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ENVIRONMENTAL FACTORS INFLUENCING SEMIDESERT GRASSLAND PERENNIAL GRASS DEMOGRAPHY

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ABSTRACT. Long-term chart quadrat records from the Jornada Experimental Range in south-central New Mexico were photographed, the negatives analyzed with a flying-spot scanner, and the information converted for computer analyses. Some 35 quadrats with data from about 30 to 50 years duration were used giving records on the life-span of 12,437 perennial grass plants of seven species. Maximum life spans varied from 28 years for *Bouteloua eripoda* to only 7 years for *Hilaria mutica.* Mean life span for plants living at least 1 year varied from 3.8 to 3.0 years for these species. Average age-specific survival rates for seven perennial grasses increased from 0.39 at age 1 up to a maximum of 0.68 at age 7 and down to 0.48 at age 12. The level of grazing over the past years had little effect on plant survival, but cattle movement and trampling caused the death of some newly established grasses. A water-budget model produced results that could be readily interpreted in understanding plant survival. The relationship between the number of days of effective moisture in a given time period and the age-specific survival rates for each age class was pronounced. The period between the second and fourth age classes was most critical as regards availability of water. For newly established plants with shallow root systems, the precipitation of the immediate growing season was more important than precipitation for longer antecedent intervals.

Continuous, reliable data, spanning long time periods are extremely rare for plant communities, particularly for herbaceous plants. Data on individual plants, necessary for examining many aspects of life history, are even more scarce. One of the major sources of such information for herbaceous communities has been through chart quadrat records in which permanently established quadrats are charted accurately over a period of years. Only limited amounts of such information are reported in the literature. For humid and subhumid grasslands Harper (1960, 1967) has reported on demographic characteristics of *Lemma minor* and *Salvina natans* and Kerster (1968) reported on *Liatris aspera.* For semiarid and arid areas Nelson (1934) reported demographic characteristics of *Bouteloua eriopoda* and Williams (1968) on *Danthonia caespitosa.* Life-span and reproduction of perennial grasses in semidesert areas were reported by Canfield (1957).

These studies have shown prairie forbs generally have life-spans of 5 to 16 years (Kerster 1968), forbs from cool, subhumid climates live about 3 to 6 years (Tamm 1956), and grasses from arid areas live 4 to 14 years, but median life expectancy may be only 3 months to 1.5 years (Nelson 1934; Canfield 1957; Williams 1969). As part of the overall present study Dittberner (1971) has presented data on life-span of several annual and perennial grasses and forbs from the Jornada. These data are referred to later herein.

Most studies of longevity of perennial herbaceous plants (e.g., Nelson 1934; Tamm 1956; Canfield 1957; Kerster 1968) have considered only the maximum longevity rather than the dynamics of plant demography. Most such work is based on limited observations over a relatively brief time span. Most researchers agree that only a few plants live to an old age (the probability of survival is low in the early years, but increases as the plant ages). Harper (1967) visualizes a constant proportional mortality throughout the life of a plant population.

The recording of chart quadrats over a long time period results in a large number of maps, each illustrating the basal cover in the plant communities. Usually, these data are processed to give only percentage cover for a given year and to plot the time trends (Nelson 1934; Paulsen and Ares 1962). Thus, individual plant data are not obtained. When the records of the individual plants are considered, extremely large amounts of data are obtained. This has required us to develop and use new techniques and instruments to permit analysis of the life history of large numbers of plants.

We investigated plant demography by developing a computer program to search the yearly records serially for a given quadrat, thus following the changes over time of individual plants (Wright and Van Dyne 1970; Wright 1972). Using this approach, we obtained reliable estimates of the time spans of existence for the major perennial grasses. Such analyses are important in evaluating both the response of systems and of specific individuals to long-term environmental alterations.

The objectives of this paper are: (1) to provide data on the life history of selected perennial grasses on the Jornada Experimental Range in terms of mean and maximum life-spans and (2) to examine the influence of important environmental factors in controlling the establishment and survival of perennial grasses.

