

VARIATION IN INSECT DENSITIES ON DESERT CREOSOTEBUSH: IS NITROGEN A FACTOR?¹

DAVID C. LIGHTFOOT AND WALTER G. WHITFORD

Department of Biology, Box 3AF, New Mexico State University, Las Cruces, New Mexico 88003 USA

Abstract. A field experiment was conducted to assess the effects of nitrogen and water on the densities and taxonomic and trophic compositions of arthropods on the foliage of desert creosotebush (*Larrea tridentata*). Nitrogen and water were manipulated through a series of fertilizer and irrigation treatments applied to naturally growing creosotebush shrubs at a site in the northern Chihuahuan Desert. Water with nitrogen, and nitrogen fertilization alone, significantly increased creosotebush foliage production and foliar nitrogen contents. Water alone had less effect on foliage production and no effect on foliar nitrogen contents. Foliage production, foliar nitrogen contents, and numbers of foliage arthropods were all higher in the late spring than in the mid or late summer. Numbers of foliage arthropods increased significantly on fertilized plants in the late spring. Water treatments alone had no effect on numbers of foliage arthropods, but a positive water-fertilizer interaction effect on numbers of foliage arthropods was evident in the late spring. Overall, there were significant positive correlations between foliage production, foliar nitrogen contents, and foliage arthropod densities. Phytophagous sap-sucking insects accounted for the majority of arthropods on creosotebush, and their densities varied most in relation to foliage production and foliar nitrogen contents. Results of our study demonstrated that sap-sucking phytophagous insects are more responsive than leaf-chewing insects to increased nitrogen content of creosotebush foliage, and that much of the between-plant variation in densities of phytophagous insects within a stand of creosotebush may be due to sap-sucking insects tracking variable foliar nitrogen.

Key words: *creosotebush; desert; fertilization; foliage; phytophagous insects; Larrea tridentata; leaf-chewing; nitrogen; sap-sucking; variable; water.*

INTRODUCTION

The dynamic relationships between phytophagous insects and their host plants are largely consequences of various host plant characteristics such as architecture, abundance, chemical defenses, nutrient content, and spatial and temporal patterns and interactions of those characteristics (Denno and McClure 1983, Strong et al. 1984). The nature of plant chemical defenses largely determines which types of insects feed on particular plants (Rhoades and Cates 1976, Rosenthal and Janzen 1979), and variations in nutrient content and chemical defenses interact to influence the population dynamics of phytophagous insects (Reese 1979, Rhoades 1983). Nitrogen availability is particularly important in regulating populations of insects on plants (McNeill and Southwood 1978, White 1978, Mattson 1980). Theoretically, insect herbivores have evolved various adaptations to maximize nitrogen consumption from their host plants, either by directly exploiting plants or plant parts with high nitrogen contents, or by counteradapting to plant chemical defenses that render plant nitrogen unavailable (Mattson 1980, Rhoades 1983).

In desert ecosystems water and nitrogen are limiting resources for plant and herbivore productivity (Hadley

and Szarek 1981). Both water and nitrogen may be available for brief periods in ample quantities to support pulses of productivity (Noy-Mier 1973, Crawford and Gosz 1982). As water and nitrogen availability to the plants varies, so does nitrogen availability to herbivores due to changes in plant growth rates and concentrations of nutrients, water, and chemical defensive compounds in the plant tissues (see Mattson 1980 and references therein). Little is known about how desert herbivores respond to temporal or spatial fluctuations in resource availability or quality.

McNeill and Southwood (1978) proposed several hypotheses to explain how phytophagous insects have adapted to varying nitrogen availability in their host plants. Variation in foliage nutrient quality among plants may partially account for spatial and temporal variation in the densities of phytophagous insects. Populations of arthropods on desert plants exhibit considerable spatial and temporal variability (Hsiao and Kirkland 1973, Orians et al. 1977, Crawford 1981), possibly reflecting variation in host plant nutrient status. We attempted to determine how foliage arthropods on desert shrubs respond to spatially and temporally variable foliage production and nitrogen content, and whether or not such responses may explain variation in numbers of foliage arthropods on desert shrubs. We examined populations of arthropods on the desert shrub, creosotebush (*Larrea tridentata* [DC] Cov.) in response

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to varying productivity and nitrogen content of their host plants, resulting from water and nitrogen fertilizer amendments. Most insects on creosotebush are host specific (Hurd and Linsley 1975, Shultz et al. 1977), providing us with a relatively simple plant-herbivore system to manipulate.

