

PERSISTENCE OF DESERTIFIED ECOSYSTEMS: EXPLANATIONS AND IMPLICATIONS *

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Abstract. Studies of rainfall partitioning by shrubs, responses of shrub-dominated ecosystems to herbicide treatment, and experiments using drought and supplemental rainfall were conducted to test the hypothesis that the shrub-dominated ecosystems that have replaced desert grasslands are resistant and resilient to disturbance. Between 16 and 25% of the intercepted rainfall is channelized to deep soil storage by stemflow and root channelization. Stemflow water is nutrient enriched and contributes to the "islands of fertility" that develop under desert shrubs. Drought and rainfall augmentation experiments during the growing season after 5 consecutive years of summer drought found that (1) growth of creosotebushes, *Larrea tridentata*, was not significantly affected, (2) perennial grasses and forbs disappeared on droughted plots, (3) nitrogen mineralization increased in the short term, and (4) densities and biomass of spring annual plants increased on the droughted plots. Doubling summer rainfall for 5 consecutive years had less-significant effects. Coppice dunes treated with herbicide in 1979 to kill mesquite (*Prosopis glandulosa*) had the same frequency of occurrence of the shrub as the untreated dunes when remeasured in 1993. These data indicate that the shrub-dominated ecosystems persist because they are resistant and resilient to climatic and anthropogenic stresses.

1. Introduction

Most examples of desertification in North America, Australia, and parts of Africa involve the replacement of grass-dominated ecosystems by shrub or small-tree-dominated ecosystems (Archer *et al.*, 1988; Buffington and Herbel, 1965; Gibbens and Beck, 1987; Grover and Musick, 1990; Hennessy *et al.*, 1983). Increases in woody plant cover and reduction or elimination of grass cover have greatly reduced the production of livestock in desertified ecosystems, but reducing or eliminating livestock grazing has resulted in neither the return of grasses nor the reduction of shrubs (Glendening, 1952; Hennessy *et al.*, 1983). Shrub-dominated ecosystems return even when challenged by herbicide treatment, root-plowing, or bulldozing (Roundy and Jordan, 1988; Rappole *et al.*, 1986). Shrub-dominated ecosystems have been suggested to represent alternative stable states replacing the predisturbance grassland or grass-dominated ecosystem (Westoby *et al.*, 1989).

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2. Resistance and Resilience of Shrub-Dominated Ecosystems

From experimental and descriptive studies, evidence is accumulating that the shrub-dominated ecosystems that have replaced grasslands in many areas of the world are resistant to perturbation and resilient following perturbation (Roundy and Jordan, 1988; Rappole *et al.*, 1986). Resistance is a measure of the degree to which the ecosystem or ecosystem variable is changed from its equilibrium state following a disturbance. Resilience is the time required for a perturbed ecosystem or ecosystem variable to return to its equilibrium value. We hypothesize that the morphological and physiological characteristics of the shrub species that dominate many of the desertified ecosystems in the southwestern United States contribute to the formation of islands of resources centered on the shrubs. Water and nutrients essential for plant growth are concentrated under desert shrubs (Charley and West, 1975, 1977; Pressland, 1975, 1976; West and Klemmedson, 1978; Parker *et al.*, 1982; Virginia and Jarrell, 1983; Lajtha and Schlesinger, 1986; Nulsen *et al.*, 1986). Moreover, woody legumes may have root symbionts that fix atmospheric nitrogen, thereby enhancing the nitrogen fertility of soils around the plant (Virginia and Jarrell, 1983; Virginia, 1986; Virginia *et al.*, 1989).

Increased soil fertility is not limited to the contributions of nitrogen fixation. Mineralization rates are higher under shrub canopies where litter is trapped and soil organic matter content is higher than intershrub soils (Fisher and Whitford, 1995, Table I). The islands of fertile soils that develop under shrubs are partly a function of litter accumulation under shrub canopies due to wind redistribution of dead plant materials. Shrubs act like rocks in a stream with respect to wind movement, producing eddy currents that result in wind-entrained debris being deposited under shrubs or immediately on the downwind side of the shrub canopy (Reichman, 1984), but litter accumulation under shrub canopies is not the only contributor to the fertile island effect.

