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Dynamics of shrub die-off in a salt desert plant community

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Abstract

Mortality of shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.) was severe in Great Basin valley bottoms between 1983 and 1988. Puddle Valley, Utah, just west of the Great Salt Lake, typifies areas of extensive shrub loss in which density decreased from over 12,000 ha^{-1} to less than 200 ha^{-1}. We analyzed vegetation along a radial transect established in the bottom of Puddle Valley in 1987. Mortality was greatest at the lowest elevations where shrubs were initially most dense. These sites occurred where soil moisture, fine-textured soils, and bulk density were greatest of all sites evaluated. Soil was most saline at the margins of the valley bottom. Higher densities of live shadscale occurred where slopes are greater, soil is more droughty, and soil moisture was lower during the 3 years of data collection. The die-off "front" continued about 5 km to the west of the valley center in 1989. Refugia of live shadscale populations were found where soil salinities were higher. Population dynamics of annuals, including summer-cypress (*Kochia scoparia* [L.] Schrader), cheatgrass (*Bromus tectorum* L.), and halogeton (*Halogeton glomeratus* [Bieb.] C.A. Mey.) were highly variable between 1987 and 1989.

Key Words: shadscale, die-off, environmental conditions, population biology, Great Basin

Shrub mortality in plant communities occupying Pleistocene lake bottoms of the Great Basin has been severe since 1983 (Nelson et al. 1989). Die-off has occurred in a number of valleys in Utah to an extent which has necessitated a reduction in livestock grazing or has eliminated it completely. A site of extensive shrub loss is Puddle Valley, located between the Great Sale Lake and Great Salt Desert in northwestern Utah. Investigations at this site are the subject of this paper.

Among the causes suggested for recent outbreaks in Utah are: (a) elevated salinities caused by saltwater intrusion from high levels of the Great Salt Lake, (b) transient soil waterlogging generated by above-average precipitation during 1982–84, (c) extended periods of cold and snow-cover during the winter of 1983, (d) summer drouth in 1984 and 1985, and (e) aggravation of environmental stresses by stocking practices.

During previous episodes of shrub die-off in the Great Basin and other areas of the West, damage has been linked to weather extremes (Nelson and Tiernan 1983). Cold damage to creosote bush (*Larrea divaricata* [DC.] Cov.), screwbean (*Prosopis pubescens* Bent.), and honey mesquite (*Prosopis glandulosa* Torr.) occurred after a cold period in southern Utah (Cottam 1937). Bitterbrush (*Purshia tridentata* [Pursh] DC.) was damaged in northern Utah by extremely cold weather following warm periods (Jensen and Urness 1979). Four-wing saltbush (*Atriplex canescens* [Pursh.] Nutt.) (Van Epps 1975) and Vasey sagebrush (*Artemisia tridentata* ssp. *vaseyana* [Rydb.] J. Boivin) (Hanson et al. 1982) have also been reported to have suffered damage from heavy snow or severe cold. Drought has been implicated in severe reductions of shadscale which occurred in 1933–34, 1942–43, 1971–72, and 1976–77 (Blaisdell and Holmgren 1984). Viscid rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.) populations were impacted during a drought in the 1950's (Ellison 1960).

Fungal association with dieback has been reported. Damage to big sagebrush (*Artemisia tridentata* Nutt.), described as a sagebrush wilt disease of unknown origin, was recorded by Nelson and Krebill (1981) at a university field station in Ephraim, Ut. Snowmold fungus damage to big sagebrush was reported in Wyoming, Colorado, and Utah (Hess et al. 1985).

Insect predation has caused specific instances of shrub loss. Infestations of the sagebrush defoliator (*Aroga websteri* Clarke) were found in populations of sagebrush and rabbitbrush near the Utah-Idaho border (Hsiao 1984). Grasshopper (*Hesperotettix viridis* Scudder) and beetle (*Crossidius pulchellus* LeConte) impacts on threadleaf snakeweed (*Gutierrezia microcephala* [DC.] Gray) were investigated in 1980 (Parker 1985). Effects of a leaf-feeding beetle (*Trirhabda pilosa* LeConte) on big sagebrush in British Columbia were reported in 1960 (Pringle 1960). Snout moth damage to shadscale has been reported in Idaho (Hutchings 1952, Sharp and Sanders 1978).

