

Diversity of Arthropod Responses to Host-plant Water Stress in a Desert Ecosystem in Southern New Mexico

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ABSTRACT.—Previous studies of insect-plant interactions have produced the contradictory Plant Stress Hypothesis (that stressed plants are more suitable hosts for phytophages) and Plant Vigor Hypothesis (that vigorous plants are more suitable hosts for phytophages). However, experimental studies of phytophage responses to host stress have involved only one, or a few, related phytophagous species, not whole communities of organisms associated with a particular plant species. We evaluated responses of various arthropods associated with creosotebush *Larrea tridentata* to manipulated water availability and plant stress in southern New Mexico during 1990–1991. Of 44 arthropod groups (taxa or functional groups) evaluated in our study only two taxa (including a lepidopteran folivore) showed significant negative response to water availability, thereby supporting the Plant Stress Hypothesis. Ten taxa (including eight phytophages) responded positively to water availability, supporting the Plant Vigor Hypothesis. One phytophage showed a nonlinear response, supporting neither hypothesis. Detrended Correspondence Analysis significantly distinguished the arthropod community on water-deprived shrubs from the communities on watered shrubs. The variation in responses among phytophagous insects on creosotebush indicated that the effect of plant water stress likely reflects the choice of phytophage, and perhaps the host plant, being studied. Therefore, neither the Plant Stress Hypothesis nor the Plant Vigor Hypothesis can explain responses of all phytophages on a particular plant species.

INTRODUCTION

Field observations that outbreaks of phytophagous arthropods are frequently associated with stressed plants generated the Plant Stress Hypothesis, *i.e.*, that stressed plants are more susceptible hosts for phytophages (White, 1969, 1976, 1984; Haglund, 1980; Schowalter *et al.*, 1986; Lightfoot and Whitford, 1987, 1989, 1991; Mattson and Haack, 1987; Heinrichs, 1988; Waring and Cobb, 1992). Experimental studies have often indicated that phytophages prefer more vigorous plants (Mispagel, 1974; Lightfoot and Whitford, 1987, 1989, 1991; Waring and Price, 1990; Waring and Cobb, 1992), leading to the alternative Plant Vigor Hypothesis (Price, 1991). Resolving the contradiction between these hypotheses is necessary for prediction of phytophage responses to environmental changes. One likely explanation for the different results is that previous studies have been limited to individual, or a few closely related, phytophage species and, therefore, have not addressed variation in response

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to gradients in plant condition among the arthropods associated with a particular plant species.

Desert ecosystems are characterized by particularly wide fluctuations in precipitation and plant-water relations (Noy-Mier, 1973; Crawford and Gosz, 1982; Kunkel *et al.*, 1990; Schlesinger *et al.*, 1990) and should provide a useful model of arthropod responses to a gradient of host conditions. Desert plants respond in various ways to chronic periods of water deprivation (*i.e.*, drought) or subsidy (Ehleringer, 1985; Reynolds, 1986; Newton and Goodin, 1989; Whitford *et al.*, 1995). Previous studies have indicated that foliage arthropods are most abundant on the most productive plants of creosotebushes, *Larrea tridentata* (Chew, 1961; Mispagel, 1974; Greenfield *et al.*, 1987; Lightfoot and Whitford, 1987, 1989, 1991; Waring and Price, 1990; Waring and Cobb, 1992), contrary to the Plant Stress Hypothesis (Lightfoot and Whitford, 1991). However, these studies have not evaluated variation in responses of the diverse arthropod community on creosotebush.

We employed a long-term rainfall manipulation experiment to test the alternative hypotheses (the Plant Stress Hypothesis and the Plant Vigor Hypothesis) on the arthropod community associated with creosotebush foliage. We compared abundances of arthropods on creosotebushes subjected to normal precipitation, summer drought and summer irrigation at a Long Term Ecological Research (LTER) site in southern New Mexico.

METHODS

Site description.—Our research was conducted on the Chihuahuan Desert Rangeland Research Center (part of the Jornada Long-Term Ecological Research Site) located at 32°N latitude and 106°W longitude, 37 km N of Las Cruces, Dona Ana County, New Mexico. The climate of this area is generally warm and arid with extreme fluctuation in precipitation. Average annual temperature is 15 C, with monthly averages ranging from 5 C in January to 26 C in July (Kunkel *et al.*, 1990). Annual precipitation averages 230 mm, with >60% falling during thunderstorms from July through September and <25% from November through April (Kunkel *et al.* 1990). Precipitation during the period of this study exceeded the long term average, especially during winter 1990–91 (Whitford *et al.*, 1995).

