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Productivity of Creosotebush Foliage and Associated Canopy Arthropods Along a Desert Roadside

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ABSTRACT.—A sampling study was designed to test the hypothesis that creosotebush (*Larrea tridentata*) shrubs along a roadside were larger, more vigorous and supported greater populations of foliage arthropods than shrubs growing 20 m away from the road margin. Structural and chemical attributes of shrubs and associated foliage arthropods were measured. Roadside shrubs were larger, had denser foliage, more flowers, higher foliar nitrogen contents and lower foliar resin contents than shrubs growing away from the road. Foliage arthropod densities were significantly higher on roadside shrubs. Sap-feeding herbivores dominated numerically and accounted for most of the differences in arthropod abundances between roadside and nonroadside shrubs. Numbers of foliage arthropods were positively correlated with shrub size, density and foliar nitrogen contents, and negatively correlated with foliar resin contents. These findings, in concordance with other studies, indicate that in arid environments productive, vigorous plants are preferred hosts for herbivorous insects.

INTRODUCTION

Roadsides are disturbed environments where the physiology and growth of plants often differ compared to nonroadside plants (Frenkel, 1977). Increased water availability from road surface run-off has beneficial effects on roadside plants, particularly in arid and semiarid regions (Frenkel, 1977). Populations of arthropods that live on roadside plants are also affected by road disturbance. Roadside insects and plants may be adversely influenced by toxic automobile pollutants or dust (Przybylski, 1979; Port and Hooton, 1982; Pratt and Sikorski, 1982; Smith, 1989). Roadside disturbance may favorably influence insects by providing suitable habitat for host plants (Fye, 1979) or by increasing the nutritional status of host plants (Port and Hooton, 1982; Braun and Flucker, 1984). For example, increased levels of nitrous oxides may serve as an additional nitrogen source to roadside plants, increasing plant growth and foliar nitrogen contents, leading to increased numbers of herbivorous insects (Port and Thompson, 1980).

In arid regions of North America, plants growing along roadsides often appear healthier and more vigorous than those growing away from roadsides (Frenkel, 1977; MacMahon, 1985). Creosotebush [*Larrea tridentata* (DC) Cov.] is a dominant shrub of the hot desert regions of North America, and creosotebush shrubs growing along roadsides often are larger with denser foliage than plants growing away from road margins (pers. observ., Fig. 1). The environmental factors accounting for these differences are not known, but long-term increased water availability from pavement run-off and subpavement soil moisture retention, may be important factors.

The purpose of this investigation was to sample shrub foliage and foliage arthropods to determine if roadside shrubs and associated arthropod assemblages differed from shrubs in an adjacent undisturbed stand. In a previous study, irrigated and fertilized creosotebush shrubs had greater foliage growth and foliar nitrogen contents and supported greater insect herbivore loads than untreated shrubs (Lightfoot and Whitford, 1987). One may predict that roadside creosotebush shrubs have access to increased moisture, and therefore should have more productive foliage and support more phytophagous insects than shrubs in adjacent undisturbed stands. One may also predict that elevated foliar water contents might be an

