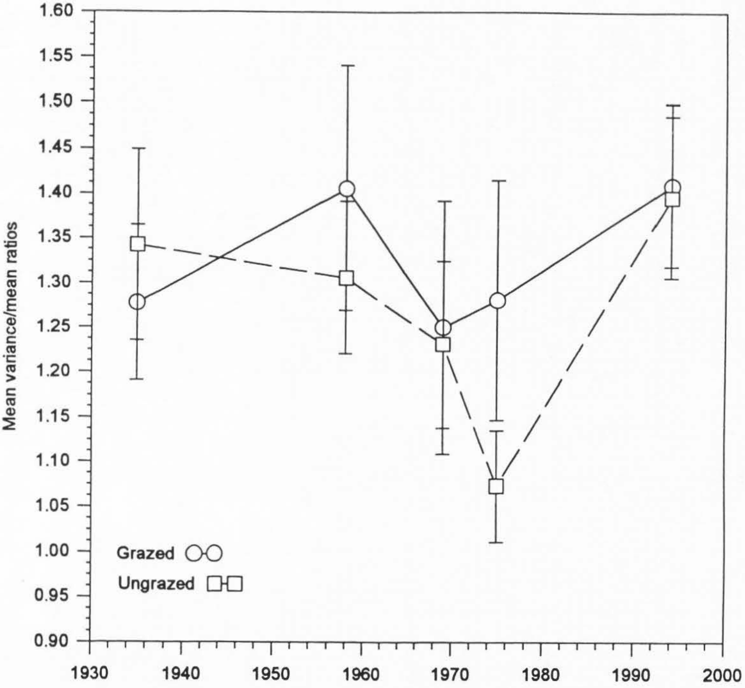


Fig. 49. Dynamics of the intensity of aggregated plant distribution for grazed and ungrazed plots for 5 sampling dates. Each point is the average of 18 variance/mean ratios.

Plant Relationships

Average climatic period (1935-58)

Significant regressions were frequent. In grazed pastures, significant and positive size-distance relationships were detected between existing ATCO focal plants and newly recruited ATCO (p=0.0002, Table 16), CELA (p=0.0051), and GRASS (p=0.0008) individuals in the grazed pastures. Of the two ungrazed treatment combinations analyzed for ATCO, only the GRASS-ATCO regression was significant (p=0.0001) .

By considering the focal species CELA, all three tested grazing treatment combinations showed significant relationships (CELA-CELA, p=0.00037; ATCO-CELA, p=0.0008; GRASS-CELA, p=0.0094; Table 16). Of the four plant combinations tested for the ungrazed treatment, only ATCO-CELA (p=0.0090) and GRASS-CELA (p=0.0001) were significant. The only combination analyzed for individual grass species was HIJA-CELA for the ungrazed treatment, and this combination was significant (p=0.0006).

Sample sizes were insufficient to consider ARSP as a focal species.

For those combinations significant in both grazing treatments, GRASS-ATCO, ATCO-CELA, and GRASS-CELA, analyses detected no significant differences in slopes (all $p \geq 0.3600$, Table 17; sample analysis using GRASS-ATCO grazed versus ungrazed is presented in Table A43). Similarly, χ^2 tests detected no significant differences in correlation coefficients (all $p \geq 0.0798$, Table 17).

Table 16. Coefficients of log transformed regressions of distance between neighbors on the canopy area of the established focal plant in grazed and ungrazed plots for the year 1958, sample size, and range of interplant distance in ft. Under the species combinations column the first code refers to the recruit species, the second to the existing focal species.

Species Combinations	Trt.	n	Dist.Range 0.1 ft*	r^2	r	Slope	p
1. ATCO-ATCO	G	59	3.1-12.0	0.21	0.46	0.18	0.0002
	U	53	3.5-16.0	0.03	0.18	0.08	0.1995
2. CELA-ATCO	G	36	2.9-11.1	0.21	0.46	0.20	0.0051
	U	-	-	-	-	-	-
3. GRASS-ATCO	G	51	1.8-14.0	0.20	0.43	0.19	0.0008
	U	36	2.3-15.0	0.48	0.69	0.33	0.0001
4. CELA-CELA	G	45	2.9-20.0	0.18	0.42	0.20	0.0037
	U	48	2.3-20.0	0.05	0.23	0.13	0.1211
5. ATCO-CELA	G	57	2.9-19.0	0.19	0.45	0.15	0.0008
	U	45	2.6-16.0	0.15	0.39	0.22	0.0090
6. ARSP-CELA	G	-	-	-	-	-	-
	U	33	2.9-13.2	0.01	0.08	0.03	0.6775
9. GRASS-CELA	G	35	0.9-12.0	0.19	0.43	0.29	0.0094
	U	59	0.4-13.1	0.24	0.49	0.29	0.0001
9.1 HIJA-CELA	G	-	-	-	-	-	-
	U	28	1.5-11.0	0.37	0.61	0.33	0.0006

*0.1 ft= 3.048 cm.

Table 17. Slope and r comparisons between grazed and ungrazed treatments for different species combinations (1958).

Species Combination	Year	Grazed n	Ungra. n	Slope P	r χ^2	P
1. GRASS-ATCO	1958	51	36	0.3600	2.9454	0.0861
2. ATCO-CELA	1958	57	45	0.5610	0.1051	0.7457
3. GRASS-CELA	1958	35	59	0.6664	3.0672	0.0798

Considering only significant regressions, the r^2 coefficients range from 0.15 (ungrazed ATCO-CELA) to 0.48 (ungrazed GRASS-ATCO) and the slopes from 0.15 (grazed ATCO-CELA) to 0.33 (ungrazed GRASS-ATCO, Table 16). The nearest distance between new recruits and focal plants was 0.04 ft in the ungrazed GRASS-CELA, while the greatest was 2 ft in the grazed and ungrazed CELA-CELA combinations. In general, the values of the coefficients and slopes can be viewed as moderate if we consider that biological data from field experiments are highly variable and dependent on more than one (generally uncontrolled) factor.

Dry/Driest Climatic Period (1958-75)

Of three tested plant combinations including ATCO as the focal species in the grazed treatment, only CELA-ATCO ($p=0.0182$) and GRASS-ATCO ($p=0.0001$) were significant (Table 18). In the ungrazed pastures, both ARSP-ATCO ($p=0.0011$) and GRASS-ATCO ($p=0.0372$), the only combinations tested, were significant (Table 18). The only two combinations with ARSP as a focal species, GRASS-ARSP and SPCR-ARSP, were tested in the ungrazed pastures, and were significant (all $p \leq 0.0002$). Intraspecific CELA-CELA ($p=0.0011$) and interspecific GRASS-CELA ($p=0.0001$) combinations were significant in ungrazed pastures, but not in the grazed companions (Table 18). By considering specific grass species, the only SPCR-CELA combination tested in the grazing and ungrazed treatments was significant (Table 18).

Table 18. Coefficients of log transformed regressions of distance between neighbors on the canopy area of the established focal plant in grazed and ungrazed plots for the year 1975, sample size, and range of interplant distance in ft. Under the species columns column the first code refers to the recruit species, the second to the existing focal species.

Species Combinations	Trt.	n	Dist.Range 0.1 ft*	r^2	r	Slope	P
1. ATCO-ATCO	G	30	2.9-18.0	0.11	0.33	0.14	0.0747
	U	-	-	-	-	-	-
2. ARSP-ATCO	G	-	-	-	-	-	-
	U	38	3.0-11.0	0.27	0.51	0.15	0.0011
3. CELA-ATCO	G	28	4.1-18.0	0.20	0.44	0.20	0.0182
	U	-	-	-	-	-	-
4. GRASS-ATCO	G	99	1.9-13.0	0.16	0.40	0.16	0.0001
	U	70	1.0-14.0	0.06	0.25	0.11	0.0372
4.1 SPCR-ATCO	G	60	2.0-10.2	0.26	0.51	0.17	0.0001
	U	35	0.5-9.7	0.12	0.35	0.15	0.0380
5. GRASS-ARSP	G	-	-	-	-	-	-
	U	94	1.0-15.0	0.14	0.37	0.19	0.0002
5.1 SPCR-ARSP	G	-	-	-	-	-	-
	U	58	2.3-10.1	0.28	0.53	0.23	0.0001
6. CELA-CELA	G	50	2.9-12.0	0.07	0.26	0.10	0.0691
	U	37	3.0-11.0	0.27	0.52	0.15	0.0011
7. GRASS-CELA	G	120	1.5-15.0	0.02	0.16	0.06	0.0855
	U	146	1.1-11.1	0.11	0.33	0.13	0.0001
7.1 SPCR-CELA	G	69	1.9-12.5	0.08	0.29	0.14	0.0165
	U	81	1.1-11.1	0.10	0.32	0.11	0.0041

*0.1 ft= 3.048 cm.

The closest distance between plants was 0.05 ft in the ungrazed SPCR-ATCO and the largest distance was 1.8 ft for the ATCO-ATCO and CELA-ATCO combinations. The analysis of significant regressions for the grazed and ungrazed GRASS-ATCO, SPCR-ATCO, and SPCR-CELA combinations yielded no significant results for differences in slopes (all $p \geq 0.1329$, Table 19), or in r coefficients (all $p \geq 0.2907$). These results suggest, in general, that importance and intensity of competition were independent of grazing during the dry period.

For significant regressions, the ranges of coefficients of determination were from 0.06% (ungrazed GRASS-ATCO) to 0.27% (ungrazed ARSP-ATCO, Table 18) and for slopes from 0.11 to 0.20. These values were lower than in 1958.

Wet Climatic Period (1975-94)

In grazed pastures, the focal species ATCO was significantly related to GRASS ($p=0.0168$) and ORHY ($p=0.004$, Table 20). The ungrazed pastures yielded significant relationships for both ARSP-ATCO ($p=0.0446$) and GRASS-ATCO ($p=0.0168$). The remaining 2 regressions, one in the grazed and the other

Table 19. Slope and r comparisons between grazed and ungrazed treatments for different species combinations (1975).

Species		Grazed	Ungra.	Slope	r	
Combination	Year	n	n	p	χ^2	p
1. GRASS-ATCO	1975	99	70	0.5874	1.1164	0.2907
2. SPCR-ATCO	1975	60	45	0.6274	0.6931	0.4051
3. SPCR-CELA	1975	69	81	0.1329	0.0389	0.8435

Table 20. Coefficients of log transformed regressions of distance between neighbors on the canopy area of the established focal plant in grazed and ungrazed plots for the year 1994, interplant distance in ft, and sample size. Under the species combination column the first code refers to the recruit species the second to the existing focal species.

Species Combinations	Trt.	n	Dist.Range 0.1 ft*	r^2	r	Slope	p
1. ARSP-ATCO	G	29	2.5-16.1	0.13	0.36	0.14	0.0534
	U	31	2.6-10.2	0.13	0.36	0.14	0.0446
2. GRASS-ATCO	G	93	1.4-13.8	0.06	0.25	0.12	0.0168
	U	49	1.7-11.4	0.11	0.36	0.14	0.0183
2.1 ORHY-ATCO	G	44	1.9-9.5	0.19	0.43	0.19	0.0040
	U	31	1.7-8.7	0.01	0.05	0.02	0.7733
3. ARSP-ARSP	G	-	-	-	-	-	-
	U	38	3.0-9.9	0.38	0.61	0.22	0.0001
4. GRASS-ARSP	G	39	1.9-14.5	0.20	0.44	0.27	0.0046
	U	77	1.4-11.0	0.06	0.24	0.12	0.0370
4.1 SPCR-ARSP	G	-	-	-	-	-	-
	U	30	2.3-10.1	0.05	0.22	0.09	0.2459
5. ARSP-CELA	G	-	-	-	-	-	-
	U	101	1.0-11.0	0.10	0.31	0.12	0.0016
6. GRASS-CELA	G	131	0.8-12.3	0.05	0.21	0.12	0.0140
	U	89	0.9-15.0	0.19	0.43	0.23	0.0001
6.1 SPCR-CELA	G	31	2.3-12.3	0.04	0.20	0.10	0.2588
	U	-	-	-	-	-	-
6.2 ORHY-CELA	G	75	1.5-15.0	0.01	0.12	0.05	0.3126
	U	47	1.2-9.0	0.11	0.33	0.20	0.0220

*0.1 ft= 3.048 cm.

in the ungrazed treatment, were not significant.

Of the 3 ungrazed combinations tested considering ARSP as the focal plant, only ARSP and GRASS were significant (all $p \leq 0.0370$). Recruits of GRASS were related to ARSP in the grazed pastures (p=0.0046, Table 20)

Considering CELA as focal plant, significant combinations were: in the grazed treatment, GRASS-CELA (p=0.0140, Table 20), and in the ungrazed treatment, ARSP-CELA (p=0.0016), GRASS-CELA (p=0.0001), and ORHY-CELA (p=0.0220).

In contrast to previous years, the range of distance between plants apparently decreased in 1994, the lowest value was 0.08 ft for the grazed GRASS-CELA, and the highest 1.6 ft for the grazed ARSP-ATCO combination.

The significant combinations in 1994 showed a high variability with coefficients of determination ranging from 0.06% for the GRASS-ATCO to 0.38% for the ungrazed ARSP-ARSP combination. Significant slopes were less variable; the lowest value was 0.12 for 4 regressions and the highest value was 0.27 for the GRASS-ARSP grazed combination.

GRASS-ATCO slopes (p=0.9322, Table 21) and r coefficients (p=0.5033) were not different. Grazed and ungrazed regressions for the GRASS-ARSP combination differed significantly in slopes (p=0.0301, Table 21), but not in r coefficients (p=0.2631), suggesting that only the intensity of competition was significantly greater in the grazed than in the ungrazed treatment. As with GRASS-ATCO, grazed and ungrazed regressions for the GRASS-CELA

Table 21. Slope and r comparisons between grazed and ungrazed treatments for different species combinations (1994).

Species		Grazed	Ungra.	Slope	r	
Combination	Year	n	n	p	x^2	p
1. GRASS-ATCO	1994	93	49	0.9322	0.4479	0.5033
2. GRASS-ARSP	1994	39	77	0.0301	1.2523	0.2631
3. GRASS-CELA	1994	131	89	0.9793	3.1306	0.0768

combination were not different in slopes (p=0.9793, Table 21) and in r coefficients (p=0.0768).

Trends in Importance and Intensity of Competition

Although statistical tests would not be valid, insight can be gained from changes in indices through time and among treatments, life forms, and species within and among years. In general, considering only significant regressions, the mean of both the importance and intensity of competition decreased from 1958 to 1994 (Table 22).

Except in the dry interval, ungrazed treatments showed generally higher values than grazed treatments (Table 22). By vegetation type, shrub-shrub combinations yielded more constant results across years than grass-shrub combinations, suggesting that competition has been more dynamic in the grass-shrub combination. For ATCO, the importance and intensity of competition tended to decrease from 1958 to 1994 (Table 22), apparently reflecting the decreasing importance of ATCO in the dynamics of the plant community. CELA followed a similar, though less clear pattern. ARSP values increased from 1975

Table 22. Importance and intensity of interference values for grazed and ungrazed pastures at the DER. Empty cells correspond to either insufficient sample sizes combinations for analysis or nonsignificant relationships.

		Importance of interference Coefficients of determination			Intensity of interference Slopes		
Combinations	TRT	1958	1975	1994	1958	1975	1994
ATCO-ATCO	G	0.21	-	-	0.18	-	-
	U	-	-	-	-	-	-
CELA-ATCO	G	0.21	0.20	-	0.20	0.20	-
	U	-	-	-	-	-	-
GRAS-ATCO	G	0.20	0.16	0.06	0.19	0.16	0.12
	U	0.48	0.06	0.11	0.33	0.11	0.14
ARSP-ATCO	G	-	-	-	-	-	-
	U	-	0.27	0.13	-	0.15	0.14
CELA-CELA	G	0.18	-	-	0.20	-	-
	U	-	0.27	-	-	0.15	-
ATCO-CELA	G	0.19	-	-	0.15	-	-
	U	0.15	-	-	0.22	-	-
ARSP-CELA	G	-	-	-	-	-	-
	U	-	-	0.10	-	-	0.12
GRAS-CELA	G	0.19	-	0.05	0.29	-	0.12
	U	0.24	0.11	0.19	0.29	0.13	0.23
ARSP-ARSP	G	-	-	-	-	-	-
	U	-	-	0.38	-	-	0.22
GRAS-ARSP	G	-	-	0.20	-	-	0.27
	U	-	0.14	0.06	-	0.19	0.12
TOTAL	Mean	0.23	0.17	0.14	0.23	0.16	0.16
Grazed	Mean	0.20	0.18	0.11	0.20	0.18	0.13
Ungrazed	Mean	0.29	0.17	0.17	0.28	0.15	0.17
SHRUB-SHRUB	Mean	0.19	0.25	0.20	0.19	0.17	0.16
GRASS-SHRUB	Mean	0.28	0.12	0.11	0.28	0.15	0.17
ALL-ATCO	Mean	0.28	0.14	0.10	0.23	0.16	0.13
ALL-CELA	Mean	0.19	0.19	0.11	0.23	0.14	0.16
ALL-ARSP	Mean	-	0.14	0.21	-	0.19	0.20

to 1994 for both the importance and intensity of competition (Table 22), perhaps reflecting the increasing importance of ARSP for the plant dynamics in the last study period (see Chapter 3).

Discussion and Conclusion

Plant Spatial Patterns

Evidence in this study suggests that patchiness is more apparent and more extreme in wet than in dry years. Similarly, Woodell et al. (1969) reported that in years with high rainfall, *Larrea divaricata* had clumped distributions and in dry years it was mainly regularly spaced. Perhaps increased water availability reduces competition, shifting the balance towards greater facilitation (such as increasing seedling establisment) for associated plants. Under this scenario, plants are able to take advantage of the resources of the "islands of fertility," leading to greater plant establishment and growth in more dense stands. Our results of plant relationships (see below) also suggest, in general, that competition may be higher in dry years than in wet years.

Other evidence also suggests that spatial patterns are dynamic through time. A high percentage of plots (75%) showed discontinuity in plant distribution across years, revealing that spatial plant patterns are highly dynamic at small scales of observation. This also suggests that extrapolation of measurements of plant distribution through time is not appropriate in the shadscale plant community because it is not constant.

There was consistency through time in where plants recruit. The total sum of plants across 5 sampling dates yielded many more aggregated distributions than did any single year. This is a clear indication that plant establishment is repeatedly occurring where plants either are or were previously present, but not in open areas. With a different analysis, Norton and Michalk (1977) came to the same conclusion. Plant establishment is not a random process, but rather is associated with specific locations that are probably more favorable for plant establishment and growth (Gasto 1969; Norton and Owens 1989, 1992; Hunter and Aarssen 1988; Bertness and Callaway 1994). This means that on average only about 7% of the total area is generally responsible for recruitment while the remaining 93% of the area is only occasionally used by perennial plants. These results confirm the importance of the "resource islands" mentioned by several authors and demonstrate that beneficial plant-plant relationships are important in these arid environments (Garcia-Moya and McKell 1970; Norton and Michalk 1978; West 1983, 1988; Hunter and Aarssen 1988; Tongway 1990; Bertness and Callaway 1994). I cannot, however, rule out the importance of seed accumulation in vegetated patches (Chambers and MacMahon 1994).

In contrast to temporal variation, there is little evidence that grazing has an impact on spatial patterns. This supports Bertness and Callaway's (1994) assertion that in stressful physical environments alleviation of stress rather than of hervibore pressure is the major advantage plants gain by growing in the presence of other plants.

As already discussed, variability in plant distributions across years is complex. As noted above, it is partly related to climatic changes, but apparently not to grazing. Plant distribution dynamics apparently are linked to other important factors such as plant cover and plant density dynamics. When graphically compared (Fig. 50), total plant cover and frequency of patchiness curves follow opposite directions; when cover increases, patchiness decreases. From previous chapters, we know that in the first study period (1935-58) small individuals dominated the plant community. Small plants are able to establish close to each other, increasing the presence of patches, while large plants tend to remain widely separated. Thus, as the community "matured," cover increased while the presence of patches decreased; conversely, random and/or uniform patterns increased. In the last study period (1975-94), which corresponds climatically to a wet period, numerous large shrubs died (Chapter 4). This mortality was linked to the establishment of numerous new small plants (see seedling emergence and establishment section). As a result, patchiness increased as total cover decreased. This interpretation is supported by plant density changes (Chapter 4) (Fig. 50). Clearly, the density curve follows the same direction as the patch curve.

Plant Relationships

Significant positive relationships between distance to newly established plants and the size of established focal plants were found in 25 of 32 analyzed

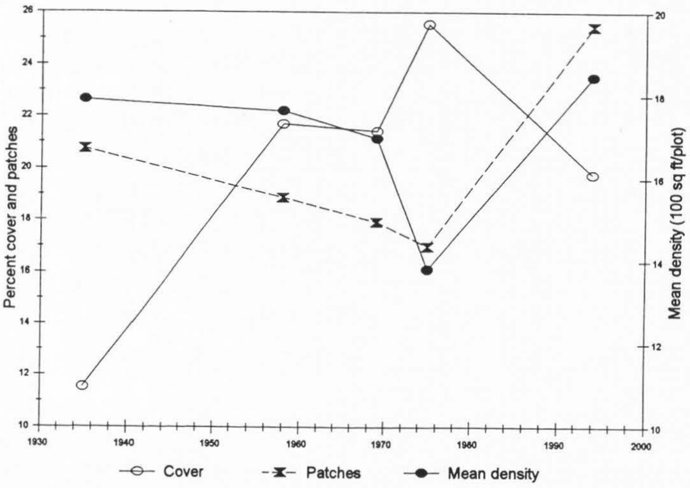


Fig. 50. Dynamics of canopy cover (%), percent of plots with aggregated distribution and mean density across years at the DER.

plant combinations, suggesting that competition from existing plants limits where new plants can recruit. It is difficult to prove, however, that these significant regressions are caused by competitive relationships between neighbors. There are other possible mechanisms in addition to competition that can lead to these spatial patterns of the plant community (Wiens 1977, Connell 1983, Welden et al. 1988). For example, disturbance, seed dispersal, asexual reproduction, local history, environmental heterogeneity, allelopathy, seed predation, herbivory, and spread of disease may all contribute to the patterns. The finding of significant size-distance regressions in every species combination, however, showed that these plants have been interacting, and that interference has a measurable intensity and importance and were interpreted to suggest that competition could be a factor affecting spatial relationships of plants in this community. As with spatial distributions, however, further study is necessary to determine the mechanisms involved. For now, we will simply refer to the process as competition, as have previous authors.

Despite the widespread evidence of competition, few cases showed high values for either importance or intensity of competition. In general, the data were interpreted to suggest that for the majority of the studied plant combinations that other sources of variation in determining plant establishment were large, and that the prevalence of "competition" as an agent of shadscale community structure is limited, as suggested by West (1988).

As with the analysis of patchiness, there is little evidence that grazing is altering the degree of competition. In only one case did grazing and non-grazing regressions differ and that case suggested that the intensity but not importance of competition between existing ARSP and recruited grasses was greater in grazed plots. ARSP was a better competitor in grazed than in ungrazed plots. Apparently this is related to the extraordinary increase of ARSP during the wet 1975-94 period. Under this condition indirect more than direct effects of grazing probably were important. Soil disturbance by trampling and other grazing activities may have favored seedling establishment and growth of ARSP. Under exceptionally good climatic conditions and moderate grazing, the palatable ARSP competed successfully with grasses.

Temporal Dynamics of Positive (i.e., Facilitation) and Negative (i.e., Competition) Interactions

Our data showed that both facilitation and competition processes operate simultaneously in the shadscale plant community (West and Tueller 1972) as in other plant communities (Bertness and Callaway 1994, Hunter and Aarssen 1988). Plant replacement in this study overwhelmingly occurred in vegetated patches, which were described as areas that ameliorate the harsh climate of a desert and provide more resources than open areas for plant establishment and growth (Garcia-Moya and McKell 1970; Norton and Michalk 1978; West 1983, 1988; Hunter and Aarssen 1988; Tongway 1990; Bertness and Callaway 1994). Competition mechanisms, however, determined how close plants can establish to existing plants. These determinants apparently changed with changes in climate. As previously mentioned, patchiness was more apparent and more extreme in wet than dry years. On the other hand, because of the numerous significant regressions reported in the results, competition cannot be negated as a factor of change in this plant community. Because of very many multiple comparisons made, some unknown significant regressions are probably due to chance alone. By using $p=0.05$, the probability to obtain 1 significant regression by chance is 1 in 20. On the other hand, the high frequency of significant regressions in relation to the total tests (25 significant regressions of 32 tests) suggests that significance is not only due to chance.