Laboratory and greenhouse experiments have linked shrub mortality to elevated salinities (Goodman and Caldwell 1971, Goodman 1973, Stutz 1975) and flooding and low concentrations of oxygen in the root zone (Lunt et al. 1973, Drew 1983). Accounts of shrub loss resulting from ephemeral soil saturation at various sites have been published (USDA 1937, Ganskopp 1986).

Many recent episodes of die-off in western Utah have begun in valley bottoms and upland depressions, especially those in which ephemeral ponds are found. The latest die-off occurred after a period of high precipitation (Nelson et al. 1989). Such conditions implicate a hydrologic or soil factor in the initiation of mortality in shrub communities which are subsequently subjected to massive losses. The spread of mortality is hypothesized to be radial, with shrub mortality proceeding contagiously and centrifugally.

This study investigated several aspects of shrub mortality, including: (1) vegetation dynamics in the Puddle Valley die-off area using field data collected in 1987, 1988, and 1989; (2) progress of the advancing die-off front during that period; (3) seedling establishment and growth within the die-off area; (4) the relationship of mortality and vegetation structure to environmental (primarily soil) variables; and (5) the relationship between environmental variables and the demographics of shrubs.

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Methods

Site Description

Puddle Valley is small (32 km by 12 km), northward trending, and partially drained (drainage out of the valley is by groundwater) (Snyder 1963). It is between the Great Salt Lake and the Great Lake Salt Lake Desert in northwestern Utah (41° 00'N Lat., 112° 55'W Long.). It is dry, sparsely populated, and used partly as a military reservation and partly as a winter range for sheep and cattle. Annual precipitation ranges from 150 mm to 300 mm, and potential evapotranspiration is as high as 1,500 mm per year (Eakin et al. 1976). In the 3 years prior to data collection for this study, annual rainfall totals at the nearest measuring station in Tooele, Utah, 75 km to the SE were: 423 mm (1987), 375 mm (1988), and 483 mm (1989). There is almost no overland runoff and little groundwater recharge. Water in sand and gravel aquifers contains 2,000 mg/l of dissolved solids in the shallowest water-bearing strata and the concentration increases with depth. Subsurface water movement is to the north, into the Great Salt Lake Desert (Price and Bolke 1970).

Soils in the valley bottom and surrounding alluvial fans are very silty at the surface with poor drainage and low permeability. There is appreciable sodium, and a duripan may form in addition to saline and clay horizons (Soil Conservation Service, Soil Survey of Tooele County, unpublished).

Vegetation is dominated by shadscale (*Atriplex confertifolia* (Torr. & Frem.) Wats.), greasewood (*Sarcobatus vermiculatus* (Hook.) Torr. in Emory), and cheatgrass (*Bromus tectorum* (L.)).

Sampling Plots

A 5,750 m long permanent transect, established across the bottom and side hills of Puddle Valley in 1987, bisected a circular area in which extensive shrub mortality had occurred. A rectangular plot (8 × 20 m) subdivided into ten 4 × 4-m quadrats was located at each of 27 stations along the transect. Data from each of the 16-m² quadrats were combined for the 160 m² plot.

Stations 1–21 encompass most of the environmental variation within the die-off area. Plots at stations 1–21 (in the valley bottom) are 250 m apart. Plots 22–27 (on the hillside) are 3.2 km to the northwest of the other plots and are located along a 250-m segment that passes through what, in 1987, was a die-off front or ecotone between healthy and dying shadscale. The total transect was divided into 2 sections to allow the upper section to cross the die-off front, but vegetation cover and composition differences in the area between the 2 segments do not seem to be great. Station 21 at the upper end of the valley section of the transect was subsequently placed by vegetation classification analysis into the same community as most of the stations in the hillside section of the transect (see following section on Community Structure). The most pronounced differences in vegetation occurred in concentric zones at the bottom of the valley (stations 1–21).