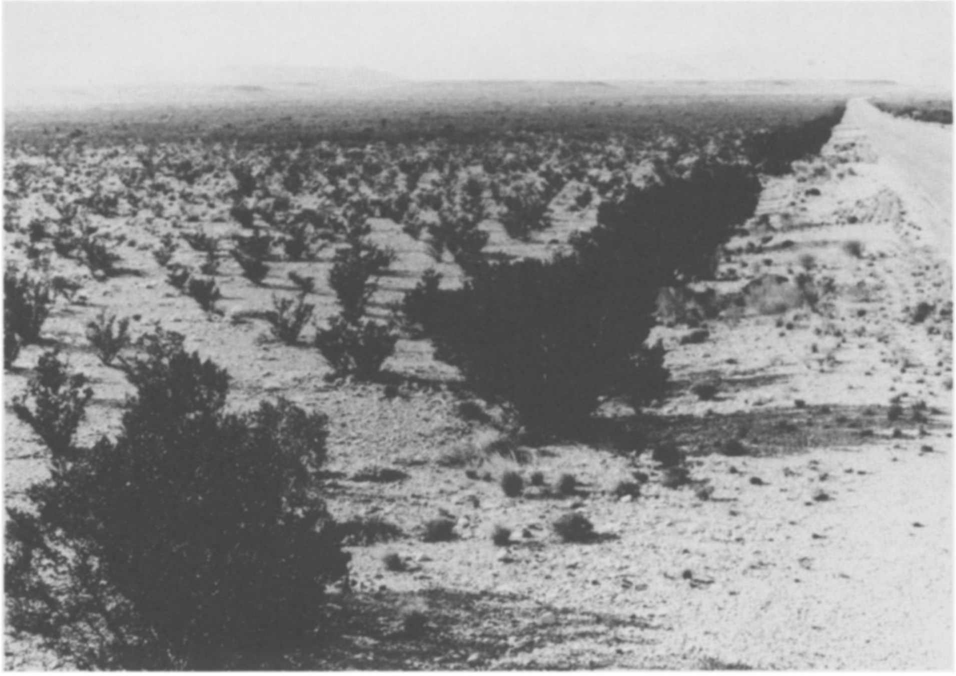

FIG. 1.—A paved highway passing through creosotebush in Big Bend National Park, Texas. Note the band of large dense shrubs along the road margin

important factor correlating with foliage arthropod abundance, particularly during the dry midsummer.

METHODS

Study site.—The study was conducted in a creosotebush dominated community on fine sandy soil near the campus of New Mexico State University in Las Cruces, New Mexico. Shrubs growing along an asphalt-paved, two-lane road through the creosotebush community were sampled. Parallel 100-m transect lines were positioned through two creosotebush stands, one through the shrubs immediately adjacent (1-3 m) to the roadside, and the other through an undisturbed stand 20 m away from and parallel to the roadside. Twenty points were randomly selected along each transect line and the shrubs closest to each point were tagged for sampling, yielding a total of 20 shrubs in each stand. Field sampling was conducted twice, once in May and once in July of 1986. Creosotebush foliage production and foliage arthropod populations generally peak in May, and are lowest in July in the northern Chihuahuan Desert (Lightfoot and Whitford, 1987).

Creosotebush shrubs.—Creosotebush shrub density and cover were measured in each of the two transects by use of the line-intercept technique (Brower *et al.,* 1989). Seven shrub foliage characteristics were measured for each of the 40 shrubs. Foliage characteristics except for canopy density and shrub volume, were measured from three randomly selected branches/shrub to account for branch to branch variability within a plant. The term foliage is used here to include stems, leaves and flowers. The small flowers and herbaceous stems of creosotebush are intermixed with leaves and all three plant parts are fed upon by phytophagous insects. The seven foliage characteristics and how they were measured are given below.

Foliage weight.—Three branch ends were randomly selected from each shrub on each sampling date, and clipped 5 cm from the terminal tips. The branch tips were weighed fresh, then placed in a drying oven at 50 C for one week and reweighed dry. The ratios of the dry weight of each branch tip to its length was used to represent foliage weight or total biomass of stems, leaves, flowers and fruit per centimeter of branch length.

Numbers of flowers and fruit.—The total numbers of flowers, flower buds, and fruit were counted from each of the harvested branch tips.

Foliar water content.—Differences between fresh and dry weights from the above branch tips were used as measures of foliar water content.

Foliar nitrogen content.—Oven-dried branch tips, including leaves, stems and flowers, were ground and analyzed for total nitrogen content by Kjeldahl digestion and colorametric measurement with an autoanalyzer.

Foliar resin content.—Three additional randomly selected 5-cm branch tips were cut from each of the 40 shrubs and weighed fresh. Foliar resin was then extracted from the three combined branch tips in ether as described by Rhoades (1977).