A clear pattern of the dynamics of intensity and importance of interference did not emerge across the 3 climatic regimes involved in this study. A tendency was present, however, toward highest coefficients of determination and slope values in the first study period, which was a climatically average period. From Fig. 50, we can see that the conditions for maximum competition--a combination of high density, high cover values, and moderately limited water resources (Chapter 2)--were perhaps present in 1958. Additionally, from the study of seedling location (Chapter 4) and plant fidelity, plants tended to establish close to each other, and the high density of recruits, as was the case during this recovery period, may increase the chances for competition. In fact, the highest average values for significant size-distance regressions of the 3 study periods occurred in 1958. The r^2 values, however, explained less than 23% of the variance, indicating that other sources of variation are large.

Importance and intensity of competition values were lower in dry/driest than in the first study period (means slope=0.17, and r^2=0.16). Cover, density, and degree of patchiness also changed, determining a new set of conditions. Higher cover (plant size) and lower density and patchiness suggested a wider spacing between plants, which eventually led to a decrease in competition. Under these conditions, competition may be less relevant than facilitation in determining plant establishment. In addition, in 1994 under favorable conditions (mean slope=0.16, and r^2=0.14), plants may have taken full advantage of the appropriate climatic conditions, competition was relaxed, and net interactions were positive. Cover and density were similar to 1958, but patches were more numerous. This was interpreted to suggest that once the stress of water scarcity was eliminated, plants tended to grow close to each other. This suggests, also, that plant size and density interact with climate in determining the degree of plant interactions. In general, then, positive and negative interactions operate simultaneously but they are not constant because they are dependent on not only climate, but also on the cover-density balance of the plant populations.

Grazing and Interference

Rasmussen and Brotherson (1986) reported strong competition between CELA and other plants in pastures released from heavy grazing. In this study, however, there is no strong evidence for the role of grazing in altering competitive relationships. The moderate grazing intensity may not have been sufficient to alter plant relationships. If grazing pressure is low, other grazing effects, such as trampling, may have little if any effect on plant spatial patterns. With low grazing pressure, the role of climate, environmental heterogeneity, and competition apparently is more important in determining the spatial structure and plant composition in the shadscale plant communities.

Conclusion

Environmental heterogeneity (patches) and climate interacting with competition are important factors in determining where plants establish. The results for this shadscale community do not support the importance of grazing in altering competitive relationships among plants. The generally low values for intensity and importance of competition and the little evidence on the effects of grazing on competitive relationships of plants suggest that under moderate grazing pressure and nongrazing conditions, negative plant interactions are low. Both competition and facilitation are variable and the variation is linked to climate and plant density, size, and cover across years. Nonetheless, it appears that positive interactions are more common and perhaps more important than negative interactions as suggested by West (1988) and others for desert environments.

CHAPTER 7

SYNTHESIS AND CONCLUSIONS

The general objective of this study was to determine if grazing affects plant community composition and structure, and if so, if it was mediated through changes in plant cover, plant recruitment and survival, and/or spatial interactions among species. To distinguish grazing effects, it was necessary to better understand the role of precipitation and spatial distributions in community dynamics. Because the focus was to study vegetation change from a multivariate approach, it is important to first justify the importance of such an approach, and then discuss the interactions among the variables and how they relate to vegetation change under grazing.

Justification for the Multivariate Approach

Grazing effects on the shadscale plant community are complex and difficult to isolate. Usually more than one factor is operating at any given time on the plant community, and the importance of any particular factor is not constant through time, but rather changes from a predominant to a subordinate role according to the circumstances.

The multiple sources of information used in this study are summarized in Fig. 51 with respect to their apparent impacts on the dynamics of the shadscale plant community under grazing. This complex control of vegetation change

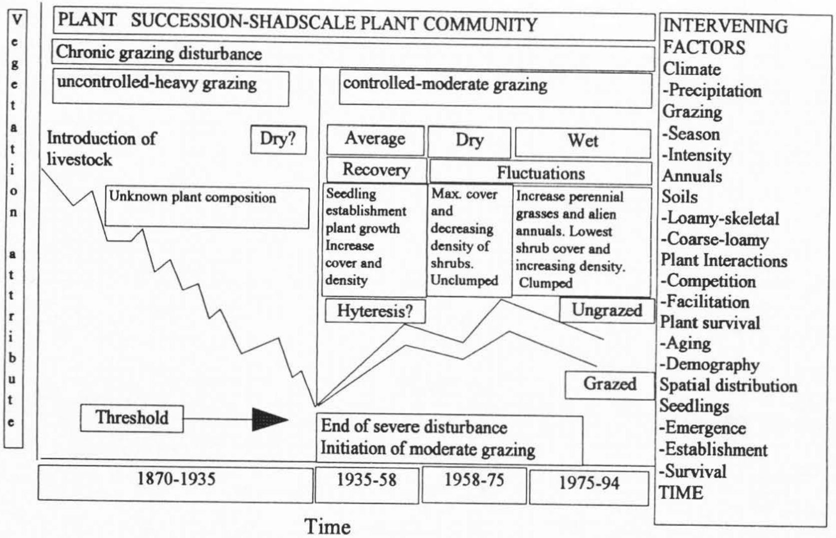


Fig. 51. Vegetation change and intervening factors in a shadscale plant community grazed by sheep at the DER. A multivariate approach to studyng plant dynamics.

supports the need for a multivariate approach that is justified by the following reasons.

First, not a single variable appears to satisfactorily explain the changes observed in the shadscale plant communities. Total plant cover suggested that grazing was not important, while individual species plant cover analyses indicated that grazing and season of grazing were influential for changes in ARSP and CELA. Long-term plant survival showed few significant results, and in general, soils did not dictate plant survival. Similarly, few significant effects of grazing on plant survival were found for all 3 shrubs investigated. The increase of annual plants was dramatic and positively correlated with changes in climate. Similarly, seedling recruitment was directly linked to precipitation, except for ATCO, while only CELA seedling and adult short-term survival were affected by grazing. Evidence suggests that both competition and facilitation occurred. The spatial distribution of plants showed primarily clumped distributions, suggesting facilitation, but both the frequency and degree of clumping were very dynamic in response mainly to climate but not to grazing. In contrast, plant-distance relationships showed low, variable values of competition with little dependence on grazing and with uncertain dependence on climate. All these factors have some degree of influence on the plant community, and this degree of importance changes according to the circumstances. It is very risky, then, to arrive at a general conclusion based only on the study of a single variable. For example, if conclusions were drawn only from the cover analysis presented in the first chapter, the conclusion would be that the ATCO population continued to decrease. However, data from plant and seedling survival analyses revealed that the number of ATCO individuals was actually increasing, despite of the decrease in plant cover. In plant community dynamics, not only changes in plant populations are important, but also changes in other components of the plant community.

Second, the multivariate approach is even more important in grazing studies where moderate grazing intensities are used (as in this study) because it is more difficult to determine grazing effects than when grazing experiments include heavy grazing. The influence of moderate grazing on ecosystem processes appears to be slight and subject to many and usually contrasting interpretations, such as the dilemma concerning whether grazing affects CELA (Norton 1978, Rasmussen and Brotherson 1986, Harper et al. 1990).

Third is the role of climate. A general outcome from this study is that temporal variation was considered greater than variation within a given period for the majority of the studied variables. Thus, climate is an important determinant of change, especially on ranges with moderate grazing. Consequently, potential subtle effects of light or moderate grazing can be overshadowed by strong climatic influences and related effects in the shadscale plant community, making it difficult to conclusively demonstrate grazing effects.

Therefore, the multivariate approach offers the possibility to overcome these limitations in long-term grazing studies in desert environments lacking clearly contrasting treatments. This approach should eventually provide information to identify critical determinants of community change and whether or not these determinants can be managed.

Vegetation Dynamics in the Shadscale Plant Community

Grazing in general and spring grazing in particular had a consistent effect on ARSP and discontinuous effects on CELA and other studied species. Overall, however, grazing apparently affected the rate more than the direction of community change. Although it was difficult to separate some grazing effects from other possible causes of change in this grazing experiment, the multivariate approach provided a means of isolating the effects of several intervening factors in the plant dynamics of this community (Fig. 51). No single factor can completely explain, however, why this plant community is changing in a given direction and at a given rate. In this scenario, the changes mediated by grazing become one more intervening factor, and sometimes with an almost insignificant role. Long-term grazing studies need to include highly contrasting grazing treatments such as heavy and no-grazing to better discriminate grazing effects on the vegetation.

The logical expectation of grazing effects in this long-term grazing experiment was partially equivocal because of the importance of climatic and inherent plants characteristics (mainly age and plant size) that emerged as important factors from the multivariate analysis of this study. The role of factors such as competition, facilitation, plant spatial patterns, annuals, and grazing interacting with climate were all moderately important for community change. Seedling recruitment and establishment clearly responded greater to climatic variation rather than grazing. Finally, other potential determinants of change such as soils and long-term plant survival appear to play a less obvious role in community dynamics than other factors.

The moderate to complete lack of grazing indirectly allowed recovery of both palatable and nonpalatable plants (except ARSP in grazed pastures). This apparently created the conditions for the decrease of ATCO through competition with these new plants. In fact, all but one interspecific plant combinations were significant for ATC0, suggesting that competition with neighbors was common although not strong for this species. Because ATCO was the major component of the plant community at the beginning of the experiment in terms of cover and density, then any change in ATCO is likely to have a strong influence on community dynamics.

The role of grazing in determining the survival of shrubs was minor, and the effects of soil types were even less important. Climate, interacting with plant age, and competition had a major role in determining plant survival of ATCO, CELA, and ARSP. This pattern occurred with little influence from grazing and mainly during dry years and during the recovery period from 1935 to 1958. Under favorable climatic conditions, the effects of grazing on plant survival were negligible.

In the short-term studies during the wet 1994-5 years, grazing did not affect survival of adult ATCO and ARSP but did affect CELA. CELA mortality was higher in grazed than in ungrazed pastures. Seedling establishment was more than 75% in all cases, while no significant effects of location and grazing were found on number of surviving seedlings except for CELA. Seedling recruitment of ATCO and ARSP was positively correlated with annual precipitation and CELA with winter precipitation. Grazing favored the recruitment of ATCO seedlings, and negatively affected the recruitment of ARSP seedlings.

Grazing effects were less obvious, however, in the plant spatial distribution study where changes in patterns roughly tracked climatic fluctuations. For example, more aggregated distributions in wet years as opposed to less aggregated distributions in dry years, coupled with higher intensity and importance of competition in dry than in wet years, suggest a strong climatic influence regardless of grazing. Similarly, it appears that facilitation mechanisms simultaneously operating in this plant community responded to climatic changes, and not to grazing. These results were interpreted to suggest a minimal role of moderate grazing in plant spatial dynamics.

Grazing effects detected in dry years, such as on CELA and ATCO in the plant cover study, were not present in the next wet period, suggesting that grazing effects are also dependent on climatic conditions. Thus, the idea of cumulative effects of moderate grazing on plant populations can be questioned because the change is not constant. This implies that management planning for changing plant communities may be very risky because it would be mainly based on climatic vagaries rather than controlled grazing pressures. However, the direct role of grazing for decreasing ARSP cannot be negated.

In conclusion, although some significant effects of moderate sheep grazing were found in several studied factors, they did not completely explain the observed changes. In general, moderate grazing, apparently interacting with climate and inherent plant attributes (shrub longevity, differential tolerance to climatic variables), was important in explaining the major changes (i.e., the shift from shrubby to grassy vegetation) in the shadscale plant community under study. Thus, management of moderate grazing pressures may play only a limited role in changing shadscale plant communities.

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APPENDIX

APPENDIX A

Table A1: Linear regression analysis for annual precipitation from 1935 to 1994.

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                         Robust Regression Report

Page                1
Database            E:\H\ADISERT\CHAPTER2\REGPRIP.S0
Time/Date           15:59:35 08-15-1996
Dependent           Precipitation (mm)

Regression Equation Section
Independent                  Regression   Standard  T-Value    Prob    Decision   Power
Variable                     Coefficient  Error     (Ho: B=0) Level    (10%)      (10%)
Intercept                    125.459      19.47513  6.4420    0.0000   Reject Ho  0.9999
Precipitation (mm)           0.5766394    0.288293  2.0002    0.05009  Reject Ho  0.6303
R-Squared                    0.063503

Regression Coefficient Section
Independent                  Regression   Standard  Lower     Upper     Standardized
Variable                     Coefficient  Error     90%C.L.   90%C.L.   Coefficient
Intercept                    125.459      19.4751   92.9142   158.003   0.00000
Time (1935-95)               0.5766394    0.28829   9.48E-02  1.0584    0.25199
T-Critical                   1.671093

Analysis of Variance Section
                                Sum of     Mean                Prob       Power
Source                   DF     Squares    Square    F-Ratio   Level      (10%)
Intercept                1      1227633    1227633
Model                    1      4840.323   4840.323  4.0007    0.050090   0.630320
Error                    59     71381.51   1209.856
Total(Adjusted)          60     76221.84   1270.364

Root Mean Square Error          34.78299   R-Square  0.063503
Mean of Dependent Variable      163.0435   Adj R-Sq  0.047630
Coefficient of Variation        0.2133357
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Table A2: Example of matrix of original data for all species.

PLOTS	TIM	SEA	TRT	ATCO	ARSP	CELA	CHST	SPCR	STHY	HIJA	BOGR	SPGR	EPNE	GUSA	ARFE	BIKI	CAspp.	TESP	SIHY	OECA	ARFR	OTHERS	UNKNW
3U11	1	S	U	293.0	7.0	21.0	0.0	0.0	0.0	120.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3U12	1	S	U	625.0	23.0	24.0	0.0	5.0	4.0	34.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3U21	1	S	U	354.0	0.0	104.0	0.0	27.0	0.0	18.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3U22	1	S	U	395.0	0.0	48.0	0.0	7.0	0.0	93.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5U11	1	W	U	81.0	53.0	56.0	0.0	0.0	15.0	324.0	0.0	5.0	22.0	4.0	2.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0
5U12	1	W	U	703.0	123.0	43.0	0.0	14.0	0.0	1.0	0.0	2.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5U21	1	W	U	128.0	22.0	2.0	0.0	2.0	32.0	151.5	0.0	5.5	0.0	0.0	2.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5U22	1	W	U	497.0	41.0	0.0	0.0	39.5	2.0	0.0	0.0	6.0	96.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6U11	1	S	U	117.0	0.0	43.5	0.0	1.0	17.0	115.0	0.0	0.0	36.0	1.5	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5
6U12	1	S	U	46.0	18.0	40.5	0.0	4.5	11.0	0.0	0.0	0.0	56.0	2.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
6U21	1	S	U	117.0	22.0	0.0	0.0	12.0	80.0	14.0	0.0	3.0	0.0	17.0	47.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6U22	1	S	U	102.0	43.0	0.0	0.0	3.0	21.0	144.0	0.0	2.0	21.0	3.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10U11	1	S	U	138.0	136.0	0.0	0.0	15.0	11.0	0.0	0.0	1.0	0.0	0.0	3.0	113.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10U12	1	S	U	36.0	37.0	0.0	0.0	85.0	10.0	28.0	0.0	3.0	31.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10U21	1	S	U	149.0	0.0	0.0	0.0	147.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10U22	1	S	U	67.0	13.0	0.0	0.0	211.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	34.5	4.0	0.0	0.0	0.0	0.0	0.0	0.0
11U11	1	W	U	185.0	0.0	0.0	0.0	179.0	4.0	0.0	0.0	1.0	0.0	0.0	0.0	14.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11U12	1	W	U	64.0	35.0	0.0	0.0	124.0	6.5	0.0	0.0	5.0	0.0	0.0	0.0	23.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11U21	1	W	U	149.0	0.0	0.0	0.0	55.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11U22	1	W	U	152.0	0.0	0.0	0.0	79.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12U11	1	W	U	151.0	31.0	0.0	0.0	73.0	16.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0
12U12	1	W	U	232.0	51.0	0.0	0.0	32.0	5.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12U21	1	W	U	174.0	0.0	2.0	0.0	38.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12U22	1	W	U	773.0	4.0	0.0	0.0	20.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13U11	1	W	U	367.0	0.0	100.0	0.0	0.0	1.0	20.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13U12	1	W	U	714.0	28.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13U21	1	W	U	135.0	0.0	38.0	0.0	1.0	0.0	186.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13U22	1	W	U	146.0	4.0	120.0	0.0	0.0	7.0	35.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14U11	1	S	U	110.0	0.0	254.0	0.0	1.0	5.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14U12	1	S	U	241.0	1.0	53.0	0.0	0.0	0.0	77.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14U21	1	S	U	561.0	9.0	73.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14U22	1	S	U	452.0	5.0	175.0	0.0	0.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15U11	1	S	U	217.0	3.0	146.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15U12	1	S	U	236.0	0.0	150.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15U21	1	S	U	386.0	28.0	44.0	0.0	8.0	1.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15U22	1	S	U	251.0	3.0	86.0	0.0	0.0	0.0	20.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16U11	1	W	U	519.0	0.0	138.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16U12	1	W	U	171.0	0.0	153.0	0.0	7.0	3.0	117.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16U21	1	W	U	130.0	0.0	271.0	0.0	0.0	11.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16U22	1	W	U	251.0	0.0	162.5	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0
3G11	1	S	G	452.0	0.0	24.0	0.0	4.0	6.0	39.0	14.0	5.0	0.0	0.0	13.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3G12	1	S	G	165.0	16.0	57.0	0.0	13.5	7.0	0.0	0.0	1.0	0.0	0.0	0.0	4.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
3G21	1	S	G	1004.0	0.0	74.0	0.0	8.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3G22	1	S	G	324.0	0.0	51.0	0.0	2.0	0.0	54.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5G11	1	W	G	201.0	23.0	76.0	6.0	0.0	1.0	118.0	0.0	16.0	0.0	8.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5G12	1	W	G	110.0	33.0	20.0	0.0	0.0	2.0	0.0	0.0	2.0	0.0	7.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5G21	1	W	G	149.0	14.0	0.0	0.0	123.0	4.0	0.0	0.0	1.0	46.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5G22	1	W	G	96.0	88.0	0.0	0.0	4.0	6.0	14.0	0.0	6.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6G11	1	S	G	173.0	0.0	12.0	0.0	22.0	1.0	40.0	0.0	19.0	0.0	0.0	4.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table A3: Results of total plant cover analysis.

```
                              REML Estimation Iteration History
                      Iteration  Evaluations      Objective      Criterion
                              0            1  7629.4612201
                              1            1  7597.4219405     0.00000000
                                    Convergence criteria met.

                                Covariance Parameter Estimates (REML)
                 Cov Parm          Ratio        Estimate       Std Error        Z  Pr > |Z|
                 DIAG CS      0.22114216  11333.358400  2794.8343840     4.06    0.0001
                 Residual     1.00000000  51249.199333  3228.3961030    15.87    0.0001

                             Model Fitting Information for TOTAL COVER
                             Description                          Value
                             Observations                      640.0000
                             Variance Estimate                 51249.20
                             Standard Deviation Estimate       226.3829
                             REML Log Likelihood               -4377.64
                             Akaike's Information Criterion    -4379.64
                             Schwarz's Bayesian Criterion      -4384.09
                             -2 REML Log Likelihood            8755.284
                             Null Model LRT Chi-Square          32.0393
                             Null Model LRT DF                   1.0000
                             Null Model LRT P-Value              0.0000

                                      Tests of Fixed Effects

                            Source        NDF    DDF  Type III F  Pr > F
                            TRT             1    126       20.98  0.0001
                            TIME            4    504       88.28  0.0001
                            TRT*TIME        4    504        2.62  0.0345

                                Differences of Least Squares Means
Level 1         Level 2           Difference      Std Error    DDF        T  Pr > |T|  Adjustment      Adj P

TIME 35(A)      TIME 58(B)      -368.3882812   28.29785751    504   -13.02    0.0001  Bonferroni     0.0000

TIME 58(B)      TIME 69(C)         8.57031250  28.29785751    504     0.30    0.7621  Bonferroni     1.0000
TIME 69(C)      TIME 75(D)      -148.6640625   28.29785751    504    -5.25    0.0001  Bonferroni     0.0000
TIME 75(D)      TIME 94(E)       201.06406250  28.29785751    504     7.11    0.0001  Bonferroni     0.0000
TIME 35(A)      TIME 94(E)      -307.4179687   28.29785751    504   -10.86    0.0001  Bonferroni     0.0000
TRT G           TRT U           -118.9628125   25.97065548    126    -4.58    0.0001  Bonferroni     0.0000
TRT*TIME G A    TRT*TIME G B    -328.5000000   40.01921387    504    -8.21    0.0001  Bonferroni     0.0000
TRT*TIME G A    TRT*TIME G E    -221.2265625   40.01921387    504    -5.53    0.0001  Bonferroni     0.0000
TRT*TIME G A    TRT*TIME U A     -34.45781250  44.22335276    504    -0.78    0.4362  Bonferroni     1.0000
TRT*TIME G B    TRT*TIME G C      -4.03125000  40.01921387    504    -0.10    0.9198  Bonferroni     1.0000
TRT*TIME G B    TRT*TIME U B    -114.2343750   44.22335276    504    -2.58    0.0101  Bonferroni     0.4532
TRT*TIME G C    TRT*TIME G D    -118.0546875   40.01921387    504    -2.95    0.0033  Bonferroni     0.1497
TRT*TIME G C    TRT*TIME U C     -89.03125000  44.22335276    504    -2.01    0.0446  Bonferroni     1.0000
TRT*TIME G D    TRT*TIME G E     229.35937500  40.01921387    504     5.73    0.0001  Bonferroni     0.0000
TRT*TIME G D    TRT*TIME U D    -150.2500000   44.22335276    504    -3.40    0.0007  Bonferroni     0.0330
TRT*TIME G E    TRT*TIME U E    -206.8406250   44.22335276    504    -4.68    0.0001  Bonferroni     0.0002
TRT*TIME U A    TRT*TIME U B    -408.2765625   40.01921387    504   -10.20    0.0001  Bonferroni     0.0000
TRT*TIME U A    TRT*TIME U E    -393.6093750   40.01921387    504    -9.84    0.0001  Bonferroni     0.0000
TRT*TIME U B    TRT*TIME U C      21.17187500  40.01921387    504     0.53    0.5970  Bonferroni     1.0000
TRT*TIME U C    TRT*TIME U D    -179.2734375   40.01921387    504    -4.48    0.0001  Bonferroni     0.0004
TRT*TIME U D    TRT*TIME U E     172.76875000  40.01921387    504     4.32    0.0001  Bonferroni     0.0009

Total Plant Cover Dynamics      1935     1958    1969    1975    1994

Total Cover Means in 1/100 ft²  417      785     776     925     724

% Total Plant Cover              4.2      7.9     7.8     9.3     7.2
```