Cover Values for Dead Shrubs

In order to take into account the recent presence of dead shadscale in the classification of vegetation data, synthetic cover values were calculated to estimate its cover when living. This was achieved by plotting the number of stems of healthy, live shadscale against measured cover values in all quadrats, in plots located in both healthy and die-off areas. Dead stems were then assigned a synthetic cover value based upon the regression equation $y = 2.87x - 0.12$, where y is the percent cover and x is the number of stems per plot ($r^2 = 0.94$). The cover value obtained with this equation was multiplied by 0.80 to make it more conservative (Ebdon 1985). This conversion was performed so that if the synthetic cover values were over-estimated by the regression equation, they would not assume a greater importance in the classification algorithm than actual measured values of shrubs which were alive. Dead shadscale cover values were then entered into TWINSPAN (Hill 1979) classification analysis as one entity and live shadscale cover values as another. This allowed measurement and comparison of prior live cover and current live cover. Before die-off, shadscale density varied appreciably across the valley because of environmental differences or competition. A potential relationship between prior density and mortality was considered to be a possibility.

Community Structure

Vegetation classification of all 27 plots was performed using TWINSPAN. Cover data were obtained in the late summer and early fall (September, October) of 1987, 1988, and 1989. In addition to the synthetic values for cover of dead shrubs, percent cover of live shrubs was obtained with a modified line-intercept method, and cover of nonshrubby species was visually estimated using the octave scale (Gauch 1984, p. 212–213). The octave scale is a 0 to 9 scale, with 0% cover = 0, 0 to 1/2% cover = 1, >1/2% to 1% cover = 2, >1% to 2% cover = 3, >2% to 4% cover = 4, >4% to 8% cover = 5, >8% to 16% cover = 6, >16% to 32% cover = 7, >32% to 64% cover = 8, and >64% cover = 9. In the line-intercept method, the distance covered by each shrub species along 3 parallel tapes, spaced evenly across a 4 × 4-m quadrat, was recorded. Cover was calculated as a percentage of the total tape distance. Ten of the 4 × m quadrats were averaged to obtain the plot value.

Vegetation data from 27 plots for each of 3 years were combined into a single data set prior to classification. This permitted tracking of potential successional changes of plots from membership in one community type to another. All cover estimates were entered as octave values.

Environmental Variables

At each of the 27 plots, the following environmental information was obtained: (1) elevation (from differential leveling); (2) slope; (3) gravimetric soil moisture, both beneath shrubs and within shrub interspaces (Gardner 1986); (4) soil bulk density beneath shrubs and within shrub interspaces (Blake and Hartge 1986); (5) infiltration rates beneath shrubs and within shrub interspaces (using a 10-cm ID double ring infiltrometer, rate recorded after 45 minutes); (6) soil texture from grab samples (soil samples from below crust to 30 cm depth were aggregated) (Gee and Bauder 1986); and (7) electrical conductivity (electrical conductivity measurements between 0–30 cm were averaged). Conductivity values were measured with a YSI model 32 conductivity meter, using aqueous extracts of saturated soil paste from each sample (Rhoades 1982); values were converted to salt concentrations in mg liter^{-1} of extract. All measurements were made in September and October 1989. Gravimetric soil moisture measurements were obtained during September 1989, at each plot. Systematic soil moisture monitoring was carried out using gravimetric as well as neutron backscatter measurements from 6 valley bottom and 6 hillside arrays starting in 1987. These measurements indicated that the 1989 soil moisture measurements are representative of the end-of-summer period, when soil moisture is at its lowest levels.

Population Variables

In addition to environmental variables at each of the 27 plots, the densities of live and dead shadscale shrubs and live seedlings, and the densities of live Gardner saltbrush (*Atriplex gardneri* [Moq.] D. Dietr.) mature shrubs and seedlings were measured in 1987, 1988, and 1989.

Numerical Analysis

After the 1989 field season, a data set comprised of values from 27 plots was compiled. Variables included community membership of each plot in 1987, 1988, and 1989, from TWINSPAN. In addition, environmental and population variables described in the previous section were used. Densities of shadscale and Gardner saltbush, of the shrubby species at the site, were specifically selected for measurement because shadscale was the species suffering mortality and Gardner saltbush was a palatable species with potential for replacing shadscale in some areas. Values for population variables measured over 3 years were pooled after first testing for homogeneity of variance. Two locational variables were used: radial distance from the center of the lowest part of the valley and radial zone. The radial zone divided the distance from the center of the valley into 5 zones (zones 1–4 were 0–3,000 m; zone 5 was 5,000–6,000 m). The zones represented increasing radial distance from the center of the valley.