Shrub canopy density.—A one-by-two-m white board partitioned into a grid of 0.25-m squares was placed on one side of each shrub, and the shrub photographed at a perpendicular angle, from the opposite side. Canopy density was then visually estimated as the percentage of the board surface obscured by foliage cover within the perimeter of the shrub canopy. The board was consistently placed on a northeast-southwest axis parallel to the central axis of each shrub to account for the southeast orientation of creosotebush branches at the site (Neufeld *et al.,* 1988).

Shrub volume.—Shrub height and diameter were measured for each of the 40 shrubs. From those dimensions, shrub volume was calculated using the mathematical formula for the volume of a circular cone ($V = \pi r^2 h/3$) (Ludwig *et al.,* 1975).

Foliage arthropods.—Foliage arthropods were sampled from each of the 40 shrubs in early morning in May and in July, when shrub characteristics were measured. Three branches, each approximately 50-cm long, were selected randomly from each shrub and shaken into an insect sweep-net. The contents of three branch samples per shrub were combined into one plastic storage bag and taken to the lab, frozen and later sorted.

A number of arthropod species are commonly found on the foliage of creosotebush, and most species are host specific to creosotebush (Hurd and Linsley, 1975; Schultz *et al.,* 1977). All arthropod taxa sampled from the foliage were included for comparisons of abundances on roadside and undisturbed stand shrubs. In addition, abundances of arthropod trophic guilds were examined by classifying the taxa into three major trophic guilds or functional feeding groups; herbivores, predators, and omnivores, following Lightfoot and Whitford (1987, 1989). Herbivores were further separated into those taxa that feed by sucking phloem, xylem, or cell sap, and those that chew and consume plant tissue. Spider mites (Tetranychidae) are sap-feeding herbivores and were also collected in the sweepnet. However, they were examined separately from other foliage arthropods because their small size and protective webbing probably resulted in a different sampling error.

Data analysis.—Multivariate analysis of variance was used to test for differences in shrub characteristics and foliage arthropod densities between the roadside and undisturbed stands. Canonical discriminant function analysis was used to further examine differences in shrub characteristics and arthropod guilds between the two stands, and to determine which combinations of variables contributed most to those differences. Multivariate canonical correlation analysis was used to examine generalized relationships between linear combinations

TABLE 1.—Mean values of creosotebush shrub characteristics sampled from shrubs in the roadside and undisturbed stands (SE of mean in parentheses)

	May		July	
Shrub characteristic	Undisturbed stand	Roadside stand	Undisturbed stand	Roadside stand
Foliage weight (mg/cm/branch)	0.25 (0.02)	0.35 (0.02)	0.37 (0.02)	0.32 (0.02)
Number of flowers (number/branch)	0.30 (0.11)	2.82 (0.45)	0.83 (0.23)	1.90 (0.28)
Shrub volume (cubic meters)	0.24 (0.04)	1.13 (0.18)	0.24 (0.03)	1.15 (0.19)
Canopy density (% cover/shrub)	44.50 (3.94)	64.50 (3.94)	29.25 (4.33)	64.00 (4.06)
Foliar nitrogen (mg/g/3 branches)	16.80 (0.81)	22.60 (0.58)	18.13 (0.57)	26.50 (0.54)
Foliar resin (mg/g/3 branches)	68.78 (1.45)	40.38 (3.04)	54.20 (1.52)	39.97 (2.00)
Foliar water (cg/g/3 branches)	42.32 (0.01)	46.35 (1.10)	39.73 (1.06)	42.83 (0.59)

of all shrub characteristics and arthropod guilds. Original data were transformed as needed to achieve normality.

RESULTS

Creosotebush shrubs.—Creosotebush shrub density and canopy cover in the roadside stand were nearly twice that in the undisturbed stand. The sampling line through the roadside stand intercepted 42 shrubs [$\bar{x} = 4.2 \pm 1.6$ (standard error of mean) shrubs/10 m], and 26 shrubs ($\bar{x} = 2.6 \pm 1.9$/10 m) in the adjacent undisturbed stand. Shrub canopy cover was 60% in the roadside stand, and only 27% in the undisturbed stand.