EXPERIMENTAL AREA. Field data were taken on the Jornada Experimental Range in southeastern New Mexico (Paulsen and Ares 1962; Buffington and Herbel 1965). The area is 1,190 to 1,495 m in elevation and is bounded by the San Andres Mountains on the east and the Rio Grande Valley on the west. The Jornada Experimental Range has 42,775 ha used for grazing.

Climate and Soils.—Records kept at the range headquarters since 1915 show an annual precipitation through 1968 of about 23 cm of which about 70% occurs between 1 April and 30 September normally in the form of high-intensity thunderstorms. Adequate temperatures for plant growth usually prevail for at least 200 days, but conditions of favorable soil water usually are found only between 90 and 100 days. Evaporation from a free-water surface averages about 236 cm a year.

The soils on the Jornada plain lack humus and show little textural change between the surface and subsoil (Gile 1961, Gile and Hawley 1966). The lime content is high in all soil types and this grades into a calcareous layer at variable depths in the coarser soils (Shreve and Mallory 1933).

Vegetation.—The Jornada is a semidesert, shrub-grass complex similar to that which occupies much of the plains area extending over southeastern Arizona, southern New Mexico, western Texas, and northern Mexico (Jardine and Forsling 1922; Campbell 1929, 1931; Campbell and Campbell 1938). Little and Campbell (1943) listed 538 species of plants found on the Jornada of which some 49 species have been encountered for at least two different years in the quadrat records used in the present research.

The majority of the chart quadrats used in this study were located in either the black grama *(Bouteloua eriopoda)* vegetation type or in the complex known as the mesquite-sandhills type *(Prosopis juliflora)*. The former is common on the well-drained sandy and gravelly soils of the dry mesas. Black grama is the dominant species. Associated species include red threeawn *(Aristida longiseta)*, mesa dropseed *(Sporobolus flexuosus)*, and poverty threeawn *(Aristida divaricata)*. Other perennial grasses of concern are ear muhly *(Muhlenbergia arenacea)*, burro grass *(Scleropogon brevifolius)*, and tobosa grass (*Hilaria mutica)*.

Where the soils are shallow, mesquite forms lateral roots that may reach out as much as 25 m from the subsurface stem, resulting in a rapid depletion of the soil water (Parker and Martin 1952). The multiple stems of the plant in turn trap blowing sand into dunes. These dual actions promote a condition whereby little cover can be established between the dunes. As early as 1929, Campbell recognized that this cycle of dune formation may be self-regenerating and spreading. The spread of mesquite has since been dramatic, and it now occupies about 58% of the range (Buffington and Herbel 1965).

METHODS. The Jornada quadrats were charted annually from 1915 through 1968, with exception of a few years from 1954 through 1967. We used data from about 35 quadrats selected out of the 90 that were charted for more than 30 years. The field procedures of charting are described by Hill (1920). The field quadrats are 1 m^2, marked by angle iron stakes, and basal cover of vegetation is mapped by species. The computer processing and analysis of these records has been described by Wright and Van Dyne (1970) and Wright (1972). Dittberner (1971) has also analyzed some of these chart quadrat data.

We retraced the original chart maps so that the basal areas of all plants were clear, then photographed these tracings on high-contrast 35-mm film and digitized them using the flying-spot scanner system located at Argonne National Laboratory (described by Butler, Butler, and Stroud 1964, 1966, 1968 and Butler and Butler 1967). The output of the scanning system provides a record for each year of each plant on the quadrat identified according to its coordinate positions and its basal area. As the scanning system cannot discriminate between species, this and other descriptive material was coded in separately and integrated for analyses.

In this research, we have used less than half of the large data base existing on the Jornada. Thus, the opportunity exists to utilize the remaining data to validate and refine the results discussed here.