We studied arthropod responses to manipulated precipitation between September 1990 and August 1991 on a desert piedmont that ranges in elevation from 1313 m to 1404 m. Our experiment was established on a site in the upper portion of the watershed where vegetation was dominated by evenly spaced creosotebushes about 1 m in diameter at 1–2 m spacing.

Experimental methods.—Twenty-four enclosures, each 3 m × 5 m and containing three creosotebushes, were constructed in a random pattern within a 1-ha area in 1987 (Whitford *et al.*, 1995). Plots were separated from each other by 10–15 m. The plots had been randomly assigned to three precipitation treatments (normal precipitation, summer drought and summer irrigation, eight plots per treatment) and each plot had been subject to the same treatment conditions for four summers at the beginning of our study. Vertebrate herbivores were excluded by means of a 1-m tall poultry wire fence and an aluminum flashing barrier inserted 25 cm in the soil and rising 25 cm aboveground. Flying insects had free access to all plots. Movement of ground dwelling invertebrates across plot boundaries was inhibited by the barriers, but their densities within plots were not manipulated.

Plots in the summer drought treatment were covered by shelters consisting of a steel frame (1.5-m high on the sides and 2.2-m high at the roof peak). Clear greenhouse polyethylene sheeting was fastened to the top of the frames from mid-June to mid-October. These shelters reduced annual precipitation about 60% but permitted air flow. Daytime air temperatures under the shelters (at 1-m height) were 3–5 C over ambient temperatures

(Whitford *et al.*, 1995), exacerbating water demands of plants but probably having little effect on arthropod communities since most species can seek sheltered microsites. Edges of the plots were trenched to 1-m depth and lined with plastic to prevent roots from accessing soil moisture outside the plots.

Irrigated plots had a sprinkler system installed around the perimeter. Sprinklers 1-m tall provided overhead irrigation from mid-June to mid-October. Sufficient water was added to these plots every 2 wk to double the long-term average precipitation for that period.

Both treatments are within the normal range of precipitation variation for 90% of years between 1851 and 1987 at this site (Kunkel *et al.*, 1990). We evaluated the extent to which our experimental gradient of water availability altered plant conditions, as a necessary criterion for evaluating the Plant Stress Hypothesis (Waring and Cobb, 1992). We measured flower production in September 1990 as a means of assessing plant stress, since previous studies have shown that flower production reflects moisture stress (*e.g.*, Cunningham *et al.*, 1979; Fisher and Whitford, 1988; Sharifi *et al.*, 1988). Each shrub was scored as 1 = <5 flowers, 2 = 5–10 flowers, 3 = 11–20 flowers, 4 = 21–50 flowers or 5 = >50 flowers.

A method for sampling arthropods that did not injure the shrubs was necessary in these long-term experimental plots. The roughly spherical form of these shrubs and the relatively even distribution of foliage at the ends of similar sized main branches suggested using individual branches as experimental units (Southwood, 1978). However, to assure that similar foliage units were sampled in each treatment, we recorded number of branches per shrub, branchlets per branch (for one randomly selected branch per shrub), leaves per branchlet (for three branchlets per shrub) and average length of 10 leaves. One branch per shrub was considered sufficient for sampling, given similar structure among branches and representation of 7% of the 14–15 branches per shrub.

We collected arthropods from three randomly selected branches from different parts of each shrub by quickly enclosing each branch in a muslin sweep net and shaking vigorously to dislodge insects into the net. Arthropod and plant matter was placed in a plastic zip-lock bag (Lightfoot and Whitford, 1987, 1989, 1991). Samples were returned to the laboratory where arthropods were sorted and counted by morphospecies and identified at the lowest taxonomic rank possible. Arthropods were sampled on each creosotebush in September (late wet season) and November (early dry season) 1990, and early March (mid-dry season), May (late dry season) and August (mid-wet season) 1991 to represent seasonal changes in arthropod abundances and community structure.

Scale insects (Homoptera: Coccoidea) and gall-forming insects (Diptera: Cecidomyiidae) were unrepresented by our branch shaking technique. Therefore, we examined each shrub in September 1990 and May 1991 for abundance of scales and gall formers by randomly selecting three branchlets from each shrub and counting all scale insects and gall formers by gall type.