Values for shrub characteristics except for foliage weight in July and foliar resin contents in May and July, were higher for roadside shrubs (Table 1). Foliar resin contents were significantly higher from shrubs in the undisturbed stand. Multivariate analysis of variance revealed that roadside shrubs had overall significantly ($P < 0.0001$) different values of foliage characteristics, compared to shrubs from the undisturbed stand, in both May and July. Single significant ($P < 0.0001$) canonical discriminant functions accounted for the separation of shrubs from the two sites based on values of shrub characteristics, and at both times of the summer (Table 2). Canonical coefficients and the canonical structure (correlations between the original variables and the discriminant function) revealed that in both May and July, foliar resin and nitrogen concentrations, numbers of flowers, foliage weight canopy density and shrub volume were the principal characteristics accounting for discrimination between roadside and undisturbed stand shrubs.

The relative values of the canonical coefficients and canonical structure varied considerably for some variables between May and July samples (Table 2). For example, foliage weight was positively correlated with the first discriminant function in May, but negatively correlated in July, and the relative importance of number of flowers was greater in May than July. The differences in the relative contributions of those variables reflects the magnitude

TABLE 2.—Results of canonical discriminant function analysis for discrimination between roadside and undisturbed stand creosotebush shrubs based on shrub characteristics

	Month	
	May	July
Discriminant function	D1	D1
Significance	0.0001	0.0001
Eigenvalue	3.14	4.14
Canonical coefficients		
Foliage weight	0.67	1.01
Number of flowers	0.14	−0.15
Shrub volume	0.44	0.31
Canopy density	0.14	0.73
Foliar nitrogen	0.52	1.66
Foliar resin	−0.75	−0.45
Foliar water	0.01	0.01
Canonical structure		
Foliage weight	0.55	−0.35
Number of flowers	0.81	0.49
Shrub volume	0.79	0.76
Canopy density	0.58	0.77
Foliar nitrogen	0.79	0.96
Foliar resin	−0.93	−0.75
Foliar water	0.51	0.43

of differences in the absolute values of those variables between roadside and undisturbed stand shrubs in May compared to July. Such differences are indicated by the means in Table 1. Shrub volume, foliar nitrogen, and foliar resin were consistently the most important variables discriminating between roadside and undisturbed stand shrubs in both May and July.

Foliage arthropods.—Foliage arthropod abundance and species richness were generally greater on shrubs growing in the roadside stand than on shrubs from the adjacent undisturbed stand (Figs. 2, 3). There was little difference in the pattern of arthropod abundance and species richness between May and July samples. Sap-feeding herbivores were the most abundant trophic guild on roadside shrubs in May and July, and on shrubs in the undisturbed stand in July (Fig. 2). Sap-feeding herbivores were the most numerous taxa on all shrubs on both dates (Fig. 3).Common species of sap-feeding taxa included *Frankliniella* sp. (*Thysanoptera*), *Phytocoris vanduzeei, P. nigripubescens* and *Dendrocoris contaminatus* (Hemiptera), and *Hysteropterum unum, Multareoides digitatus* and *Multareis cornutus* (Homoptera). Leaf-chewing herbivores were not nearly as abundant as sap-feeders. Common leaf-chewers included *Bootettix argentatus* (Orthoptera), *Diapheromera covilleae* (Phasmatodea), and *Semiothesia colorata* (Lepidoptera).

