# Vegetative Responses of Some Great Basin Shrub Communities Protected against Jackrabbits or Domestic Stock

BARBARA RICE AND MARK WESTOBY

We surveyed the vegetation at 19 locations inside and outside 12 exclosures built at various times in Curlew Valley, northern Utah. The exclosures were in semidesert shrub vegetation and included several communities definable by a dominant perennial shrub distribution having sharp boundaries. At the level of the individual quadrat, there was no correlation between the density of any of the abundant annuals and the percentage of the soil surface that was bare, or covered by rock, dead plant matter, or cryptogam crust. The communities as defined by dominants arranged themselves in the order winterfat, shadscale, shadscale and perennial grasses, sagebrush, black sage. These communities are known to be found on progressively less xeric sites. The changes which resulted from protecting samples of these communities from grazers were fairly consistent within each community, but differed among communities; and moreover these changes were not correlated with a trend from more to less xeric sites. Protection against sheep, with or without protection against jackrabbits, did not have very many effects even over 15 years: halogeton generally decreased; peppergrass increased where present; winterfat increased in vigor but not in density where it was dominant. Other dominant shrubs and perennial grasses did not respond to protection. Protection against jackrabbits had no consistent extra effect on the parameters studied. The classical concept of range succession is that recovery from overgrazing moves a community through secondary succession parallel to a gradient towards relatively more mesic conditions. On the whole, this concept has not been useful in interpreting the results of excluding grazers from these semiarid shrublands.

It is generally accepted that vegetation on many semiarid rangelands has changed during the last century, partly because of poor grazing practices (Martin 1975). A number of reports document shifts from grassland to shrub-dominated vegetation in New Mexico (Buffington and Herbel 1965) and central Utah (Christensen and Johnson 1964). Vale (1975) suggested that northern Great Basin semiarid ranges may always have been dominated by shrub species. Under continued grazing pressure vegetational change in northern Nevada may be toward annual grasses and forbs replacing desirable browse species (Robertson and Kennedy 1954).

Studies of grazing successions are frequently based on comparisons of protected and grazed vegetation, and results vary considerably. Stoddart et al. (1975) state that secondary succession should follow the same sequence as primary succession, although the process may be extremely slow. On some Arizona ranges the shrub component continues to increase, regardless of grazing treatment (Smith and Schmutz 1975). Gardner (1950) found an increase in grass cover on protected areas in New Mexico, but little difference in floristic composition after 30 years. In Texas Smeins et al. (1976) recorded little change in plant composition within an exclosure protected for 25 years, and Reardon and Merrill (1976) found that litter production was greater under continuous light grazing than under no grazing. In western Colorado, Turner (1971) found little response to protection which could be clearly attributed to livestock exclusion, although an increase in litter and moss cover within exclosures was attributed to the lack of trampling. However, Robertson (1971) reported that 30 years' exclusion of livestock on a Nevada sagebrush-grass range resulted in an increase of shrub, forb, and grass cover.

In Curlew Valley, northern Utah, different range scientists have at various times built exclosures against livestock, and sometimes against jackrabbits. The exclosures are spread over a range of vegetation types along a slope and have been protected from 6 to 15 years. They provide an opportunity to study differences between protected and unprotected vegetation and also the relation of those differences to variation among different vegetation types. In this paper we report results of a vegetation survey designed to investigate those matters.

## Study Area

Curlew Valley runs north from the shore of the Great Salt Lake across the Utah/Idaho border. Vegetation ranges from sagebrush (*Artemisia tridentata*) types in the north to saltbush types (*Atriplex* spp.) in the south and at lower elevations. Total year-round precipitation ranges from 150–200 mm in the south to 350–400 mm in the north. Most falls in the winter, a substantial portion as snow. Besides decreasing precipitation, another probable cause of changing vegetation down the valley is the increasing salinity of soils left behind by Pleistocene Lake Bonneville during its retreat. Attempts to define the correlation of soil properties with plant distribution in the study area have not been successful (Mitchell et al. 1966).

Gates et al. (1956) show that abrupt changes in soil chemistry do not necessarily induce concomitant, or consistent, shifts in vegetation. Even the relatively strong patterning in winterfat and shadscale vegetation types is apparently independent of soil salinity (Mitchell et al. 1966), although salinity would seem the strongest factor operating on distribution in the area.