Climatic Data.—Climatic records were available from the range headquarters since 1914. Additional precipitation data were taken from a network established in 1920 of 20 storage rain gauges distributed over the range. The semidesert climate is one of the more variable grassland climates within western North America (Smith 1970). Over a 60-year period, the mean precipitation was about 23 cm with a coefficient of variation of 87%.

Variation in precipitation has promoted the establishment and maintenance of a plant community adapted to take immediate advantage of the least effective rainfall. Green (1960) computed the probability of drought and rainy periods during the growing season for nearby Las Cruces, New Mexico. Even during July and August, the "wet" season, the probability that any given day would be the start of a 5-day drought was approximately 20%, and in June and September the probability was greater than 50%.

Animal Use Data.—Records on the use of the experimental range by cattle have been kept since 1912 on a pasture basis. Older records show as early as 1860 herds of sheep, cattle, goats, and horses were driven across the Jornada plain from Chihuahua, Mexico, to Santa Fe. By the turn of the century, overgrazing was generally the case on most New Mexico rangeland (Wooton 1908, Pingrey 1948). Before 1912 the Jornada and surrounding area was heavily grazed by cattle. In 1916 the stocking was at about 17 ha per animal whereas in recent years there have been about 95 ha per animal unit.

A seasonal suitability system (Valentine 1967) has long been used for experimental grazing management on the Jornada. Cattle were removed from the black grama pastures during the summer-fall growing season, and returned to them for October to July (Ares 1943, Pearse 1950, USDA 1951). Canfield (1939) noted that when a black grama range on the Jornada was shifted from year-long to primarily winter-spring use, the perennial grass cover increased by 300%. Herbel and Nelson (1966*a*, 1966*b*) and Herbel, Dittberner, and Bickle (1970) introduced a "best pasture" grazing system which incorporated seasonal suitability and attempted to maximize the use of all forages at the period of their optimum palatability.

Since management strategy has been based on the concept of conservatively utilizing all parts of the pasture, stocking records for the Jornada vary greatly in the number of cattle supported per unit area in the different pastures.

Age-specific Survival.—The quadrat data by species, soil, and grazing level were arranged in matrices, Q, of dimension n years by m age classes, the first age class representing the number of plants established in a given year. An example segment of this Q matrix for one species is as follows:

Time in Years (n)	Age Classes (m)			
	1	2	3	4
1	21	5	3	3
2	15	10	3	1
3	19	7	9	1
4	17	12	5	2

Each row gives the number of plants alive in each of the possible age classes. The rows are the consecutive years in which the quadrat was field plotted. The sum of all entries for one row gives the total number of plants alive for any one year (example, 36 on year 3).

In recoding the data for use in climatic analysis, all elements of Q, i.e., each q_{ij}, are first converted into age-specific survival probabilities q_{ii}^* defined as:

$$q_{ij}^* = q_{i+1,j+l}/q_{ij}$$

The elements of this new matrix represent the age specific survival rates between age class j and $j+l$ from year i to $i+l$.

Many factors can cause a plant to die short of reaching its physiologic maximum life-span. The vagaries of climate are paramount on semidesert grasslands. A host of secondary factors, however, can come into play including overgrazing by domestic animals or rodents, trampling, erosion, and factors within the plant itself that include size, vigor, nutrient uptake ability, and period of growth (Daubenmire 1968). All of these latter factors can be combined under "competitive ability."

We cataloged the deaths from various causes for each species by means of a life table. As many of the secondary causes (such as grazing and variation in precipitation) of death operate independently of plant age and time, they might be considered random. Given a large enough sample, the life tables for each species yield a fairly accurate assessment of the age-specific survival rates (p_j). The data are reduced by calculating for each species matrices D by subtracting the age specific population survival rates from the sample rates as illustrated by the following equation:

$$d_{ij} = q_{ij}^* - p_j$$

for $i = 1, n$ years, $j = 1, m$ age classes.