Data analysis.—Plant and arthropod data were pooled across shrubs and seasons within plots for statistical analyses, producing eight replicates for each moisture treatment. Data for individual shrubs within plots were not statistically independent, and low and highly variable abundances of individual taxa by sample date limited evaluation of treatment effects by season. Evaluation of treatment effects for annual data are appropriate since most arthropods have annual life histories. Infrequent species were combined by higher taxonomic ranks and then by functional groups (based on food source and feeding type), as necessary, to provide sufficient numbers for analysis. In addition to these taxonomic and functional groups, two arthropods (a creosotebush grasshopper *Boottettix argentatus* Bruner and a heteropterid *Parthenicus* sp.) were sufficiently abundant to explore potentially different responses by sexes and/or life stages.

TABLE 1.—Mean (and standard deviation) host plant variables by precipitation treatment during 1990–91. n = 8 plots per treatment

Variable	Precipitation level			χ^2
	Reduced	Reference	Irrigated	
Leaf length (mm)	6.4 (1.4)	7.4 (1.1)	7.4 (1.0)	2.8 ¹
Leaves/branchlet	35 (8.0)	40 (8.5)	38 (7.7)	0.6
Branchlets/branch	150 (38)	150 (35)	180 (43)	2.6
Branches/shrub	15 (5.2)	15 (6.5)	14 (5.2)	2.9
Flower score ²	4.0 (0.8)	2.1 (1.1)	1.4 (1.0)	14

¹ Significant ($P < 0.05$) responses to treatments indicated by $\chi^2 > 5.8$, rank sum difference > 66 (Kruskal-Wallis test)

² 1 = < 5 flowers, 2 = 6–10, 3 = 11–20, 4 = 21–50, 5 = > 50

Because flower and arthropod data were non-normally distributed, the Kruskal-Wallis test was used on ranked data to evaluate the significance of treatment effects (Steel and Torrie, 1980). The degree to which precipitation treatments affected the integrated arthropod community was assessed using Detrended Correspondence Analysis, verified by the Kruskal-Wallis test. Detrended Correspondence Analysis was chosen because of the frequency of nonlinear responses to the moisture gradient (Hill and Gauch, 1980). SAS software (SAS Inst. Inc., 1982) was used for the Kruskal-Wallis test and DECORANA (Hill, 1979) for Detrended Correspondence Analysis.

RESULTS

Water-deprived shrubs produced significantly ($P < 0.05$) more flowers (Class 4, 21–50 flowers) than shrubs in the other treatments (< 10 flowers). However, shrubs were similar in structure, with no significant differences among treatments in numbers of branches per shrub, branchlets per branch, leaves per branchlet or average leaf length (Table 1). Hence, our samples were comparable among treatments and represented about 20% of each shrub.

We collected 147 morphospecies of arthropods, but combination of infrequent species resulted in 44 species or groups for analyses. Thirteen species or groups (30%) showed significant ($P < 0.05$) responses to precipitation level (Table 2). Only two (5%) were negatively related to precipitation (a lepidopteran defoliator *Semiothesia* sp. and a flower-feeding thrips *Frankliniella* sp.). Ten groups (23%) were positively related to precipitation (leaf-feeding Coleoptera; Aleyrodidae (Homoptera); a membracid *Multireoides* sp.; four gall midges (Diptera: Cecidomyiidae); predaceous thrips (Phlaeothripidae); and salticid spiders) and one (2%) showed a nonlinear response (a mirid *Parthenicus* sp. significantly most abundant in the reference plots).

For the two taxa whose life stages were analyzed separately, different responses to treatments were observed among life stages (Table 2). Female *Boottettix argentatus* were significantly more abundant in irrigated plots, whereas males and nymphs were more evenly distributed among treatments. Abundance of *Parthenicus* adults was significantly highest in the reference plots, whereas abundance of nymphs did not change with moisture availability.

Detrended Correspondence Analysis indicated that the arthropod community in the sheltered treatment was distinct from the communities in the reference and irrigated treatments (Fig. 1). Axis 1 significantly distinguished the sheltered treatment from the reference and irrigated treatments ($\chi^2 = 15$ $P = 0.005$). Additional axes were not significant. Reference and irrigated plots could not be distinguished.