ANOVA and subsequent pairwise analysis of community types were performed in order to determine how the environment and plant population responses varied between communities. ANOVA was performed twice, first using vegetation community membership as the class variable, and again with radial zone as the class variable. When the ANOVA showed that a significant relationship existed, pairwise comparisons were made using Duncan's multiple range test ($\alpha = 0.05$). Correlations were performed on the data set, excluding class variables.

Results and Discussion

Vegetation Analysis

TWINSPAN classified plots from the combined 1987, 1988, and 1989 data sets, based upon species presence and cover. The resulting community membership for the 27 plots was compared over the 3 years to assess successional change, gross shrub mortality, and shrub regeneration. Five community types were designated using TWINSPAN classification.

The TWINSPAN algorithm uses a species-stand matrix and divides all stands (plots) into smaller and smaller groupings. The first division separated communities designated as 1, 2, and 3 from communities 4 and 5. The former grouping (1, 2, and 3) contained all plots with Gardner saltbush and most with gray molly (*Kochia americana* Wats.), summer-cypress (*Kochia scoparia* (L.) Schrader), and greasewood, and had the higher densities of dead shadscale. The latter grouping contained the plots with the greater coverage of live shadscale and halogeton (*Halogeton glomeratus* (Bieb.) C.A. Mey.). Subsequent division resulted in the following 5 community types:

Community 1. Dominated by high coverage (20–30%) of Gardner saltbush and large numbers (>4,000 ha^{-1}) of dead shadscale shrubs. Located on the east end of the transect.

Community 2. High coverage of summer-cypress and cheatgrass (30–60%), with the highest density of dead shadscale shrubs (>9,000 ha^{-1}). Primarily at the lowest elevations in the valley.

Community 3. Plots in which greasewood is dominant, with scattered live and dead shadscale shrubs. Annuals such as summer-cypress and cheatgrass are sub-dominants. This community type has a patchy distribution in the valley bottom and is concentrated on the western edge of the flat bottom.

Community 4. Dominated by live shadscale, mostly on the hillside at the west end of the transect.

Community 5. Dominated by halogeton. Seems to occur behind the advancing front of shadscale die-off. Mostly on the hillside at the west end of the transect. This community type did not occur in the 1988 data set because of low survival rates for halogeton and other annuals; 1988 had lower than average rainfall totals at the nearest recording station.

Vegetation Composition Shifts, 1987–1989

Figure 1 shows community affinities along the transect for each of the 3 years. Membership in community 1, dominated by Gardner saltbush, was stable over the 3-year period. Membership in community 2 showed a striking change from 1987 to 1988, shifting from membership of contiguous plots 6 through 17 in 1987 to a patchy affiliation of these plots with community 2 and community 3 (dominated by greasewood). The shift was not due to changes in the cover or presence of the dominant greasewood, but to a large decrease in the cover of the annuals summer-cypress and cheatgrass in 1988. In 1989, cover for these annuals had increased. Community 4 is characterized by dominance of live shadscale; it occurs primarily on the west end of the transect, especially at the hillside site. Community 5 occurs when there is high cover of halogeton, and halogeton seems to appear in areas where shadscale shrubs have recently died. In 1987, halogeton-dominated community 5 occurred at one plot (22), just behind the die-off front. In 1988, halogeton cover was very low, as was cover for other annuals. In 1989, 3 of the plots at the hillside site (22, 23, 24), and 3 in the lower transect (15, 16, 17) were assigned to community 5 by TWINSPAN.