Rainfall intercepted by shrub canopies is redistributed to stemflow and throughfall in addition to the fraction that is evaporated from the leaf and stem surfaces (Martinez-Meza and Whitford, in press). In creosotebush (*Larrea tridentata*) stands stemflow that accounts for between 16 and 25% of the intercepted rainfall is nutrient enriched (Figure 1). There is a lesser enrichment of the throughfall water. Stemflow water enters the soil at the root crown. The soil immediately adjacent to the root crown has higher concentrations of many soil nutrients than the soil at mid-crown under a shrub (Figure 1). The root crown soil enrichment results mainly from stemflow water since in this shrub species the soil immediately adjacent to the root crown is generally litter free. The stemflow water enters the soil and follows preferential root pathways to deep storage. This movement has been documented in three of the dominant Chihuahuan Desert shrubs: honey mesquite (*Prosopis glandulosa*), creosotebush (*L. tridentata*), and tarbush (*Flourensia cernua*) (Martinez-Meza and Whitford, in press).

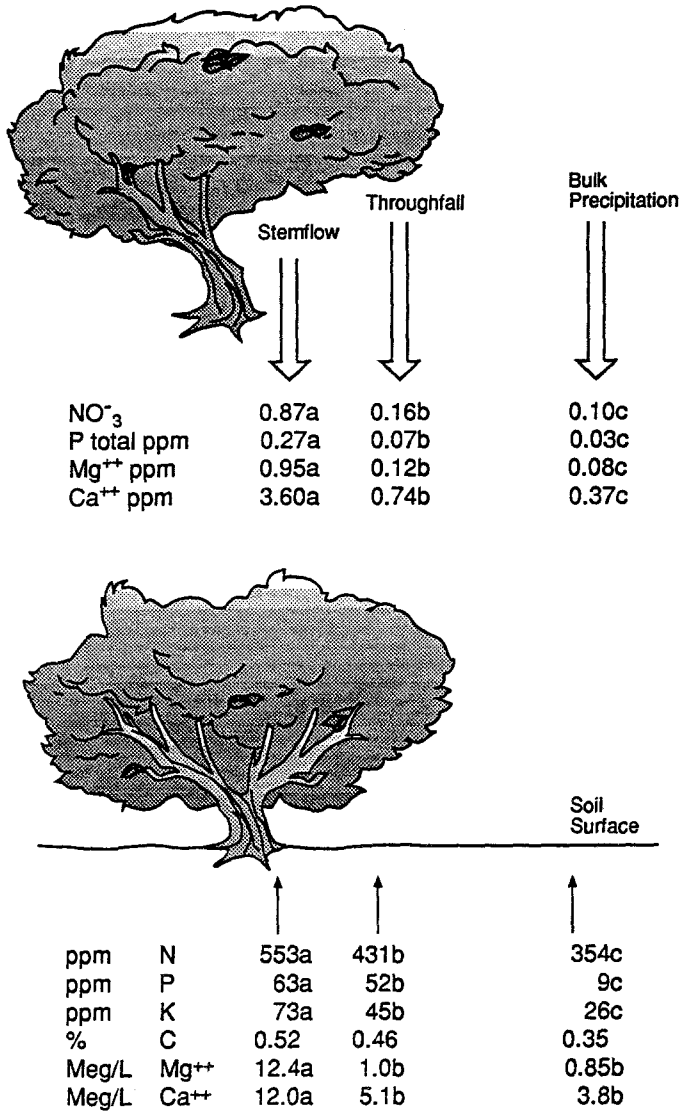


Fig. 1. Chemical composition of stemflow, throughfall, bulk precipitation, and soil chemistry affected by creosotebush (*Larrea tridentata*). Upper panel compares concentrations (ppm) of chemicals measured in stemflow, throughfall, and bulk precipitation. The bottom panel compares chemical concentrations in the soils adjacent to the stem of the shrub, soil under mid-canopy, and soil at the mid-point of the intershrub space. Letters following the numbers show significant differences in concentration of a chemical in different locations or sources at $p < 0.05$.