DISCUSSION

Our study demonstrated that all four responses, in terms of arthropod abundance (increased, decreased, nonlinear and no change), to increasing water availability (Waring and Cobb, 1992) could be observed among arthropod taxa on an individual plant species. A preponderance of significant responses (10 of the 44 taxa) supported the Plant Vigor Hypothesis. Two taxa supported the Plant Stress Hypothesis, and one taxon showed peak abundance in reference plots, supporting neither hypothesis. Furthermore, we observed variation in the type of response within functional groups, *e.g.*, defoliators and sap-suckers. The diversity of responses among taxa in this experiment indicates that the different results from other studies largely reflect the choice of arthropod(s) studied.

A critical test of arthropod response to plant condition requires that the treatments create differences in plant condition (Waring and Cobb, 1992). Our precipitation treatments clearly created differences in plant conditions. We demonstrated that water-deprived shrubs produced significantly more flowers than watered shrubs, consistent with previous studies indicating greater flowering by stressed creosotebushes (Cunningham *et al.*, 1979; Fisher *et al.*, 1988; Sharifi *et al.*, 1988). In addition, Whitford *et al.* (1995) reported that irrigated shrubs showed significantly higher biomass production than water-deprived shrubs (reference shrubs intermediate).

Although we analyzed responses of a large number of arthropod taxa, the tests for significance of treatment effects for each taxon or group are statistically independent of each other. Including many taxa into a single study permitted simultaneous evaluation of treatment effects on abundances of all the taxa present. Although some Type I errors can occur among a large number of taxa, simultaneous evaluation provides better understanding of responses to environmental variables than a focus on individual taxa that ignores interactions among taxa. Presentation of a separate set of tests for each taxon shows general patterns of response across the groups, but conclusions for specific taxa or functional groups should be avoided. We also note that pooling across seasons was necessary to obtain sufficient numbers for analysis of treatment effects, but may have masked seasonal differences in results.

Multivariate assessment of arthropod assemblages among treatments distinguished the fauna on water-deprived shrubs from the fauna in the other treatments. These data, together with results for individual taxa, indicated that creosotebush arthropods may be more sensitive to reduced water than to increased water. We note, however, that precipitation during our study was above average. The water available to reference shrubs approached that available to irrigated shrubs, perhaps explaining nonlinear responses by some taxa.

Our study was not designed to identify specific factors influencing arthropod responses to altered precipitation. We expect that the variety of responses among arthropod taxa represents a similar variety of mechanisms affecting arthropod-plant interactions. Arthropod responses to our precipitation treatments likely reflected direct effects of water availability and desiccation and/or indirect effects of changes in host plant conditions or predator and parasite abundances.

We do not know the degree to which precipitation level influenced creosotebush physiology or biochemistry. Rhoades (1974) reported increased resin concentration in water-deprived creosotebushes, but Rundel *et al.* (1994) found that neither leaf resin content nor concentrations of the major anti-herbivore compound, nordihydroguaiaretic acid, were significantly affected by additions of water or nitrogen. Changes in plant growth and flower production in our study indicated reallocation of plant resources between vegetative growth and reproduction. Such effects of water limitation would affect resource quantity and quality for phytophages, as suggested by the following examples.

TABLE 2.—Mean (and standard deviation) abundances of arthropod taxa and functional groups per plot by precipitation treatment during 1990–91¹