Predators and omnivores were usually considerably less abundant than herbivores. Common predators included Phlaeothripidae (Thysanoptera), *Anthocoris* sp. and *Zelus socius* (Hemiptera), Chalcidoidea (parasites) (Hymenoptera), and *Sassacus papenhoei* and *Misumenops coloradensis* (Araneae). Omnivores (ants) were the most abundant trophic guild on shrubs from the undisturbed stand in May. The most common ant species was *Forelius*

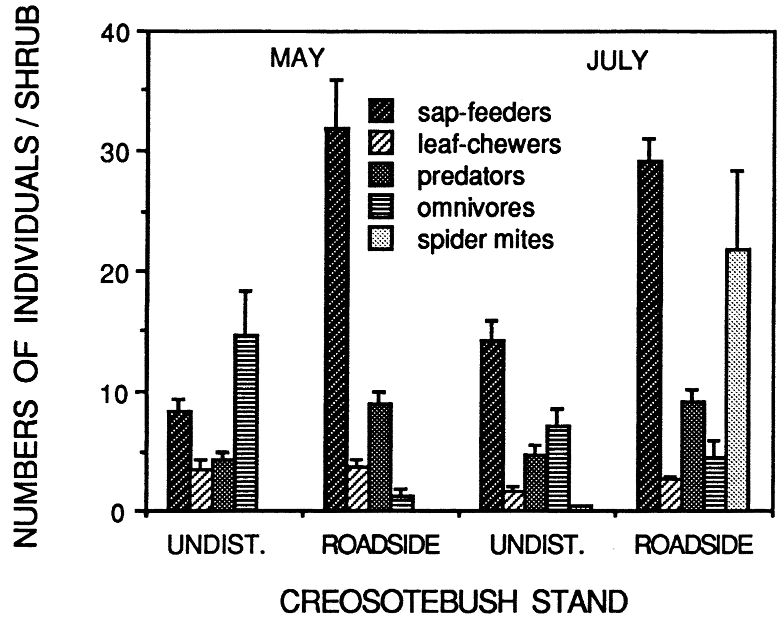

FIG. 2.—Mean numbers of foliage arthropods in the major trophic guilds sampled from 20 roadside and 20 undisturbed stand creosotebush shrubs in May and July. Error bars represent standard errors of the means

foetidus. Spider mites, absent from creosotebush shrubs in May, were present in July and were considerably more abundant on roadside shrubs.

Multivariate analysis of variance revealed that roadside shrubs had significantly ($P < 0.0001$) higher numbers of foliage arthropods than shrubs in the undisturbed stand, in both May and July. Single significant ($P < 0.0001$) canonical discriminant functions accounted for separation of roadside and undisturbed stand shrubs in both May and July (Table 3). Differences in abundances of sap-feeding herbivores and omnivores accounted for the separation of shrubs from roadside and undisturbed stands in May, and differences in sap-feeding herbivores, spider mites and predators accounted for separation of roadside and undisturbed stand shrubs in July (Table 3). Note that numbers of omnivores or ants were inversely related to the discriminant functions in both May and June.

Relationships between shrub characteristics and foliage arthropods.—Canonical correlation analysis showed significant correlations between the first canonical variables representing shrub characteristics and foliage arthropod guilds from all 40 shrubs in May ($P < 0.002$) and July ($P < 0.0008$) (Table 4). Examination of the canonical coefficients and the canonical structure reveals that in May, relationships between the shrub characteristics foliar nitrogen, foliar resin and shrub volume, and sap-feeding herbivores and predators, contributed most to the canonical correlation (Table 4). In July, the shrub characteristics foliar nitrogen and canopy density, and sap-feeding herbivores and spider mites (which are also sap-feeders), contributed most to the canonical correlation. Again, note that omnivores or ants were inversely related to the discriminant functions in both May and July.