Table A4: Results of multivariate analysis of species cover.

```
Manova Test Criteria and F Approximations for the Hypothesis of no Overall TIME*GRAZE*SEASON
        Effect
          H = Type III SS&CP Matrix for TIME*GRAZE*SEASON   E = Error SS&CP Matrix

                                S=4    M=0.5    N=306.5

        Statistic                    Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda           0.98018220     0.5147        24  2146.689  0.9753
        Pillai's Trace          0.01990958     0.5152        24      2472  0.9752
        Hotelling-Lawley Trace  0.02012498     0.5144        24      2454  0.9754
        Roy's Greatest Root     0.01425243     1.4680         6       618  0.1867

Manova Test Criteria and F Approximations for the Hypothesis of no Overall TIME*GRAZE Effect
           H = Type III SS&CP Matrix for TIME*GRAZE   E = Error SS&CP Matrix
                                S=4    M=0.5    N=306.5

        Statistic                    Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda           0.90602865     2.5663        24  2146.689  0.0001
        Pillai's Trace          0.09571165     2.5250        24      2472  0.0001
        Hotelling-Lawley Trace  0.10180723     2.6024        24      2454  0.0001
        Roy's Greatest Root     0.07950395     8.1889         6       618  0.0001

Manova Test Criteria and F Approximations for the Hypothesis of no Overall TIME*SEASON Effect
           H = Type III SS&CP Matrix for TIME*SEASON   E = Error SS&CP Matrix
                                S=4    M=0.5    N=306.5

        Statistic                    Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda           0.95785487     1.1109        24  2146.689  0.3219
        Pillai's Trace          0.04256928     1.1080        24      2472  0.3251
        Hotelling-Lawley Trace  0.04355826     1.1135        24      2454  0.3188
        Roy's Greatest Root     0.03092250     3.1850         6       618  0.0044


Manova Test Criteria and Exact F Statistics for the Hypothesis of no Overall GRAZE*SEASON Effect
                       H = Type III SS&CP Matrix for GRAZE*SEASON   E = Error SS&CP Matrix

                                S=1    M=2    N=306.5

        Statistic                    Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda           0.93888828     6.6717         6       615  0.0001
        Pillai's Trace          0.06111172     6.6717         6       615  0.0001
        Hotelling-Lawley Trace  0.06508944     6.6717         6       615  0.0001
        Roy's Greatest Root     0.06508944     6.6717         6       615  0.0001


Manova Test Criteria and F Approximations for the Hypothesis of no Overall TIME Effect
             H = Type III SS&CP Matrix for TIME   E = Error SS&CP Matrix
                                S=4    M=0.5    N=306.5

        Statistic                    Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda           0.51010317    19.0366        24  2146.689  0.0001
        Pillai's Trace          0.55144505    16.4703        24      2472  0.0001
        Hotelling-Lawley Trace  0.84270959    21.5418        24      2454  0.0001
        Roy's Greatest Root     0.68059751    70.1015         6       618  0.0001
```

Table A4: (Continued).

```
Manova Test Criteria and Exact F Statistics for the Hypothesis of no Overall GRAZE Effect
               H = Type III SS&CP Matrix for GRAZE   E = Error SS&CP Matrix
                                   S=1    M=2    N=306.5

        Statistic                      Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda             0.79073046    27.1270         6       615  0.0001
        Pillai's Trace            0.20926954    27.1270         6       615  0.0001
        Hotelling-Lawley Trace    0.26465345    27.1270         6       615  0.0001
        Roy's Greatest Root       0.26465345    27.1270         6       615  0.0001

Manova Test Criteria and Exact F Statistics for the Hypothesis of no Overall SEASON Effect
              H = Type III SS&CP Matrix for SEASON   E = Error SS&CP Matrix
                                   S=1    M=2    N=306.5

        Statistic                      Value          F      Num DF    Den DF  Pr > F

        Wilks' Lambda             0.89388182    12.1684         6       615  0.0001
        Pillai's Trace            0.10611818    12.1684         6       615  0.0001
        Hotelling-Lawley Trace    0.11871612    12.1684         6       615  0.0001
        Roy's Greatest Root       0.11871612    12.1684         6       615  0.0001
```

Table A5: Results of univariate analysis of species cover.

```
Dependent Variable: ATCO

Source                    DF        Sum of Squares        Mean Square      F Value          Pr > F
Model                     19          445.25860648        23.43466350         9.72          0.0001
Error                    620         1495.44336695         2.41200543
Corrected Total          639         1940.70197343

                    R-Square                  C.V.           Root MSE                   LATCO Mean
                    0.229432              33.07138         1.55306324                   4.69609476

Source                    DF           Type III SS        Mean Square      F Value          Pr > F

TIME                       4          295.24879513        73.81219878        30.60          0.0001
GRAZE                      1           40.11056331        40.11056331        16.63          0.0001
TIME*GRAZE                 4           20.04741524         5.01185381         2.08          0.0822
SEASON                     1            0.58488749         0.58488749         0.24          0.6226
TIME*SEASON                4            5.54953786         1.38738447         0.58          0.6807
GRAZE*SEASON               1            8.74329370         8.74329370         3.62          0.0574
TIME*GRAZE*SEASON          4            5.44615466         1.36153866         0.56          0.6885

Contrast                  DF           Contrast SS        Mean Square      F Value          Pr > F

T1 vs T2                   1            2.47633318         2.47633318         1.03          0.3113
T2 vs T3                   1           37.96964385        37.96964385        15.74          0.0001
T3 vs T4                   1           21.51168770        21.51168770         8.92          0.0029
T4 vs T5                   1           13.01926040        13.01926040         5.40          0.0205
T1 vs T5                   1          164.72708529       164.72708529        68.29          0.0001
[T1*T2]*(Grazed*Ungr)      1            5.26555543         5.26555543         2.18          0.1400
[T3*T4]*(Grazed*Ungr)      1            1.10315990         1.10315990         0.46          0.4991
[T1*T5]*(Grazed*Ungr)      1            1.24522431         1.24522431         0.52          0.4727
[T4*T5]*(Grazed*Ungr)      1            3.54585532         3.54585532         1.47          0.2258
[T2*T3]*(Grazed*Ungr)      1            3.07853251         3.07853251         1.28          0.2590
Grazed(1) vs Ungraze       1           40.11056331        40.11056331        16.63          0.0001
Spring(1) vs Winter        1            0.58488749         0.58488749         0.24          0.6226

Dependent Variable: CELA

Source                    DF        Sum of Squares        Mean Square      F Value          Pr > F
Model                     19          288.73492170        15.19657483         2.99          0.0001
Error                    620         3154.58790053         5.08804500
Corrected Total          639         3443.32282223

                    R-Square                  C.V.           Root MSE                   LCELA Mean

                    0.083854              63.68913         2.25566952                   3.54168707

Source                    DF           Type III SS        Mean Square      F Value          Pr > F

TIME                       4          158.84917480        39.71229370         7.81          0.0001
GRAZE                      1           29.99857618        29.99857618         5.90          0.0155
TIME*GRAZE                 4           13.43151054         3.35787763         0.66          0.6200
SEASON                     1           27.14850908        27.14850908         5.34          0.0212
TIME*SEASON                4            8.07862587         2.01965647         0.40          0.8109
GRAZE*SEASON               1            2.57682333         2.57682333         0.51          0.4769
TIME*GRAZE*SEASON          4            1.82763613         0.45690903         0.09          0.9856

Contrast                  DF           Contrast SS        Mean Square      F Value          Pr > F

T1 vs T2                   1           20.79622265        20.79622265         4.09          0.0436
T2 vs T3                   1            1.26950575         1.26950575         0.25          0.6176
T3 vs T4                   1            3.05447032         3.05447032         0.60          0.4388
```

Table A5: (Continued).

```
T4 vs T5                   1        117.81772622       117.81772622       23.16        0.0001
T1 vs T5                   1         11.69415727        11.69415727        2.30        0.1300
[T1*T2]*(Grazed*Ungr       1          9.06280627         9.06280627        1.78        0.1825
[T3*T4]*(Grazed*Ungr       1          0.01523871         0.01523871        0.00        0.9564
[T1*T5]*(Grazed*Ungr)      1          9.65285381         9.65285381        1.90        0.1689
[T4*T5]*(Grazed*Ungr)      1          0.25605942         0.25605942        0.05        0.8226
[T2*T3]*(Grazed*Ungr)      1          0.08186652         0.08186652        0.02        0.8991
Grazed(1) vs Ungraze       1         29.99857618        29.99857618        5.90        0.0155
Spring(1) vs Winter        1         27.14850908        27.14850908        5.34        0.0212


Dependent Variable: ARSP

Source                    DF      Sum of Squares        Mean Square     F Value        Pr > F
Model                     19        885.82865964        46.62256103       12.29        0.0001
Error                    620       2351.36799873         3.79252903
Corrected Total          639       3237.19665836

                    R-Square                C.V.           Root MSE                LARSP Mean

                    0.273641            71.72145         1.94744166                2.71528482

Source                    DF         Type III SS        Mean Square     F Value        Pr > F

TIME                       4         71.96378341        17.99094585        4.74        0.0009
GRAZE                      1        439.30450113       439.30450113      115.83        0.0001
TIME*GRAZE                 4        136.55577095        34.13894274        9.00        0.0001
SEASON                     1        125.31084950       125.31084950       33.04        0.0001
TIME*SEASON                4         39.09569401         9.77392350        2.58        0.0366
GRAZE*SEASON               1        111.01284151       111.01284151       29.27        0.0001
TIME*GRAZE*SEASON          4         26.08762795         6.52190699        1.72        0.1439

Contrast                  DF         Contrast SS        Mean Square     F Value        Pr > F
T1 vs T2                   1         35.02404278        35.02404278        9.24        0.0025
T2 vs T3                   1          0.77553040         0.77553040        0.20        0.6513
T3 vs T4                   1          0.00300004         0.00300004        0.00        0.9776
T4 vs T5                   1          0.01820076         0.01820076        0.00        0.9448
T1 vs T5                   1         48.83824127        48.83824127       12.88        0.0004
[T1*T2]*(Grazed*Ungr)      1         33.94116825        33.94116825        8.95        0.0029
[T3*T4]*(Grazed*Ungr)      1          0.36663595         0.36663595        0.10        0.7560
[T1*T5]*(Grazed*Ungr)      1        116.36549045       116.36549045       30.68        0.0001
[T4*T5]*(Grazed*Ungr)      1          4.37195775         4.37195775        1.15        0.2834
[T2*T3]*(Grazed*Ungr)      1          5.13000484         5.13000484        1.35        0.2453
Grazed(1) vs Ungraze       1        439.30450113       439.30450113      115.83        0.0001
Spring(1) vs Winter        1        125.31084950       125.31084950       33.04        0.0001


Dependent Variable: SPCR

Source                    DF      Sum of Squares        Mean Square     F Value        Pr > F
Model                     19        343.69580819        18.08925306        4.94        0.0001
Error                    620       2272.13183299         3.66472876
Corrected Total          639       2615.82764118

                    R-Square                C.V.           Root MSE                LSPCR Mean

                    0.131391            64.95661         1.91434813                2.94711838

Source                    DF         Type III SS        Mean Square     F Value        Pr > F
TIME                       4        237.41398560        59.35349640       16.20        0.0001
GRAZE                      1         15.31580393        15.31580393        4.18        0.0413
TIME*GRAZE                 4          6.04199109         1.51049777        0.41        0.7999
SEASON                     1         22.98131017        22.98131017        6.27        0.0125
TIME*SEASON                4          7.54822915         1.88705729        0.51        0.7248
GRAZE*SEASON               1          0.54541329         0.54541329        0.15        0.6998
TIME*GRAZE*SEASON          4          2.83316854         0.70829214        0.19        0.9419
```

Table A5: (Continued).

```
Contrast                  DF          Contrast SS          Mean Square      F Value        Pr > F

T1 vs T2                   1          21.19610863          21.19610863         5.78        0.0165
T2 vs T3                   1          20.56508306          20.56508306         5.61        0.0181
T3 vs T4                   1           1.25500229           1.25500229         0.34        0.5586
T4 vs T5                   1          14.92140642          14.92140642         4.07        0.0440
T1 vs T5                   1         199.42777022         199.42777022        54.42        0.0001
[T1*T2]*(Grazed*Ungr)      1           1.59272371           1.59272371         0.43        0.5100
[T3*T4]*(Grazed*Ungr)      1           1.37355237           1.37355237         0.37        0.5406
[T1*T5]*(Grazed*Ungr)      1           4.61878076           4.61878076         1.26        0.2620
[T4*T5]*(Grazed*Ungr)      1           0.15360460           0.15360460         0.04        0.8379
[T2*T3]*(Grazed*Ungr)      1           0.45806829           0.45806829         0.12        0.7238
Grazed(1) vs Ungraze       1          15.31580393          15.31580393         4.18        0.0413
Spring(1) vs Winter        1          22.98131017          22.98131017         6.27        0.0125


Dependent Variable: ORHY

Source                    DF       Sum of Squares          Mean Square      F Value        Pr > F
Model                     19         667.23503425          35.11763338      15.42          0.0001
Error                    620        1411.57934914           2.27674089
Corrected Total          639        2078.81438339

                    R-Square                 C.V.             Root MSE                 LSTHY Mean

                    0.320969             74.41094           1.50888730                 2.02777614


Source                    DF          Type III SS          Mean Square      F Value        Pr > F

TIME                       4         504.46036404         126.11509101        55.39        0.0001
GRAZE                      1           0.47235785           0.47235785         0.21        0.6489
TIME*GRAZE                 4          18.15851591           4.53962898         1.99        0.0939
SEASON                     1           4.67371368           4.67371368         2.05        0.1524
TIME*SEASON                4           8.42700111           2.10675028         0.93        0.4487
GRAZE*SEASON               1           1.17816489           1.17816489         0.52        0.4722
TIME*GRAZE*SEASON          4           2.16772293           0.54193073         0.24        0.9168

Contrast                  DF          Contrast SS          Mean Square      F Value        Pr > F
T1 vs T2                   1          19.70694093          19.70694093         8.66        0.0034
T2 vs T3                   1           5.02659871           5.02659871         2.21        0.1378
T3 vs T4                   1           2.80528697           2.80528697         1.23        0.2674
T4 vs T5                   1         164.50908906         164.50908906        72.26        0.0001
T1 vs T5                   1         448.68841567         448.68841567       197.07        0.0001
[T1*T2]*(Grazed*Ungr       1           3.10452677           3.10452677         1.36        0.2434
[T3*T4]*(Grazed*Ungr       1           0.46087782           0.46087782         0.20        0.6529
[T1*T5]*(Grazed*Ungr)      1           1.99684347           1.99684347         0.88        0.3494
[T4*T5]*(Grazed*Ungr)      1           0.34428542           0.34428542         0.15        0.6975
[T2*T3]*(Grazed*Ungr)      1           9.50453396           9.50453396         4.17        0.0415
Grazed(1) vs Ungraze       1           0.47235785           0.47235785         0.21        0.6489
Spring(1) vs Winter        1           4.67371368           4.67371368         2.05        0.1524


Dependent Variable: HIJA

Source                    DF       Sum of Squares          Mean Square      F Value        Pr > F
Model                     19         275.66531685          14.50870089         2.52        0.0004
Error                    620        3573.52634884           5.76375218
Corrected Total          639        3849.19166569

                    R-Square                 C.V.             Root MSE                 LHIJA Mean

                    0.071616             107.2031           2.40078158                 2.23946973
```

Table A5: (Continued).

Source	DF	Type III SS	Mean Square	F Value	Pr > F
TIME	4	126.68169378	31.67042344	5.49	0.0002
GRAZE	1	3.14397681	3.14397681	0.55	0.4605
TIME*GRAZE	4	5.14127680	1.28531920	0.22	0.9256
SEASON	1	134.99155531	134.99155531	23.42	0.0001
TIME*SEASON	4	10.12071691	2.53017923	0.44	0.7805
GRAZE*SEASON	1	0.86128278	0.86128278	0.15	0.6992
TIME*GRAZE*SEASON	4	1.91212241	0.47803060	0.08	0.9876
Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
T1 vs T2	1	34.00022658	34.00022658	5.90	0.0154
T2 vs T3	1	7.60082462	7.60082462	1.32	0.2513
T3 vs T4	1	0.85594493	0.85594493	0.15	0.7001
T4 vs T5	1	0.09865704	0.09865704	0.02	0.8960
T1 vs T5	1	84.62171825	84.62171825	14.68	0.0001
[T1*T2]*(Grazed*Ungr)	1	2.59544064	2.59544064	0.45	0.5024
[T3*T4]*(Grazed*Ungr)	1	1.18421125	1.18421125	0.21	0.6505
[T1*T5]*(Grazed*Ungr)	1	1.71858084	1.71858084	0.30	0.5852
[T4*T5]*(Grazed*Ungr)	1	0.05235622	0.05235622	0.01	0.9241
[T2*T3]*(Grazed*Ungr)	1	0.31282689	0.31282689	0.05	0.8159
Grazed(1) vs Ungraze	1	3.14397681	3.14397681	0.55	0.4605
Spring(1) vs Winter	1	134.99155531	134.99155531	23.42	0.0001