Water translocated to deep storage along root channels serves to initiate spring growth even in years with no effective winter-spring rainfall. The importance of this deep water source is evident in the phenologies of both creosotebush and mesquite and to a lesser extent tarbush. Mesquite and creosotebush initiate leaf production

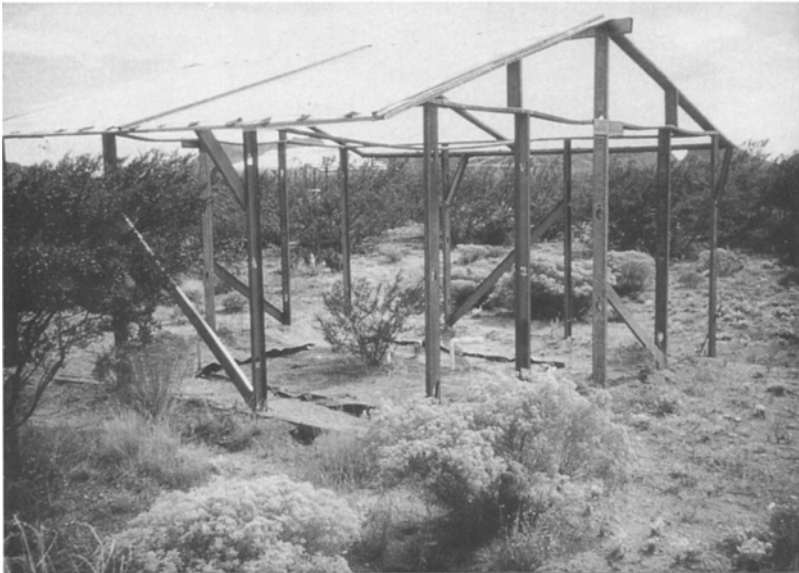


Fig. 2. Rain-out shelter used to impose drought conditions on the shrub and surrounding soil in the enclosed, trenched plot.

and growth between mid-April and mid-May every year, even when winter-spring moisture is inadequate to initiate growth of herbaceous perennials or annuals. In drought years, tarbush will produce extremely small leaves in late spring and early summer. The ability to produce foliage despite inadequate rainfall to support that production is an important adaptation of these desert shrubs that allows them to dominate sites. Thus water redistribution, together with the enhanced mineral nutrient content of soils under shrub canopies, should provide the resources needed to make shrubs relatively independent of climatic constraints and contribute to the resistance and resilience of shrub-dominated ecosystems. This hypothesis was tested experimentally using repeated, consecutive summer drought and irrigation to examine the responses of a creosotebush (*Larrea tridentata*) ecosystem.

3. Drought and Rainfall Augmentation Experiments

One test of the resilience of an arid ecosystem is the recovery of that system from drought. We had an opportunity to examine the resistance and resilience of a creosotebush-dominated ecosystem in which we had 24, 3 m × 5 m plots assigned at random to drought, 2 X summer rainfall, and unmanipulated controls. Eight plots were irrigated at 2-week intervals with enough water to double the long-term monthly mean. Because of the variability of rainfall, the irrigated plots regularly

received more than twice the long-term monthly average. Drought was achieved by "rain-out" shelters built of a steel frame (1.5 m high on the sides and 2.2 m high at the roof peak). The steel roof beams were covered with large-mesh chicken wire, which supported the ultraviolet-light-resistant greenhouse polyethylene covering the roof to exclude rain (Figure 2). In 1987 and 1988 the roof plastic sheets were rolled down at night and as storms approached. During that time period research focused on nitrogen mineralization patterns, and growth increments of the creosotebushes were not measured. From June 1989 through October 1991 rain-out shelter roof covers were installed in mid-June and removed in mid-September. With permanent roof coverings, the daytime air temperatures under the roofs were elevated 3–5 °C higher than in the control plots. This increase in temperature exacerbated the drought conditions of the plot, adding stress to the system and thereby more exactly testing the resistance and resilience of the stressed system.