METHODS

Study site

Our investigation was conducted in the northern Chihuahuan Desert at the Jornada Long-Term Ecological Research site near Las Cruces, New Mexico. The study site was situated in an extensive stand of creosotebush (*Larrea tridentata*) on the eastern slope of the Dona Ana Mountains. Other less abundant plants included the shrubs snakeweed (*Xanthocephalum sarothrae*) and mormon tea (*Ephedra trifurca*), the succulents prickly pear cactus (*Opuntia violacea*) and soap-tree yucca (*Yucca elata*), the perennial grasses fluffgrass (*Erioneuron pulchellum*) and bush-muhly (*Muhlenbergia porteri*), and numerous annual herbs.

Sampling techniques

To assess the effects of variable water and nitrogen on creosotebush plants and foliage arthropods, a series of nine plots was constructed and amended with water and nitrogen in a split-plot factorial experimental design. Each of the plots measured 5 × 10 m and received the following treatments: (1) simulated rainfall: three treatments randomly assigned to plots, each replicated three times, consisting of three plots as controls, three plots receiving 6 mm of water once a week, and three plots each receiving 25 mm of water once every 4 wk; (2) one-half of each of the plots was treated with ammonium nitrate fertilizer, with the total nitrogen equivalent of 100 kg/ha, by one application in February 1983. Simulated rainfall was applied through a series of sprinklers that were above the shrub canopy. Water was obtained from a well-fed concrete storage pond prior to transport to the plots. The combination of simulated rainfall and nitrogen fertilizer treatments resulted in a total of five treatments and one absolute control, each replicated three times. All plots were fenced with chicken wire to exclude rabbits.

Five similar-sized shrubs in each of the half plots were measured and sampled for plant growth and foliage arthropods. Ten branches on each of the five plants per treatment were tagged with yarn and marked with a small spot of permanent paint 4 cm from the terminal bud. Those branches were measured once every 3 wk throughout the year (1983) to determine growth increments. Separate 5-cm branch ends (leaves and stems) from shrubs in each treatment were clipped off and analyzed for tissue nitrogen content using a Kjeldahl digest and autoanalyzer colorimetric analysis. Samples for nitrogen content analyses were taken once in late May, and once in mid-July.

Foliage arthropods were sampled from one branch on each of the tagged shrubs at three times during the spring and summer of 1983: early June, mid-July, and late September. We attempted to sample similar-sized branches from all shrubs. Each branch was placed into a 40 cm diameter insect sweep net and shaken vigorously to dislodge arthropods from the branch into the net. Initial testing of sampling techniques for creosotebush foliage arthropods revealed that shaking branches into sweep nets was more effective and consistent than sweeping the foliage or using a mechanical vacuum device. Insecticide fumigations of entire shrubs revealed that branch shaking adequately sampled the variety of arthropod taxa present on creosotebush plants. Branch shaking is appropriate for creosotebush because individual shrubs consist of series of similar-sized branches with foliage largely limited to the ends of the branches. Only one branch per shrub was sampled at each date to minimize the effects on samples taken at later dates. All plots were sampled at sunrise when arthropod activity was lowest and flying insects were not likely to escape. The net contents from each branch were emptied into individual zip-lock plastic storage bags, and taken to the lab where the arthropods were sorted to taxa and trophic groups.

Data analysis

Data for creosotebush branch growth increments, nitrogen contents of leaves, and foliage arthropod numbers were analyzed by SAS GLM factorial analysis of variance models (SAS Institute 1982). Normality of data was verified by using PROC UNIVARIATE (SAS Institute 1982). With these models, we could test for response differences between the various treatments and sample dates, and test for interaction effects. In all analyses, plots were used as replicates, and the mean values of growth increments, nitrogen contents, or numbers of arthropods (arthropod data were log transformed) were used as response variables. Differences between the levels of class variables were tested by using orthogonal contrasts and Duncan's multiple-range tests for main effect means.