Table A6: Least square means and probability values for pairwise time by grazing comparison.

```
TIME  GRAZE         ATCO  T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

                    LSMEAN i/j         1         2         3         4         5         6         7         8         9        10
1     G         5.34810664  1          .  -0.08104  -1.76124  0.247254  0.245433  3.851633  2.835343  5.485131  5.335506  6.270601
                                            0.9354    0.0787    0.8048    0.8062    0.0001    0.0047    0.0001    0.0001    0.0001
1     U         5.37210600  2  0.081036         .   -1.6802  0.328289  0.326469  3.932669  2.916379  5.566167  5.416542  6.351637
                                  0.9354              0.0934    0.7428    0.7442    0.0001    0.0037    0.0001    0.0001    0.0001
2     G         5.86971036  3  1.761237  1.680202         .  2.008491   2.00667  5.612871  4.596581  7.246369  7.096743  8.031839
                                  0.0787    0.0934              0.0450    0.0452    0.0001    0.0001    0.0001    0.0001    0.0001
2     U         5.27488060  4  -0.24725  -0.32829  -2.00849         .  -0.00182  3.604379   2.58809  5.237878  5.088252  6.023348
                                  0.8048    0.7428    0.0450              0.9985    0.0003    0.0099    0.0001    0.0001    0.0001
3     G         5.27541983  5  -0.24543  -0.32647  -2.00667  0.001821         .    3.6062   2.58991  5.239698  5.090073  6.025168
                                  0.8062    0.7442    0.0452    0.9985              0.0003    0.0098    0.0001    0.0001    0.0001
3     U         4.20741644  6  -3.85163  -3.93267  -5.61287  -3.60438   -3.6062         .  -1.01629  1.633498  1.483873  2.418968
                                  0.0001    0.0001    0.0001    0.0003    0.0003              0.3099    0.1029    0.1384    0.0159
4     G         4.50839834  7  -2.83534  -2.91638  -4.59658  -2.58809  -2.58991   1.01629         .  2.649788  2.500163  3.435258
                                  0.0047    0.0037    0.0001    0.0099    0.0098    0.3099              0.0083    0.0127    0.0006
4     U         3.72364363  8  -5.48513  -5.56617  -7.24637  -5.23788   -5.2397   -1.6335  -2.64979         .  -0.14963   0.78547
                                  0.0001    0.0001    0.0001    0.0001    0.0001    0.1029    0.0083              0.8811    0.4325
5     G         3.76795627  9  -5.33551  -5.41654  -7.09674  -5.08825  -5.09007  -1.48387  -2.50016  0.149625         .  0.935095
                                  0.0001    0.0001    0.0001    0.0001    0.0001    0.1384    0.0127    0.8811              0.3501
5     U         3.49102080 10   -6.2706  -6.35164  -8.03184  -6.02335  -6.02517  -2.41897  -3.43526  -0.78547   -0.9351         .
                                  0.0001    0.0001    0.0001    0.0001    0.0001    0.0159    0.0006    0.4325    0.3501


TIME  GRAZE         CELA  T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

                    LSMEAN i/j         1         2         3         4         5         6         7         8         9        10

1     G         3.14878415  1          .  0.348905  -0.48584  -2.02437  -0.92874  -2.28788  -1.51531  -2.79705   2.04595  0.446951
                                            0.7273    0.6273    0.0434    0.3534    0.0225    0.1302    0.0053    0.0412    0.6551
1     U         2.99870659  2   -0.3489         .  -0.83475  -2.37327  -1.27765  -2.63678  -1.86421  -3.14596  1.697045  0.098046
                                  0.7273              0.4042    0.0179    0.2019    0.0086    0.0628    0.0017    0.0902    0.9219
2     G         3.35776427  3  0.485843  0.834747         .  -1.53853   -0.4429  -1.80204  -1.02947  -2.31121  2.531793  0.932794
                                  0.6273    0.4042              0.1244    0.6580    0.0720    0.3037    0.0211    0.0116    0.3513
2     U         4.01954456  4  2.024368  2.373273  1.538526         .  1.095627  -0.26351  0.509059  -0.77268  4.070318  2.471319
                                  0.0434    0.0179    0.1244              0.2737    0.7922    0.6109    0.4400    0.0001    0.0137
3     G         3.54827248  5  0.928742  1.277646  0.442899  -1.09563         .  -1.35914  -0.58657  -1.86831  2.974691  1.375693
                                  0.3534    0.2019    0.6580    0.2737              0.1746    0.5577    0.0622    0.0030    0.1694
3     U         4.13289107  6   2.28788  2.636784  1.802037  0.263511  1.359138         .   0.77257  -0.50917  4.333829  2.734831
                                  0.0225    0.0086    0.0720    0.7922    0.1746              0.4401    0.6108    0.0001    0.0064
4     G         3.80057823  7  1.515309  1.864214  1.029466  -0.50906  0.586568  -0.77257         .  -1.28174  3.561259   1.96226
                                  0.1302    0.0628    0.3037    0.6109    0.5577    0.4401              0.2004    0.0004    0.0502
4     U         4.35190613  8  2.797052  3.145957  2.311209  0.772684   1.86831  0.509172  1.281743         .  4.843002  3.244003
                                  0.0053    0.0017    0.0211    0.4400    0.0622    0.6108    0.2004              0.0001    0.0012
5     G         2.26874078  9  -2.04595  -1.69705  -2.53179  -4.07032  -2.97469  -4.33383  -3.56126    -4.843         .    -1.599
                                  0.0412    0.0902    0.0116    0.0001    0.0030    0.0001    0.0004    0.0001              0.1103
5     U         2.95653297 10  -0.44695  -0.09805  -0.93279  -2.47132  -1.37569  -2.73483  -1.96226    -3.244  1.598999         .
                                  0.6551    0.9219    0.3513    0.0137    0.1694    0.0064    0.0502    0.0012    0.1103

TIME  GRAZE         ARSP  T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

                    LSMEAN i/j         1         2         3         4         5         6         7         8         9        10
1     G         1.82707208  1          .  0.037817  -0.03348  -4.22638  0.469156  -5.36853  0.669125  -5.60827  1.379343  -6.41646
                                            0.9698    0.9733    0.0001    0.6391    0.0001    0.5037    0.0001    0.1683    0.0001
1     U         1.81302817  2  -0.03782         .   -0.0713   -4.2642  0.431339  -5.40635  0.631307  -5.64609  1.341526  -6.45428
                                  0.9698              0.9432    0.0001    0.6664    0.0001    0.5281    0.0001    0.1802    0.0001
2     G         1.83950520  3   0.03348  0.071297         .   -4.1929  0.502636  -5.33505  0.702604  -5.57479  1.412823  -6.38298
                                  0.9733    0.9432              0.0001    0.6154    0.0001    0.4826    0.0001    0.1582    0.0001
2     U         3.39659101  4  4.226379  4.264196  4.192899         .  4.695535  -1.14215  4.895504  -1.38189  5.605722  -2.19008
                                  0.0001    0.0001    0.0001              0.0001    0.2538    0.0001    0.1675    0.0001    0.0289
3     G         1.65284497  5  -0.46916  -0.43134  -0.50264  -4.69554         .  -5.83769  0.199968  -6.07743  0.910187  -6.88562
                                  0.6391    0.6664    0.6154    0.0001              0.0001    0.8416    0.0001    0.3631    0.0001
3     U         3.82074275  6  5.368529  5.406346  5.335049   1.14215  5.837685         .  6.037654  -0.23974  6.747872  -1.04793
                                  0.0001    0.0001    0.0001    0.2538    0.0001              0.0001    0.8106    0.0001    0.2951
4     G         1.57858426  7  -0.66912  -0.63131   -0.7026   -4.8955  -0.19997  -6.03765         .   -6.2774  0.710219  -7.08559
                                  0.5037    0.5281    0.4826    0.0001    0.8416    0.0001              0.0001    0.4778    0.0001
4     U         3.90977452  8  5.608273   5.64609  5.574793  1.381894  6.077429  0.239744  6.277397         .  6.987616  -0.80819
                                  0.0001    0.0001    0.0001    0.1675    0.0001    0.8106    0.0001              0.0001    0.4193
5     G         1.31483559  9  -1.37934  -1.34153  -1.41282  -5.60572  -0.91019  -6.74787  -0.71022  -6.98762         .  -7.79581
                                  0.1683    0.1802    0.1582    0.0001    0.3631    0.0001    0.4778    0.0001              0.0001
5     U         4.20990577 10  6.416462  6.454279  6.382982  2.190083  6.885618  1.047933  7.085587  0.808189  7.795805         .
                                  0.0001    0.0001    0.0001    0.0289    0.0001    0.2951    0.0001    0.4193    0.0001

TIME  GRAZE         SPCR  T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

                    LSMEAN i/j         1         2         3         4         5         6         7         8         9        10
1     G         1.85405572  1          .   0.06416  -2.16672  -1.17024  -3.59178  -3.09529  -4.43848  -3.07619  -6.01006  -4.35824
                                            0.9489    0.0306    0.2424    0.0004    0.0021    0.0001    0.0022    0.0001    0.0001
1     U         1.83063398  2  -0.06416         .  -2.23088   -1.2344  -3.65594  -3.15945  -4.50264  -3.14035  -6.07422   -4.4224
                                  0.9489              0.0260    0.2175    0.0003    0.0017    0.0001    0.0018    0.0001    0.0001
2     G         2.64502089  3   2.16672   2.23088         .  0.996479  -1.42506  -0.92857  -2.27176  -0.90947  -3.84334  -2.19152
                                  0.0306    0.0260              0.3194    0.1546    0.3535    0.0234    0.3635    0.0001    0.0288
2     U         2.28125456  4  1.170241  1.234402  -0.99648         .  -2.42154  -1.92505  -3.26824  -1.90595  -4.83982    -3.188
                                  0.2424    0.2175    0.3194              0.0157    0.0547    0.0011    0.0571    0.0001    0.0015
3     G         3.16524250  5  3.591782  3.655942  1.425062  2.421541         .  0.496491   -0.8467  0.515594  -2.41828  -0.76646
                                  0.0004    0.0003    0.1546    0.0157              0.6197    0.3975    0.6063    0.0159    0.4437
3     U         2.98399755  6  3.095291  3.159451  0.928571   1.92505  -0.49649         .  -1.34319  0.019103  -2.91477  -1.26295
                                  0.0021    0.0017    0.3535    0.0547    0.6197              0.1797    0.9848    0.0037    0.2071
4     G         3.47433015  7  4.438477  4.502637  2.271757  3.268236  0.846695  1.343186         .  1.362289  -1.57159  0.080236
                                  0.0001    0.0001    0.0234    0.0011    0.3975    0.1797              0.1736    0.1166    0.9361
4     U         2.97702394  8  3.076188  3.140348  0.909468  1.905947  -0.51559   -0.0191  -1.36229         .  -2.93387  -1.28205
                                  0.0022    0.0018    0.3635    0.0571    0.6063    0.9848    0.1736              0.0035    0.2003
5     G         4.04804023  9  6.010062  6.074222  3.843342  4.839821   2.41828  2.914771  1.571585  2.933874         .  1.651821
                                  0.0001    0.0001    0.0001    0.0001    0.0159    0.0037    0.1166    0.0035              0.0991
5     U         3.44503992 10  4.358242  4.422402  2.191522     3.188  0.766459   1.26295  -0.08024  1.282053  -1.65182         .
                                  0.0001    0.0001    0.0288    0.0015    0.4437    0.2071    0.9361    0.2003    0.0991
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Table A6: (Continued).

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TIME    GRAZE             ORHY   T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

                         LSMEAN i/j         1         2         3         4         5         6         7         8         9        10
1       G            0.91501284   1         .   -0.3534  -1.25465  -3.25946  -3.75007  -2.86537  -4.85312  -3.33214  -10.5888  -9.61778
                                                0.7239    0.2101    0.0012    0.0002    0.0043    0.0001    0.0009    0.0001    0.0001
1       U            1.01669684   2  0.353396         .  -0.90125  -2.90606  -3.39667  -2.51198  -4.49972  -2.97874  -10.2354  -9.26439
                                      0.7239              0.3678    0.0038    0.0007    0.0123    0.0001    0.0030    0.0001    0.0001
2       G            1.27601764   3   1.25465  0.901253         .  -2.00481  -2.49542  -1.61072  -3.59847  -2.07749  -9.33417  -8.36313
                                      0.2101    0.3678              0.0454    0.0128    0.1077    0.0003    0.0382    0.0001    0.0001
2       U            1.85286874   4   3.25946  2.906064   2.00481         .  -0.49061  0.394086  -1.59366  -0.07268  -7.32936  -6.35832
                                      0.0012    0.0038    0.0454              0.6239    0.6937    0.1115    0.9421    0.0001    0.0001
3       G            1.99403378   5   3.75007  3.396674  2.495421   0.49061         .  0.884696  -1.10305  0.417933  -6.83875  -5.86771
                                      0.0002    0.0007    0.0128    0.6239              0.3767    0.2704    0.6761    0.0001    0.0001
3       U            1.73947713   6  2.865375  2.511978  1.610725  -0.39409   -0.8847         .  -1.98774  -0.46676  -7.72344  -6.75241
                                      0.0043    0.0123    0.1077    0.6937    0.3767              0.0473    0.6408    0.0001    0.0001
4       G            2.31141726   7  4.853117  4.499721  3.598467  1.593657  1.103047  1.987742         .   1.52098   -5.7357  -4.76467
                                      0.0001    0.0001    0.0003    0.1115    0.2704    0.0473              0.1288    0.0001    0.0001
4       U            1.87378034   8  3.332137  2.978741  2.077487  0.072677  -0.41793  0.466762  -1.52098         .  -7.25668  -6.28565
                                      0.0009    0.0030    0.0382    0.9421    0.6761    0.6408    0.1288              0.0001    0.0001
5       G            3.96177105   9  10.58882  10.23542  9.334169  7.329359  6.838749  7.723445  5.735702  7.256682         .  0.971037
                                      0.0001    0.0001    0.0001    0.0001    0.0001    0.0001    0.0001    0.0001              0.3319
5       U            3.68237110  10  9.617782  9.264386  8.363132  6.358322  5.867712  6.752408  4.764665  6.285645  -0.97104         .
                                      0.0001    0.0001    0.0001    0.0001    0.0001    0.0001    0.0001    0.0001    0.3319

TIME    GRAZE             HIJA   T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

                         LSMEAN i/j         1         2         3         4         5         6         7         8         9        10
1       G            1.44086811   1         .  -0.39714  -2.19191  -1.64004  -3.16866  -2.28732  -3.12063  -2.88033  -3.09552  -2.72042
                                                0.6914    0.0288    0.1015    0.0016    0.0225    0.0019    0.0041    0.0021    0.0067
1       U            1.62268110   2  0.397135         .  -1.79477  -1.24291  -2.77152  -1.89018   -2.7235  -2.48319  -2.69838  -2.32329
                                      0.6914              0.0732    0.2144    0.0057    0.0592    0.0066    0.0133    0.0072    0.0205
2       G            2.44434833   3  2.191909  1.794774         .  0.551868  -0.97675  -0.09541  -0.92873  -0.68842  -0.90361  -0.52851
                                      0.0288    0.0732              0.5812    0.3291    0.9240    0.3534    0.4914    0.3666    0.5973
2       U            2.19169691   4  1.640041  1.242905  -0.55187         .  -1.52862  -0.64728  -1.48059  -1.24028  -1.45548  -1.08038
                                      0.1015    0.2144    0.5812              0.1269    0.5177    0.1392    0.2153    0.1460    0.2804
3       G            2.89151389   5  3.168656   2.77152  0.976747  1.528615         .  0.881337  0.048021   0.28833  0.073139  0.448235
                                      0.0016    0.0057    0.3291    0.1269              0.3785    0.9617    0.7732    0.9417    0.6541
3       U            2.48802798   6  2.287319  1.890183   0.09541  0.647278  -0.88134         .  -0.83332  -0.59301   -0.8082   -0.4331
                                      0.0225    0.0592    0.9240    0.5177    0.3785              0.4050    0.5534    0.4193    0.6651
4       G            2.86952934   7  3.120635  2.723499  0.928726  1.480594  -0.04802  0.833316         .  0.240309  0.025118  0.400214
                                      0.0019    0.0066    0.3534    0.1392    0.9617    0.4050              0.8102    0.9800    0.6891
4       U            2.75951311   8  2.880326   2.48319  0.688417  1.240285  -0.28833  0.593007  -0.24031         .  -0.21519  0.159905
                                      0.0041    0.0133    0.4914    0.2153    0.7732    0.5534    0.8102              0.8297    0.8730
5       G            2.85802987   9  3.095516  2.698381  0.903608  1.455476  -0.07314  0.808198  -0.02512  0.215191         .  0.375096
                                      0.0021    0.0072    0.3666    0.1460    0.9417    0.4193    0.9800    0.8297              0.7077
5       U            2.68630687  10  2.720421  2.323285  0.528512   1.08038  -0.44824  0.433102  -0.40021   -0.1599   -0.3751         .
                                      0.0067    0.0205    0.5973    0.2804    0.6541    0.6651    0.6891    0.8730    0.7077
```

Table A7: Least square means and probability values for pairwise time by season comparison.

```
                         TIME   SEASON         ATCO   LSMEAN
                                             LSMEAN   Number
                          1       S      5.28180733     1
                          1       W      5.43840531     2
                          2       S      5.39418011     3
                          2       W      5.75041085     4
                          3       S      4.84324595     5
                          3       W      4.63959032     6
                          4       S      4.05052288     7
                          4       W      4.18151909     8
                          5       S      3.68652168     9
                          5       W      3.57245539    10

                        T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

i/j          1          2          3          4          5          6          7          8          9         10
1            .   -0.52877   -0.32358   -1.58228   1.262863   2.168498   3.545555   3.715213   4.593718   5.771766
                   0.5972     0.7464     0.1141     0.2071     0.0305     0.0004     0.0002     0.0001     0.0001
2     0.528766          .    0.14933    -1.3326   2.009604   3.411799   4.686298   5.368255   5.915377   7.969612
        0.5972               0.8813     0.1832     0.0449     0.0007     0.0001     0.0001     0.0001     0.0001
3     0.323584   -0.14933          .   -1.20284   1.586447   2.547934   3.869139   4.094648   4.917302   6.151202
        0.7464     0.8813                0.2295     0.1131     0.0111     0.0001     0.0001     0.0001     0.0001
4     1.582278   1.332599   1.202842          .   3.063116   4.744398    5.73981   6.700854    6.96889   9.302211
        0.1141     0.1832     0.2295                0.0023     0.0001     0.0001     0.0001     0.0001     0.0001
5     -1.26286    -2.0096   -1.58645   -3.06312          .    0.68766   2.282692   2.234375   3.330855   4.290928
        0.2071     0.0449     0.1131     0.0023                0.4919     0.0228     0.0258     0.0009     0.0001
6      -2.1685    -3.4118   -2.54793    -4.7444   -0.68766          .   1.989034   1.956457   3.218114   4.557813
        0.0305     0.0007     0.0111     0.0001     0.4919                0.0471     0.0509     0.0014     0.0001
7     -3.54556    -4.6863   -3.86914   -5.73981   -2.28269   -1.98903          .   -0.44232   1.048163   1.614234
        0.0004     0.0001     0.0001     0.0001     0.0228     0.0471                0.6584     0.2950     0.1070
8     -3.71521   -5.36826   -4.09465   -6.70085   -2.23437   -1.95646   0.442319          .   1.671399   2.601357
        0.0002     0.0001     0.0001     0.0001     0.0258     0.0509     0.6584                0.0951     0.0095
9     -4.59372   -5.91538    -4.9173   -6.96889   -3.33085   -3.21811   -1.04816    -1.6714          .   0.385154
        0.0001     0.0001     0.0001     0.0001     0.0009     0.0014     0.2950     0.0951                0.7003
10    -5.77177   -7.96961    -6.1512   -9.30221   -4.29093   -4.55781   -1.61423   -2.60136   -0.38515          .
        0.0001     0.0001     0.0001     0.0001     0.0001     0.0001     0.1070     0.0095     0.7003
```

```
                         TIME   SEASON         CELA   LSMEAN
                                             LSMEAN   Number
                          1       S      3.00301654     1
                          1       W      3.14447420     2
                          2       S      3.41724863     3
                          2       W      3.96006021     4
                          3       S      3.41526921     5
                          3       W      4.26589435     6
                          4       S      3.87517287     7
                          4       W      4.27731149     8
                          5       S      2.47028743     9
                          5       W      2.75498632    10

                      Least Squares Means for effect TIME*SEASO
                        T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|
Dependent Variable: LCELA
i/j          1          2          3          4          5          6          7          8          9         10
1            .   -0.32886   -0.82126   -2.22496   -0.81734   -2.93597   -1.72915   -2.96252   1.056199   0.576628
                   0.7424     0.4118     0.0264     0.4140     0.0034     0.0843     0.0032     0.2913     0.5644
2     0.328865          .   -0.63415   -2.39839   -0.62955   -3.29776   -1.69875   -3.33134   1.567368   1.145367
        0.7424               0.5262     0.0168     0.5292     0.0010     0.0899     0.0009     0.1175     0.2525
3     0.821265   0.634154          .   -1.26194   0.003924   -1.97296   -0.90789    -1.9995   1.877464   1.539646
        0.4118     0.5262                0.2074     0.9969     0.0489     0.3643     0.0460     0.0609     0.1242
4     2.224962   2.398395   1.261944          .   1.266545   -0.89937   0.197348   -0.93294   3.463466   3.543762
        0.0264     0.0168     0.2074                0.2058     0.3688     0.8436     0.3512     0.0006     0.0004
5      0.81734   0.629552   -0.00392   -1.26655          .   -1.97756   -0.91181    -2.0041    1.87354   1.535044
        0.4140     0.5292     0.9969     0.2058                0.0484     0.3622     0.0455     0.0615     0.1253
6     2.935974   3.297761   1.972956   0.899367   1.977557          .    0.90836   -0.03357   4.174478   4.443129
        0.0034     0.0010     0.0489     0.3688     0.0484                0.3640     0.9732     0.0001     0.0001
7     1.729155   1.698749    0.90789   -0.19735   0.911814   -0.90836          .    -0.9349   2.785354   2.604241
        0.0843     0.0899     0.3643     0.8436     0.3622     0.3640                0.3502     0.0055     0.0094
8     2.962517   3.331336   1.999498   0.932941     2.0041   0.033574   0.934903          .   4.201021   4.476703
        0.0032     0.0009     0.0460     0.3512     0.0455     0.9732     0.3502                0.0001     0.0001
9      -1.0562   -1.56737   -1.87746   -3.46347   -1.87354   -4.17448   -2.78535   -4.20102          .   -0.66188
        0.2913     0.1175     0.0609     0.0006     0.0615     0.0001     0.0055     0.0001                0.5083
10    -0.57663   -1.14537   -1.53965   -3.54376   -1.53504   -4.44313   -2.60424    -4.4767   0.661876          .
        0.5644     0.2525     0.1242     0.0004     0.1253     0.0001     0.0094     0.0001     0.5083
```

Table A7: (Continued).

```
                                TIME   SEASON        ARSP   LSMEAN
                                                   LSMEAN   Number
                                  1      S     1.83482265      1
                                  1      W     1.80527761      2
                                  2      S     2.21021629      3
                                  2      W     3.02587992      4
                                  3      S     2.11857379      5
                                  3      W     3.35501392      6
                                  4      S     2.04998886      7
                                  4      W     3.43836992      8
                                  5      S     2.08122211      9
                                  5      W     3.44351925     10

                         T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

i/j         1          2          3          4          5          6          7          8          9         10
1           .   0.079558   -0.86206   -3.20726   -0.65161   -4.09355   -0.49411   -4.31801   -0.56584   -4.33188
                  0.9366     0.3890     0.0014     0.5149     0.0001     0.6214     0.0001     0.5717     0.0001
2    -0.07956          .   -1.09041   -4.15754   -0.84364   -5.27861   -0.65896   -5.56253   -0.74306   -5.58007
       0.9366                0.2760     0.0001     0.3992     0.0001     0.5102     0.0001     0.4577     0.0001
3     0.86206   1.090413          .   -2.19641   0.210449    -3.0827   0.367949   -3.30716   0.296224   -3.32102
       0.3890     0.2760                0.0284     0.8334     0.0021     0.7130     0.0010     0.7672     0.0009
4    3.207263   4.157537   2.196408          .   2.443182   -1.12107   2.627866     -1.405   2.543762   -1.42254
       0.0014     0.0001     0.0284                0.0148     0.2627     0.0088     0.1605     0.0112     0.1554
5    0.651611    0.84364   -0.21045   -2.44318          .   -3.32947     0.1575   -3.55393   0.085775   -3.56779
       0.5149     0.3992     0.8334     0.0148                0.0009     0.8749     0.0004     0.9317     0.0004
6     4.09355   5.278611   3.082695   1.121075   3.329469          .   3.514154   -0.28392   3.430049   -0.30146
       0.0001     0.0001     0.0021     0.2627     0.0009                0.0005     0.7766     0.0006     0.7632
7    0.494111   0.658955   -0.36795   -2.62787    -0.1575   -3.51415          .   -3.73861   -0.07172   -3.75248
       0.6214     0.5102     0.7130     0.0088     0.8749     0.0005                0.0002     0.9428     0.0002
8     4.31801   5.562533   3.307155   1.404997   3.553929   0.283922   3.738614          .   3.654509   -0.01754
       0.0001     0.0001     0.0010     0.1605     0.0004     0.7766     0.0002                0.0003     0.9860
9    0.565836    0.74306   -0.29622   -2.54376   -0.08578   -3.43005   0.071725   -3.65451          .   -3.66838
       0.5717     0.4577     0.7672     0.0112     0.9317     0.0006     0.9428     0.0003                0.0003
10   4.331876   5.580073   3.321021   1.422536   3.567795   0.301461    3.75248   0.017539   3.668375          .
       0.0001     0.0001     0.0009     0.1554     0.0004     0.7632     0.0002     0.9860     0.0003
```

```
                                TIME   SEASON    SPCR LSMEAN   Number
                                  1      S        1.79668971      1
                                  1      W        1.88799999      2
                                  2      S        2.22193457      3
                                  2      W        2.70434088      4
                                  3      S        2.70642980      5
                                  3      W        3.44281024      6
                                  4      S        2.95742073      7
                                  4      W        3.49393335      8
                                  5      S        3.64778571      9
                                  5      W        3.84529445     10

                         T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

i/j       1          2          3          4          5          6          7          8          9          10
     1      .        -0.25013   -0.99342   -2.48636   -2.12526   -4.50928    -2.7116   -4.64932   -4.32437   -5.61182
                       0.8026     0.3209     0.0132     0.0340     0.0001     0.0069     0.0001     0.0001     0.0001
     2    0.25013       .       -0.91476   -2.82864   -2.24195   -5.38744    -2.9295   -5.56459   -4.82065   -6.78206
           0.8026                 0.3607     0.0048     0.0253     0.0001     0.0035     0.0001     0.0001     0.0001
     3   0.993421   0.914759        .      -1.32147   -1.13184   -3.34439   -1.71818   -3.48443   -3.33095   -4.44693
           0.3209     0.3607                 0.1868     0.2581     0.0009     0.0863     0.0005     0.0009     0.0001
     4   2.486362   2.828635   1.321473        .      -0.00572   -2.55881   -0.69327   -2.73595   -2.58441   -3.95342
           0.0132     0.0048     0.1868                 0.9954     0.0107     0.4884     0.0064     0.0100     0.0001
     5   2.125257   2.241955   1.131836   0.005722        .      -2.01719   -0.58634   -2.15724   -2.19911   -3.11973
           0.0340     0.0253     0.2581     0.9954                 0.0441     0.5579     0.0314     0.0282     0.0019
     6   4.509279   5.387445    3.34439   2.558809   2.017194        .       1.329645   -0.17714    -0.5615   -1.39461
           0.0001     0.0001     0.0009     0.0107     0.0441                 0.1841     0.8595     0.5747     0.1636
     7     2.7116   2.929504    1.71818   0.693271   0.586343   -1.32965        .      -1.46969   -1.61277   -2.43219
           0.0069     0.0035     0.0863     0.4884     0.5579     0.1841                 0.1422     0.1073     0.0153
     8   4.649322   5.564587   3.484433   2.735952   2.157237   0.177142   1.469689        .      -0.42145   -1.21747
           0.0001     0.0001     0.0005     0.0064     0.0314     0.8595     0.1422                 0.6736     0.2239
     9   4.324372   4.820646   3.330951   2.584413   2.199115   0.561497   1.612771   0.421453        .      -0.54104
           0.0001     0.0001     0.0009     0.0100     0.0282     0.5747     0.1073     0.6736                 0.5887
    10   5.611818   6.782059   4.446929   3.953424   3.119734   1.394615   2.432185   1.217472   0.541043        .
           0.0001     0.0001     0.0001     0.0001     0.0019     0.1636     0.0153     0.2239     0.5887
```

Table A7: (Continued).

```
                              TIME   SEASON    ORHY LSMEAN    Number

                                1      S        1.19658004       1
                                1      W        0.73512964       2
                                2      S        1.64430314       3
                                2      W        1.48458324       4
                                3      S        1.86529416       5
                                3      W        1.86821674       6
                                4      S        2.32335411       7
                                4      W        1.86184349       8
                                5      S        3.74310570       9
                                5      W        3.90103645      10

                             T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|
 i/j        1          2          3          4          5          6          7          8          9         10
 1          .   1.603742   -1.32699   -1.00094   -1.98198   -2.33423    -3.3396   -2.31208   -7.54755   -9.39917
                  0.1093     0.1850     0.3172     0.0479     0.0199     0.0009     0.0211     0.0001     0.0001
 2   -1.60374          .   -3.15978   -3.29469   -3.92782   -4.98119   -5.51978   -4.95317    -10.454   -13.9177
       0.1093                0.0017     0.0010     0.0001     0.0001     0.0001     0.0001     0.0001     0.0001
 3    1.32699   3.159776          .   0.555097   -0.65499    -0.7782   -2.01261   -0.75605   -6.22056   -7.84314
       0.1850     0.0017                0.5790     0.5127     0.4367     0.0446     0.4499     0.0001     0.0001
 4   1.000937   3.294688    -0.5551          .   -1.32314    -1.6865    -2.9151   -1.65848   -7.84935    -10.623
       0.3172     0.0010     0.5790                0.1863     0.0922     0.0037     0.0977     0.0001     0.0001
 5   1.981977   3.927817   0.654987   1.323137          .   -0.01016   -1.35763   0.011993   -5.56558    -7.0751
       0.0479     0.0001     0.5127     0.1863                0.9919     0.1751     0.9904     0.0001     0.0001
 6   2.334232   4.981187   0.778198   1.686499   0.010157          .    -1.5818   0.028018   -6.51606   -8.93652
       0.0199     0.0001     0.4367     0.0922     0.9919                0.1142     0.9777     0.0001     0.0001
 7   3.339605   5.519776   2.012614   2.915096   1.357627   1.581802          .   1.603952   -4.20795   -5.48314
       0.0009     0.0001     0.0446     0.0037     0.1751     0.1142                0.1092     0.0001     0.0001
 8   2.312082   4.953169   0.756048   1.658481   -0.01199   -0.02802   -1.60395          .   -6.53821   -8.96454
       0.0211     0.0001     0.4499     0.0977     0.9904     0.9777     0.1092                0.0001     0.0001
 9   7.547554   10.45403   6.220564   7.849355   5.565577    6.51606    4.20795    6.53821          .   -0.54888
       0.0001     0.0001     0.0001     0.0001     0.0001     0.0001     0.0001     0.0001                0.5833
10   9.399171   13.91771   7.843137   10.62302   7.075096   8.936519   5.483137   8.964537   0.548878          .
       0.0001     0.0001     0.0001     0.0001     0.0001     0.0001     0.0001     0.0001     0.5833


                              TIME   SEASON          HIJA    LSMEAN
                                                    LSMEAN   Number
                                1      S        1.81254463       1
                                1      W        1.25100459       2
                                2      S        2.73123859       3
                                2      W        1.90480665       4
                                3      S        3.30291523       5
                                3      W        2.07662665       6
                                4      S        3.46759445       7
                                4    . W        2.16144800       8
                                5      S        3.28905587       9
                                5      W        2.25528088      10

                              T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|

 i/j        1          2          3          4          5          6          7          8          9         10
 1          .   1.226576   -1.71133   -0.20153   -2.77624   -0.57684     -3.083   -0.76211   -2.75042   -0.96707
                  0.2204     0.0875     0.8404     0.0057     0.5643     0.0021     0.4463     0.0061     0.3339
 2   -1.22658          .   -3.23329   -1.80643     -4.482   -2.28116   -4.84171   -2.51551   -4.45173   -2.77477
       0.2204                0.0013     0.0713     0.0001     0.0229     0.0001     0.0121     0.0001     0.0057
 3   1.711328   3.233286          .   1.805181   -1.06491   1.429874   -1.37167   1.244598   -1.03909   1.039638
       0.0875     0.0013                0.0715     0.2873     0.1533     0.1707     0.2137     0.2992     0.2989
 4   0.201529   1.806425   -1.80518          .    -3.0539   -0.47473   -3.41361   -0.70909   -3.02363   -0.96834
       0.8404     0.0713     0.0715                0.0024     0.6351     0.0007     0.4785     0.0026     0.3333
 5   2.776238   4.482003    1.06491   3.053898          .   2.678591   -0.30676   2.493315   0.025817   2.288355
       0.0057     0.0001     0.2873     0.0024                0.0076     0.7591     0.0129     0.9794     0.0225
 6   0.576836   2.281156   -1.42987   0.474731   -2.67859          .    -3.0383   -0.23436   -2.64832   -0.49361
       0.5643     0.0229     0.1533     0.6351     0.0076                0.0025     0.8148     0.0083     0.6218
 7   3.082999   4.841713   1.371671   3.413608   0.306762   3.038301          .   2.853025   0.332579   2.648065
       0.0021     0.0001     0.1707     0.0007     0.7591     0.0025                0.0045     0.7396     0.0083
 8   0.762112   2.515513    -1.2446   0.709088   -2.49331   0.234358   -2.85302          .   -2.46304   -0.25926
       0.4463     0.0121     0.2137     0.4785     0.0129     0.8148     0.0045                0.0140     0.7955
 9   2.750421    4.45173   1.039093   3.023625   -0.02582   2.648318   -0.33258   2.463042          .   2.258082
       0.0061     0.0001     0.2992     0.0026     0.9794     0.0083     0.7396     0.0140                0.0243
10   0.967072   2.774769   -1.03964   0.968344   -2.28836   0.493613   -2.64807   0.259256   -2.25808          .
       0.3339     0.0057     0.2989     0.3333     0.0225     0.6218     0.0083     0.7955     0.0243
```