Growth was measured by painting a reference point on a terminal growth point 1 mm from the stem apex (approximately two leaf nodes) and measuring the total new-stem length added over a specified time period. Reference branches were tagged in late October-early November and were measured in late April-mid-May. Different branches were tagged in May and measured in September-late October, depending upon the year. Branch growth in creosotebushes exhibits an early summer growth spurt, a leveling off of growth in mid-summer, and a small late-summer growth surge (Fisher *et al.*, 1988).

Litter fall was collected in 30 cm × 30 cm trays built of aluminum window screen. Two trays were placed at random under the canopy of each shrub in a plot. Trays were emptied into plastic bags at the end of a sample period, returned to the laboratory, dried at 60 °C for 72 hours, and weighed.

The nitrogen mineralization potential and soil nitrogen content were measured on soil samples collected from under the canopy of shrubs in each plot. Nitrogen mineralization was measured by the batch incubation method of Fisher *et al.* (1987).

Residual effects of the experimental treatments were monitored by censusing all perennial plants in the plots in 1992 and 1993. Annual plants were censused on all plots in 1992. In 1993 densities of annual plants were estimated by a count of all annuals within five 40 cm × 40 cm quadrats placed at random within each plot.

Leaf litter decomposition was measured in 240 creosotebush leaf litter bags, 15 cm × 15 cm (fiberglass mesh 1.5 mm) filled with approximately 7.0 g (initial weight) of oven-dried creosotebush leaves. Sets of 10 litter bags were assigned at random to each plot of each treatment. Litter bags were placed under the shrub canopy at the mid-point of the canopy in July 1990. One leaf litter bag per plot was then retrieved at 6-month intervals and dried, cleaned, and weighed. Root decomposition was measured on 96 roots of the perennial herb, *Cassia bauhinoides*. Roots were washed and oven dried at 50 °C for 72 hours. Two roots per set were weighed and tagged with an aluminum tag, and two sets of roots were buried