A sketch-map of the part of the valley in which our studies were located is shown in Figure 1. The Wildcat Hills, on the east in Figure 1, rise in the center of the valley. The lowest point on the east-
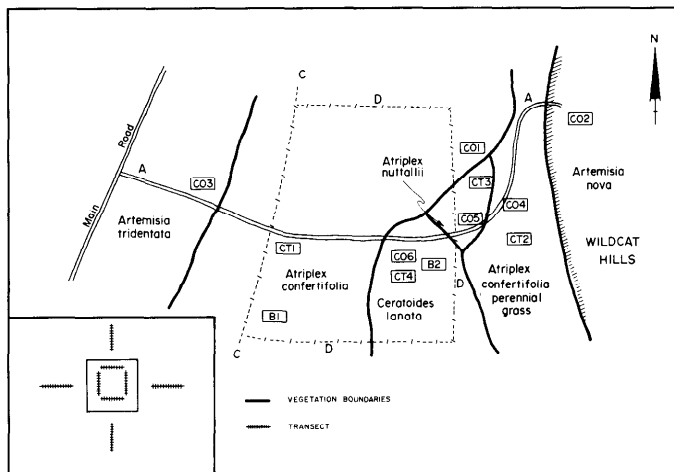
**Fig. 1.** *Sketch map of the study area. A is the access road, C and D indicate relevant fences, small rectangles with two- or three-digit names are exclosures. Further explanation in text.*

west road A lies at about B. The dominant shrubs are mapped over the area. This mapping is not exact but serves to show which shrubs dominate the vegetation of particular exclosures. For example, exclosure CO3 is dominated by sagebrush. To the east on the map, the road A turns north under a sharp slope upwards to the Wildcat Hills. Thus exclosure CO2 lies higher than the others, on coarser soils, and is dominated by black sage (*Artemisia nova*). Exclosure CT2 lies at the mouth of a small valley into the Wildcat Hills, and its soil is also coarser, presumably derived from material washed out of the valley.

What is known of the grazing history of the area is as follows. (We are grateful to Dr. N. E. West for this information.) From 1869–1914, Kelton, a few miles south, was a major railhead for shipping stock. Over this period the study area probably was grazed intensely by sheep being driven to Kelton and held waiting for shipment. After 1919 the main east-west railway route shifted south of the Great Salt Lake, and Kelton was no longer used. More recently the valley to the south of the study area has been grazed in winter under Bureau of Land Management permit. In the study area itself, the area west of the fence C has been grazed year-round by cattle. The center of the valley, bounded by fence C and fence D, was privately owned and used as a lambing ground until 1969. Since then it has not been grazed. The corridor between Fence D, on the west, and the slope of the Wildcat Hills, on the east, is the route through which sheep are driven south in early winter to use the grazing in the lower valley, and north again in spring. While there is no fence restraining sheep to the east, the absence of dung indicates that they do not usually have time to spread up onto the high ground.

The area shown in Figure 1 has been much used since the 1950's for various studies of range ecology. The exclosures shown there have mostly been established in order to protect from defoliation individual plants whose physiology was being studied. Those exclosures prefixed CO were established in 1956 (Cook 1971); except for CO1 they were made proof against jackrabbits (*Lepus californicus* only in this area) in 1957. The studies in them ended in 1969; the protection of CO2 and CO4 against jackrabbits has lapsed since then (Westoby 1973). Exclosures prefixed CT were established in 1966 (Coyne 1969; Trlica 1971). None of these were made jackrabbit-proof. Those prefixed B were established in 1968 (Bjerregaard 1971) and were made jackrabbit-proof.

## Methods

### Data Collection

Data were collected at a total of 19 "locations." These were inside each of the 12 exclosures and close by, but outside, seven of them—exclosures B1, CO1, CO2, CO3, CO4, CO5, and CO6. Locations in exclosures are referred to by the suffix P (e.g. B1P) and those outside by the suffix U (e.g. B1U). The inset in Figure 1 shows the arrangement within and outside the exclosures. Four 30-m transects were

placed at each location. At 1.5-m intervals along each transect, twenty 0.1 m² (50 cm × 20 cm) quadrats were sampled. Within each quadrat percent cover and rooting density of shrubs were recorded. The soil surface was described as percentages of bare soil, cryptogam cover (algal crust), and litter; plant bases were considered litter. For perennial grasses, a cover value was recorded for each individual whose center lay inside the quadrat. Percent cover for each such individual was estimated as if it lay entirely inside the quadrat. Individuals some part of which fell inside the quadrat were not recorded if their center was not inside.

At each end of the quadrat, two 10 cm × 20 cm areas were marked off with wire. The densities of annual species were recorded in these two subquadrats.

These data were collected between May 6 and 12, 1973. At this date all annuals had germinated but most had not flowered. Identification was therefore speculative at the time the data were collected. In most cases the species were given arbitrary names and successfully identified later. In one case, however, seedlings of two *Descurainia* species were given the same arbitrary designation, and these data could not be properly separated afterwards. Generally they occurred together only in the Wildcat Hills, while over the rest of the area *Descurainia pinnata* was found.

### Data Analysis

In the Results section, besides presenting the basic data on vegetation properties of the 19 locations, we describe results of analyzing the data in three ways.