Table A8: Least square means and probability values for pairwise grazing by season comparison.

```
                           Least Squares Means
GRAZE    SEASON         ATCO  T for H0: LSMEAN(i)=LSMEAN(j) / Pr > |T|
                      LSMEAN   i/j         1          2          3          4
ATCO
G        S        5.04739089    1          .   0.998071   3.607193   2.535332
                                                 0.3186     0.0003     0.0115
G        W        4.86044569    2   -0.99807          .   3.231738   1.944499
                                      0.3186                0.0013     0.0523
U        S        4.25512029    3   -3.60719   -3.23174          .   -1.69448
                                      0.0003     0.0013                0.0907
U        W        4.57250670    4   -2.53533    -1.9445   1.694476          .
                                      0.0115     0.0523     0.0907
CELA

G        S        2.93420676    1          .   -2.13658   -1.89337   -3.35032
                                                 0.0330     0.0588     0.0009
G        W        3.51544920    2   2.136575          .    -0.0836   -1.53528
                                      0.0330                0.9334     0.1252
U        S        3.53819111    3   1.893369   0.083596          .   -1.13015
                                      0.0588     0.9334                0.2589
U        W        3.84564142    4   3.350321    1.53528   1.130149          .
                                      0.0009     0.1252     0.2589
ARSP

G        S        0.71597696    1          .   -7.89024   -9.75265   -11.6749
                                                 0.0001     0.0001     0.0001
G        W        2.56915989    2   7.890239          .   -3.54576   -4.78726
                                      0.0001                0.0004     0.0001
U        S        3.40195252    3   9.752649   3.545755          .   -0.23891
                                      0.0001     0.0004                0.8113
U        W        3.45806437    4    11.6749    4.78726   0.238906          .
                                      0.0001     0.0001     0.8113
SPCR

G        S        2.86441670    1          .   -1.49794   1.465407   -0.32517
                                                 0.1347     0.1433     0.7452
G        W        3.21025909    2   1.497937          .   3.216279   1.483442
                                      0.1347                0.0014     0.1385
U        S        2.46768751    3   -1.46541   -3.21628          .   -2.04352
                                      0.1433     0.0014                0.0414
U        W        2.93949247    4   0.325174   -1.48344   2.043516          .
                                      0.7452     0.1385     0.0414
ORHY

G        S        2.13755025    1          .   0.504452   -0.15912   1.335196
                                                 0.6141     0.8736     0.1823
G        W        2.04575078    2   -0.50445          .   -0.69104   1.050818
                                      0.6141                0.4898     0.2938
U        S        2.17150461    3    0.15912   0.691036          .    1.52178
                                      0.8736     0.4898                0.1286
U        W        1.89457305    4    -1.3352   -1.05082   -1.52178          .
                                      0.1823     0.2938     0.1286
HIJA

G        S        3.03584843    1          .   3.695386   0.678476   3.944287
                                                 0.0002     0.4977     0.0001
G        W        1.96586739    2   -3.69539          .    -2.8998   0.314838
                                      0.0002                0.0039     0.7530
U        S        2.80549107    3   -0.67848   2.899802          .   3.148703
                                      0.4977     0.0039                0.0017
U        W        1.89379932    4   -3.94429   -0.31484    -3.1487          .
                                      0.0001     0.7530     0.0017
```

Table A9: Multivariate and univariate analysis of variance for time effects on shrubs and grasses.

```
           Manova Test Criteria and F Approximations for the Hypothesis of no Overall TIME Effect
                       H = Type III SS&CP Matrix for TIME   E = Error SS&CP Matrix
                                     S=2    M=0.5    N=308.5

                  Statistic                       Value          F      Num DF   Den DF  Pr > F
                  Wilks' Lambda              0.70100368    30.0792          8      1238  0.0001
                  Pillai's Trace             0.31633746    29.1224          8      1240  0.0001
                  Hotelling-Lawley Trace     0.40178845    31.0382          8      1236  0.0001
                  Roy's Greatest Root        0.32587786    50.5111          4       620  0.0001

                                   General Linear Models Procedure

Dependent Variable: SHRUB

Source                  DF          Sum of Squares          Mean Square       F Value        Pr > F
Model                   19          1633.92333583          85.99596504          8.87         0.0001
Error                  620          6011.39141427           9.69579260
Corrected Total        639          7645.31475009

                  R-Square                   C.V.             Root MSE                   SHRUB Mean
                  0.213716               28.42863           3.11380677                  10.95306664

Source                  DF            Type III SS          Mean Square       F Value        Pr > F
TIME                     4           539.03064991         134.75766248         13.90         0.0001
GRAZE                    1           404.14659566         404.14659566         41.68         0.0001
TIME*GRAZE               4           168.52650421          42.13162605          4.35         0.0018
SEASON                   1           294.78951065         294.78951065         30.40         0.0001
TIME*SEASON              4            51.75567880          12.93891970          1.33         0.2557
GRAZE*SEASON             1            84.35698269          84.35698269          8.70         0.0033
TIME*GRAZE*SEASON        4            26.72665060           6.68166265          0.69         0.5997

Contrast                DF            Contrast SS          Mean Square       F Value        Pr > F

T1 vs T2                 1           145.25156957         145.25156957         14.98         0.0001
T2 vs T3                 1            17.26058323          17.26058323          1.78         0.1826
T3 vs T4                 1             8.04058481           8.04058481          0.83         0.3628
T4 vs T5                 1           205.28294263         205.28294263         21.17         0.0001
T1 vs T5                 1            85.85580641          85.85580641          8.85         0.0030

Dependent Variable: GRASS

Source                  DF          Sum of Squares          Mean Square       F Value        Pr > F
Model                   19          2718.47548634         143.07765718         13.32         0.0001
Error                  620          6658.62870207          10.73972371
Corrected Total        639          9377.10418840

                  R-Square                   C.V.             Root MSE                   GRASS Mean
                  0.289906               45.42537           3.27715177                   7.21436425
Source                  DF            Type III SS          Mean Square       F Value        Pr > F
TIME                     4          2167.58507865         541.89626966         50.46         0.0001
GRAZE                    1            40.62724277          40.62724277          3.78         0.0522
TIME*GRAZE               4            41.23267080          10.30816770          0.96         0.4290
SEASON                   1            80.75864534          80.75864534          7.52         0.0063
TIME*SEASON              4            10.94830206           2.73707552          0.25         0.9067
GRAZE*SEASON             1             0.33772509           0.33772509          0.03         0.8593
TIME*GRAZE*SEASON        4             9.26494892           2.31623723          0.22         0.9297

Contrast                DF            Contrast SS          Mean Square       F Value        Pr > F
T1 vs T2                 1           221.24017589         221.24017589         20.60         0.0001
T2 vs T3                 1            90.89412694          90.89412694          8.46         0.0038
T3 vs T4                 1            13.84093611          13.84093611          1.29         0.2567
T4 vs T5                 1           268.13525793         268.13525793         24.97         0.0001
T1 vs T5                 1          1980.53148712        1980.53148712        184.41         0.0001
```

Table A10: Results of the analysis of grazing treatments by presence of exotic annuals for study periods.

```
Bonferroni Correction to adjust the 0.05 probability
for four independent tests
p=.05/k
k=4 independent tests
p=0.0125

        ANALYSIS OF 2 BY 2 TABLE FOR 1958
         TABLE OF TRT BY PRESENCE-TEST 1.
   TRT       PRESENCE
   Frequency|
   Percent  |
   Row Pct  |
   Col Pct  |absent  |present |  Total
   ---------+--------+--------+
   grazed   |    121 |      7 |    128
            |  47.27 |   2.73 |  50.00
            |  94.53 |   5.47 |
            |  49.59 |  58.33 |
   ---------+--------+--------+
   ungrazed |    123 |      5 |    128
            |  48.05 |   1.95 |  50.00
            |  96.09 |   3.91 |
            |  50.41 |  41.67 |
   ---------+--------+--------+
   Total         244       12      256
               95.31     4.69   100.00

STATISTICS FOR TABLE OF TRT BY PRESENCE

Statistic                     DF       Value      Prob
------------------------------------------------------
Chi-Square                     1       0.350     0.554
Likelihood Ratio Chi-Square    1       0.351     0.553
Continuity Adj. Chi-Square     1       0.087     0.767
Mantel-Haenszel Chi-Square     1       0.348     0.555
Fisher's Exact Test (Left)                       0.384
                    (Right)                      0.812
                    (2-Tail)                     0.769
Sample Size = 256
-------------------------------------------------------

          ANALYSIS OF 2 BY 2 TABLE FOR 1969

           TABLE OF TRT BY PRESENCE-TEST 2.

   TRT       PRESENCE
   Frequency|
   Percent  |
   Row Pct  |
   Col Pct  |absent  |present |  Total
   ---------+--------+--------+
   grazed   |    104 |     24 |    128
            |  40.63 |   9.38 |  50.00
            |  81.25 |  18.75 |
            |  49.29 |  53.33 |
   ---------+--------+--------+
   ungrazed |    107 |     21 |    128
            |  41.80 |   8.20 |  50.00
            |  83.59 |  16.41 |
            |  50.71 |  46.67 |
   ---------+--------+--------+
   Total         211       45      256
               82.42    17.58   100.00
```

Table A10: (Continued).

```
                 ANALYSIS OF 2 BY 2 TABLE FOR 1969

        STATISTICS FOR TABLE OF TRT BY PRESENCE

        Statistic                     DF       Value       Prob
        ------------------------------------------------------
        Chi-Square                     1       0.243      0.622
        Likelihood Ratio Chi-Square    1       0.243      0.622
        Continuity Adj. Chi-Square     1       0.108      0.743
        Mantel-Haenszel Chi-Square     1       0.242      0.623
        Fisher's Exact Test (Left)                        0.371
                            (Right)                       0.744
                            (2-Tail)                      0.743

         Sample Size = 256
        ------------------------------------------------------
```

```
                 ANALYSIS OF 2 BY 2 TABLE FOR 1975

                      TABLE OF TRT BY PRESENCE-TEST 3.

                 TRT          PRESENCE

                 Frequency|
                 Percent  |
                 Row Pct  |
                 Col Pct  |absent  |present |  Total
                 ---------+--------+--------+
                 grazed   |    101 |     27 |    128
                          |  39.45 |  10.55 |  50.00
                          |  78.91 |  21.09 |
                          |  48.79 |  55.10 |
                 ---------+--------+--------+
                 ungrazed |    106 |     22 |    128
                          |  41.41 |   8.59 |  50.00
                          |  82.81 |  17.19 |
                          |  51.21 |  44.90 |
                 ---------+--------+--------+
                 Total         207       49      256
                             80.86    19.14   100.00

             STATISTICS FOR TABLE OF TRT BY PRESENCE

        Statistic                     DF       Value       Prob
        ------------------------------------------------------
        Chi-Square                     1       0.631      0.427
        Likelihood Ratio Chi-Square    1       0.632      0.427
        Continuity Adj. Chi-Square     1       0.404      0.525
        Mantel-Haenszel Chi-Square     1       0.629      0.428
        Fisher's Exact Test (Left)                        0.263
                            (Right)                       0.830
                            (2-Tail)                      0.525
        Sample Size = 256
        ------------------------------------------------------
```

Table A10: (Continued).

```
              ANALYSIS OF 2 BY 2 TABLE FOR 1994

               TABLE OF TRT BY PRESENCE-TEST 4.

          TRT        PRESENCE

          Frequency|
          Percent  |
          Row Pct  |
          Col Pct  |absent  |present |  Total
          ---------+--------+--------+
          grazed   |     71 |     57 |    128
                   |  27.73 |  22.27 |  50.00
                   |  55.47 |  44.53 |
                   |  40.57 |  70.37 |
          ---------+--------+--------+
          ungrazed |    104 |     24 |    128
                   |  40.63 |   9.38 |  50.00
                   |  81.25 |  18.75 |
                   |  59.43 |  29.63 |
          ---------+--------+--------+
          Total         175       81      256
                      68.36    31.64   100.00

           STATISTICS FOR TABLE OF TRT BY PRESENCE

   Statistic                     DF       Value        Prob
   ------------------------------------------------------
   Chi-Square                     1      19.667       0.000
   Likelihood Ratio Chi-Square    1      20.104       0.000
   Continuity Adj. Chi-Square     1      18.493       0.000
   Mantel-Haenszel Chi-Square     1      19.590       0.000
   Fisher's Exact Test (Left)                      7.05E-06
                       (Right)                        1.000
                       (2-Tail)                    1.41E-05

   Sample Size = 256
   ------------------------------------------------------
```

Table A11: Analysis of the intensity of invasion by annuals for grazing treatments in 1994.

```
INTENSIT     TRT

Frequency|
Percent  |
Row Pct  |
Col Pct  |grazed  |ungrazed|  Total
---------+--------+--------+
heavy    |     16 |      9 |     25
         |  19.75 |  11.11 |  30.86
         |  64.00 |  36.00 |
         |  28.07 |  37.50 |
---------+--------+--------+
ligth    |     41 |     15 |     56
         |  50.62 |  18.52 |  69.14
         |  73.21 |  26.79 |
         |  71.93 |  62.50 |
---------+--------+--------+
Total          57       24       81
            70.37    29.63   100.00


         STATISTICS FOR TABLE OF INTENSIT BY TRT

Statistic                     DF       Value       Prob
------------------------------------------------------
Chi-Square                     1       0.704      0.402
Likelihood Ratio Chi-Square    1       0.690      0.406
Continuity Adj. Chi-Square     1       0.331      0.565
Mantel-Haenszel Chi-Square     1       0.695      0.404
Fisher's Exact Test (Left)                        0.280
                    (Right)                       0.864
                    (2-Tail)                      0.437

Sample Size = 81
------------------------------------------------------
```

Table A12: Matrices for the analysis of ATCO plant survival.

General plant survival matrix. Number of individuals surviving in 5 ATCO cohorts.

FACTOR	n	Cohort	1935	1958	1969	1975	1994
Time	128	C1	1312	500	161	58	14
		C2		858	385	180	61
		C3			351	197	76
		C4				146	51
		C5					353
		Total	1312	1358	897	581	555

Matrix for the analysis of plant survival of ATCO by soil type.

FACTOR	n	Cohort	1935	1958	1969	1975	1994
C-Soil	76	C1	819	323	118	47	12
		C2		600	292	145	53
		C3			250	148	63
		C4				108	37
		C5					273
D-Soil	52	C1	493	177	43	11	2
		C2		258	93	35	8
		C3			101	49	13
		C4				38	14
		C5					80
		Total	1312	1358	897	581	555

Matrix for the analysis of plant survival of ATCO by grazing treatment.

TREAT.	n	Cohort	1935	1958	1969	1975	1994
Ungrazed	64	C1	642	233	51	20	3
		C2		359	144	69	29
		C3			136	71	30
		C4				70	30
		C5					124
Grazed	64	C1	670	267	110	38	11
		C2		499	241	111	32
		C3			215	126	46
		C4				76	21
		C5					229
		Total	1312	1358	897	581	555

n=number of plots sampled

Table A13: Matrices for the analysis of CELA plant survival.

General plant survival matrix. Number of individuals surviving in 5 CELA cohorts.

FACTOR	n	Cohort	1935	1958	1969	1975	1994
Time	128	1	2182	1237	931	728	370
		2		607	392	279	124
		3			447	297	129
		4				255	83
		5					334
			2182	1844	1770	1559	1040

Matrix for the analysis of plant survival of CELA by soil type.

FACTOR	n	Cohort	1935	1958	1969	1975	1994
C-SOIL	76	1	1054	567	430	330	196
		2		250	160	104	50
		3			176	110	49
		4				98	37
		5					152
D-SOIL	52	1	1128	670	501	398	174
		2		357	232	175	74
		3			271	187	80
		4				157	46
		5					182
			2182	1844	1770	1559	1040

Matrix for the analysis of plant survival of CELA by grazing treatment.

TREAT.	n	Cohort	1935	1958	1969	1975	1994
UNGRA.	64	1	1052	657	490	384	220
		2		263	177	128	62
		3			176	121	54
		4				100	38
		5					174
GRAZED	64	1	1130	580	441	344	150
		2		344	215	151	62
		3			271	176	75
		4				155	45
		5					160
			2182	1844	1770	1559	1040

n=number of plots sampled

Table A14: Matrices for the analysis of ARSP plant survival.

General plant survival matrix. Number of individuals surviving in 5 ARSP cohorts.

FACTOR	n	Cohort	1935	1958	1969	1975	1994
Time	128	1	494	252	182	123	46
		2		315	238	189	99
		3			260	135	68
		4				144	58
		5					1261
			494	567	680	591	1532

Matrix for the analysis of plant survival of ARSP by soil type.

FACTOR	n	Cohort	1935	1958	1969	1975	1994
C-SOIL	76	1	384	196	143	100	37
		2		196	154	119	61
		3			177	83	39
		4				86	40
		5					887
D-SOIL	52	1	110	56	39	23	9
		2		119	84	70	38
		3			83	52	29
		4				58	18
		5					374
			494	567	680	591	1532

Matrix for the analysis of plant survival of ARSP by grazing treatment.

TREAT.	n	Cohort	1935	1958	1969	1975	1994
UNGRA.	64	1	260	159	128	89	35
		2		218	170	137	80
		3			159	88	47
		4				115	48
		5					1037
GRAZED	64	1	234	93	54	34	11
		2		97	68	52	19
		3			101	47	21
		4				29	10
		5					224
			494	567	680	591	1532

n=number of plots sampled

Table A15: Example of survival analysis for *Artemisia spinescens*.

```
  Model 1.

  Hypothesis: Plant survival during any one period is constant.

  - INPUT --- Proc Title ARSP SURVIVAL OVERALL;

        CPU time in seconds for last procedure was     0.00
  - INPUT --- Proc Model  NPAR=10;
  0 INPUT ---      COHORT= 494 /*1935 COHORT*/;
    INPUT ---         242:(1-S(1)**2.3);
    INPUT ---         70:S(1)**2.3*(1-S(2)**1.1);
    INPUT ---         59:S(1)**2.3*S(2)**1.1*(1-S(3)**.6);
    INPUT ---         77:S(1)**2.3*S(2)**1.1*S(3)**.6*(1-S(4)**1.9);
  0 INPUT ---      COHORT =315 /*1958 COHORT*/;
    INPUT ---         77:(1-S(5)**1.1);
    INPUT ---         49:S(5)**1.1*(1-S(6)**.6);
    INPUT ---         90:S(5)**1.1*S(6)**.6*(1-S(7)**1.9);
  0 INPUT ---      COHORT= 260 /*1969 COHORT*/;
    INPUT ---         125:(1-S(8)**.6);
    INPUT ---         67:S(8)**.6*(1-S(9)**1.9);
  0 INPUT ---      COHORT=144 /*1975 COHORT*/;
    INPUT ---         86:(1-S(10)**1.9);
  0 INPUT ---      LABELS;
    INPUT ---         S(1)=C135-58;
    INPUT ---         S(2)=C158-69;
    INPUT ---         S(3)=C169-75;
    INPUT ---         S(4)=C175-94;
    INPUT ---         S(5)=C258-69;
    INPUT ---         S(6)=C269-75;
    INPUT ---         S(7)=C275-94;
    INPUT ---         S(8)=C369-75;
    INPUT ---         S(9)=C375-94;
    INPUT ---         S(10)=C475-94;

        CPU time in seconds for last procedure was     0.27


  - INPUT --- PROC ESTIMATE NSIG=5 MAXFN=2000 NAME=TIMEEQ;
  0 INPUT ---      INITIAL;
    INPUT ---         ALL=0.50;
  0 INPUT ---      CONSTRAINTS;
    INPUT ---         S(2)=S(5);
    INPUT ---         S(3)=S(6);
    INPUT ---         S(3)=S(8);
    INPUT ---         S(4)=S(7);
    INPUT ---         S(4)=S(9);
    INPUT ---         S(4)=S(10);

        Number of parameters in model  = 10

        Number of parameters set equal =  6

        Number of parameters fixed     =  0

        Number of parameters estimated =  4

        Final function value  1511.5004     (Error Return =   0)

        Number of significant digits       9

        Number of function evaluations     91
```