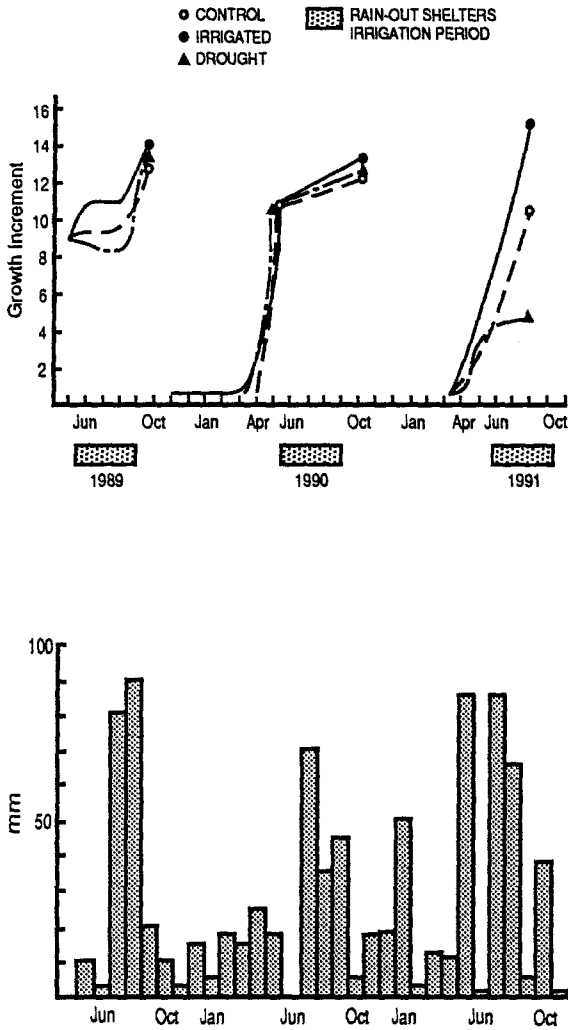


Fig. 3. The effects of drought and irrigation on incremental growth in *Larrea tridentata*. The bottom panel shows the monthly rainfall during the years of the experimental study. Symbols indicate actual measurements. Trajectory lines of growth have been inferred from data in Fisher *et al.*, 1988 and Lajtha and Whitford, 1989.

(parallel to the soil surface) at 5 cm depth in each plot. Sets of roots were retrieved at the end of October 1990 (end of the summer rainy season) and in March 1990. Root material remaining was brushed to remove adhering soil particles, oven dried at 50 °C for 72 hours, and weighed to estimate mass loss.

Data on growth measurements, annual and perennial plant densities, and decomposition were analyzed by ANOVA using the General Linear Model Procedure (PROC GLM) of SAS (SAS Institute Inc., 1985). Statistically significant treatment

TABLE I

Effects of rain exclusion (dry) and irrigation (wet) on soil inorganic N ($\text{NH}_4 + \text{NO}_3 + \text{NO}_2$) and on mineralization potentials (inorganic N accumulated in a 2-week incubation). Data are for soil samples collected approximately 2 weeks after the end of treatments. Numbers followed by different letters significantly differ at $p < 0.05$

	Soil Inorganic N mg N/kg soil	Mineralization potential mg N/kg soil
Control	2.1 a	9.6 a
Dry	3.7 b	10.7 b
Wet	2.3 a	9.2 a

effects were identified with the Least Significant Difference means comparison test.

4. Results and Discussion of Drought-Rainfall Augmentation Experiments

Summer rainfall during the years of the experiment was above average for July through September, the period of drought application and irrigation (Figure 3). In 1989 and 1990 growth increments were measured more than 30 days after the rain-out shelter roofs were removed. Exposure of the droughted plots to even a small amount of rainfall following the "drought" period resulted in growth increments that did not differ among treatments (Figure 3). Since the pattern of measurement produced no difference due to drought, growth increments were measured in 1991 immediately after the roof covers were removed and before rainfall affected the uncovered plots. Treatments significantly differed at that time. Growth increments, however, were not further measured in 1991 to determine if the plants on the control and drought plots reached the growth increment of the shrubs on the irrigated plots. Because of the large coefficients of variation (30% irrigated, 85% control, and 50% drought), the growth increments significantly differed at $p < 0.05$ between the drought and irrigated plot shrubs, but the growth of shrubs in the control plots did not significantly differ from shrubs receiving treatments.

The growth increment data demonstrate that creosotebush (*L. tridentata*) rapidly recovers following drought and that irrigation does not benefit this species in the long term. The resilience of this dominant species following drought is an important factor contributing to the persistence of creosotebush-dominated ecosystems in areas that were historically grass dominated. The failure of irrigation to provide a long-term differential in stem elongation and biomass production is the result of the depletion of available nitrogen and the nitrogen requirements of this species (Fisher

TABLE II

Effects of rain exclusion (dry) and irrigation (wet) on creosotebush litter fall collected in 30 cm × 30 cm litter traps. Data are average g/litter trap. Rainfall was excluded for periods marked with *. Dates represent beginning of a sampling period, which ran until the next date listed. Letters show significant difference at $p < 0.10$

	7/7/87*	10/28/87	3/30/88	6/30/88–10/7/88*
Control	82 a	50	48	98 ab
Dry	45 b	53	46	72 b
Wet	84 a	58	54	126 a

TABLE III

Effects of rain exclusion (dry) and irrigation (wet) on biomass (g/m^2) of annual plants collected on the dates shown. U indicates under shrubs, O indicates intershrub space, and OU indicates data combined for both locations because there was no location effect. Letters show significant difference at $p < 0.10$