Taxon/group (No. of combined taxa)	Precipitation level			χ^2
	Reduced	Reference	Irrigated	
Defoliators				
Lepidoptera				
<i>Semiothesia</i> sp.	0.65(0.34)b ²	0.39(0.16)ab	0.31(0.12)a	6.4
Other Lepidoptera (3)	0.01(0.02)	0.02(0.03)	0.03(0.05)	1.5
Orthoptera				
<i>Boottettix argentatus</i>	0.43(0.19)	0.28(0.19)	0.48(0.19)	4.6
Females	0.09(0.07)ab	0.05(0.03)a	0.15(0.08)b	8.0
Males	0.08(0.05)	0.04(0.05)	0.11(0.07)	4.1
Nymphs	0.27(0.16)	0.19(0.15)	0.23(0.18)	1.3
Other Orthoptera (6)	0.09(0.07)	0.12(0.10)	0.04(0.07)	3.4
Phytophagous Coleoptera (8)	0.10(0.10)a	0.27(0.08)b	0.28(0.14)b	9.0
Sap-suckers				
Homoptera				
Scale insects				
<i>Tachardiella larreae</i>	0.35(0.47)	0.15(0.24)	0.40(0.50)	1.4
Other scale insects	0.23(0.48)	0.31(0.88)	0.78(0.88)	5.5
Aleyrodidae	0.06(0.08)ab	0.05(0.06)a	0.16(0.10)b	5.8
Psyllidae	1.20(0.45)	1.40(0.74)	1.00(0.40)	1.6
Cicadellidae				
Cicadellid 1	0.29(0.16)	0.29(0.26)	0.23(0.18)	1.1
Cicadellid 2	0.09(0.09)	0.20(0.09)	0.14(0.10)	4.7
Membracidae				
<i>Multireoides</i>	0.90(0.52)a	3.21(1.56)b	3.31(0.94)b	15
Other Membracidae (2)	0.10(0.12)	0.08(0.06)	0.25(0.22)	3.6
Other Homoptera (5)	0.27(0.18)	0.26(0.13)	0.33(0.10)	0.7
Heteroptera				
Miridae				
Mirid 1	0.08(0.11)	0.03(0.04)	0.01(0.02)	3.6
<i>Parthenicus</i> sp.	0.67(0.37)a	1.16(0.40)b	0.70(0.31)a	7.9
Adults	0.39(0.22)a	0.93(0.30)b	0.57(0.26)a	11
Nymphs	0.28(0.16)	0.23(0.15)	0.14(0.13)	4.5
<i>Phytocoris nigrinus</i>	0.46(0.26)	0.65(0.34)	0.70(0.31)	3.6
<i>Phytocoris vanduzee</i>	1.76(0.49)	1.83(0.63)	2.27(0.65)	3.2
Other Miridae (2)	0.02(0.04)	0.01(0.02)	0	2.3
Other Heteroptera (2)	0.01(0.02)	0	0.01 (0.02)	1.0
Gall formers				
Cecidomyiidae				
<i>Asphondylia clavata</i>	0.04(0.12)a	0.65(0.33)b	0.56(0.59)b	12
<i>A. digitata</i>	2.96(2.94)a	10.0(7.05)b	8.68(3.64)b	11
<i>A. silicula</i>	0a	0.48(0.39)b	0.31(0.24)b	12
<i>A. villosa</i>	1.23(0.86)a	3.35(1.51)b	3.15(1.05)b	11
<i>A. resinosa</i>	0.36(0.64)	0.71(0.48)	0.65(0.75)	3.2
Other gall midges (4)	0.91(1.31)	0.33(0.37)	1.13(2.01)	1.4

TABLE 2.—Continued

Taxon/group (No. of combined taxa)	Precipitation level			χ^2
	Reduced	Reference	Irrigated	
Flower feeders				
Thysanoptera				
<i>Frankliniella</i> sp.	3.50(2.34)b	0.33(0.33)a	0.16(0.25)a	14
Omnivores				
Formicidae				
<i>Crematogaster larreae</i>	0.32(0.30)	0.40(0.78)	0.20(0.19)	1.2
<i>Forelius</i> sp.	0.43(0.58)	0.10(0.15)	0.83(1.93)	4.3
Other ants (3)	0.06(0.11)	0.08(0.09)	0.02(0.03)	2.8
Predators				
Thysanoptera				
Phlaeothripidae	0.52(0.31)a	0.81(0.23)ab	0.96(0.32)b	6.2
Heteroptera (5)	0.04(0.08)	0.02(0.03)	0.02(0.04)	0.5
Neuroptera (2)	0.01(0.02)	0.05(0.05)	0.03(0.05)	4.4
Coleoptera				
Coccinellidae (3)	0.17(0.12)	0.17(0.13)	0.14(0.08)	2.8
Parasitic Hymenoptera (12)	0.43(0.26)	0.69(0.41)	0.79(0.43)	3.7
Bdellid mites	0.19(0.21)	0.08(0.08)	0.03(0.05)	5.6
Spiders				
Araneids	1.13(0.61)	1.15(0.48)	1.31(0.66)	0.4
Salticids	0.39(0.26)a	0.41(0.24)ab	0.70(0.24)b	6.4
Thomisids	1.46(0.48)	1.54(0.35)	1.55(0.44)	0.4
Other predators (3)	0.03(0.05)	0.04(0.03)	0.03(0.05)	
Detritivores				
Collembola (2)	0.07(0.07)	0.02(0.03)	0.02(0.03)	5.1
Psocoptera	0.05(0.15)	0.03(0.03)	0.04(0.07)	1.0
Other detritivores (2)	0.01(0.02)	0.02(0.03)	0.02(0.04)	0.6
Miscellaneous (4)	0.28(0.19)b	0.04(0.05)a	0.05(0.10)a	13