First, we studied the distribution of herbaceous species in the 0.1-m² quadrats with respect to their relation to soil surface properties and the percentage cover of half-shrubs and whole shrubs, by correlation of these factors for all 1,520 quadrats. Second, we ordinated the 19 locations to find the main directions of variation in vegetation composition over the whole study area, in order to see whether changes in vegetation after exclusion were consistently related to their direction of variation. A Bray-Curtis ordination method was used (Bray and Curtis 1957). Third, we considered the specific effects of protection by comparing particular pairs of samples (grazed and ungrazed) at locations which probably had similar shrub dominants before undergoing different grazing histories.

The basic data which come out of a vegetation study take the form of a table, with species along one side, locations along the other, and a measure of the abundance of each species at each location in each cell of the table. Such a table contains too much information for the main patterns to be readily apparent. Ordination is one of several methods for reducing such a data table to a simpler picture, but without discarding too much information in the process. The first step is to convert the basic data table to a similarity table. This is a table with the list of locations along both sides. Each cell of the table contains a measure of how different two locations are. The diagonal contains zero values, and the matrix is symmetrical about the diagonal.

Various measures of how different two locations are can be used. The results we present used percentage similarity, obtained by summing over all species the smallest abundance of each divided by the sum of its abundances in the two sites.

The similarity matrix can be used in various ways. In ordination procedures the locations are arranged along a few axes (usually two, so that the resulting figure can be shown on a page) in such a way that distances between locations in the arrangement are as close as possible in proportion to the differences between them in the similarity matrix.

We carried out several Bray-Curtis ordinations and a principal components ordination. In Bray-Curtis ordination axes are defined by choosing very dissimilar sites as endpoints; principal components ordination uses measures of how much variance between sites is explained to choose axes. For our data all analyses gave similar results. Gauch and Whittaker (1973) describe and assess the merits of different ordination methods.

Before carrying out ordinations, we reduced somewhat the basic data table. First, we removed those species which occurred in only a few locations because the mathematics of ordination make two locations appear similar if they both lack the same species as well as if

**Table 1.** Vegetation composition as percentage cover and densities at the 19 locations studied. Locations are arranged with similar ones adjacent. Zero values indicate cover of less than 0.05%.

| Measure of abundance / Species | Location | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | CO2U | CO2P | CT2P | CO3U | CO3P | B1U | B1P | CT1P | CO1U | CO1P | CO4U | CO4P | CO6U | CO6P | CT4P | B2P | CO5U | CO5P | CT3P |
| **Percent cover** | | | | | | | | | | | | | | | | | | | |
| *Artemisia nova* | 26 | 25 | | | | | | | | | | | | | | | | | |
| *Artemisia tridentata* | | 1 | 6 | 9 | 10 | | | | | | 2 | 3 | 0.1 | 1 | 0.1 | | | | |
| *Atriplex confertifolia* | | 0.1 | | | | 12 | 19 | 20 | 6 | 7 | 8 | 9 | 0 | | | | | | |
| *Ceratoides lanata* | | | | | | 0.3 | | | 0 | | | 2 | 16 | 25 | 21 | 29 | | | |
| *Atriplex nuttallii* | | | | | | | | | | | | | | 0.3 | | | 18 | 15 | 22 |
| *Chrysothamnus viscidiflorus* | 0.4 | 2 | 8 | | | | | | | | | | | | | | | | |
| *Grayia spinosa* | 1 | 0.1 | 5 | | | | | | | | | | | | | | | | |
| *Artemisia spinescens* | | | | | | 2 | | | | | 1 | 2 | | | | | | | |
| *Kochia americana* | | | | | | | | | | | 0.3 | 0.8 | | | | | | | |
| **Rooting density/m$^2$** | | | | | | | | | | | | | | | | | | | |
| *Artemisia nova* | 5 | 4 | | | | | | | | | | | | | | | | | |
| *Artemisia tridentata* | | | 0.3 | 1 | 1 | | | | | | 0.3 | 2 | | | 0.5 | 0.3 | | | |
| *Atriplex confertifolia* | | | 0.3 | | | 4 | 5 | 3 | 2 | 2 | 2 | 1 | 0.1 | | | | | | |
| *Ceratoides lanata* | | | | | | 0.3 | | | 0.1 | | | 1 | 19 | 21 | 23 | 27 | | | |
| *Atriplex nuttallii* | | | | | | | | | | | | | | | | | 49 | 28 | 42 |
| *Chrysothamnus viscidiflorus* | 0.3 | | | | | | | | | | | | | | | | | | |
| *Grayia spinosa* | 0.3 | 0.1 | 0.1 | | | | | | | | | | | | | | | | |
| *Artemisia spinescens* | | | | | | 1 | | | 0.4 | 0.3 | | | | | | | | | |
| *Kochia americana* | | | | | | | | | 2 | 2 | | | | | | | | | |
| *Malcolmia africana* | 4 | 1 | 1 | | | | | | 0.3 | | | 11 | 1 | 3 | | 4 | 15 | 94 | 313 |
| *Halogeton glomeratus* | | | 69 | 150 | 53 | | 141 | 21 | 701 | 247 | 558 | 2 | 285 | | 25 | 2 | 88 | | 26 |
| *Descurainia* spp. | 19 | 71 | 5 | 75 | 129 | 23 | 32 | 2 | 15 | 77 | 0.3 | 12 | 16 | 19 | 9 | 2 | 3 | 4 | 5 |
| *Cryptantha* sp. (annual) | 3 | 1 | 4 | 3 | 2 | 13 | 31 | 3 | 7 | 25 | 11 | 7 | 13 | 2 | 3 | 4 | 45 | 3 | 21 |
| *Bromus tectorum* | 20 | 21 | 95 | 673 | 776 | 164 | 225 | 62 | 642 | 609 | 446 | 232 | 7 | 5 | 55 | 7 | 34 | 466 | 84 |
| *Lepidium perfoliatum* | | | | | | 45 | 4 | 558 | | 7 | 9 | 72 | | | | | | | |