	May 88 U	May 88 O	Oct 88 OU
Control	16.3	3.9 a	6.9 a
Dry	14.6	14.9 b	0.8 b
Wet	15.9	7.0 b	2.9 ab

et al., 1988). In earlier studies of drought and irrigation effects on available nitrogen and nitrogen mineralization potential, the increases in available nitrogen and the rate of mineralization approximately 2 weeks after termination of treatments were higher in the drought plot soils than in the control or irrigated plot soils (Table I). These data suggest that the rapid recovery in growth following drought can be attributed to the increase in available nitrogen in the droughted plots.

Another feature of the growth dynamics of creosotebush in response to drought and irrigation is change in the dynamics of litter fall. During drought litter fall significantly decreased but was not significantly affected by irrigation (Table II). When treatments were terminated, litter fall amounts were the same on all plots (Table II). This feature of the growth of creosotebush exhibited the same resilience pattern that stem growth showed in later years of the experiment.

Litter fall patterns are related to leaf production and stem growth, with leaves being retained during periods with little or no growth (Lajtha and Whitford, 1989). This pattern of leaf demography allows for rapid carbon gain as soon as water is

TABLE IV

Average densities (no./m²) of the perennials: fluff grass (*Erioneuron pulchellum*) and the forb *Bahia absinthifolia* on plots subjected to drought and irrigation in the growing season for 6 consecutive years (1987–1992). Data were collected in May 1992 and May 1993. No perennial grasses or forbs were in the drought plots. Data for species that occurred in fewer than four plots are reported as present. Numbers followed by different letters are significantly different at $p < 0.05$

	1992		1993	
	Control	Irrigated	Control	Irrigated
<i>Erioneuron pulchellum</i>	10.3 ± 12.7	18.9 ± 10.5	3.0 ± 3.6a	22.3 ± 10.2b
<i>Bahia absinthifolia</i>	4.4 ± 4.3	6.9 ± 4.5	3.8 ± 3.9	6.6 ± 7.1
Number of plots with species present				
<i>Muhlenbergia porteri</i>	2	3	3	2
<i>Opuntia phaeacantha</i>	2	5	2	3
<i>Zinnia acerosa</i>	2	1	2	2
<i>Gutierrezia sarothrae</i>	1	2	1	2
<i>Aristida longiseta</i>	0	1	0	1
Average cover: cm ² /plant				
<i>Erioneuron pulchellum</i>	23.4 ± 3.2a	5.1 ± 0.7b		No data
<i>Bahia absinthifolia</i>	23.2 ± 9.0a	6.9 ± 1.5b		No data

available following a drought. This pattern of leaf demography contributes to the resilience of the system by allowing for immediate response to rainfall.

By changing the timing and quantities of available water and nutrients, drought and irrigation changed the production patterns of annual plants on the experimental plots. Drought during the previous growing season resulted in increased biomass production of spring annual plants and marked differences in the biomass production of annual plants in the intershrub space compared to controls (Table III). But the drought treatment resulted in a significant decrease in the biomass of summer annuals, and the irrigation also reduced the biomass of summer annuals compared to controls (Table III).

After 5 consecutive years of growing season drought and irrigation, perennial grasses and forbs had disappeared on the drought plots. Repeated growing-season irrigation significantly affected the density and size of the dominant perennials (Table IV). The higher densities of fluff grass and *Bahia absinthifolia* in the irrigated plots were offset by the smaller size of the plants in comparison to those in the control plots. The decrease in fluff grass on the control plots in 1992 was not matched on the irrigated plots (Table IV). The changes in fluff grass between 1992 and 1993 may reflect demographic differences in the fluff grass populations in the treatment and control plots. Numbers of other species of perennials on the irrigated plots slightly increased in comparison to the controls (Table IV). The other

TABLE V

Densities of spring annual plants (number/m² ± standard deviation) on plots subjected to repetitive drought and/or irrigation from 1987–1991. Numbers in parentheses are numbers of plots on which a species was found