Table A15: (Continued).

```
                                                     95% Confidence Interval
 I    Parameter       S(I)          Standard Error       Lower          Upper
---   ---------   -------------    --------------  -------------  -------------
 1        1        0.74627958       0.14306912E-01  0.71823803      0.77432113
 2        2        0.76122801       0.17193596E-01  0.72752856      0.79492746
 3        3        0.49697098       0.22931941E-01  0.45202437      0.54191758
 4        4        0.66340677       0.15607827E-01  0.63281543      0.69399811
 5        2        0.76122801       0.17193596E-01  0.72752856      0.79492746
 6        3        0.49697098       0.22931941E-01  0.45202437      0.54191758
 7        4        0.66340677       0.15607827E-01  0.63281543      0.69399811
 8        3        0.49697098       0.22931941E-01  0.45202437      0.54191758
 9        4        0.66340677       0.15607827E-01  0.63281543      0.69399811
10        4        0.66340677       0.15607827E-01  0.63281543      0.69399811


              Variance-Covariance matrix of estimates on diagonal and below,

               Correlation matrix of estimates above diagonal.

   |      1              2              3              4              5              6              7              8               9             10
---+-------------------------------------------------------------------------------------------------------------------------------------------------------
   |
 1 | 0.20468773E-03-0.24659948E-12-0.61971663E-12-0.43673941E-12-0.24659948E-12-0.61971663E-12-0.43673941E-12-0.61971663E-12  -0.43673941E-12-0.43673941E-12
   |
 2 |-0.60660334E-16 0.29561976E-03 0.58260523E-12 0.65093621E-12  1.0000000      0.58260523E-12 0.65093621E-12 0.58260523E-12   0.65093621E-12 0.65093621E-12
   |
 3 |-0.20331989E-15 0.22971107E-15 0.52587392E-03 0.24432145E-12-0.51567055E-12  1.0000000      0.24432145E-12  1.0000000       0.24432145E-12 0.24432145E-12
   |
 4 |-0.97523828E-16 0.17468178E-15 0.87446990E-16 0.24360427E-03 0.85599798E-12-0.27247551E-12  1.0000000     -0.27247551E-12   1.0000000      1.0000000
   |
 5 |-0.60660334E-16 0.29561976E-03-0.20331989E-15 0.22971107E-15 0.29561976E-03 0.58260523E-12 0.65093621E-12 0.58260523E-12   0.65093621E-12 0.65093621E-12
   |
 6 |-0.20331989E-15 0.22971107E-15 0.52587392E-03-0.97523828E-16 0.22971107E-15 0.52587392E-03 0.24432145E-12  1.0000000       0.24432145E-12 0.24432145E-12
   |
 7 |-0.97523828E-16 0.17468178E-15 0.87446990E-16 0.24360427E-03 0.17468178E-15 0.87446990E-16 0.24360427E-03-0.27247551E-12   1.0000000      1.0000000
   |
 8 |-0.20331989E-15 0.22971107E-15 0.52587392E-03-0.97523828E-16 0.22971107E-15 0.52587392E-03-0.97523828E-16 0.52587392E-03   0.24432145E-12 0.24432145E-12
   |
 9 |-0.97523828E-16 0.17468178E-15 0.87446990E-16 0.24360427E-03 0.17468178E-15 0.87446990E-16 0.24360427E-03 0.87446990E-16   0.24360427E-03 1.0000000
   |
10 |-0.97523828E-16 0.17468178E-15 0.87446990E-16 0.24360427E-03 0.17468178E-15 0.87446990E-16 0.24360427E-03 0.87446990E-16   0.24360427E-03 0.24360427E-03


 0  Cohort  Cell   Observed  Expected  Chi-square  Note
    ------  ----   --------  --------  ----------  -------------
      1       1       242    242.000      0.000    0 < P < 1
      1       2        70     65.333      0.333    0 < P < 1
      1       3        59     63.961      0.385    0 < P < 1
      1       4        77     66.440      1.679    0 < P < 1
      1       5        46     56.266      1.873    0 < P < 1
      2       1        77     81.667      0.267    0 < P < 1
      2       2        49     79.951     11.982    0 < P < 1
      2       3        90     83.050      0.582    0 < P < 1
      2       4        99     70.333     11.685    0 < P < 1
      3       1       125     89.088     14.476    0 < P < 1
      3       2        67     92.541      7.049    0 < P < 1
      3       3        68     78.371      1.372    0 < P < 1
      4       1        86     77.970      0.827    0 < P < 1
      4       2        58     66.030      0.977    0 < P < 1
    -----------------------------------------------------------
    Total (Degrees of freedom =   6)     53.486
    Pr(Larger Chi-square) = 0.0000
    With pooling, Degrees of freedom =  6  Chi-square =      53.486
    Pr(Larger Chi-square) = 0.0000


    Log-likelihood = -55.175481

    CPU time in seconds for last procedure was     0.44
```

Table A15: (Continued).

```
Hypothesis 2: Survival rate for each recruit class for each period is equal (Model 2).

 - INPUT --- PROC ESTIMATE NSIG=5 MAXFN=2000 NAME=AGEEQ;
 0 INPUT ---     INITIAL;
   INPUT ---        ALL=0.50;
 0 INPUT ---     CONSTRAINTS;
   INPUT ---        S(1)=S(5);
   INPUT ---        S(1)=S(8);
   INPUT ---        S(1)=S(10);
   INPUT ---        S(2)=S(6);
   INPUT ---        S(2)=S(9);
   INPUT ---        S(3)=S(7);

       Number of parameters in model  = 10

       Number of parameters set equal =  6

       Number of parameters fixed     =  0

       Number of parameters estimated =  4

      Final function value  1560.0639     (Error Return =   0)

      Number of significant digits        7

      Number of function evaluations     93

                                                             95% Confidence Interval
     I    Parameter     S(I)          Standard Error        Lower            Upper
    ---   ---------  --------------   --------------   --------------   --------------
     1        1       0.68835906      0.11558827E-01    0.66570376       0.71101436
     2        2       0.71306644      0.17151501E-01    0.67944950       0.74668338
     3        3       0.65570827      0.25130945E-01    0.60645161       0.70496492
     4        4       0.59591681      0.38347105E-01    0.52075648       0.67107713
     5        1       0.68835906      0.11558827E-01    0.66570376       0.71101436
     6        2       0.71306644      0.17151501E-01    0.67944950       0.74668338
     7        3       0.65570827      0.25130945E-01    0.60645161       0.70496492
     8        1       0.68835906      0.11558827E-01    0.66570376       0.71101436
     9        2       0.71306644      0.17151501E-01    0.67944950       0.74668338
    10        1       0.68835906      0.11558827E-01    0.66570376       0.71101436
```

```
Variance-Covariance matrix of estimates on diagonal and below,

Correlation matrix of estimates above diagonal.

          1              2              3              4              5              6              7              8              9              10
---+------------------------------------------------------------------------------------------------------------------------------------------------------
   |
 1 | 0.13360648E-03 0.36643865E-13 0.44047323E-12 0.14086083E-11  1.0000000     0.36643865E-13 0.44047323E-12  1.0000000     0.36643865E-13 1.0000000
   |
 2 | 0.72646912E-17 0.29417397E-03 0.71529054E-12-0.52114766E-12 0.36643865E-13 1.0000000      0.71529054E-12 0.36643865E-13 1.0000000      0.36643865E-13
   |
 3 | 0.12795054E-15 0.30831413E-15 0.63156442E-03 0.14868644E-11  1.0127020     0.29684597E-12  1.0000000      1.0127020     0.29684597E-12 1.0127020
   |
 4 | 0.62436219E-15-0.34276423E-15 0.14328936E-14 0.14705004E-02 0.28866609E-12 0.46876884E-12 0.64788092E-12 0.28866609E-12 0.46876884E-12 0.28866609E-12
   |
 5 | 0.13360648E-03 0.72646912E-17 0.29417397E-03 0.12795054E-15 0.13360648E-03 0.36643865E-13 0.44047323E-12  1.0000000     0.36643865E-13 1.0000000
   |
 6 | 0.72646912E-17 0.29417397E-03 0.12795054E-15 0.30831413E-15 0.72646912E-17 0.29417397E-03 0.71529054E-12 0.36643865E-13 1.0000000      0.36643865E-13
   |
 7 | 0.12795054E-15 0.30831413E-15 0.63156442E-03 0.62436219E-15 0.12795054E-15 0.30831413E-15 0.63156442E-03  1.0127020     0.29684597E-12 1.0127020
   |
 8 | 0.13360648E-03 0.72646912E-17 0.29417397E-03 0.12795054E-15 0.13360648E-03 0.72646912E-17 0.29417397E-03 0.13360648E-03 0.36643865E-13 1.0000000
   |
 9 | 0.72646912E-17 0.29417397E-03 0.12795054E-15 0.30831413E-15 0.72646912E-17 0.29417397E-03 0.12795054E-15 0.72646912E-17 0.29417397E-03 0.36643865E-13
   |
10 | 0.13360648E-03 0.72646912E-17 0.29417397E-03 0.12795054E-15 0.13360648E-03 0.72646912E-17 0.29417397E-03 0.13360648E-03 0.72646912E-17 0.13360648E-03
```

Table A15: (Continued).

```
0  Cohort  Cell   Observed  Expected  Chi-square  Note
   ------  ----   --------  --------  ----------  ------------
       1     1       242    284.733      6.413    0 < P < 1
       1     2        70     65.008      0.383    0 < P < 1
       1     3        59     32.272     22.137    0 < P < 1
       1     4        77     70.106      0.678    0 < P < 1
       1     5        46     41.882      0.405    0 < P < 1
       2     1        77    106.115      7.988    0 < P < 1
       2     2        49     38.361      2.951    0 < P < 1
       2     3        90     94.046      0.174    0 < P < 1
       2     4        99     76.478      6.633    0 < P < 1
       3     1       125     52.192    101.568    0 < P < 1
       3     2        67     98.511     10.079    0 < P < 1
       3     3        68    109.297     15.604    0 < P < 1
       4     1        86     73.171      2.249    0 < P < 1
       4     2        58     70.829      2.324    0 < P < 1
   ------------------------------------------------------------
   Total (Degrees of freedom =   6)      179.586
   Pr(Larger Chi-square) = 0.0000
   With pooling, Degrees of freedom =   6  Chi-square =     179.586
   Pr(Larger Chi-square) = 0.0000

   Log-likelihood = -103.73897

   CPU time in seconds for last procedure was     0.44

Model 0.

This model does not test a hypothesis but to obtain real estimates
of the mean and variance of the survival estimates.

- INPUT --- PROC ESTIMATE NSIG=5 MAXFN=2000 NAME=GENERAL;
0 INPUT ---     INITIAL;
  INPUT ---        ALL=0.50;

      Number of parameters in model  = 10
      Number of parameters set equal =  0
      Number of parameters fixed     =  0
      Number of parameters estimated = 10

     Final function value  1484.8288      (Error Return =   0)

     Number of significant digits        8

     Number of function evaluations   306
Appendix 9. Page 5.
                                                    95% Confidence Interval
   I   Parameter      S(I)           Standard Error      Lower          Upper
  ---  ---------  --------------     --------------  -------------  -------------
   1       1      0.74627958         0.14306912E-01  0.71823803     0.77432113
   2       2      0.74390753         0.26420528E-01  0.69212329     0.79569177
   3       3      0.52046263         0.44531503E-01  0.43318088     0.60774437
   4       4      0.59591681         0.36590259E-01  0.52419991     0.66763372
   5       5      0.77505602         0.22581053E-01  0.73079716     0.81931489
   6       6      0.68099107         0.37459340E-01  0.60757076     0.75441138
   7       7      0.71153541         0.25973784E-01  0.66062679     0.76244403
   8       8      0.33542909         0.33361242E-01  0.27004105     0.40081712
   9       9      0.69702776         0.31342388E-01  0.63559668     0.75845884
  10      10      0.61964041         0.33094793E-01  0.55477462     0.68450621
```

Table A15: (Continued).

```
Variance-Covariance matrix of estimates on diagonal and below,
Correlation matrix of estimates above diagonal.

   |       1             2             3             4             5             6             7             8              9            10
---+-------------------------------------------------------------------------------------------------------------------------------------------------
   |
 1 | 0.20468773E-03-0.18763989E-12 0.18671889E-11 0.10347168E-11 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 2 |-0.70927158E-16 0.69804428E-03 0.11598942E-11-0.73999797E-12 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 3 | 0.11896015E-14 0.13646687E-14 0.19830547E-02 0.31154028E-11 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 4 | 0.54166764E-15-0.71538116E-15 0.50762972E-14 0.13388470E-02 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 5 | 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.50990393E-03-0.19212258E-12 0.26100415E-12 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 6 | 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00-0.16251098E-15 0.14032022E-02 0.20181941E-12 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 7 | 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.15308295E-15 0.19636238E-15 0.67463746E-03 0.00000000E+00  0.00000000E+00 0.00000000E+00
   |
 8 | 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.11129725E-02  0.92394408E-12 0.00000000E+00
   |
 9 | 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.96609534E-15  0.98234530E-03 0.00000000E+00
   |
10 | 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00 0.00000000E+00  0.00000000E+00 0.10952653E-02
```

```
 0   Cohort  Cell   Observed  Expected  Chi-square  Note
     ------  ----   --------  --------  ----------  -------------
        1      1       242     242.000      0.000   0 < P < 1
        1      2        70      70.000      0.000   0 < P < 1
        1      3        59      59.000      0.000   0 < P < 1
        1      4        77      77.000      0.000   0 < P < 1
        1      5        46      46.000      0.000   0 < P < 1
        2      1        77      77.000      0.000   0 < P < 1
        2      2        49      49.000      0.000   0 < P < 1
        2      3        90      90.000      0.000   0 < P < 1
        2      4        99      99.000      0.000   0 < P < 1
        3      1       125     125.000      0.000   0 < P < 1
        3      2        67      67.000      0.000   0 < P < 1
        3      3        68      68.000      0.000   0 < P < 1
        4      1        86      86.000      0.000   0 < P < 1
        4      2        58      58.000      0.000   0 < P < 1

 * *  WARNING  * *   ERROR with chi-square probability.
     ---------------------------------------------------------
     Total (Degrees of freedom =   0)        0.000
     Pr(Larger Chi-square) = ***** Log-likelihood = -28.503823
       CPU time in seconds for last procedure was     0.82

 - INPUT --- PROC TEST;

       Submodel     Name        Log-likelihood  NDF   G-O-P
           1      TIMEEQ        -55.175481        6  0.0000
           2      AGEEQ         -103.73897        6  0.0000
           3      GENERAL       -28.503823        0  ******
  * *  WARNING  * *   Sequence of models reinitialized to zero.
 CPU time in seconds for last procedure was     0.00
 - INPUT --- PROC STOP;
 CPU time in minutes for this job was     0.03

 E X E C U T I O N   S U C C E S S F U L
```

Table A16: Model comparisons for soil and grazing treatments using the Likelihood Ratio Test technique.

Comparisons	Log-Likelihood		X^2	df	P
	Model 2 vs Model 1				
ATCO-soil	-93.298	-71.002	44.591	6	0.000
ATCO-grazing	-95.176	-72.880	44.591	6	0.000
CELA-soil	-110.659	-79.392	62.534	6	0.000
CELA-grazing	-119.696	-83.706	71.981	6	0.000
ARSP-soil	-83.682	-57.010	53.344	6	0.000
ARSP-grazing	-101.722	-75.050	53.344	6	0.000

In each case, a more general model, Model 1 (i.e., survival rates are equal across grazing treatments) that had fewer constraints (10 constraints) was compared with Model 2 (i.e., survival rates are equal across both grazing treatments and across all cohorts) that had more constraints (16 constraints). The results of the tests for all species suggested that Model 2 with 16 constraints does not fit the data much better than Model 1 because the p value is $p=0.0000$ in all tests. From this information we would want to use the parameter estimates under Model 1.

Table A17: Approximate χ^2 values for testing the hypothesis that ATCO survival rates during any one study interval are equal across cohorts.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
C1-35-58	Mortality	812	812.000	0.000	1	1.0000
C1-58-69	Mortality	339	298.969	5.360	1	0.0206
C1-69-75	Mortality	103	103.541	0.003	1	0.9563
C1-75-94	Mortality	44	63.595	6.038	1	0.0140
C1-94	Survival	14	33.895	11.678	1	0.0006
Total				23.075	4	0.0001
C2-58-69	Mortality	473	513.031	3.124	1	0.0771
C2-69-75	Mortality	205	177.676	4.202	1	0.0404
C2-75-94	Mortality	119	109.129	0.893	1	0.3447
C2-94	Survival	61	58.164	0.138	1	0.7103
Total				8.357	3	0.0392
C3-69-75	Mortality	154	180.783	3.968	1	0.0463
C3-75-94	Mortality	121	111.037	0.894	1	0.3444
C3-94	Survival	76	59.181	4.780	1	0.0288
Total				9.642	2	0.0081
C4-75-94	Mortality	95	95.239	0.001	1	0.9748
C4-94	Survival	51	50.761	0.001	1	0.9748
Total				0.002	1	0.9643
Total				41.078	6	0.0000

With pooling, Degrees of freedom=6 Chi-square=41.078
Log-likelihood = -52.413795

Table A18: Approximate χ^2 values for testing the hypothesis that ATCO survival rates are equal across soil types.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	p
			SOIL C			
C1-35-58	Mortality	496	506.881	0.234	1	0.6286
C1-58-69	Mortality	205	211.617	0.207	1	0.6491
C1-69-75	Mortality	71	64.296	0.699	1	0.4031
C1-75-94	Mortality	35	27.466	2.066	1	0.1506
C1-94	Survival	12	8.739	1.217	1	0.2699
Total				4.423	4	0.3518
C2-58-69	Mortality	308	330.769	1.567	1	0.2115
C2-69-75	Mortality	147	143.357	0.093	1	0.7604
C2-75-94	Mortality	92	83.217	0.927	1	0.3356
C2-94	Survival	53	42.657	2.508	1	0.1133
Total				5.095	3	0.1649
C3-69-75	Mortality	102	109.687	0.539	1	0.4628
C3-75-94	Mortality	85	86.182	0.016	1	0.8993
C3-94	Survival	63	54.131	1.453	1	0.2280
Total				2.008	1	0.3664
C4-75-94	Mortality	71	70.274	0.008	1	0.9287
C4-94	Survival	37	37.726	0.014	1	0.9058
Total				0.022	1	0.8821
			SOIL-D			
C1-35-58	Mortality	316	305.119	0.388	1	0.5333
C1-58-69	Mortality	134	127.383	0.344	1	0.5575
C1-69-75	Mortality	32	38.704	1.161	1	0.2813
C1-75-94	Mortality	9	16.534	3.433	1	0.0639
C1-94	Survival	2	5.261	2.021	1	0.1551
	Total			7.347	4	0.1186
C2-58-69	Mortality	165	142.231	3.645	1	0.0562
C2-69-75	Mortality	58	61.643	0.215	1	0.6429
C2-75-94	Mortality	27	35.783	2.156	1	0.1420
C2-94	Survival	8	18.343	5.832	1	0.0157
Total				11.848	3	0.0079
C3-69-75	Mortality	52	44.313	1.333	1	0.2483
C3-75-94	Mortality	36	34.818	0.040	1	0.8414
C-94	Survival	13	21.869	3.597	1	0.0580
	Total			4.970	2	0.0833
C4-75-94	Mortality	24	24.726	0.021	1	0.8848
C4-94	Survival	14	13.274	0.040	1	0.8415
	Total			0.061	1	0.8049
Total				35.772	10	0.0000

With pooling, Degrees of freedom=10 Chi-square=35.772
Log-likelihood = -71.002399

Table A19: Approximate χ^2 values for testing the hypothesis that ATCO survival rates are equal across grazing treatments.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
			UNGRAZED			
C1-35-58	Mortality	409	397.335	0.342	1	0.5587
C1-58-69	Mortality	182	165.883	1.566	1	0.2108
C1-69-75	Mortality	31	50.401	7.468	1	0.0063
C1-75-94	Mortality	17	27.466	0.953	1	0.3290
C1-94	Survival	3	6.851	2.164	1	0.1413
Total				12.493	4	0.0140
C2-58-69	Mortality	215	197.910	1.476	1	0.2244
C2-69-75	Mortality	75	85.775	1.354	1	0.2445
C2-75-94	Mortality	40	49.791	1.925	1	0.1653
C2-94	Survival	29	25.523	0.474	1	0.4911
Total				5.229	3	0.1558
C3-69-75	Mortality	65	59.670	0.476	1	0.4924
C3-75-94	Mortality	41	46.883	0.738	1	0.3903
C3-94	Survival	30	29.447	0.010	1	0.9203
Total				1.224	2	0.5423
C4-75-94	Mortality	40	45.548	0.676	1	0.4109
C4-94	Survival	30	24.452	1.259	1	0.2618
Total				1.935	1	0.1642
			GRAZED			
C1-35-58	Mortality	403	414.665	0.328	1	0.8563
C1-58-69	Mortality	157	173.117	1.501	1	0.2205
C1-69-75	Mortality	72	52.599	7.156	1	0.0075
C1-75-94	Mortality	27	22.470	0.913	1	0.3393
C1-94	Survival	11	7.149	2.074	1	0.1498
Total				11.972	4	0.0176
C2-58-69	Mortality	258	275.090	1.062	1	0.3027
C2-69-75	Mortality	130	119.225	0.974	1	0.3236
C2-75-94	Mortality	79	69.209	1.385	1	0.2392
C2-94	Survival	32	35.477	0.341	1	0.5592
Total				3.762	3	0.2883
C3-69-75	Mortality	89	94.330	0.301	1	0.5832
C3-75-94	Mortality	80	34.117	0.467	1	0.4944
C3-94	Survival	46	46.553	0.007	1	0.9333
Total				0.775	2	0.6787
C4-75-94	Mortality	55	49.452	0.622	1	0.4303
C4-94	Survival	21	26.548	1.159	1	0.2817
Total				1.781	1	0.1821
Total				39.172	10	0.0000

With pooling, Degrees of freedom=10 Chi-square=39.172
Log-likelihood = -72.880268

Table A20: Approximate χ^2 values for testing the hypothesis that CELA survival rates during any one study interval are equal across cohorts.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
C1-35-58	Mortality	945	945.000	0.000	1	1.0000
C1-58-69	Mortality	306	349.499	5.414	1	0.0200
C1-69-75	Mortality	203	233.658	4.023	1	0.0449
C1-75-94	Mortality	358	357.747	0.000	1	1.0000
C1-94	Survival	370	296.095	18.446	1	0.0000
Total				27.883	4	0.0000
C2-58-69	Mortality	215	171.501	11.033	1	0.0009
C2-69-75	Mortality	113	114.657	0.024	1	0.8769
C2-75-94	Mortality	155	175.548	2.405	1	0.1209
C2-94	Survival	124	145.295	3.121	1	0.0773
Total				16.583	3	0.0009
C3-69-75	Mortality	150	117.685	8.874	1	0.0029
C3-75-94	Mortality	168	180.183	0.824	1	0.3640
C3-94	Survival	129	149.132	2.718	1	0.0992
Total				14.416	2	0.0007
C4-75-94	Mortality	172	139.522	7.560	1	0.0060
C4-94	Survival	83	115.478	9.134	1	0.0025
Total				16.694	1	0.0000
Total				73.576	6	0.0000

With pooling, Degrees of freedom=6 Chi-square=73.576

Log-likelihood = -69.417845

Table A21: Approximate χ^2 values for testing the hypothesis that CELA survival rates are equal across soil types.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
			SOIL C			
C1-35-58	Mortality	487	467.103	0.848	1	0.3571
C1-58-69	Mortality	137	147.811	0.791	1	0.3738
C1-69-75	Mortality	100	98.058	0.038	1	0.8454
C1-75-94	Mortality	134	172.929	8.764	1	0.0031
C1-94	Survival	196	168.099	4.631	1	0.0314
Total				15.072	4	0.0045
C2-58-69	Mortality	90	88.550	0.024	1	0.8769
C2-69-75	Mortality	56	46.540	1.923	1	0.1655
C2-75-94	Mortality	54	63.839	1.516	1	0.2182
C2-94	Survival	50	51.071	0.022	1	0.8821
Total				3.485	3	0.3327
C3-69-69	Mortality	66	59.060	0.815	1	0.3666
C3-75-94	Mortality	61	66.148	0.401	1	0.5266
C3-94	Survival	49	50.792	0.063	1	0.8018
Total				1.279	2	0.5298
C4-75-94	Mortality	61	66.102	0.394	1	0.5302
C4-94	Survival	37	31.898	0.816	1	0.3663
Total				1.210	1	0.2713
			SOIL D			
C1-35-58	Mortality	480	499.897	0.792	1	0.3735
C1-58-69	Mortality	169	158.189	0.739	1	0.3900
C1-69-75	Mortality	103	104.942	0.036	1	0.8495
C1-75-94	Mortality	224	185.071	8.189	1	0.0042
C1-94	Survival	152	179.901	4.327	1	0.0375
Total				14.083	4	0.0070
C2-58-69	Mortality	125	126.450	0.017	1	0.8962
C2-69-75	Mortality	57	66.460	1.346	1	0.2459
C2-75-94	Mortality	101	91.161	1.062	1	0.3027
C2-94	Survival	74	72.929	0.016	1	0.8969
Total				2.401	3	0.4934
C3-69-75	Mortality	84	90.940	0.530	1	0.4666
C3-75-94	Mortality	107	101.852	0.260	1	0.6101
C3-94	Survival	80	78.208	0.041	1	0.8395
Total				0.831	2	0.6600
C4-75-94	Mortality	111	105.898	0.246	1	0.6199
C4-94	Survival	46	51.102	0.509	1	0.4756
Total				0.755	1	0.3849
Total				39.155	10	0.0000