they have the same species. Thus too many zero values in the table can produce misleading results. Second, we divided all percentage cover values in the table by the largest single percentage cover, and all densities by the largest single density. This has the effect of making species measured by cover (shrubs and perennial grasses) of roughly equal importance in the ordination to species measured by density (annuals).

## Results

### Vegetation Composition

Table 1 shows the vegetation composition of the 19 locations studied. On the basis of the dominant shrubs, the locations fall into six subjectively recognizable communities. These correspond to the types indicated in Figure 1. They are communities dominated by sagebrush, shadscale, winterfat (*Ceratoides lanata*), Nuttall saltbush (*Atriplex nuttallii*), black sage, and shadscale-mixed shrub-grass community.

Of the minor perennials, white sage (*Kochia americana*) and bud sage (*Artemisia spinescens*) were found exclusively in certain shadscale communities on the east side of the valley. *Phlox hoodii* and rabbitbrush (*Chrysothamnus viscidiflorus*) occurred in all full-shrub communities. *Grayia spinosa* was found in sagebrush with black sage communities. Pricklypear (*Opuntia polyacantha*) was found occasionally in all communities.

Of the herbaceous species, three of the most important, halogeton (*Halogeton glomeratus*), *Malcolmia africana,* and cheatgrass (*Bromus tectorum*), are introduced. Halogeton was found in all communities except those dominated by black sage, but reached its greatest abundance in certain shadscale and winterfat communities. *Malcolmia africana* was also found in several communities, including those dominated by black sage, but only reached great abundance in Nuttall saltbush communities. Cheatgrass was found in all communities, but was most abundant in sagebrush communities, where it formed an almost continuous understory.

Of the native herbaceous species, the annual *Cryptantha* was found in moderate amounts in all communities, never reaching the abundance of halogeton, cheatgrass, or *Lepidium perfoliatum.* The latter was found only in shadscale communities. *Lepidium densiflorum* was found only in winterfat communities. *Allium nevadense, Phlox longifolia,* and *Gilia inconspicua* were virtually restricted to black sage communities.

By far the most important perennial grass was squirreltail (*Sitanion hystrix*). It occurred in all six communities, but rarely exceeded 10% cover; it did not compare with the dominant shrubs in abundance. Indian ricegrass (*Oryzopsis hymenoides*) was less common. Sandberg bluegrass (*Poa sandbergii*) equalled squirreltail in importance in the black sage community.

### Correlation between Herbaceous Species and Microscale Properties

We attempted to determine the microscale habitat preferences of the more abundant annuals and of perennial grass seedlings by correlating their density in individual quadrats with factors that might be expected to influence their densities, such as the percentages of the soil surface covered with litter, a cryptogam crust, or bare ground, and the shrub cover over the quadrat.

We plotted scattergrams of densities against these factors, after appropriate transformations (square root for densities, angular for percentages). None of these scattergrams showed any consistent patterns. Accordingly we did not calculate correlation coefficients.

### Ordination

Figure 2 shows the results of a typical Bray–Curtis ordination. In this figure, locations which were similar (as measured by percentage similarity) are close together, while very different sites are far apart. The dotted lines separate sets of locations
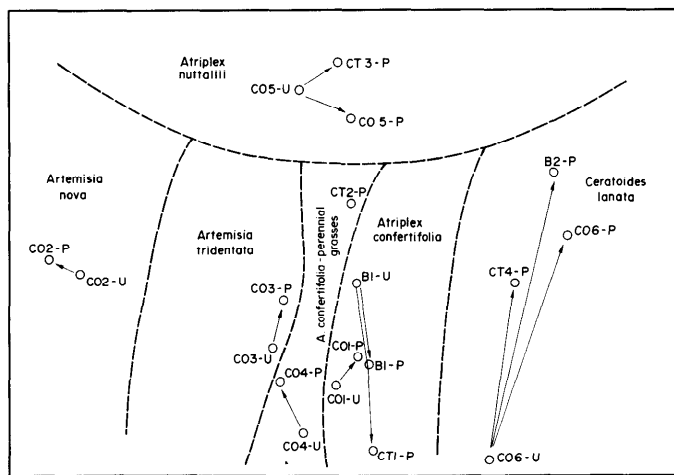
**Fig. 2.** *Results of a two-dimensional Bray-Curtis ordination of sample sites. The closer two sites on this figure, the more similar was their vegetation. Arrows go from grazed sites to protected sites with the same dominants, and therefore indicate the directions of change after protection. Further explanation in text.*