¹ Abundances are per three branches on each of three creosotebushes per plot (n = 8 plots) sampled in September and November 1990 and March, May and August 1991, except for *Tachardiella larreae*, other scale insects and gall midges. Abundances for these taxa are per branchlet on three creosotebushes per plot (n = 8 plots) surveyed in September 1990 and May 1991

² For arthropods showing significant ($P < 0.05$) responses to treatments by the Kruskal-Wallis test ($\chi^2 > 5.8$, rank sum difference > 66), means in rows followed by the same letter are not significantly different

Increased abundance of the flower-feeding thrips, *Frankliniella* sp., on water-deprived shrubs reflects increased production of flowers, on which these insects feed. Abundances of other folivores, especially folivorous beetles and female *Boottettix argentatus*, and gall formers were positively related to precipitation level, as found by others (Schowalter and Whitford, 1979; Lightfoot and Whitford, 1987, 1989, 1991; Waring and Price, 1990; Price, 1991), and thereby supported the Plant Vigor Hypothesis. Male *B. argentatus* are territorial (Schowalter and Whitford 1979), behavior that would tend to mask any preference for shrub condition, but females prefer more productive shrubs for unknown reasons (Schow-

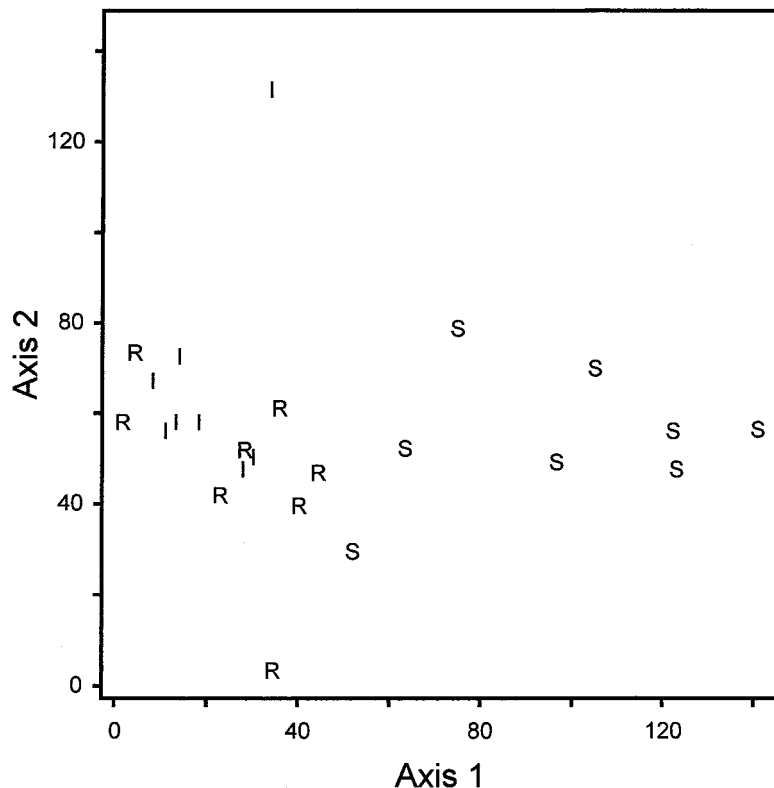


FIG. 1.—Detrended Correspondence Analysis for arthropods associated with creosotebushes in sheltered (S), reference (R) and irrigated (I) plots during 1990–91. Data are from Table 2

alter and Whitford, 1979; Rundel *et al.*, 1994). The positive response of scale insects and other sap-suckers to precipitation level reflects water-dependent sap flow on which these insects depend.

Arthropods showing nonsignificant responses fell into one of the following three categories. Uncommon taxa occurred too infrequently to detect responses. Combinations of rare taxa probably masked responses of individual taxa, as demonstrated by our data for individual taxa within functional groups (*e.g.*, compare *Semiothesia* and *Boottettix argentatus*, among defoliators). Movement of highly mobile taxa also masks responses.

This study demonstrated that the arthropod community on creosotebush represented a wide diversity of responses to precipitation level, and that each arthropod functional group included species that responded in different ways to changes in plant condition. These results indicate that arthropod species within functional groups are not “redundant”, but respond differentially to environmental changes. Diversity maintained by environmental heterogeneity, in turn, maintains ecological functions, such as herbivory and nutrient turnover, during environmental changes, such as fluctuating precipitation level.

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