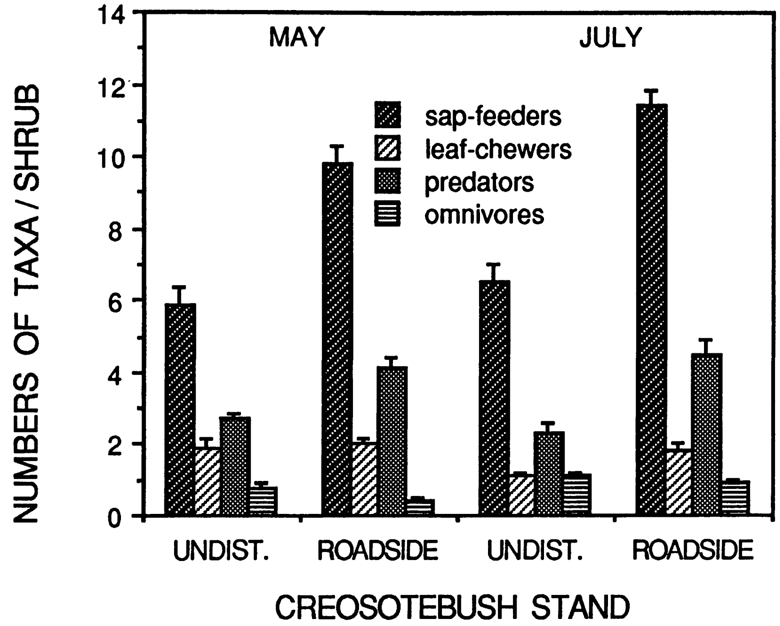

FIG. 3.—Mean numbers of taxa of foliage arthropods in the major trophic guilds sampled from 20 roadside and 20 undisturbed stand creosotebush shrubs in May and July. Error bars represent standard errors of the means

DISCUSSION

Creosotebush shrubs growing along the roadside examined in this study were larger and more vigorous than shrubs in the adjacent undisturbed stand, and densities of foliage arthropods, particularly sap-feeding herbivores, were significantly higher on the more productive roadside shrubs. This pattern was evident in both the spring when creosotebush productivity tends to be high, and in the midsummer dry period when creosotebush productivity tends to be low in the northern Chihuahuan Desert (Cunningham *et al.,* 1979; Fisher *et al.,* 1988). Sampling was not repeated at other sites, so caution must be exercised in generalizing from these results. However, creosotebush shrubs tend to be visibly large and dense along roadsides throughout the Southwest, and the patterns found in this study are likely to be widespread.

Creosotebush shrubs growing along the roadside were probably more productive than those farther away because water availability was greater along the roadside than in the undisturbed stand. Surface run-off from precipitation collects along road edges, providing more water to the soil along the road margin than precipitation alone would provide to soil away from the road. A paved surface should increase water retention under the edge of the pavement for long periods after precipitation events by retarding evaporation of the soil moisture. In arid environments, such increased soil water availability should enhance plant productivity.

Higher foliar nitrogen contents of roadside shrubs indicates that there was increased nitrogen available to roadside shrubs. Port and Thompson (1980) found elevated levels of foliar nitrogen in roadside vegetation in Britain, and suggested that roadside plants acquired

TABLE 3.—Results of canonical discriminant function analysis for discrimination between roadside and undisturbed stand creosotebush shrubs based on foliage arthropods

	Date	
	May	July
Discriminant functions	D1	D1
Significance	0.0001	0.0001
Eigenvalue	2.66	1.54
Canonical coefficients		
Sap-feeding herbivores	1.15	0.95
Leaf-chewing herbivores	−0.15	0.04
Predators	0.43	0.04
Omnivores	−0.82	−0.35
Spider mites	0.00	0.61
Canonical structure		
Sap-feeding herbivores	0.92	0.93
Leaf-chewing herbivores	0.14	0.36
Predators	0.53	0.61
Omnivores	−0.75	−0.43
Spider mites	0.00	0.82

additional nitrogen from nitrous oxides emitted by passing automobiles. Roadside plants may also acquire nitrogen from compounds leached from asphalt pavement, or road surface residues washing off to the soil. However, increased rates of soil nitrogen mineralization in roadside soils resulting from elevated soil moisture availability may have accounted for the higher nitrogen levels found in roadside creosotebush shrubs. Nitrogen mineralization rates in desert soils are highest under conditions of high soil moisture and organic carbon availability (West and Klemmedson, 1978; Skujins, 1981). Rain run-off along roadsides probably increases soil moisture and nitrogen mineralization above levels found in soils of adjacent undisturbed creosotebush stands away from the road margins.