dominated by different perennial species or species-combinations. The main sequence of these subjectively recognizable communities, from left to right, is black sage, sagebrush, shadscale-mixed shrub-grass, shadscale, and winterfat. This is the same sequence as is found typically in Curlew Valley going towards lower elevations and more saline soils. The ordination has placed the Nuttall saltbush communities to one side of this main sequence, though these are normally found interspersed in a mosaic with the winterfat communities. Although surrounded by shadscale-mixed shrub-grass community, exclosure CT2P is dominated by sagebrush and rabbit-brush. This may be due to its position on coarse alluvial soils washed down from the Wildcat Hills.

Just as two sites with different vegetation would occur in different places in a two-dimensional ordination such as Figure 2, a change in the vegetation of one site would cause it to change its position, and the direction of the move would indicate the nature of the change which had occurred.

Therefore on Figure 2 we have drawn arrows from locations which are unprotected to those which have the same perennial dominants and which have been protected from large herbivores to various degrees and for various times. These arrows represent

in length the amount of vegetation change suggested, and in direction the nature of the change.

First, it is clear that within each subjectively recognizable community the effects of protection from herbivores are reasonably consistent. Second, however, the trends were different in each community. Even in two communities with a good deal in common, the shadscale (*A. confertifolia*) and the shadscale-mixed shrub-grass communities, the effects of herbivore exclusion moved the composition of the vegetation in directly opposite directions.

In particular, the trends that resulted from herbivore exclusion apparently did not bear any regular relation to the main trend of vegetation variation along the topographic-rainfall-soil salinity gradient. Thus the effect of protection on the shadscale-dominated communities was not to make them more like the more mesic sagebrush-dominated communities. Similarly, protection did not make sagebrush-dominated communities more like the more diverse black sage-dominated communities.

### Specific Effects of Protection

Table 2 describes what is known of the history of protection of the 12 enclosures. It is of course hard to guarantee that a fence is jackrabbit-proof. We tested this by estimating the standing crop of pellets inside and outside each exclosure during 1973 (Table 2). Westoby and Wagner (1973) found in a nearby area that the standing crop of pellets was 2–3 times as great as a yearly deposition rate which can be calculated from literature values. Therefore it is assumed here that the standing crop of pellets can reasonably be used as a crude estimator of jackrabbit grazing pressure at a location over the last 2–3 years. If the 95% confidence limits of pellet density inside and outside an exclosure do not overlap, the exclosure has probably provided effective protection since 1969. Non-overlap of confidence limits is a conservative test for the difference between means (Sokal and Rohlf 1969). The two peaks of jackrabbit density in Curlew Valley during the history of these exclosures have been in 1959–61 and in 1970–72. From the data presented in Table 2, it is possible to decide which exclosures were rabbit-proof during those peaks.

It might be thought that exclosures which had been protected against sheep grazing but not made rabbit-proof would be subject to heavier jackrabbit use than the community at large; but the pellet counts show no evidence of this. However, a higher rate of pellet deposition may have been counteracted by a

**Table 2. History and characteristics of some exclosures in Curlew Valley up to 1973.**

| Vegetation type | Exclosure name | Sheep-proof since | Jackrabbit pellets per m² (95% confidence limits) | | Dates definitely jackrabbit-proof |
| | | | Inside | Outside | |
| --- | --- | --- | --- | --- | --- |
| *Atriplex confertifolia* | CO1 | 1957 | 34 ± 28 | 155 ± 148 | Never |
| | CT1 | 1966 | 29 ± 17 | 28 ± 13 | Never |
| | B1 | 1968 | 1 ± 1 | 29 ± 37 | 1968–1973 |
| *Artemisia nova* | CO2 | 1957 | 24 ± 31 | 30 ± 39 | 1958–1969 |
| *Artemisia tridentata*[1] | CO3 | 1957 | 29 ± 26 | 92 ± 52 | Never |
| *Atriplex confertifolia* and perennial grasses | CO4 | 1957 | 73 ± 52 | 57 ± 31 | 1958–1969 |
| | CT2 | 1966 | 53 ± 52 | 54 ± 49 | Never |
| *Atriplex nuttallii* | CO5 | 1957 | 19 ± 11 | 125 ± 51 | 1958–1973 |
| | CT3 | 1966 | 99 ± 31 | 131 ± 90 | Never |
| *Ceratoides lanata*[2] | CO6 | 1957 | 0 ± 0 | 155 ± 148 | 1958–1973 |
| | CT4 | 1966 | 70 ± 17 | 90 ± 47 | Never |
| | B2 | 1968 | 3 ± 4 | 92 ± 34 | 1968–1973 |

[1] Area grazed by cattle.
[2] Sheep grazing in this community stopped in 1969.

higher rate of decomposition inside the exclosures, resulting from a more uneven (less trampled) soil surface and a denser herb layer (Flux 1967).