Analysis of variance procedures were performed on branch growth increments, numbers of foliage arthropods for each of the three sample dates separately, and over all three dates using date as a class variable. The same was done for nitrogen contents, but only for the two dates that nitrogen content samples were taken. In this way, seasonal differences in water and nitrogen responses within and between the different dates could be examined. The relationships between creosotebush foliage growth, leaf nitrogen contents, and arthropod densities were further examined by regression analysis. Regressions were performed on the mean number of arthropods per branch per half plot, against the mean growth increments of terminal branches per plot, and the mean total nitrogen content of branches (milligrams per gram of foliage) per half plot. Data from

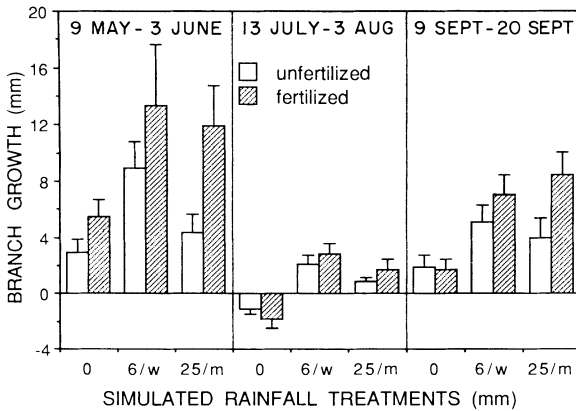


FIG. 1. Three-week growth of creosotebush branch ends in response to simulated rainfall (6 mm/wk or 25 mm/mo) and nitrogen fertilizer treatments, at different times of the year. Graphed values are the mean growth increments from 10 branches per shrub, from 15 shrubs per treatment, +1 SE.

individual sample dates were analyzed both separately and combined. The response of foliage arthropod species diversity to nitrogen fertilization was determined by the use of Shannon's information index; $H' = -\sum p_i \log_2 p_i$.

RESULTS

Effects of water and fertilizer treatments on creosotebush

Water and nitrogen amendments to creosotebush plants resulted in significant increases in shrub foliage production. The terminal branches grew more than the controls in response to both simulated rainfall and nitrogen fertilization (Fig. 1). Growth increments of creosotebush branches were significantly ($P < .001$) greater in plots treated with simulated rainfall than in unwatered plots over each of the three sample periods. Growth responses to the two water treatments did not differ. In the plots treated with 25 mm of water every 4 wk, branch growth during May-June was not significantly different from growth during September, but growth over both dates was significantly greater ($P < .05$) than in July. On all watered and unwatered plots, branch growth increments recorded during May-June were significantly ($P < .001$) greater than growth recorded in July or September, and growth in September was significantly ($P < .001$) greater than in July.

Nitrogen fertilization resulted in significantly greater branch growth during May-June and September, but not in July (Fig. 1). Growth increments of fertilized and unfertilized plants were significantly ($P < .001$) greater during May-June than in July or September. Fertilized and unfertilized plants that received water exhibited significantly ($P < .001$) more growth than unwatered plants. Significant ($P < .05$) water-nitrogen interaction effects on growth occurred in September. Additive effects of water and nitrogen on branch growth were evident in May-June. The nitrogen content of

creosotebush foliage increased in response to nitrogen fertilization. At each of the two sample dates, foliar nitrogen contents from plants on the fertilized plots were significantly ($P < .001$) higher than unfertilized plants, but water treatments alone had no effect on foliar nitrogen content. Across all treatments and controls, foliar nitrogen contents were significantly ($P < .001$) higher in late May than in mid-July.

Effects of water and fertilizer treatments on foliage arthropods

Foliage arthropod densities were considerably greater in early June than in either July or September (Fig. 2). In June, arthropod densities on plants supplemented with nitrogen were significantly ($P < .001$) higher than densities on unfertilized plants. Arthropod densities on fertilized plants were significantly ($P < .001$) higher in June than the densities on the same plants in July or September. Foliage arthropod densities were not significantly different between July and September samples. Water augmentations alone had no significant effects on arthropod populations at any date. A significant ($P < .05$) water-nitrogen interaction effect on number of arthropods was present in June for plants receiving 25 mm of water per month. Foliage arthropod species diversity was analyzed for June data only, when arthropods exhibited significant responses to resource augmentation. Results show that although species richness increased slightly, evenness and overall diversity decreased in response to fertilization (Table 1).