	1992			1993		
	Control	Wet	Dry	Control	Wet	Dry
Erdi	3.8 ± 1.9	1.9 ± 1.0	20.3 ± 4.8	8.3 ± 5.8	7.1 ± 5.7	39.2 ± 34.7
Depi	0.6 ± 0.2	0.2 ± 0.2	0.6 ± 0.3	15.7 ± 19.0	13.0 ± 7.3	33.2 ± 8.8
Lela	0.9(2)	0.1(2)	1.6(6)	0.4(2)	0	2.6(5)
Ertr	0.6(3)	0.3(3)	1.6(3)	0.2(2)	0.3(2)	0.4(2)
Erab	0.2(2)	0.3(3)	0.3(3)	0	0	0
Cran	0	0.4(4)	2.1(5)	0.1(1)	0.5(3)	7.5(5)
Crmi	2.3(4)	5.3(4)	8.0(7)	4.1 ± 3	8.7 ± 10	7.6 ± 9
Total	6.5 ± 2.7	2.9 ± 1.9	22.5 ± 18.4	29.5 ± 6.2	28.9 ± 11.4	104.0 ± 62.0

Erdi – *Eriastrum diffusum*, Depi – *Descurainia pinnata*, Lela – *Lepidium lasiocarpum*, Ertr – *Eriogonum trichopes*, Cran – *Crypthantha angustifolia*, Crmi – *Crypthantha micrantha*.

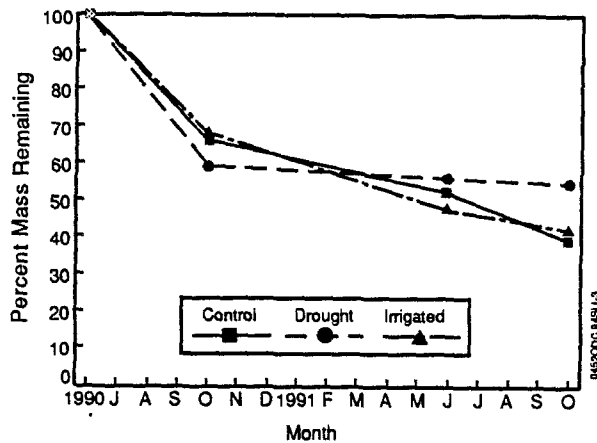


Fig. 4. The effects of drought and irrigation on the decomposition of creosotebush (*Larrea tridentata*) leaf litter.

species were present on fewer than half of the plots, and no statistical analysis was performed.

The absence of perennial grasses and forbs on the drought plots may be the primary reason for the increased densities of spring annuals on the drought plots in 1992 and 1993 (Table V). The differences in spring annuals appear not to be related to soil nutrient differences among treatments because the most responsive species are those shown not to respond to fertilization (Gutierrez and Whitford, 1987).

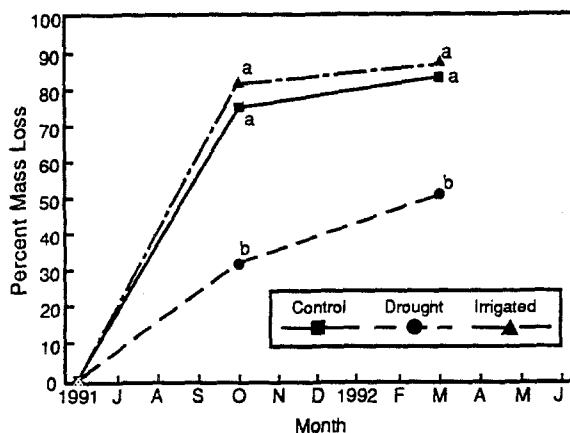


Fig. 5. The effects of drought and irrigation on the decomposition of roots of the perennial herb, *Cassia bauhinooides*. Points with different letters significantly differ at $p < 0.01$.