Precipitation Influences.—We used three approaches to relate precipitation to plant surival: (1) Multiple regression analysis was used to relate the monthly precipitation values to yearly survival probabilities. Although several combinations of rainfall values were tried, none of the analyses gave significant results. (2) The pattern of rainfall was incorporated into the analysis by calculating rainfall distribution coefficients by fitting orthogonal polynomials to the rainfall distribution over some time period (according to the method of Fisher 1925). These coefficients are then used in a multiple regression analysis. This technique proved adequate in explaining a large but uninterpretable proportion of the variance in the age-specific survival rates. (3) We then converted actual precipitation records into units of "effective rainfall" in order to partially limit the changes in soil water over time. The effective rainfall at a particular time is that which is required to maintain soil water in a range for suitable plant growth. It is not a constant but rather a dynamic process, i.e., a function of time, soil characteristics, plant development, and evaporation (Green and Martin 1967).

RESULTS AND DISCUSSION. *Grazing Impact and Survival.*—The variation in the numbers of plants established and in their life-spans as a response to grazing was tested by an analysis of variance. The data were stratified by four soil types and two grazing categories, i.e., those quadrats receiving differential summer use and those receiving year-long use. Distance from water was the criterion for testing the responses to grazing. In most cases, the quadrats ranged from 1 to 5 km from water. Areas near water were presumed to be grazed more intensively over the long run than areas further away from water. Quadrats in exclosures (thus ungrazed) were treated as being a greater distance from water than any other quadrat analyzed.

Grazing, as tested in this manner, has a significant effect on the mean life-span in only two cases, both on species growing on loamy soils grazed during the summer. The reason for this is not clear. The results of all analyses are shown in Table 1.

The influence of grazing on species establishment was more pronounced as indicated in Table 1. On one half of the categories, there was a significant increase in black grama as distance from water increased. In most cases, the effect of grazing measured in this manner did not significantly alter the number of red threeawn and mesa dropseed plants established. In those cases where the results were significant, both species showed a decline in the number of plants established as grazing lessened.

Significant results were obtained only for those plants located on sandy soils. On these soils, it appears that the rooting of new black grama sets is more easily disturbed by cattle trampling than on heavier textured soils.

It appears that trampling by cattle had a more important effect on black grama establishment than did grazing per se. For red threeawn and mesa dropseed, the results are not easily interpreted, but they may indicate that the above species increase as a result of decreased black grama competition and a broken soil surface thus promoting better establishment conditions.

On the semidesert ranges, a general measure of grazing intensity is the distance of an area from a permanent source of water, particularly when no attempts are made to distribute the cattle more evenly. On unfenced public range, originally similar in character to the Jornada, serious overgrazing extended to about 7 km from per-

TABLE 1

Results of a single-classification analysis of variance testing the effect of grazing (as measured in distance from watering points) on the mean life-spans and plant establishment for the species listed.

Soil Type	Quadrats	Total Observations	F value of influence of grazing on: Mean life-span	Establishment
		Black grama		
Shallow, sandy loam†	4	1246	2.8	3.4*
Loamy sand†	4	946	3.0	3.5*
Shallow, sandy loam‡	5	1309	2.2	2.3
Loamy sand‡	11	2583	2.9*	3.3*
Deep sand‡	3	169	0.5	1.6
		Red threeawn		
Shallow, sandy loam†	3	67	1.1	3.7*
Shallow, sandy loam‡	2	99	0.9	3.2*
Deep sand‡	4	198	3.0	0.7
		Poverty threeawn		
Deep sand‡	6	376	2.4	1.6
		Mesa dropseed		
Shallow, sandy loam†	3	185	0.8	2.1
Loamy sand†	4	393	11.8*	3.6*
Shallow, sandy loam‡	4	281	2.2	0.8
Loamy sand‡	6	363	2.1	3.2*
Deep sand‡	6	115	2.9	1.6

† Quadrats receiving differential summer use.
* Significant at 0.025 level.
‡ Quadrats receiving year-long use.