Roadside shrubs were expected to have elevated foliar water concentrations, and foliar water was expected to be an important factor accounting for differences in numbers of foliage arthropods on roadside and undisturbed stand shrubs. Instead, foliar water concentrations differed little between the two stands, but foliar nitrogen was higher and resin concentrations lower in roadside shrubs. Densities of phytophagous insects on creosotebush shrubs have been found to be positively correlated with foliar nitrogen contents of shrubs that were nitrogen fertilized or growing in naturally nitrogen-rich sites (Lightfoot and Whitford, 1987, 1989). Foliar nitrogen is an important resource to phytophagous insects, and insects tend to select plant foliage that is high in available nitrogen (McNeill and Southwood, 1978; Mattson, 1980).

The availability of foliar nitrogen to herbivores is often reduced by plant defensive chemicals (Mattson, 1980; Reese, 1979; Rhoades, 1983). The foliar resin of creosotebush apparently deters phytophagous insects from feeding, and functions like a tannin, complexing with proteins and reducing nitrogen assimilation in the guts of phytophagous insects (Rhoades, 1977). Increased concentrations of foliar nitrogen, and decreased concentrations of foliar resin apparently provided better quality foliage for increased numbers of arthropods on roadside shrubs, particularly sap-feeding insects. Increased nitrogen and decreased resin

TABLE 4.—Canonical correlations between foliage arthropod guilds and creosotebush shrub characteristics. Analysis was done on all 40 shrubs at once, per date

	Month	
	May	July
Canonical variables	VI	VI
Canonical correlations	0.80	0.81
Significance	0.002	0.0008
% Variance extracted	83	75

Canonical coefficients by date

Shrub variables	May	July	Arthropods	May	July
Foliage weight	0.15	−0.17	Sap-feeding	0.44	0.61
Flowers	−0.03	0.24	Leaf-chewing	−0.01	0.15
Shrub volume	0.34	0.10	Predators	0.51	0.13
Canopy density	0.13	0.37	Omnivores	−0.38	−0.09
Foliar nitrogen	0.46	0.27	Mites	0	0.29
Foliar resin	−0.10	−0.08			
Foliar water	0.19	0.17			

Canonical structure by date

Shrub variables	May	July	Arthropods	May	July
Foliage weight	0.52	−0.36	Sap-feeding	0.88	0.94
Flowers	0.74	0.67	Leaf-chewing	0.17	0.49
Shrub volume	0.84	0.74	Predators	0.73	0.70
Canopy density	0.48	0.82	Omnivores	−0.63	−0.29
Foliar nitrogen	0.85	0.89	Mites	0	0.80
Foliar resin	−0.83	−0.77			
Foliar water	0.58	0.55			

were probably a consequence of greater numbers of flowers and fruit found on roadside shrubs. Creosotebush flowers and fruit are fed upon by many of the same insects that typically feed on leaves.

Creosotebush foliage growth, foliage quality to herbivores and associated arthropod abundances all vary seasonally, depending largely on water availability to creosotebush plants. Both creosotebush foliage production and foliage arthropod abundances tend to be high in the late spring, and low during the midsummer dry period (Barbour *et al.,* 1977; Lightfoot and Whitford, 1987). In the present study, sampling was conducted in the late spring and midsummer to compare roadside and undisturbed shrubs during times of favorable growing conditions, and during a period of water stress. If roadside shrubs were growing in moisture enhanced soil, then one should expect roadside shrubs to be less affected by the midsummer dry period than shrubs in the undisturbed stand.

There was little direct evidence for reduced water stress in roadside compared to undisturbed stand shrubs based on foliage water content in either late spring or during the dry midsummer. However, the marked decrease in canopy cover of shrubs in the undisturbed stand from spring to summer, compared to little change in the canopy cover of roadside shrubs, does indicate that foliage senescence and leaf drop were much greater among shrubs growing in the undisturbed stand. Creosotebush is drought deciduous, and leaf loss in the summer is a symptom of water stress (Barbour *et al.,* 1977; Cunningham *et al.,* 1979).