With pooling, Degrees of freedom=10 Chi-square=39.155

Log-likelihood = -84.166171

Table A22: Approximate χ^2 values for testing the hypothesis that CELA survival rates are equal across grazing treatments.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
			UNGRAZED			
C1-35-58	Mortality	395	455.610	8.063	1	0.0045
C1-58-69	Mortality	167	147.531	2.569	1	0.1090
C1-69-75	Mortality	106	97.872	0.675	1	0.4113
C1-75-94	Mortality	164	172.574	0.429	1	0.5125
C1-94	Survival	220	178.387	9.707	1	0.0018
Total				21.443	4	0.0003
C2-58-69	Mortality	86	93.155	0.550	1	0.4583
C2-69-75	Mortality	49	48.960	0.000	1	0.9920
C2-75-94	Mortality	66	67.158	0.020	1	0.8875
C2-94	Survival	62	53.727	1.274	1	0.2590
Total				1.844	3	0.6054
C3-69-75	Mortality	55	59.060	0.279	1	0.5973
C3-75-94	Mortality	67	66.148	0.011	1	0.9164
C3-94	Survival	54	50.792	0.203	1	0.6523
Total				0.493	2	0.7815
C4-75-94	Mortality	62	67.451	0.441	1	0.5066
C4-94	Survival	38	32.549	0.913	1	0.3393
Total				1.354	1	0.2446
			GRAZED			
C1-35-58	Mortality	550	489.390	7.506	1	0.0061
C1-58-69	Mortality	139	158.469	2.392	1	0.1220
C1-69-75	Mortality	97	105.128	0.628	1	0.4281
C1-75-94	Mortality	194	185.399	0.399	1	0.5276
C1-94	Survival	150	191.613	9.037	1	0.0026
Total				19.962	4	0.0005
C2-58-69	Mortality	129	121.845	0.420	1	0.5169
C2-69-75	Mortality	64	64.040	0.000	1	0.9920
C2-75-94	Mortality	89	87.842	0.015	1	0.9025
C2-94	Survival	62	70.273	0.974	1	0.3236
Total				1.309	3	0.7269
C3-69-75	Mortality	95	90.940	0.181	1	0.6705
C3-75-94	Mortality	101	101.852	0.007	1	0.9333
C3-94	Survival	75	78.208	0.132	1	0.7163
Total				0.320	2	0.8521
C4-75-94	Mortality	110	104.549	0.284	1	0.5940
C4-94	Survival	45	50.451	0.589	1	0.4428
Total				0.873	1	0.3501
Total				47.699	10	0.0000

With pooling, Degrees of freedom=10 Chi-square=47.699
Log-likelihood = -83.705710

Table A23: Approximate x^2 values for testing the hypothesis that ARSP survival rates during any one study interval are equal across cohorts.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
C1-35-58	Mortality	242	242.000	0.000	1	1.0000
C1-58-69	Mortality	70	65.333	0.333	1	0.5639
C1-69-75	Mortality	59	63.961	0.385	1	0.5349
C1-75-94	Mortality	77	66.440	1.679	1	0.1951
C1-94	Survival	46	56.266	1.873	1	0.1711
Total				4.270	4	0.3707
C2-58-69	Mortality	77	81.667	0.267	1	0.6054
C2-69-75	Mortality	49	79.951	11.982	1	0.0005
C2-75-94	Mortality	90	83.050	0.582	1	0.4455
C2-94	Survival	99	70.333	11.685	1	0.0006
Total				24.516	3	0.0000
C3-69-75	Mortality	125	89.088	14.476	1	0.0001
C3-75-94	Mortality	67	92.541	7.049	1	0.0079
C3-94	Survival	68	78.371	1.372	1	0.2415
Total				22.897	2	0.0000
C4-75-94	Mortality	86	77.970	0.827	1	0.3631
C4-94	Survival	58	66.030	0.977	1	0.3229
Total				1.804	1	0.1792
Total				53.486	6	0.0000

With pooling, Degrees of freedom=6 Chi-square=53.486
Log-likelihood = -55.175481

Table A24: Approximate χ^2 values for testing the hypothesis that ARSP survival rates are equal across soil types.

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	p
		SOIL C				
C1-35-58	Mortality	188	188.113	0.000	1	1.0000
C1-58-69	Mortality	53	54.413	0.037	1	0.8474
C1-69-75	Mortality	43	45.862	0.179	1	0.6722
C1-75-94	Mortality	63	59.854	0.165	1	0.6885
C1-94	Survival	37	35.757	0.043	1	0.8357
Total				0.424	4	0.9804
C2-35-58	Mortality	42	47.911	0.729	1	0.3922
C2-58-69	Mortality	35	30.489	0.667	1	0.4141
C2-75-94	Mortality	58	56.000	0.071	1	0.7899
C2-94	Survival	61	61.600	0.006	1	0.9382
Total				1.483	3	0.6861
C3-58-69	Mortality	94	85.096	0.932	1	0.3343
C3-75-94	Mortality	44	45.612	0.057	1	0.8113
C3-94	Survival	39	46.292	1.149	1	0.2837
Total				2.138	2	0.3433
C4-75-94	Mortality	46	51.361	0.560	1	0.4543
C4-94	Survival	40	34.639	0.830	1	0.3622
Total				1.390	1	0.2384
		SOIL D				
C1-35-58	Mortality	54	53.887	0.000	1	1.0000
C1-58-69	Mortality	17	15.587	0.128	1	0.7205
C1-69-75	Mortality	16	13.138	0.624	1	0.4295
C1-75-94	Mortality	14	17.146	0.577	1	0.4474
C1-94	Survival	9	10.243	0.151	1	0.6975
Total				1.480	4	0.8302
C2-58-69	Mortality	35	29.089	1.201	1	0.2731
C2-69-75	Mortality	14	18.511	1.099	1	0.2944
C2-75-94	Mortality	32	34.000	0.118	1	0.7312
C2-94	Survival	38	37.400	0.010	1	0.9203
Total				2.328	3	0.5071
C3-58-69	Mortality	31	39.904	1.987	1	0.1597
C3-75-94	Mortality	23	21.388	0.121	1	0.7269
C3-94	Survival	29	21.708	2.450	1	0.1175
Total				4.558	2	0.1023
C4-75-94	Mortality	40	34.639	0.830	1	0.3622
C4-94	Survival	18	23.361	1.230	1	0.2674
Total				1.060	1	0.3032

Total (Degrees of freedom = 10 15.950
Pr(Larger Chi-square) = 0.1011
Log-likelihood = -57.009964

Table A25: Approximate χ^2 values for testing the hypothesis that ARSP survival rates are equal across grazing treatments

Cohort and Interval	Fate	Observed	Expected	Chi-square	df	P
		UNGRAZED				
C1-35-58	Mortality	101	127.368	5.459	1	0.0195
C1-58-69	Mortality	31	36.842	0.926	1	0.3359
C1-69-75	Mortality	39	31.053	2.034	1	0.1538
C1-75-94	Mortality	54	40.526	4.480	1	0.0343
C1-94	Survival	35	24.211	4.808	1	0.0283
Total				17.707	4	0.0014
C2-58-69	Mortality	48	53.289	0.525	1	0.4687
C2-69-75	Mortality	33	33.911	0.024	1	0.8768
C2-75-94	Mortality	57	62.286	0.449	1	0.5028
C2-94	Survival	80	68.514	1.925	1	0.1653
Total				2.923	3	0.4036
C3-69-75	Mortality	71	76.442	0.387	1	0.5339
C3-75-94	Mortality	41	40.973	0.000	1	1.0000
C3-94	Survival	47	41.585	0.705	1	0.3756
Total				1.092	2	0.5792
C4-75-94	Mortality	67	68.681	0.041	1	0.8395
C4-94	Survival	48	46.319	0.061	1	0.8049
Total				0.102	1	0.7494
		GRAZED				
C1-35-58	Mortality	141	114.632	6.065	1	0.0138
C1-58-69	Mortality	39	33.158	1.029	1	0.3104
C1-69-75	Mortality	20	27.947	2.260	1	0.1328
C1-75-94	Mortality	23	36.474	4.977	1	0.0257
C1-94	Survival	11	21.789	5.343	1	0.0208
Total				16.674	4	0.0022
C2-58-69	Mortality	29	23.711	1.180	1	0.2773
C2-69-75	Mortality	16	15.089	0.055	1	0.8145
C2-75-94	Mortality	33	27.714	1.008	1	0.3153
C2-94	Survival	19	30.486	4.327	1	0.0375
Total				6.570	3	0.0869
C3-69-75	Mortality	54	48.558	0.610	1	0.4347
C3-75-94	Mortality	26	26.027	0.000	1	1.0000
C3-94	Survival	21	26.415	1.110	1	0.2920
Total				1.720	2	0.4231
C4-75-94	Mortality	19	17.319	0.163	1	0.6864
C4-94	Survival	10	11.681	0.242	1	0.6227
Total				0.405	1	0.5245
Total				50.195	10	0.0000

With pooling, Degrees of freedom=10 Chi-square=50.195
Log-likelihood = -75.050270

Table A26: Correlation analysis between shrub seedlings and precipitation variables.

```
                                          Correlation Analysis

                      6 'WITH' Variables:  TOTALP    WINTER    SPRING    SUMMER    WINSPR    WINSUM
                      4 'VAR'  Variables:  ATCO      CELA      ARSP      TSEED

                                                    Simple Statistics
Variable           N         Mean            Std Dev         Median          Minimum          Maximum

TOTAL PRECIP.      7    196.285714        43.522846      195.000000       148.000000       270.000000
WINTER PRECIP.     7     73.857143        27.297305       71.000000        37.000000       112.000000
SPRING PRECIP.     7     58.714286        42.484171       55.000000        19.000000       148.000000
SUMMER PRECIP.     7     63.714286        31.255476       58.000000        21.000000       104.000000
WIN-SPR PRECIP.    7    132.571429        54.902511      128.000000        90.000000       248.000000
WIN-SUM PRECIP.    7    137.714286        19.939193      139.000000       118.000000       175.000000
ATCO               7     88.571429        87.849980       62.000000         4.000000       217.000000
CELA               7     27.285714        13.960830       27.000000         9.000000        48.000000
ARSP               7     42.571429        49.949498       34.000000                0       119.000000
TOTAL-SEEDLINGS    7    158.428571       148.342910      124.000000        22.000000       371.000000



Spearman Correlation Coefficients / Prob > |R| under Ho: Rho=0 / N = 7

TSEED              ATCO               CELA               ARSP

TOTALP            0.82143            0.35714            0.81084            0.78571
                  0.0234             0.4316             0.0269             0.0362

WINTER            0.60714            0.85714            0.55858            0.64286
                  0.1482             0.0137             0.1925             0.1194

SPRING            0.42857            0.00000            0.48651            0.39286
                  0.3374             1.0000             0.2682             0.3833

SUMMER           -0.10714           -0.60714           -0.09009           -0.14286
                  0.8192             0.1482             0.8477             0.7599

WINSPR            0.71429            0.64286            0.72075            0.75000
                  0.0713             0.1194             0.0676             0.0522

WINSUM            0.66669            0.27028            0.58182            0.72075
                  0.1019             0.5577             0.1706             0.0676
```

Table A27: Grazed versus ungrazed Wilcoxon Signed Rank tests for all seedlings and seedlings by species.

1. All seedlings

Descriptive Statistics Section

Variable	**Count**	**Mean**	**Standard Deviation**	**Standard Error**	**95% LCL of Mean**	**95% UCL of Mean**
ungraall	6	68.83334	46.6494	19.04454	19.87779	117.7889
grazall	6	110.6667	104.8116	42.78915	0.6736623	220.6597
Difference	6	-41.83333	60.3835	24.65146	-105.2019	21.53526

T for Confidence Limits = 2.5706

Wilcoxon Signed-Rank Test

	Exact Probability		**Approximation Without Continuity Correction**			**Approximation With Continuity Correction**		
Alternative Hypothesis	**Prob Level**	**Decision (5%)**	**Z-Value**	**Prob Level**	**Decision (5%)**	**Z-Value**	**Prob Level**	**Decision (5%)**
X1-X2<>0	0.156250	Accept Ho	1.5724	0.115851	Accept Ho	1.4676	0.142213	Accept Ho
X1-X2<0	0.078125	Accept Ho	-1.5724	0.057926	Accept Ho	-1.4676	0.071107	Accept Ho
X1-X2>0	0.953125	Accept Ho	-1.5724	0.942074	Accept Ho	-1.6773	0.953254	Accept Ho

2. ATCO

Descriptive Statistics Section

Variable	**Count**	**Mean**	**Standard Deviation**	**Standard Error**	**95% LCL of Mean**	**95% UCL of Mean**
Ungrazed ATCO	6	24	18.89973	7.715785	4.165944	43.83406
Grazed ATCO	6	75.66666	74.54037	30.43098	-2.558654	153.892
Difference	6	-51.66667	59.99889	24.49444	-114.6316	11.29831

T for Confidence Limits = 2.5706

Wilcoxon Signed-Rank Test

	Exact Probability		**Approximation Without Continuity Correction**			**Approximation With Continuity Correction**		
Alternative **Hypothesis**	Prob **Level**	Decision **(5%)**	**Z-Value**	Prob **Level**	Decision **(5%)**	**Z-Value**	Prob **Level**	Decision **(5%)**
1-X2<>0	0.062500	Accept Ho	1.9917	0.046399	Reject Ho	1.8869	0.059172	Accept Ho
X1-X2<0	0.031250	Reject Ho	-1.9917	0.023200	Reject Ho	-1.8869	0.029586	Reject Ho
X1-X2>0	0.984375	Accept Ho	-1.9917	0.976800	Accept Ho	-2.0966	0.981984	Accept Ho

3. CELA

Descriptive Statistics Section

Variable	**Count**	**Mean**	**Standard Deviation**	**Standard Error**	**95% LCL of Mean**	**95% UCL of Mean**
Ungrazed CELA	6	16	7.211102	2.94392	8.432412	23.56759
Grazed CELA	6	14.33333	9.309493	3.800585	4.563619	24.10305
Difference	6	1.666667	11.02119	4.499382	-9.899364	13.2327

T for Confidence Limits = 2.5706

Wilcoxon Signed-Rank Test

	Exact Probability		**Approximation Without Continuity Correction**			**Approximation With Continuity Correction**		
Alternative Hypothesis	**Prob Level**	**Decision (5%)**	**Z-Value**	**Prob Level**	**Decision (5%)**	**Z-Value**	**Prob Level**	**Decision (5%)**
X1-X2<>0	0.843750	Accept Ho	0.3145	0.753152	Accept Ho	0.2097	0.833935	Accept Ho
X1-X2<0	0.656250	Accept Ho	0.3145	0.623424	Accept Ho	0.4193	0.662507	Accept Ho
X1-X2>0	0.421875	Accept Ho	0.3145	0.376576	Accept Ho	0.2097	0.416968	Accept Ho

Table A27: (Continued).

4. ARSP

Descriptive Statistics Section

Variable	Count	Mean	Standard Deviation	Standard Error	95% LCL of Mean	95% UCL of Mean
Ungrazed ARSP	6	28.83333	29.34223	11.97892	-1.959452	59.62612
Grazed ARSP	6	20.66667	22.57137	9.214723	-3.020532	44.35387
Difference	6	8.166667	12.25425	5.002777	-4.693381	21.02671

T for Confidence Limits = 2.5706

Wilcoxon Signed-Rank Test

	Exact Probability		Approximation Without Continuity Correction			Approximation With Continuity Correction		
Alternative Hypothesis	Prob Level	Decision (5%)	Z-Value	Prob Level	Decision (5%)	Z-Value	Prob Level	Decision (5%)
X1-X2<>0	0.218750	Accept Ho	1.4757	0.140017	Accept Ho	1.3703	0.170587	Accept Ho
X1-X2<0	0.921875	Accept Ho	1.4757	0.929992	Accept Ho	1.5811	0.943077	Accept Ho
X1-X2>0	0.109375	Accept Ho	1.4757	0.070008	Accept Ho	1.3703	0.085293	Accept Ho

Table A28: ATCO seedling survival from 1994 to 1995 by treatment.

```
                TABLE OF TRT BY FATE

        TRT       FATE

        Frequency|
        Percent  |
        Row Pct  |
        Col Pct  |DIED    |SURVIVED|  Total
        ---------+--------+--------+
        GRAZED   |     43 |    135 |    178
                 |  19.82 |  62.21 |  82.03
                 |  24.16 |  75.84 |
                 |  87.76 |  80.36 |
        ---------+--------+--------+
        UNGRAZED |      6 |     33 |     39
                 |   2.76 |  15.21 |  17.97
                 |  15.38 |  84.62 |
                 |  12.24 |  19.64 |
        ---------+--------+--------+
        Total          49      168      217
                    22.58    77.42   100.00


        STATISTICS FOR TABLE OF TRT BY FATE

Statistic                     DF       Value        Prob
------------------------------------------------------
Chi-Square                     1       1.408       0.235
Likelihood Ratio Chi-Square    1       1.510       0.219
Continuity Adj. Chi-Square     1       0.951       0.329
Mantel-Haenszel Chi-Square     1       1.402       0.236
Fisher's Exact Test (Left)                         0.923
                    (Right)                        0.165
                    (2-Tail)                       0.293
Phi Coefficient                        0.081
Contingency Coefficient                0.080
Cramer's V                             0.081
------------------------------------------------------
```

Table A29: CELA seedling survival from 1994 to 1995 by treatment.

```
                    TABLE OF TRT BY FATE

                    INSUFICIENT SAMPLE SIZE

                         TRT        FATE

              Frequency|
              Percent  |
              Row Pct  |
              Col Pct  |DIED    |SURVIVED|  Total
              ---------+--------+--------+
              GRAZED   |      3 |     21 |     24
                       |   8.57 |  60.00 |  68.57
                       |  12.50 |  87.50 |
                       |  42.86 |  75.00 |
              ---------+--------+--------+
              UNGRAZED |      4 |      7 |     11
                       |  11.43 |  20.00 |  31.43
                       |  36.36 |  63.64 |
                       |  57.14 |  25.00 |
              ---------+--------+--------+
              Total           7       28       35
                          20.00    80.00   100.00

              STATISTICS FOR TABLE OF TRT BY FATE

Statistic                       DF       Value        Prob
------------------------------------------------------
Chi-Square                       1       2.685       0.101
Likelihood Ratio Chi-Square      1       2.523       0.112
Continuity Adj. Chi-Square       1       1.400       0.237
Mantel-Haenszel Chi-Square       1       2.608       0.106
Fisher's Exact Test (Left)                           0.120
                    (Right)                          0.979
                    (2-Tail)                         0.171
Phi Coefficient                         -0.277
Contingency Coefficient                  0.267
Cramer's V                              -0.277

------------------------------------------------------
```

Table A30: ARSP seedling survival from 1994 to 1995 by treatment.

```
                  TABLE OF TRT BY FATE

         TRT       FATE
         Frequency|
         Percent  |
         Row Pct  |
         Col Pct  |DIED    |SURVIVED|  Total
         ---------+--------+--------+
         GRAZED   |     10 |     34 |     44
                  |   8.40 |  28.57 |  36.97
                  |  22.73 |  77.27 |
                  |  31.25 |  39.08 |
         ---------+--------+--------+
         UNGRAZED |     22 |     53 |     75
                  |  18.49 |  44.54 |  63.03
                  |  29.33 |  70.67 |
                  |  68.75 |  60.92 |
         ---------+--------+--------+
         Total          32       87      119
                     26.89    73.11   100.00

         STATISTICS FOR TABLE OF TRT BY FATE

Statistic                     DF       Value        Prob
------------------------------------------------------
Chi-Square                     1       0.616       0.433
Likelihood Ratio Chi-Square    1       0.625       0.429
Continuity Adj. Chi-Square     1       0.325       0.568
Mantel-Haenszel Chi-Square     1       0.610       0.435
Fisher's Exact Test (Left)                         0.286
                    (Right)                        0.841
                    (2-Tail)                       0.523
Phi Coefficient                       -0.072
Contingency Coefficient                0.072
Cramer's V                            -0.072

------------------------------------------------------
```

Table A31: ATCO seedling survival from 1994 to 1995 by location.

```
                TABLE OF LOCATION BY FATE

        LOCATION      FATE

        Frequency|
        Percent  |
        Row Pct  |
        Col Pct  |DIED    |SURVIVED|  Total
        ---------+--------+--------+
        BARE     |     27 |     87 |    114
                 |  12.44 |  40.09 |  52.53
                 |  23.68 |  76.32 |
                 |  55.10 |  51.79 |
        ---------+--------+--------+
        PATCH    |     22 |     81 |    103
                 |  10.14 |  37.33 |  47.47
                 |  21.36 |  78.64 |
                 |  44.90 |  48.21 |
        ---------+--------+--------+
        Total          49      168      217
                    22.58    77.42   100.00


           STATISTICS FOR TABLE OF LOCATION BY FATE

   Statistic                     DF       Value        Prob
   ------------------------------------------------------
   Chi-Square                     1       0.167       0.683
   Likelihood Ratio Chi-Square    1       0.168       0.682
   Continuity Adj. Chi-Square     1       0.061       0.805
   Mantel-Haenszel Chi-Square     1       0.167       0.683
   Fisher's Exact Test (Left)                         0.716
                       (Right)                        0.403
                       (2-Tail)                       0.746
   Phi Coefficient                        0.028
   Contingency Coefficient                0.028
   Cramer's V                             0.028

   ------------------------------------------------------
```

Table A32: CELA seedling survival from 1994 to 1995 by location.

```
                 TABLE OF TRT BY FATE

        TRT       FATE

        Frequency|
        Percent  |
        Row Pct  |
        Col Pct  |DIED    |SURVIVED|  Total
        ---------+--------+--------+
        BARE     |      6 |     11 |     17
                 |  17.14 |  31.43 |  48.57
                 |  35.29 |  64.71 |
                 |  85.71 |  39.29 |
        ---------+--------+--------+
        PATCH    |      1 |     17 |     18
                 |   2.86 |  48.57 |  51.43
                 |   5.56 |  94.44 |
                 |  14.29 |  60.71 |
        ---------+--------+--------+
        Total           7       28       35
                    20.00    80.00   100.00


        STATISTICS FOR TABLE OF TRT BY FATE

Statistic                     DF     Value      Prob
------------------------------------------------------
Chi-Square                     1     4.833     0.028
Likelihood Ratio Chi-Square    1     5.230     0.022
Continuity Adj. Chi-Square     1     3.153     0.076
Mantel-Haenszel Chi-Square     1     4.694     0.030
Fisher's Exact Test (Left)                     0.997
                    (Right)                    0.036
                    (2-Tail)                   0.041
Phi Coefficient                      0.372
Contingency Coefficient              0.348
Cramer's V                           0.372

------------------------------------------------------
```

Table A33: ARSP seedling survival from 1994 to 1995 by location.

```
TRT       FATE

Frequency|
Percent  |
Row Pct  |
Col Pct  |DIED    |SURVIVED|  Total
---------+--------+--------+
BARE     |     19 |     40 |     59
         |  15.97 |  33.61 |  49.58
         |  32.20 |  67.80 |
         |  59.38 |  45.98 |
---------+--------+--------+
PATCH    |     13 |     47 |     60
         |  10.92 |  39.50 |  50.42
         |  21.67 |  78.33 |
         |  40.63 |  54.02 |
---------+--------+--------+
Total          32       87      119
            26.89    73.11   100.00


         STATISTICS FOR TABLE OF TRT BY FATE

Statistic                     DF       Value        Prob
--------------------------------------------------------
Chi-Square                     1       1.680       0.195
Likelihood Ratio Chi-Square    1       1.687       0.194
Continuity Adj. Chi-Square     1       1.187       0.276
Mantel-Haenszel Chi-Square     1       1.666       0.197
Fisher's Exact Test (Left)                         0.934
                    (Right)                        0.138
                    (2-Tail)                       0.220
Phi Coefficient                        0.119
Contingency Coefficient                0.118
Cramer's V                             0.119

--------------------------------------------------------
```