manent water sources. The combined basal area of black grama, red threeawn, and the dropseed grasses at 1 km from watering places on the Jornada was equal to that found 7.2 km from water on the unfenced range (Jardine and Hurtt 1917, Nelson 1934). According to Little and Campbell (1943), the utilization of black grama decreased from water on the Jornada at a rate of 7% km^{-1} for the first 5.6 km. Herbel, Ares, and Nelson (1967) point out, however, that those studies which indicate a decline in grazing use with increased distance from water were conducted in pastures where the vegetation was uniformly good black grama. Their studies show a close relationship between acreage of a zone and grazing time of a zone; animal distribution was not a major problem. This may be due to the relatively level terrain and marginal condition of the pastures. The procedure on the Jornada has been to avoid overuse of certain areas of the range, such as around water sources, through the use of salt and supplemental feed.

In summary here, even though grazing management is considerably improved and grazing intensities greatly decreased on the Jornada in the past 60 years as compared to the earlier half century, grazing still had a negative influence on plant establishment, but relatively little impact on life-span of established plants.

Year-of-Establishment Influence.—To test whether some of the variations between the life-spans of the respective species might be due to the year of establishment, each of the stratified groups of quadrats were analyzed using a two-way analyses of variance with years included. There was no significant difference among the years of establishment within quadrats, or on any of the groups for the respective species. Given these results, the life-spans over all stratifications were combined and are listed in Table 2.

Based on data from about 7,000 black grama plants, 1,600 mesa dropseed plants, and less than 400 of the threeawns, calculated over all locations and treatments, mean life-spans vary from only 2.2 to 1.7 years. Data in Table 2 represent a few more quadrats than used in the analyses reported in Table 1; thus the sample sizes are different. There was, as expected, a high degree of variability in these data and frequently the standard deviation approached or exceeded the mean. As will be noted below, maximum life-spans differ greatly from the mean life-span.

The Effect of Climate on Survival.—The age-specific survival data are plotted in Fig. 1 for three individual species and for the weighted

TABLE 2

Mean life-spans (years), standard deviations, and number of occurrences for principal grasses on the Jornada summed over all soil types and years.

Species	Mean	Standard deviation	Number of observations
Black grama	2.2	2.4	6909
Red threeawn	1.9	1.7	355
Poverty threeawn	1.8	1.5	380
Mesa dropseed	1.7	1.4	1582
Ear muhly	1.8	1.3	1492
Burro grass	1.8	1.5	1607
Tobosa grass	2.0	1.5	112

average of seven perennial grasses representing 12,437 observations for age class 1 and successively fewer plants for older age classes.

Somewhat less than 40% of the perennial grasses established and charted in a given year survive to be charted in the next year. Maximum survival is for 7-year old plants for which almost 70% survive to the next year. After 7 years of age there is an approximately linear decrease in survival of about 0.05 per year.

Two facets of survival are combined in the yearly age specific survival rates calculated above. One is the ability of a plant to survive between effective amounts of rainfall during the thunderstorm season, and the second is the ability to survive between the yearly thunderstorm seasons. The first type of survival implies opportunism, the second is drought resistance. The spectre of drought on the Jornada is always present. The long, catastrophic droughts such as occurred in the early 1920's and 1950's on the Jornada are devastating, but they are probably not as important as short-term droughts in affecting age-specific population survival rates. The long-term droughts tend to be less selective in their influence and probably are not as important in influencing the yearly plant survival rates, but instead play an important role in restricting the life-spans of those few long-lived plants. The short-term drought operates differently in regard to different age classes in different years, making its relationship more difficult to determine.