From Table 2 various comparisons among specific locations can be identified which allow us to explore the effects of particular kinds of protection in different communities. The effects of protecting against jackrabbits specifically can be seen by comparing B1P with CT1P in shadscale communities, and B2P with CT4P in winterfat communities. Notice that sheep are absent from both sides of these comparisons. The effects of protecting against both sheep and jackrabbits can be seen by comparing CO2P with CO2U in black sage communities, CO4P with CO4U in shadscale-perennial grass communities, CO5P with CO5U in Nuttall saltbush communities, and CO6P with CO6U in winterfat communities. The effect of excluding cattle can be seen by comparing CO3P with CO3U in sagebrush communities.

For each of these pairs of locations, we compared the value of all measured quantities by $t$-test after appropriate transformation. We do not show the detailed results of these tests here, although mean values are shown in Table 1. The results are summarized in Table 3, where a + means that protection caused a significant ($P < .05$) increase in the parameter, 0 means there was no change, a − indicates a significant decrease under protection, and a blank means that the value was zero in both locations being compared.

In interpreting Table 3 it should be borne in mind that 1 in 20 contrasts would be expected to show a "significant" change

Table 3. Herbivores excluded and the resulting increase (+), decrease (−), or no change (0) in vegetation parameters from plant communities subjectively defined by their dominants. Blanks indicate that the species was absent from both locations being compared. Increases and decreases defined at $P = .05$.

| Measure and species or other parameters | Rabbits | | Sheep | | | Sheep and rabbits | | | | Cattle |
|---|---|---|---|---|---|---|---|---|---|---|
| | Atriplex confertifolia | Ceratoides lanata | Atriplex confertifolia | Atriplex nuttallii | Ceratoides lanata | Ceratoides lanata | Artemisia nova | A. confertifolia perennial grass | Atriplex nuttallii | Artemisia tridentata |
| **Percentage cover** | | | | | | | | | | |
| Chrysothamnus viscidiflorus | | | | | | | 0 | | | |
| Artemisia nova | | | | | | | 0 | | | |
| Artemisia spinescens | | | | | | | | 0 | | |
| Artemisia tridentata | | 0 | | | 0 | 0 | 0 | 0 | | 0 |
| Atriplex confertifolia | 0 | | + | 0 | 0 | 0 | 0 | 0 | | |
| Atriplex nuttallii | | | | 0 | | | 0 | | 0 | |
| Ceratoides lanata | | + | 0 | 0 | + | + | | + | | |
| Grayia spinosa | | | | | | | 0 | | | |
| Juniperus osteospermum | | | | | | | 0 | | | |
| Kochia americana | | | | | | | | 0 | | |
| Opuntia polyacantha | | | 0 | | | | 0 | | | |
| Phlox hoodii | | | | | | | 0 | | | |
| Sitanion hystrix | 0 | 0 | − | 0 | 0 | 0 | 0 | 0 | + | 0 |
| Poa secunda | | 0 | 0 | | | 0 | 0 | 0 | + | 0 |
| Oryzopsis hymenoides | | 0 | 0 | 0 | 0 | | − | 0 | | |
| Bare soil | 0 | − | 0 | 0 | − | 0 | 0 | − | − | 0 |
| Littered soil | 0 | 0 | 0 | 0 | 0 | 0 | − | 0 | + | − |
| Cryptogam-crusted soil | 0 | + | 0 | 0 | + | 0 | 0 | + | + | 0 |
| Rock | | | | | | | 0 | 0 | | + |
| **Density** | | | | | | | | | | |
| Chrysothamnus viscidiflorus | | | | | | | 0 | | | |
| Artemisia nova | | | | | | | 0 | | | |
| Artemisia spinescens | | | − | | | | | 0 | | |
| Artemisia tridentata | | 0 | | | 0 | 0 | | 0 | | 0 |
| Atriplex confertifolia | 0 | | 0 | 0 | 0 | 0 | | 0 | | |
| Atriplex nuttallii | | | | 0 | | | | | − | |
| Ceratoides lanata | | 0 | 0 | 0 | 0 | 0 | | + | | |
| Grayia spinosa | | | | | | | 0 | | | |
| Kochia americana | | | | | | | 0 | | | |
| Opuntia polyacantha | | | 0 | | | | 0 | | | 0 |
| Phlox hoodii | | | | | | | 0 | | | |
| Allium nevadense | | | | | | | 0 | | | 0 |
| Bromus tectorum | + | − | − | 0 | + | + | 0 | − | + | 0 |
| Cryptantha nana | | | | | | | 0 | | | |
| Cryptantha sp. (annual) | + | 0 | − | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cymopteris longipes | | | | | | | 0 | | | |
| Descurainia spp. | 0 | − | 0 | 0 | 0 | 0 | + | + | 0 | + |
| Delphinium nelsonii | | | | | | | 0 | | | |
| Brigeron pumilis | | | | | | | 0 | | | |
| Camilina microcarpa | 0 | | | | | | | | | |
| Gilia polyclador | | | | | | | − | | | |
| Halogeton glomeratus | + | − | + | − | − | − | 0 | | − | − |
| Lepidium montanum | | | | | | | + | | | |
| Lepidium perfoliatum | − | | + | + | | | | + | | |
| Lepidium densiflorum | | + | | | − | − | | | | |
| Malcolmia africana | | + | 0 | + | 0 | − | 0 | | − | |
| Phlox longifolia | | | | | | | − | | | |
| Ranunculus testiculatus | | 0 | | | 0 | | | 0 | | |
| Rumex acetosella | | | | | | | | | | 0 |
| Sphaeralcea collina | | | | | | | 0 | 0 | | |