Decomposition rates of surface litter were slightly affected by drought and not at all by irrigation (Figure 4). Root decomposition was not affected by irrigation but was affected by drought (Figure 5). In roots most of the mass was lost within the first 4 months in the control and dry plots. During the next 6 months the roots in irrigated and control plots lost approximately 8% of their initial mass, while the roots in the drought plots lost 37% of their initial mass (Figure 5). Extrapolating the results of these measurements to a second full year would be unlikely to reveal large differences in the mass remaining among treatments, suggesting that in this ecosystem, recovery from drought and/or above-average rainfall has little long-term effect on decomposition and release of nutrients from dead plant material.

These studies confirm the hypothesis that islands of resources develop under creosotebush (*L. tridentata*) and that the concentration of these resources results in an ecosystem that is extremely resilient to drought stress. The rates of recovery of components and processes within this ecosystem differ, but all reach predisturbance levels within 2 years. The experiments were conducted over five consecutive growing seasons during which summer drought was not found to measurably harm the shrubs. Drought and supplemental rainfall, however, did affect the density and biomass of perennial herbaceous plants (Whitford, 1994). Drought reduced the abundance and biomass of one perennial forb, *Bahia absinthifolia*, and one grass, *Erioneuron pulchellum*. Irrigation affected only the fluff grass, *E. pulchellum*, (Whitford, 1994).

Although drought affected the decomposition of roots, it had little effect on the decomposition of leaf litter. The decomposition of roots and the effects of drought on the microbial biomass were translated into temporal changes in the pulses of available nutrients. The increased availability of nitrogen in the droughted

plots contributed to the rapid recovery of the shrubs and to the increased biomass production of spring annual plants.

4.1. SHRUB REMOVAL AND RECOVERY

One measure of the resilience of shrub-dominated ecosystems is the recovery of those systems after disturbance. We examined the recovery of plots treated in 1979 with the herbicide tebuthiuron applied at rates varying between 1.3 kg/ha and 2.6 kg/ha. The treatment resulted in nearly a complete kill of the coppice dune mesquite (*Prosopis glandulosa*). In 1993, we ran ten 100 m line transects across the treated area and ten 100 m line transects across an adjacent, untreated, mesquite coppice dune area. The average grass cover was 2.3% on the herbicide-treated coppice dune area and 10.2% on the untreated area. Mesa dropseed (*Sporobolus flexuosus*) and fluff grass (*Erioneuron pulchellum*) were the dominant grasses on both sites. The frequency of *P. glandulosa* on the treated and untreated plots in 1993 did not differ: 15.7 ± 7.1 /line treated; 14.3 ± 3.7 /line untreated reference area. The average canopy cover per plant was 0.28 m² on the treated area and 9.8 m² for the coppice dune plants. Thus, only 14 years after shrub removal, mesquite had re-established on a site that was mesquite free in 1979. Most of the young mesquites in the herbicide-treated area were growing on the residual mounds of the treated coppice dunes. Despite the smaller size of the shrubs in the herbicide-treated area, these shrubs will eventually reach the size of those on the untreated coppice dunes.

5. Conclusions

The historical trend of desertification in North America has been the replacement of perennial grassland ecosystems with shrub-dominated ecosystems (Grover and Musick, 1990). This experimental study demonstrates that the creosotebush ecosystem remains relatively unchanged after 5 consecutive years of growing season drought. The persistence of this ecosystem when subjected to long-term stress suggests that there is little probability that the shrub-dominated ecosystem will revert to grassland or that the ecosystem will undergo a transition to another state. Applying herbicide to kill shrubs often results in a short-term shrub-free ecosystem that reverts to a shrub-dominated ecosystem. The permanence and resilience of the "desertified" ecosystems implies that these ecosystems should be managed for the values that can be derived from them in their present state. The failure of shrub-control measures and other manipulations to change structure and function of the desertified ecosystems in the long term is further evidence that management should focus on the values that can be derived from the degraded systems or on improving one ecosystem service such as enhanced water storage rather than attempting large-scale reconstruction.

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