Our water budget model (i.e., (3) in the section on *Precipitation Influences*) was developed using daily precipitation and evaporation

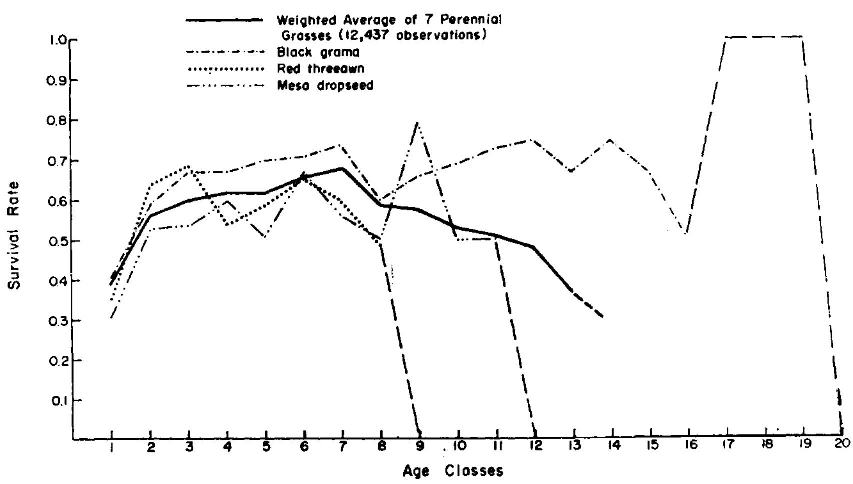

Fig. 1. Population age-specific survival rates for major perennial grasses on the Jornada.

values to compute the number of days for a time period in which the rainfall was above a threshold level. Each day above this level was termed "an effective moisture day." Threshold levels varied with soil type and they were computed from soils data reported by Herbel et al. (1970). We determined the number of days of effective moisture over three time periods prior to the date the quadrats were recorded in the field—the growing season, a year, and a 15-month period. We determined the simple correlation between the number of effective moisture days calculated over any of these three periods and plant survival data. This approach is particularly applicable to the sandy plains of the Jornada which neither receive nor produce runoff. They are also underlain with an impervious caliche layer. Correlations of 0.37 to 0.46 were obtained between the survival of all plant age classes with either 15-month or growing season moisture (Table 3).

The general relationship between the number of days of effective moisture for a given time period and the age-specific survival rates can also be examined using the mean regression coefficients from a series of linear regression equations. These equations are calculated for the combination of effective days and threshold values yielding the highest correlation in the model for each compartment and age class. These coefficients, in essence, give the mean effect of moisture on the age-specific survival rates (Fig. 2).

Effective moisture had more impact on increasing survival rate of 3 to 5 year old blue grama plants than on either younger or older plants. This may be due to the shallower root system of the young plants. Plants with shallow root systems can more easily obtain surface soil water from rainfall that does not effectively add to soil water storage. The decrease in moisture requirements for older plants is probably due to the more effective moisture-gathering mechanisms.

TABLE 3

Results of water-budget model analysis. Correlation of survival of plant age classes averaged over all soil-grazing categories and species.

Plant age class	Time period/effective moisture	correlation coefficient
1	15 months	0.39
2	15 months	0.41
3	15 months	0.39
4	Growing season	0.41
5	Growing season	0.42
6	Growing season	0.37
7	Growing season	0.46
8	Growing season	0.44

Many of the older plants die in the center and split into several individual clumps.

The relation of effective moisture and survival rate for mesa dropseed shows a less pronounced but similar pattern to black grama. The exception is that the initial age class requires slightly more moisture for survival than those age classes immediately following it. This is most probably due to the different mode of establishment of mesa dropseed as compared with black grama.

Effect of Climate on Establishment.—The vectors of the numbers of plants of each species established each year were also related to various classifications of precipitation. Linear regression was used to relate yearly establishment to growing season rainfall of the current year (Table 4). Our data suggest that the production of lateral culms (the chief method of reproduction in black grama) is triggered rather quickly when a sufficient moisture level is reached. A similar phenomenon occurs with respect to seed germination. There was no indication in any of the analyses that the length of the effective moisture period was important to perennial grass establishment.