Relationships between creosotebush and arthropod responses

Regression analysis of creosotebush foliage growth, foliar nitrogen contents, and foliage arthropod densities, for all treatments over all dates, indicated positive relationships between foliage productivity and arthro-

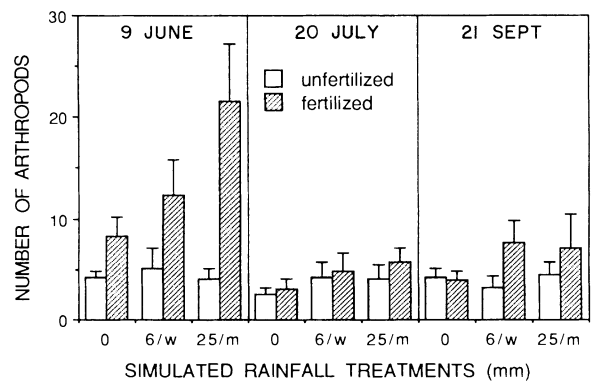


FIG. 2. Numbers of foliage arthropods on creosotebush branches in response to simulated rainfall (6 mm/wk or 25 mm/mo) and nitrogen fertilizer treatments, at different times of the year. Graphed values are the mean number of arthropods sampled from one branch per shrub, from 15 shrubs per treatment, +1 SE.

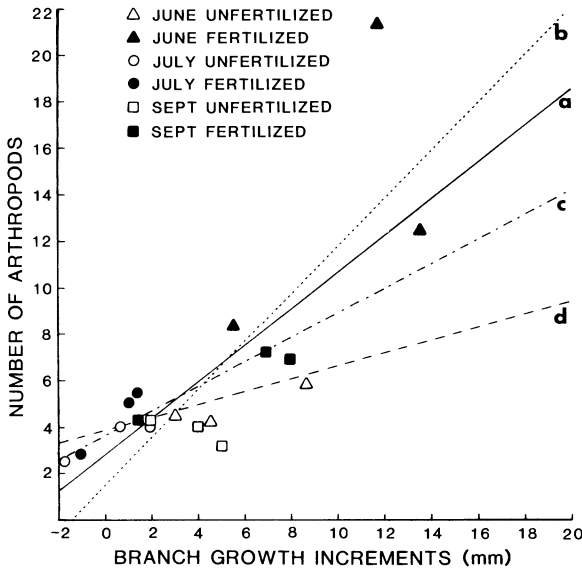


FIG. 3. Relationships between numbers of foliage arthropods, creosotebush branch growth, and the time of year. Regression models fitted to data for all dates combined and each date separately are as follows: (a) all dates combined; $y = 2.7 + 0.8x$, $r^2 = 0.4354$, $P < .001$. (b) June; $y = 1.5 + 1.0x$, $r^2 = 0.3750$, $P < .005$. (c) July; $y = 3.5 + 0.5x$, $r^2 = .3096$, $P < .01$. (d) September; $y = 3.4 + 0.3x$, $r^2 = 0.0961$, $P > .1$. Only means per fertilizer treatment per water treatment are plotted.

pod densities. There was a significant positive linear relationship between branch growth and arthropod densities for all dates combined (Fig. 3). Additional regression analysis for each sample date showed that foliage production and arthropod densities were most highly correlated in late June, less so in July, and no significant relationship was evident in September (Fig. 3). Regression analysis of foliar nitrogen contents and foliage arthropod densities yielded similar results. However, arthropod densities increased exponentially with increasing foliar nitrogen contents. Overall, foliage arthropod densities were significantly correlated with increasing foliar nitrogen contents (Fig. 4). In June, this positive relationship was evident, but there was no significant relationship in July (Fig. 4).

Trophic structure of foliage arthropods

Foliage arthropods were classified into three main trophic groups: herbivores, predators, and omnivores.

TABLE 1. Foliage arthropod species diversity on creosotebush in response to nitrogen fertilizer. Data for June samples only.