One should also expect foliage arthropods on moisture enhanced roadside shrubs to be less affected by the summer dry period than arthropods on the foliage of shrubs in the undisturbed stand. Instead, sap-feeding herbivores increased on the foliage of shrubs growing in the undisturbed stand between May and July, and densities remained similar on roadside shrubs over the same period. These results indicate that there was little seasonal decline of foliage quality in shrubs growing along the roadside or in the undisturbed stand (*see* Table 1).

In addition to chemical characteristics, structural features of roadside shrubs differed from undisturbed stand shrubs and may have contributed to differences in foliage arthropods between the two stands. Creosotebush shrubs growing along the roadside were large shrubs arranged in a continuous band across the landscape. The size and shape of such a band of productive foliage probably incurred higher immigration rates from phytophagous insects than the smaller, spatially scattered shrubs in the undisturbed stand. The spatial distribution of host plants can have a major influence on densities of phytophagous insects (Kareiva, 1983). Additionally, the combined effects of positive species-area relationships and the resource concentration hypothesis (Root, 1973) may explain increased densities of insects on larger host patches. Large patches of productive creosotebush foliage such as the roadside shrubs, provided larger concentrations of food and habitat for phytophagous insects than smaller patches as found in the undisturbed creosotebush stand.

The size and density of plants also influences the quality of foliage as habitat to insects (Lawton, 1983). Predator escape space is an important aspect of animal habitats (Jefferies and Lawton, 1984). Schultz *et al.* (1977) discussed the characteristics of creosotebush foliage as a refuge for herbivorous insects. Schultz *et al.* (1977) also showed that most insects that live on creosotebush foliage are host specific, and have morphological and behavioral adaptations that render them cryptic on particular parts of the foliage. The high foliage densities of roadside shrubs probably provided better habitat to foliage arthropods than the sparser foliage of shrubs growing in the undisturbed stand, contributing to the generally higher densities of arthropods on roadside shrubs.

The productive, nutrient-rich roadside creosotebush shrubs apparently had access to increased water and nitrogen, and were clearly preferred by foliage arthropods to the shrubs growing in the undisturbed stand. Port and Thompson (1980) concluded that increased levels of nitrogen in the foliage of roadside plants was the major factor accounting for increased numbers of insect herbivores on roadside plants in Britain. The present study demonstrates that increased foliar nitrogen and density of roadside shrubs, apparently facilitated by increased water and nitrogen availability in roadside soils, supported increased densities of foliage arthropods. Roadsides in desert environments appear to provide favorable conditions for increased vigor of creosotebush plants and their associated foliage arthropods.

Lightfoot and Whitford (1989) asserted that the positive relationship between creosotebush productivity and foliage arthropod abundance is contrary to the tenet that phytophagous insects are more successful on physiologically stressed host plants (Mattson and Haack, 1987; Heinrichs, 1988, and chapters therein). The pattern of foliage arthropods favoring productive creosotebush foliage may be indicative of a more general pattern between host plant physiological stress and quality to phytophagous insects in arid environments. However, gall forming insects appear to show an opposite relationship to plant water stress (Waring, 1986).

In arid environments where water stress is common and shrubs tend to be drought tolerant (Reynolds, 1986; Newton and Goodin, 1989), plant foliar chemical defenses may be high and/or nutrients low under conditions of water deficit. Optimal growing conditions may be infrequent and characterized by vigorous plants which have better quality foliage to herbivores, but are more difficult for herbivores to track in space and time. Such a scenario is similar to the concept of spring feeders of mesic forest trees (Feeny, 1970; Mattson, 1980; Faeth, 1986). Perennial desert plants such as creosotebush apparently have relatively predictable low quality foliage most of the time, and infrequent good quality foliage during temporally unpredictable productivity pulses. Roadside or watered and fertilized shrubs may provide relatively predictable or temporally persistent good quality foliage, and thus attract and support large populations of phytophagous insects. Studies of more desert plant species and their associated insects under varying environmental conditions will be necessary to test these ideas.

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