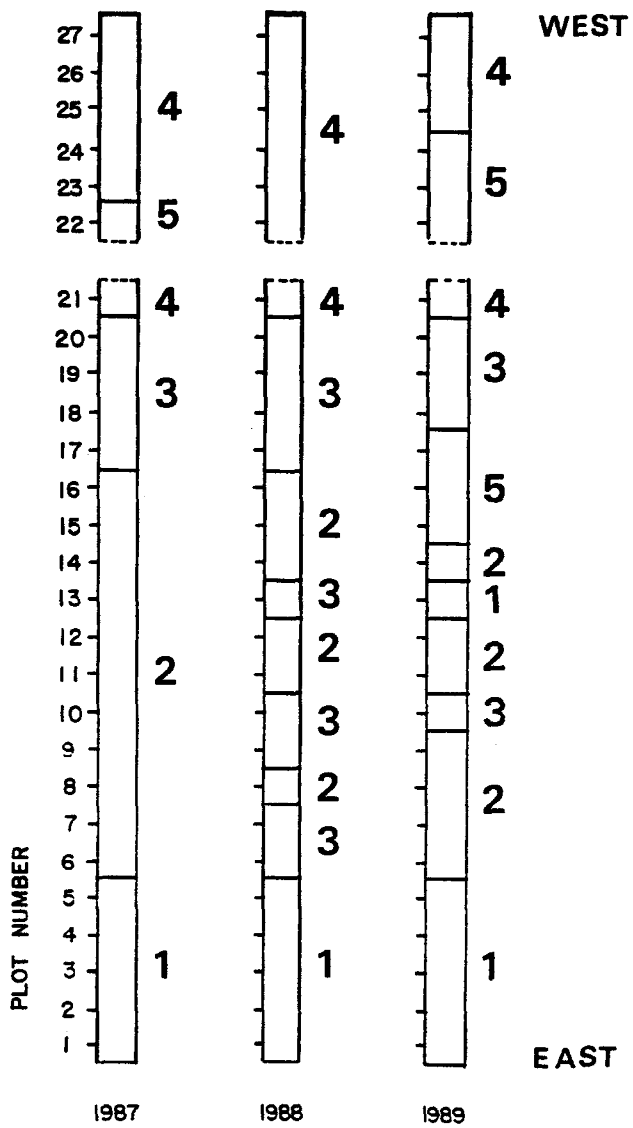

Fig. 1. Community membership of vegetation plots 1–27 for 1987, 1988, and 1989. Dominant species for each community are: 1) Gardner saltbush, 2) dead shadscale, summer-cypress, 3) greasewood, summer-cypress, 4) live shadscale, 5) halogeton.

Relationship of Plant Community Types, Environmental Conditions and Shrub Populations

The classification of plots into communities using TWINSPAN

Table 1. Mean values of environmental and population variables for TWINSPAN-derived plant community types. Row values which are not significantly different ($\alpha = 0.05$, Duncan's multiple range test) have the same superscript. Dead shadscale density and percent of shadscale alive are the averaged values for 1987, 1988, and 1989. All other variables are the result of one-time measurements.

	Plant Community Types				
	1	2	3	4	5
Location	East end of transect	Valley bottom	West slope next to bottom	West hillside die-off front	West end of transect
Dominant Form	Gardner saltbush	Dead shadscale Live summer-cypress	Greasewood Summer-cypress	Live Live shadscale	Halogeton
Dead Shadscale (ha^{-1})	4590^{AB}	9790^{A}	2890^{B}	2180^{B}	3790^{B}
Percent of Shadscale Alive	11.4^{B}	16.1^{B}	37.3^{AB}	63.7^{A}	29.4^{AB}
Moisture Under Shrubs (%)	7.9^{AB}	8.3^{AB}	8.9^{A}	4.6^{B}	6.3^{AB}
Moisture Between Shrubs (%)	6.3^{A}	6.9^{A}	5.2^{AB}	3.6^{B}	3.8^{B}
Bulk Density Under Shrubs ($g\ cm^{-3}$)	1.19^{A}	1.15^{AB}	1.11^{ABC}	1.00^{BC}	0.96^{C}
Soil Salinity at 30 cm ($mg\ l^{-1}$)	3918^{A}	1527^{AB}	1884^{AB}	952^{B}	384^{B}
Elevation (m)	1321^{B}	1317^{B}	1318^{B}	1341^{A}	1344^{A}
Slope (m/m)	0.005^{B}	0.001^{C}	0.001^{C}	0.009^{A}	0.009^{A}
Sand in Soil (%)	30^{A}	11^{B}	2^{B}	35^{A}	60^{A}

assumes that there are underlying environmental differences between different community types and that plants are integrating these differences and responding. There may also be underlying historical differences between communities, e.g., differences resulting from events such as fire, flooding, disease, grazing, priority of establishment, etc. The current mortality is another source of differences in vegetation structure in the valley. An underlying environmental factor may also have contributed to the outbreak of episodes of mortality or conversely may result in greater resistance to die-off among shrubs.