Nitrogen treatment	Number of species	Number of individuals	Species diversity (H')	Species evenness (J)
Control	28	187	2.60	0.78
Fertilized	33	632	2.02	0.58

Herbivores were further separated into those species that feed by sucking phloem, xylem, or cell sap, and those that chew and consume plant tissue. Some of the more common taxa from each trophic group are listed in the Appendix. Trophic structure of foliage arthropod assemblages among the various treatments and dates were examined by comparing each trophic group as a percentage of the total number of arthropods from each treatment and date (Fig. 5). In June, when total arthropod densities were highest, herbivores accounted for the majority of the arthropod fauna in all treatments. In July all trophic groups had proportionately similar numbers over all treatments. In September, herbivores again dominated, but not to the extent that they did in June.

Sucking herbivores outnumbered chewing herbivores over all treatments at all times (Table 2). Sucking herbivores also increased significantly ($P < .001$) on plants treated with nitrogen fertilizer in June, less so ($P < .05$) in response to a water-nitrogen interaction effect in June, and showed no response to water alone at any date. Chewing herbivores showed no significant ($P > .05$) response to any treatments. In June, sucking herbivores outnumbered chewing herbivores by 8:1, in July by 4:1, and in September by 11:1. Thus, of all the foliage arthropods on creosotebush, sucking herbivores were most prevalent, exhibited the most pronounced response to water and nitrogen augmentation, and to seasonal variation in creosotebush foliage production.

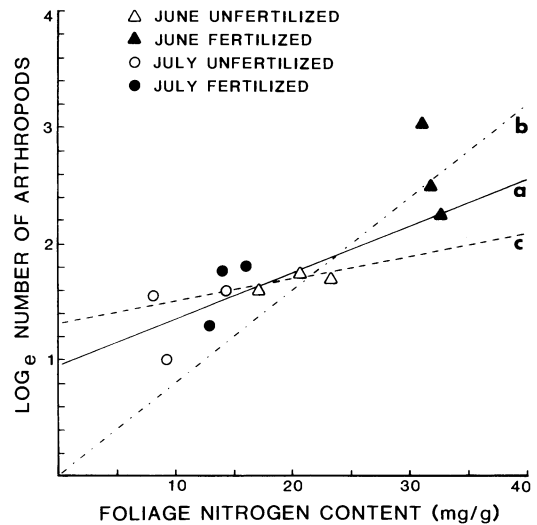


FIG. 4. Relationships between numbers of foliage arthropods, creosotebush foliar nitrogen content, and the time of year. Regression models fitted to data for both dates combined and each separately are as follows: (a) both dates combined; $\log_e y = 0.96 + 0.04x$, $r^2 = 0.4055$, $P < .001$. (b) June; $\log_e y = 0.01 + 0.08x$, $r^2 = 0.4953$, $P < .05$. (c) July; $\log_e y = 1.28 + 0.02x$, $r^2 = 0.0450$, $P > .05$. Only means per fertilizer treatment per water treatment are plotted.

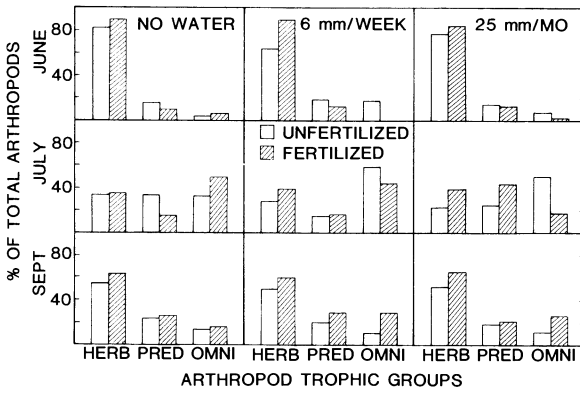


FIG. 5. Trophic structure of foliage arthropods on creosotebush in response to simulated rainfall and nitrogen fertilizer treatments at different times of the year. Graphed values are the percentage of total arthropods from each trophic group sampled from one branch/shrub, from 15 shrubs per treatment.