randomly. Thus we would expect as many as 9 of the +'s and −'s in Table 3 to be spurious. Conclusions must be based on repeated patterns. rather than on single comparisons.

Looking first at the effects attributable specifically to excluding rabbits, we see that there were no changes in particular species which were repeated in both the communities for which we have data. In some cases where there was a significant increase in one community, there was a significant decrease in the other. These results are documented in more detail by Westoby (1973).

There seem to be two species consistently affected by the exclusion of sheep but not jackrabbits. *Lepidium perfoliatum* increased consistently in the *Atriplex confertifolia* communities in which it was found. Halogeton decreased in most cases, although in one case in a shadscale community it had increased. This increase was smaller and less significant ($P < .05$) than the decreases ($P < .0005$). This situation may be explained by the fact that the "unprotected" half of this comparison had not been grazed by sheep for 3 years before the data were collected. Perhaps the response of halogeton to sheep exclusion is a rapid one.

In the winterfat community, winterfat has increased in percentage cover but not in rooting density as a result of sheep exclusion; that is, the individual plants have increased in vigor, but not in number.

Considering now the effects of excluding both sheep and jackrabbits, we see first that some of the patterns found when sheep alone were excluded are confirmed. *Lepidium perfoliatum* increased where it was present, *Halogeton* usually decreased, and winterfat increased in percentage cover but not in density where it was a dominant. Interestingly, winterfat increased in density as well as percentage cover in the shadscale-perennial grass community where it was not a dominant. *Malcolmia africana* seemed to decrease when both sheep and jackrabbits were excluded, but this was contradicted by increases found when either sheep or jackrabbits were excluded separately.

Across all kinds of exclusion, the percentage of soil with cryptogam crust tended to increase, and the percentage of bare soil to decrease correspondingly. This was presumably the result of trampling pressures being removed.

## Conclusions and Discussion

From these results we drew the following conclusions:
1) Although the communities in the study area have sharp boundaries as defined by the dominants, ordination arranged them as a series dominated by winterfat, Nuttall saltbush, shadscale, sagebrush, and black sage. These communities occur on progressively less saline soils, at higher elevations, and commonly under higher rainfall. Adjacent communities in the series tend to have annual species in common.
2) The vegetation changes in these communities which result when they are protected against domestic stock, jackrabbits, or both are different among communities. These changes do not tend to move the communities either higher or lower along the environmental progression described.
3) Protection against grazers tended to increase the percentage of the soil surface covered with cryptogam crust, and conversely to decrease the percentage of bare soil. This presumably resulted from the absence of trampling.
4) At the level of the 20 × 50 cm quadrat, there appeared to be no correlation between soil surface properties (percentages of litter, cryptogam crust, etc.) and the abundance of any of the

common annuals or perennial grass seedlings.
5) In most communities the following tendencies of particular species either to increase or decrease under protection were found: *halogeton* tended to decrease; peppergrass (*L. perfoliatum*) to increase where present; winterfat plants increased in vigor where it was a dominant (i.e. there was an increase in percentage cover but not in density).
6) Protection from jackrabbits had no consistent effects.
7) A number of plant species which might have been expected to respond to protection did not do so. The other abundant annuals besides halogeton and peppergrass (*Malcolmia africana, Bromus tectorum, Descurainia* spp., and *Cryptantha* sp.) did not show a consistent response. Perennial grasses did not respond, either in percentage cover, density, or the number of seedlings present. The dominant perennial shrubs, with the exception of winterfat, did not increase under protection.

Three general points can be made from these conclusions. First, the difficulties of intepreting exclosure experiments should be emphasized. Our results from cold deserts are much like those documented for warm, arid zones (Smeins et al. 1976; Smith and Schmutz 1975), indicating common problems over different types of rangelands. While quadrats can be replicated inside and outside an exclosure, it is unusual to have replicated exclosures; that is, replicated samples of the original vegetation subjected to an exclosure treatment. Moreover, in most cases including this one, the sample protected is arbitrarily rather than randomly chosen from the original vegetation. Other factors complicating interpretation in this study are the varied history of the exclosures, and the varied history of grazing patterns to which the areas outside the exclosures have been subjected.