Generalizations may be made about environmental relationships in Puddle Valley: at higher elevations, slopes are greater and there is a greater proportion of coarse-grained soil. Where soil salinity is higher, soil bulk density is also higher, and infiltration rates are lower.

Plant Environments

When correlations between environmental and demographic variables are assessed, dead shadscale is negatively correlated with slope and elevation; the greatest densities of dead shrubs are in the flat valley bottom. Where slopes are minimal, the clay content of soils is greater, and soil moisture under shrubs and between shrubs is greater (Table 1). Live shrubs are found more often on sandier sites where soil water retention capacity is less, and on slopes, where residence time for surface runoff is short.

Evaluation of the relationship between the percentage of live shadscale and soil salinity in exclusively valley-bottom sites shows a definite positive correlation. Sites of higher salinity (>1,000 $mg\ l^{-1}$) have greater rates of survival (30–45% live) than do surrounding plots ($r = 0.82$, $P < 0.001$).

Seedlings of shadscale are found where there are live plants ($r = 0.81$, $P < 0.001$) and dead plants ($r = 0.45$, $P < 0.05$). There is also a correlation between soil salinity and the presence of seedlings of both shadscale ($r = 0.45$, $P < 0.05$) and Gardner saltbush ($r = 0.42$ $P > 0.05$), possibly because the elevated salinities are eliminating competition from annuals such as summer-cypress and cheatgrass.

Conditions within Community Type

Of those environmental conditions measured at all 27 plots, several showed significant ($\alpha = 0.05$) differences when an analysis of variance was performed on the data set with plant community as the class variable (Table 1). This indicated that plant communities were different in respect to the particular environmental variable being tested. Environmental variables showing significant differences between communities were: soil moisture under shrubs, soil moisture within shrub interspaces, soil bulk density under shrubs, elevation, slope of terrain, mean soil salinity in the top 30 cm, and soil texture. Does a relationship between environmental conditions and shadscale mortality exist? TWINSPAN community structure reflects die-off because it was generated using both the cover values for live shrubs and artificial cover values for dead shrubs. Therefore, relationships between environmental conditions, spatial distribution and community types will show conditions under which die-off has been most intense, where it was probably initiated, and where, if at all, it has been avoided by shadscale populations.

Both soil moisture under shrubs and soil moisture within interspaces between shrubs were greatest in the valley bottom communities (2, 3) and less in the hillside community (4) at the west end of the transect. Community 4 had the highest percentage of live shrubs and so plant uptake must account for some of the decrease in soil moisture, but percentage of fines in the soil is higher in the valley bottom, so moisture retention capacity of those soils is also higher.

Soil bulk density under shrubs is highest in community 1 on the east end of the transect where soil salinity is also quite high. Bulk density is lowest in soils on the hillside at the west end of the transect. Soil salinity is substantially higher in the first 5 plots on the east end of the transect (comprising community 1), and lowest on the hillside plots to the west; it is intermediate in the valley bottom (communities 2, 3). Salinity differences along the transect may be due to differential deposition by flowing water and airborne transport (*sensu* Dobrowolski et al. 1990). Soils are sandy on the west end of the transect and slopes are steepest. Therefore, water does not pond. Rainfall or snowmelt will pond and slowly infiltrate in the valley bottom. High salinities on the east end of the transect may be the result of airborne transport of salt from the soil surface in the valley bottom by prevailing winds which move from west to east (Dobrowloski et al. 1990).