Maximum Life-spans.—There is a considerable difference between the maximum and mean measured life-spans in the quadrat records (compare Tables 2 and 5). The longest-lived plant on any of the quadrats analyzed was a black grama clump which persisted for

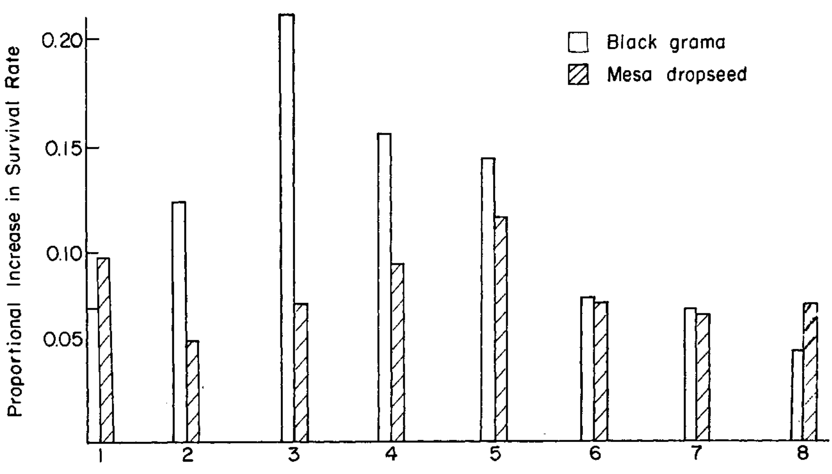

Fig. 2. The mean effect due to a change in effective moisture on the survival rates of black grama and mesa dropseed for given age classes.

TABLE 4

Results of linear regression analysis relating growing season rainfall to plant establishment. Table shows simple correlation coefficients for species categorized by soil type.

Species	Soil: Deep sand	Shallow sandy loam	Loamy sand	Silt clay loam
Black grama	0.39	0.36	0.46	0.34
Mesa dropseed	0.47	0.34	0.27	—
Red threeawn	0.47	—	—	—

about 28 years. Several black grama clumps persisted for 20 years. Likewise, while the longest lived mesa dropseed plant persisted for 18 years, several lived for 12 years. Maximum life-span for the threeawns was about 9 years. The more data that are available, the more chance there is of finding those few longlived plants. But increasing the amount of data does not seem to alter the mean life-spans. The effect of environmental adaptation, indicated by the means of those plants living at least one year as a percentage of the maximum, is illustrated in Table 5. The percentages are, in many cases, almost double those calculated from establishment and point out that the number of survivors between the first and second age classes is low.

Robbins (1957) had discussed the difficulties with respect to the physiological aging in plants. Probably all plants have a physiological maximum life-span which is invariant. The mean life-span of a species is probably not fixed but differs from the physiological maxi-

TABLE 5

Maximum life-span in years and mean life-span as a percent of maximum longevity and mean life-span of those plants living more than 1 year as a percent of maximum attained.

Species	Maximum life-span	Mean life-span of those established as a percent of maximum life-span	Mean life-span of those living at least 1 year as a percent of maximum life-span
Poverty threeawn	9.5	19	33
Red threeawn	9.0	21	40
Black grama	27.5	8	14
Mesa dropseed	18.9	9	18
Ear muhly	9.0	20	31
Burro grass	12.0	15	25
Tobosa grass	6.9	29	44

mum in response to many factors. The proximity of the two measures depends in part on the success of a given species in "learning" how to cope with environmental fluctuations in order to stretch its mean lifespan toward the maximum. In this respect, the perennial grasses in the Jornada have only nominally succeeded.

The lack of fully clearcut causality between survival and establishment to key environmental factors indicates that the effects of environmental factors are more subtle than might be anticipated. It also indicates that a larger role is played by the so-called random environmental factors such as disease.

These analyses are possible only because of dedicated effort of numerous employees on the Jornada Experimental Range since 1915. Carlton Herbel, Agricultural Research Service, made the old records available to us and facilitated our rereading of the quadrats in 1968. J. W. Butler supervised the electronic processing of the negatives of the chart quadrats. Phil Dittberner aided in reading quadrats and discussing procedures of analyses.

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