Second, even given these reservations about the imperfections of the "experimental design," we feel we can conclude that any changes which ensue on protection in these communities are at best slow, and probably almost nonexistent. With the exception of winterfat, none of the dominant shrubs or the perennial grasses responded to protection even after periods of 15 years. This must mean either that these populations were not reduced by intense grazing earlier, or that the concept of the grazing succession is not meaningful in these semiarid shrublands, or that recovery has been prevented by some new factor such as *Halogeton* invasion.

Third, we conclude that those changes which do occur after protection are not correlated with changes occurring along the gradient from relatively xeric to relatively mesic sites which dominates the distribution of communities over the area. Again, this is in conflict with the classical concept of range succession (Stoddart et al. 1975).

## Literature Cited

**Bjerregaard, R. S. 1971.** The nitrogen budget of two salt desert shrub plant communities of Western Utah. PhD Diss., Utah State Univ., Logan. 100 p.

**Bray, R. J., and J. T. Curtis. 1957.** An ordination of the upland forest communities of Southern Wisconsin. Ecol. Monogr. 27:325-349.

**Buffington, L. C., and C. H. Herbel. 1965.** Vegetational changes on a semi-desert grassland range from 1858–1963. Ecol. Monogr. 35:135-164.

**Christensen, E. M., and H. B. Johnson. 1964.** Presettlement vegetation and vegetational change in three valleys in Central Utah. Brigham Young Univ. Sci. Bull. Biol. Ser. IV, No. 4. 16 p.

**Cook, C. W. 1971.** Effects of season and intensity of use on desert vegetation. Utah Agr. Exp. Sta. Bull. 382. 57 p.

**Coyne, P. I. 1969.** Seasonal trends in total available carbohydrates with respect to phenological stage of development in eight desert range species. PhD Diss., Utah State Univ., Logan. 164 p.

**Flux, J. E. C. 1967.** Hare numbers and diet in an alpine basin in New Zealand. Proc. N. Z. Ecol. Soc. 14:27-33.

Gardner, J. L. 1950. Effects of thirty years of protection from grazing in desert grassland. Ecology 31:44-50.

Gates, D. H., L. A. Stoddart, and D. W. Cook. 1956. Soil as a factor influencing plant distribution on salt-deserts of Utah. Ecol. Monogr. 26: 155-175.

Gauch, H. F., and R. H. Whittaker. 1972. Comparison of ordination techniques. Ecology 53:868-875.

Martin, S. C. 1975. Ecology and management of south-western semidesert grass-shrub ranges: the status of our knowledge. U.S. Dep. Agr., Forest Serv. Res. Pap. RM-156. 39 p.

Mitchell, J. E., N. E. West, and R. W. Miller. 1966. Soil physical patterns in the shadscale zone of northwestern Utah. Ecology 47:627-630.

Reardon, P. O., and L. B. Merrill. 1976. Vegetative response under various grazing management systems in the Edwards Plateau of Texas. J. Range Manage. 29:195-198.

Robertson, J. H. 1971. Changes on a sagebrush-grass range in Nevada ungrazed for 30 years. J. Range Manage. 24:397-400.

Robertson, J. H., and P. B. Kennedy. 1954. Half-century changes on northern Nevada ranges. J. Range Manage. 7:117-121.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco. 776 p.

Smeins, F. E., T. W. Taylor, and L. B. Merrill. 1976. Vegetation of a 25-year exclosure on the Edwards Plateau, Texas. J. Range Manage. 29:24-29.

Smith, D. A., and E. M. Schmutz. 1975. Vegetative changes on protected versus grazed desert grassland ranges in Arizona. J. Range Manage. 28: 453-458.

Stoddart, L. A., A. D. Smith, and T. W. Box. 1975. Range Management. 3rd edition. McGraw-Hill Book Co., Inc., New York. 532 p.

Trlica, M. J., Jr. 1971. Defoliation and soil moisture regime effects on plant regrowth and carbohydrate reserve utilization and storage in eight desert range species. PhD Diss., Utah State Univ., Logan. 122 p.

Turner, G. T. 1971. Soil and grazing influences on a salt-desert shrub range in western Colorado. J. Range Manage. 24:31-37.

Vale, T. R. 1975. Presettlement vegetation in the sagebrush-grass area of the intermountain west. J. Range Manage. 28:33-36.

Westoby, M. 1973. Impact of black-tailed jackrabbits (Lepus californicus) on vegetation in Curlew Valley, Northern Utah. PhD Diss., Utah State Univ., Logan. 164 p.

Westoby, M., and F. H. Wagner. 1973. Use of a crested wheatgrass seeding by black-tailed jackrabbits. J. Range Manage. 26:349-352.