Table A34: ATCO adult survival from 1994 to 1995 by treatment.

```
                 TABLE OF TRT BY FATE

      TRT        FATE

      Frequency|
      Percent  |
      Row Pct  |
      Col Pct  |DIED    |SURVIVED|  Total
      ---------+--------+--------+
      GRAZED   |     91 |    248 |    339
               |  16.40 |  44.68 |  61.08
               |  26.84 |  73.16 |
               |  66.91 |  59.19 |
      ---------+--------+--------+
      UNGRAZED |     45 |    171 |    216
               |   8.11 |  30.81 |  38.92
               |  20.83 |  79.17 |
               |  33.09 |  40.81 |
      ---------+--------+--------+
      Total         136      419      555
                  24.50    75.50   100.00


      STATISTICS FOR TABLE OF TRT BY FATE

Statistic                     DF       Value        Prob
------------------------------------------------------
Chi-Square                     1       2.576       0.108
Likelihood Ratio Chi-Square    1       2.614       0.106
Continuity Adj. Chi-Square     1       2.262       0.133
Mantel-Haenszel Chi-Square     1       2.572       0.109
Fisher's Exact Test (Left)                         0.957
                    (Right)                        0.066
                    (2-Tail)                       0.129
Phi Coefficient                        0.068
Contingency Coefficient                0.068
Cramer's V                             0.068

------------------------------------------------------
```

Table A35: CELA adult survival from 1994 to 1995 by treatment.

```
                    TABLE OF TRT BY FATE

            TRT       FATE

            Frequency|
            Percent  |
            Row Pct  |
            Col Pct  |DIED    |SURVIVED|  Total
            ---------+--------+--------+
            GRAZED   |     56 |    436 |    492
                     |   5.41 |  42.13 |  47.54
                     |  11.38 |  88.62 |
                     |  57.14 |  46.53 |
            ---------+--------+--------+
            UNGRAZED |     42 |    501 |    543
                     |   4.06 |  48.41 |  52.46
                     |   7.73 |  92.27 |
                     |  42.86 |  53.47 |
            ---------+--------+--------+
            Total          98      937     1035
                         9.47    90.53   100.00


            STATISTICS FOR TABLE OF TRT BY FATE

   Statistic                     DF       Value      Prob
   ------------------------------------------------------
   Chi-Square                     1       4.006     0.045
   Likelihood Ratio Chi-Square    1       4.005     0.045
   Continuity Adj. Chi-Square     1       3.592     0.058
   Mantel-Haenszel Chi-Square     1       4.002     0.045
   Fisher's Exact Test (Left)                       0.982
                       (Right)                      0.029
                       (2-Tail)                     0.055
   Phi Coefficient                        0.062
   Contingency Coefficient                0.062
   Cramer's V                             0.062


   ------------------------------------------------------
```

Table A36: ARSP adult survival from 1994 to 1995 by treatment.

```
                 TABLE OF TRT BY FATE

          TRT       FATE

          Frequency|
          Percent  |
          Row Pct  |
          Col Pct  |DIED    |SURVIVED|  Total
          ---------+--------+--------+
          GRAZED   |     41 |    242 |    283
                   |   2.68 |  15.80 |  18.47
                   |  14.49 |  85.51 |
                   |  15.36 |  19.13 |
          ---------+--------+--------+
          UNGRAZED |    226 |   1023 |   1249
                   |  14.75 |  66.78 |  81.53
                   |  18.09 |  81.91 |
                   |  84.64 |  80.87 |
          ---------+--------+--------+
          Total         267     1265     1532
                      17.43    82.57   100.00


          STATISTICS FOR TABLE OF TRT BY FATE

Statistic                     DF       Value        Prob
------------------------------------------------------
Chi-Square                     1       2.086       0.149
Likelihood Ratio Chi-Square    1       2.165       0.141
Continuity Adj. Chi-Square     1       1.843       0.175
Mantel-Haenszel Chi-Square     1       2.084       0.149
Fisher's Exact Test (Left)                         0.086
                    (Right)                        0.939
                    (2-Tail)                       0.165
Phi Coefficient                       -0.037
Contingency Coefficient                0.037
Cramer's V                            -0.037


------------------------------------------------------
```

Table A37: Example of fuzzy graph analysis for the spring ungrazed pastures for the period 1935 to 1994

```
Third definition of succession. Alpha cut of 0.05.

AT=ATCO, AR=ARSP, CE=CELA, SP=SPCR, ST=ORHY, and HI=HIJA

        U5-9
BASED ON MAX (0, MIN(-DX,DY))

        AT     AR     CE     SP     ST     HI
AT    0.00031.400 0.000 2.900 9.50011.000
AR    0.00031.400 0.000 0.000 0.000 0.000
CE    0.000 2.800 0.000 2.800 2.800 2.800
SP    0.000 0.000 0.000 2.900 0.000 0.000
ST    0.000 0.000 0.000 0.000 9.500 0.000
HI    0.000 0.000 0.000 0.000 0.00011.000

TRANSITIVE CLOSURE

        AT     AR     CE     SP     ST     HI
AT    0.00031.400 0.000 2.900 9.50011.000
AR    0.00031.400 0.000 0.000 0.000 0.000
CE    0.000 2.800 0.000 2.800 2.800 2.800
SP    0.000 0.000 0.000 2.900 0.000 0.000
ST    0.000 0.000 0.000 0.000 9.500 0.000
HI    0.000 0.000 0.000 0.000 0.00011.000

ALPHA-CUT OF TRANSITIVE CLOSURE     ALPHA =  0.050

          1-AT  2-AR  3-CE  4-SP  5-ST  6-HI
1-AT        0     1     0     1     1     1
2-AR        0     1     0     0     0     0
3-CE        0     1     0     1     1     1
4-SP        0     0     0     1     0     0
5-ST        0     0     0     0     1     0
6-HI        0     0     0     0     0     1

REACHABILITY SET (UPPER LINE) AND INTERSECTION (LOWER LINE)
FOR ALL SPECIES ABOVE THE ALPHA-CUT

0  1  2     4  5  6
0  1
0
0     2
0     2
0
0     2  3  4  5  6
0        3
0
0           4
0           4
0
0              5
0              5
0
0                 6
0                 6

1 TIERS FOR FUZZY GRAPHS
0 CONNECT UP SPECIES TO SPECIES IN THEIR REACHABILITY SET

0  2  4  5  6
0  1  3
```

Table A38: Rank correlation analysis of grazed and ungrazed spring pastures.

1935

```
Spearman Correlation Coefficients / Prob > |R| under Ho: Rho=0 / N = 6

                              GRAZED          UNGRAZED

          GRAZED             1.00000           0.94286
                              0.0               0.0048

          UNGRAZED           0.94286           1.00000
                              0.0048            0.0

Kendall Tau b Correlation Coefficients / Prob > |R| under Ho: Rho=0 / N = 6

                              GRAZED          UNGRAZED

          GRAZED             1.00000           0.86667
                              0.0               0.0146

          UNGRAZED           0.86667           1.00000
                              0.0146            0.0
```

1994

```
Spearman Correlation Coefficients / Prob > |R| under Ho: Rho=0 / N = 6

                              GRAZED          UNGRAZED

          GRAZED             1.00000          -0.54286
                              0.0               0.2657

          UNGRAZED          -0.54286           1.00000
                              0.2657            0.0

                          Correlation Analysis

Kendall Tau b Correlation Coefficients / Prob > |R| under Ho: Rho=0 / N = 6

                              GRAZED          UNGRAZED

          GRAZED             1.00000          -0.46667
                              0.0               0.1885

          UNGRAZED          -0.46667           1.00000
                              0.1885            0.0
```

Table A35: Analysis of clumped and unclumped plant distribution across years.

```
                  N P A R 1 W A Y   P R O C E D U R E

            Analysis of Variance for Variable COUNT
                   Classified by Variable TRT

TRT         N         Mean                      Among MS    Within MS
                                              102.400000   12.7000000
c           5   21.2000000
u           5   14.8000000                       F Value    Prob > F
                                                   8.063      0.0218
                 Average Scores were used for Ties
            clumped and unclumpend plant distributions



        Wilcoxon Scores (Rank Sums) for Variable COUNT
                   Classified by Variable TRT

                    Sum of     Expected      Std Dev          Mean
TRT         N       Scores     Under H0     Under H0         Score

c           5   39.5000000   27.5000000   4.77260702    7.90000000
u           5   15.5000000   27.5000000   4.77260702    3.10000000
                 Average Scores were used for Ties

   Wilcoxon 2-Sample Test (Normal Approximation)
   (with Continuity Correction of .5)

   S=  39.5000  Z=  2.40958  Prob > |Z| =    0.0160

   T-Test approx. Significance =        0.0393
```

Table A40: Analysis of clumped and unclumped plant distribution by grazing treatments from 1935 to 1994.

1935

```
BONFERRONI CORRECTION 0.05/5=0.01

         TABLE OF TRT BY DISTR
TRT       DISTR
Frequency|
Percent  |
Row Pct  |
Col Pct  |Clumped |Unclumpe|  Total
---------+--------+--------+
GRAZED   |     10 |      8 |     18
         |  27.78 |  22.22 |  50.00
         |  55.56 |  44.44 |
         |  45.45 |  57.14 |
---------+--------+--------+
UNGRAZED |     12 |      6 |     18
         |  33.33 |  16.67 |  50.00
         |  66.67 |  33.33 |
         |  54.55 |  42.86 |
---------+--------+--------+
Total          22       14       36
            61.11    38.89   100.00

         STATISTICS FOR TABLE OF TRT BY DISTR
Statistic                     DF       Value        Prob
------------------------------------------------------
Chi-Square                     1       0.468       0.494
Likelihood Ratio Chi-Square    1       0.469       0.494
Continuity Adj. Chi-Square     1       0.117       0.732
Mantel-Haenszel Chi-Square     1       0.455       0.500
Fisher's Exact Test (Left)                         0.367
                    (Right)                        0.847
                    (2-Tail)                       0.733
------------------------------------------------------
```

1958

```
         TABLE OF TRT BY DISTR
TRT       DISTR

Frequency|
Percent  |
Row Pct  |
Col Pct  |Clumped |Unclumpe|  Total
---------+--------+--------+
GRAZED   |      9 |      9 |     18
         |  25.00 |  25.00 |  50.00
         |  50.00 |  50.00 |
         |  45.00 |  56.25 |
---------+--------+--------+
UNGRAZED |     11 |      7 |     18
         |  30.56 |  19.44 |  50.00
         |  61.11 |  38.89 |
         |  55.00 |  43.75 |
---------+--------+--------+
Total          20       16       36
            55.56    44.44   100.00
```

Table A40: (Continued).

```
          STATISTICS FOR TABLE OF TRT BY DISTR

Statistic                     DF       Value      Prob
------------------------------------------------------
Chi-Square                     1       0.450     0.502
Likelihood Ratio Chi-Square    1       0.451     0.502
Continuity Adj. Chi-Square     1       0.113     0.737
Mantel-Haenszel Chi-Square     1       0.437     0.508
Fisher's Exact Test (Left)                       0.369
                    (Right)                      0.843
                    (2-Tail)                     0.738


------------------------------------------------------
```

1969

```
                TABLE OF TRT BY DISTR
        TRT       DISTR
        Frequency|
        Percent  |
        Row Pct  |
        Col Pct  |Clumped |Unclumpe|  Total
        ---------+--------+--------+
        GRAZED   |      8 |     10 |     18
                 |  22.22 |  27.78 |  50.00
                 |  44.44 |  55.56 |
                 |  42.11 |  58.82 |
        ---------+--------+--------+
        UNGRAZED |     11 |      7 |     18
                 |  30.56 |  19.44 |  50.00
                 |  61.11 |  38.89 |
                 |  57.89 |  41.18 |
        ---------+--------+--------+
        Total          19       17       36
                    52.78    47.22   100.00

          STATISTICS FOR TABLE OF TRT BY DISTR

Statistic                     DF       Value      Prob
------------------------------------------------------
Chi-Square                     1       1.003     0.317
Likelihood Ratio Chi-Square    1       1.008     0.315
Continuity Adj. Chi-Square     1       0.446     0.504
Mantel-Haenszel Chi-Square     1       0.975     0.323
Fisher's Exact Test (Left)                       0.253
                    (Right)                      0.909
                    (2-Tail)                     0.505
------------------------------------------------------
```

Table A40: (Continued).

1975

```
             TABLE OF TRT BY DISTR
TRT          DISTR
Frequency|
Percent  |
Row Pct  |
Col Pct  |Clumped |Unclumpe|  Total
---------+--------+--------+
GRAZED   |      9 |      9 |     18
         |  25.00 |  25.00 |  50.00
         |  50.00 |  50.00 |
         |  50.00 |  50.00 |
---------+--------+--------+
UNGRAZED |      9 |      9 |     18
         |  25.00 |  25.00 |  50.00
         |  50.00 |  50.00 |
         |  50.00 |  50.00 |
---------+--------+--------+
Total          18       18       36
            50.00    50.00   100.00

        STATISTICS FOR TABLE OF TRT BY DISTR
Statistic                      DF      Value        Prob
--------------------------------------------------------
Chi-Square                      1      0.000       1.000
Likelihood Ratio Chi-Square     1      0.000       1.000
Continuity Adj. Chi-Square      1      0.000       1.000
Mantel-Haenszel Chi-Square      1      0.000       1.000
Fisher's Exact Test (Left)                         0.630
                    (Right)                        0.630
                    (2-Tail)                       1.000
--------------------------------------------------------
```

1994

```
             TABLE OF TRT BY DISTR
TRT          DISTR
Frequency|
Percent  |
Row Pct  |
Col Pct  |Clumped |Unclumpe|  Total
---------+--------+--------+
GRAZED   |     13 |      5 |     18
         |  36.11 |  13.89 |  50.00
         |  72.22 |  27.78 |
         |  48.15 |  55.56 |
---------+--------+--------+
UNGRAZED |     14 |      4 |     18
         |  38.89 |  11.11 |  50.00
         |  77.78 |  22.22 |
         |  51.85 |  44.44 |
---------+--------+--------+
Total          27        9       36
            75.00    25.00   100.00
```

Table A40: (Continued).

```
             STATISTICS FOR TABLE OF TRT BY DISTR

Statistic                     DF       Value      Prob
------------------------------------------------------
Chi-Square                     1       0.148     0.700
Likelihood Ratio Chi-Square    1       0.148     0.700
Continuity Adj. Chi-Square     1       0.000     1.000
Mantel-Haenszel Chi-Square     1       0.144     0.704
Fisher's Exact Test (Left)                       0.500
                    (Right)                      0.778
------------------------------------------------------
```

Table A41: Continuous and discontinuous plant distribution by grazing treatments

```
          TABLE OF TRT BY DISTR
TRT          DISTR

Frequency|
Percent  |
Row Pct  |
Col Pct  |Continou|Disconti|  Total
---------+--------+--------+
GRAZED   |      5 |     13 |     18
         |  13.89 |  36.11 |  50.00
         |  27.78 |  72.22 |
         |  55.56 |  48.15 |
---------+--------+--------+
UNGRAZED |      4 |     14 |     18
         |  11.11 |  38.89 |  50.00
         |  22.22 |  77.78 |
         |  44.44 |  51.85 |
---------+--------+--------+
Total           9       27       36
            25.00    75.00   100.00


        STATISTICS FOR TABLE OF TRT BY DISTR

Statistic                     DF     Value      Prob
------------------------------------------------------
Chi-Square                     1     0.148     0.700
Likelihood Ratio Chi-Square    1     0.148     0.700
Continuity Adj. Chi-Square     1     0.000     1.000
Mantel-Haenszel Chi-Square     1     0.144     0.704
Fisher's Exact Test (Left)                     0.778
                    (Right)                    0.500
                    (2-Tail)                   1.000
------------------------------------------------------
```

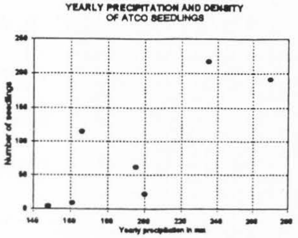
Table A42: Analysis of grazing and time effects on plant distribution 1935 to 1994.

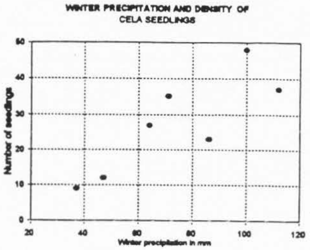
```
                          The SAS System

                        The MIXED Procedure
                      Class Level Information
                          TRT           2  g u
                          TIM           5  1 2 3 4 5

                      REML Estimation Iteration History
             Iteration  Evaluations      Objective     Criterion

                     0            1  -76.59667744
                     1            1  -131.5326761    0.00000000

                Convergence criteria met.
                Covariance Parameter Estimates (REML)

             Cov Parm         Ratio      Estimate      Std Error        Z  Pr > |Z|
              PLOT       0.96527427    0.09714356     0.02854699     3.40    0.0007
              Residual   1.00000000    0.10063830     0.01220419     8.25    0.0001

                          Model Fitting Information for VAME
             Description                            Value
             Observations                        180.0000
             Variance Estimate                     0.1006
             Standard Deviation Estimate           0.3172
             REML Log Likelihood                 -90.4532
             Akaike's Information Criterion      -92.4532
             Schwarz's Bayesian Criterion        -95.5890
             -2 REML Log Likelihood              180.9064

                         Tests of Fixed Effects

             Source     NDF   DDF  Type III F  Pr > F
              TRT         1   136        0.25  0.6197
              TIM         4   136        2.79  0.0290
              TRT*TIM     4   136        0.99  0.4148

                         Least Squares Means

             Level              LSMEAN     Std Error   DDF        T   Pr > |T|
             TIM 1          1.31000000    0.07412112   136    17.67     0.0001

                         Differences of Least Squares Means

Level 1        Level 2       Difference      Std Error   DDF        T   Pr > |T|  Adjustment       Adj P

TIM 1          TIM 2        -0.04527778     0.07477310   136    -0.61     0.5458  Bonferroni      1.0000
TIM 1          TIM 3         0.06805556     0.07477310   136     0.91     0.3643  Bonferroni      1.0000
TIM 1          TIM 4         0.12972222     0.07477310   136     1.73     0.0850  Bonferroni      0.8503
TIM 1          TIM 5        -0.09166667     0.07477310   136    -1.23     0.2223  Bonferroni      1.0000
TIM 2          TIM 3         0.11333333     0.07477310   136     1.52     0.1319  Bonferroni      1.0000
TIM 2          TIM 4         0.17500000     0.07477310   136     2.34     0.0207  Bonferroni      0.2072
TIM 2          TIM 5        -0.04638889     0.07477310   136    -0.62     0.5360  Bonferroni      1.0000
TIM 3          TIM 4         0.06166667     0.07477310   136     0.82     0.4110  Bonferroni      1.0000
TIM 3          TIM 5        -0.15972222     0.07477310   136    -2.14     0.0345  Bonferroni      0.3446
TIM 4          TIM 5        -0.22138889     0.07477310   136    -2.96     0.0036  Bonferroni      0.0362
TRT g          TRT u         0.05677778     0.11414962   136     0.50     0.6197  Bonferroni      0.6197
```

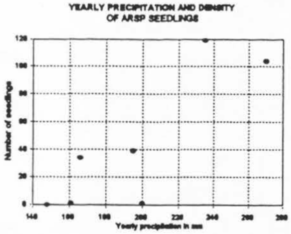
Table A43: Analysis to test differences between slopes of grazed and ungrazed significant regressions.

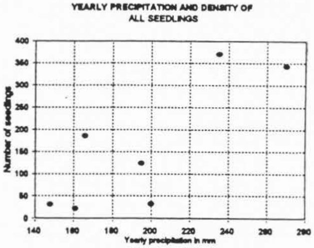
```
                          The SAS System

                       The MIXED Procedure

                     Class Level Information

                     Class      Levels  Values

                     TRT             2  G U

                       The MIXED Procedure

                Model Fitting Information for DIS

          Description                            Value

          Observations                         86.0000
          Variance Estimate                     4.7468
          Standard Deviation Estimate           2.1787
          REML Log Likelihood                 -195.586
          Akaike's Information Criterion      -196.586
          Schwarz's Bayesian Criterion        -197.790
          -2 REML Log Likelihood              391.1726

                       The MIXED Procedure

                      Tests of Fixed Effects

         Source       NDF   DDF  Type III F  Pr > F

         TRT            1    82        0.55  0.4612 Intercept
         SIZF           1    82       22.70  0.0000 Covariate
         SIZF*TRT       1    82        0.85  0.3600 Slope

                       The MIXED Procedure

                       Least Squares Means

    Level              LSMEAN      Std Error   DDF        T  Pr > |T|

    TRT G          6.10484174     0.30213613    82    20.21    0.0000
    TRT U          6.08726863     0.37365847    82    16.29    0.0000
    TRT 1-2        0.01757311     0.48052772    82     0.04    0.9709
```

Figure A1: Correlations between seedlings emerged in the 7 sampling dates and precipitation variables.









CURRICULUM VITAE

Full name: Humberto Alzérreca Angelo
Citizenship: Bolivia (Tupiza)

Education and Training:

1968-1973	B.Sc. (University of San Simón, Cochabamba, Bolivia). Agronomy.
1976-1978	M.Sc. (Utah State University, Logan, Utah). Range Science.
1992-1996	Ph.D. (Utah State University, Logan Utah). Range Science.
1977	Range management (Colorado State University).
1980	Animal production in semi-arid and arid rangelands (UNEP-Soviet Union).
1983	Assessment of desertification and techniques for soil stabilization and revegetation (FAO-Italy).
1988	Range management and forage production (New Mexico Sta. Uni.).

Work experience:

1973-1976	Assistant technician in animal, forage, range research and production (Patacamaya Research Station, Bolivia).
1979-1992	Technician for the Bolivian Institute of Agricultural Technology (IBTA) in forage and range research, production and development programs. As a private consultant in the same subjects named above.
1990-1992	Director of the animal and forage research program at IBTA.

Research Interest:

1975	B. Sc. Evaluación de la pradera nativa en el Altiplano Central de Bolivia.
1978	M.Sc. Condition and development of the Altiplano range in Bolivia.

1996 Ph.D. Spatial and temporal dynamics of plant populations in salt-desert shrub vegetation grazed by sheep.

Publications:

1986 Lara, R. y Alzérreca H. 1986. Pastizales, p. 82-96. *In*: C. Brockman (ed.) Perfil Ambiental de Bolivia. Agencia Internacional para el Desarrollo. Ins. Int. Para el Desarrollo del Medio Ambiente. La Paz, Bolivia.

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1991 Cardozo, A. y Alzérreca H. 1991. Valor de los alimento para la ganadería Andina. Serie técnica-IBTA/SR-CRSP/001. LA Paz, Bolivia. 82 p.

1991 Alzérreca, H. 1991. Overview of small ruminant research in the Bolivian Andean Zone, p. 165-207. *In:* C. Valdivia (ed.), Sustainable Crop-Livestock Systems for the Bolivian Highlands. Proceedings of an SR-CRSP Workshop.

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1995 Genin, D. y Alzérreca, H. Reseña de la vegetación de la zona de Turco, p. 35-56. *In*: D. Genin and H. Picht (eds.), Waira Pampa-Un sistema pastoril camélidos-ovinos del Altiplano árido Boliviano. ORSTOM/IBTA. 299 p.

1976-1994. Sixteen research articles (author and coauthor) published in the research series of the Bolivian Institute of Agricultural Technology numbered VI, VII, VIII, IX, X and XI.

Awards:

Vice-president of the Bolivian Association of Animal Production (ABOPA), two terms.

Assistant and Director of the grass and forage section of the Latin-American Association of Animal Production (ALPA), one term.