The number of dead shadscale stems is greatest in community 2 in the valley bottom and lowest in community 4 on the hillside to the west. A similar relationship occurs when the percentage of live shadscale cover is the variable. Both communities 1 and 2 have low percentage of live shadscale. Shadscale seedlings show no significant association with any plant community, although seedlings correlate highly with both mature live and dead shadscale shrubs. Gardner saltbush seedlings are found only where live mature shrubs are, which is in community 1.

Distance from the Valley Center

When the radial distance from the center of the valley bottom to a plot is entered as a variable in the correlation matrix, the greatest correlation between population variables and the radius are for the percentage of live shadscale ($r = 0.60$, $P<0.001$), and the density of dead shadscale ($r = -0.60$, $P<0.001$). ANOVA and Duncan's multiple range test ($\alpha = 0.05$) with radial zone as the class variable show the zone closest to the center (0–700 m) with significantly higher numbers of dead shadscale (mean = 12,160 ha^{-1}) than zones more distal. The most distant radial zone (5,000–7,000 m) retains a significantly higher percentage of live shadscale (60%) than do the two zones (0–700 m, 701–1,400 m) closest to the center (17% and 9%, respectively).

Progress of Die-Off Front

Comparison of the numbers of live shadscale shrubs at stations 22–27 in 1987, 1988, and 1989 indicates that there is a trend of decreasing numbers of live shrubs over the 3-year period and that the die-off is continuing. The numbers of live shadscale ha^{-1}, from plot 22 (behind the die-off front in 1987) to plot 27 (outside the die-off front in 1987) are presented in Figure 2. The substantial loss

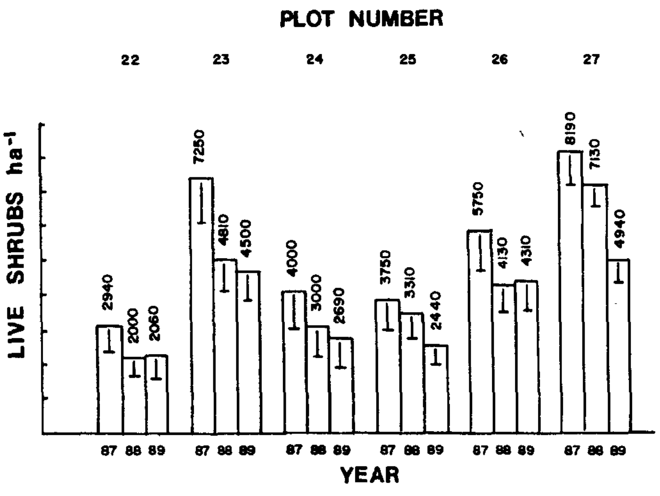

Fig. 2. Live shadscale densities (shrubs ha^{-1}) in plots 22-27 for the years 1987, 1988, and 1989. Die-off front was advancing from plot 22 toward plot 27. Plots are 50 m apart. Standard errors are shown within bars of histogram.

of live shrubs between 1988 and 1989 in plot 27 indicates that this entire section of the transect is now within the die-off front.

Conclusions

The analysis indicates that the current die-off of shadscale was initiated at lower elevations in Puddle Valley and has spread up the sides of the valley. The valley bottom is associated with higher soil moisture and finer grained soils, with low slopes and potential ponding of snowmelt, rainfall, and runoff water in the spring. Higher densities of live shadscale are found where slopes are greater, soil is more droughty, and soil moisture content is lower. Dead shrub densities are not generally correlated with soil salinity. There are, however, refugia along the transect where the percentage of shadscale shrubs which are alive is higher than in the surrounding die-off. All of these sites have elevated soil salinities (>1,000 mg l^{-1}). Both shadscale and Gardner saltbush seedling growth is positively correlated with soil salinity, possibly because competing annual herbs are suppressed by elevated salinities. The die-off front has advanced through the short transect established across the live-dead ecotone in 1987, and shadscale shrubs are continuing to die. There has been no re-establishment of mature communities dominated by healthy shadscale within the die-off zone, although seedling growth is vigorous where densities of live or dead shadscale are high. The apparent release of resources in the valley bottom after the death of large numbers of shrubs has allowed annuals to dominate some areas, but year-to-year fluctuation of cover and dominance for annuals has been considerable.

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