DISCUSSION

Water and nitrogen as limiting resources to creosotebush productivity

The importance of water in the regulation of primary production in desert ecosystems is well known (Hadley and Szarek 1981, Ludwig and Whitford 1981). The importance of nitrogen as a factor limiting primary production in deserts has been suggested by Ettershank et al. (1978), West and Skujins (1978), Floret et al. (1982), and Penning de Vries and Djiteye (1982). Results from our experiment demonstrated that both water and nitrogen augmentation significantly increased foliage production of creosotebush plants. A pronounced

seasonal effect was also evident, in that growth was considerably higher in the late spring (May–June) than in the middle (July) or late (September) summer.

The seasonal growth patterns that we observed with resource supplementation are similar to the findings of Cunningham et al. (1979) and Romney et al. (1978). Our results indicate that water significantly increased foliage growth in July. However, the significant difference that we observed between the control and water plots at that time resulted from negative growth on the unwatered plots due to branch tip mortality caused by water stress. Water augmentation apparently maintained the status of terminal stems in the watered plots rather than actually inducing growth. Consequently, there was no significant nitrogen fertilizer response in July because there was probably no actual growth.

The nitrogen content of creosotebush foliage was correlated with foliage production. Increases in foliar nitrogen content may have resulted from increased growth, since young growing plant tissue is generally high in soluble nitrogen. Foliar nitrogen content probably also increased as a result of plants taking up additional nitrogen from fertilized soil. We were not able to determine the cause of increased foliar nitrogen contents, but we assume that the increase was due to elevated growth rates facilitated by nitrogen uptake from the fertilized soil.

Variation in phytophagous insects and variable creosotebush nitrogen

Nitrogen is known to be an important limiting resource for phytophagous insects, and variation in nitrogen availability affects their population dynamics (McNeill and Southwood 1978, Onuf 1978, Mattson

TABLE 2. Numbers of chewing and sucking phytophagous insects on creosotebush foliage in response to simulated rainfall and nitrogen fertilizer treatments at different times of the year.

Date	Resource augmentation treatments		Feeding mode					
	Water	Nitrogen	Sucking			Chewing		
			<i>N</i>	\bar{X}	<i>s</i>	<i>N</i>	\bar{X}	<i>s</i>
No. inds./branch, from 15 branches/trt.								
June	C*	C	41	2.73	1.87	13	0.87	1.06
	C	+*	93	6.20	5.75	17	1.13	1.46
	6 mm/wk	C	45	3.00	3.84	10	0.67	1.13
	6 mm/wk	+	150	10.00	8.52	14	0.93	0.88
	25 mm/mo	C	33	2.20	2.78	14	0.93	0.80
	25 mm/mo	+	259	17.27	14.09	15	1.00	1.36
July	C	C	11	0.73	0.79	2	0.13	0.35
	C	+	10	0.67	0.82	5	0.33	0.48
	6 mm/wk	C	11	0.73	0.79	5	0.33	0.48
	6 mm/wk	+	26	1.73	1.33	4	0.27	0.46
	25 mm/mo	C	11	0.73	0.79	3	0.24	0.41
	25 mm/mo	+	24	1.62	1.43	7	0.47	0.52
September	C	C	29	1.93	1.75	7	0.47	0.74
	C	+	32	2.13	2.67	5	0.33	0.49
	6 mm/wk	C	21	1.40	1.05	3	0.21	0.41
	6 mm/wk	+	62	4.13	4.91	2	0.13	0.35
	25 mm/mo	C	31	2.07	1.39	2	0.13	0.35
	25 mm/mo	+	63	4.27	5.90	2	0.13	0.35

* C = control; + = fertilizer added.

1980, White 1978, Strong et al. 1984). McNeill and Southwood (1978) proposed several ways in which phytophagous insects have adapted to variable nitrogen contents of their host plants. Results from our investigation are consistent with two of those strategies: (1) plant-plant movements, and (2) phenological adaptations.

The significant increases in arthropod densities that we observed on fertilized creosotebush plants may have resulted from mobile insects selecting better quality host plants. The majority of abundant insect species (Hemiptera, Homoptera, Thysanoptera) sampled from fertilized plants are mobile, and plant-to-plant movements by individuals were often observed in the field. In addition, growth and survival rates of insects may have been higher on fertilized plants. Vince et al. (1981) attributed increased numbers of phytophagous insects on fertilized *Spartina* to increased survival and growth rates of immature insects on their individual host plants. A combination of plant-to-plant movements and increased survivorship probably accounted for overall higher numbers of arthropods on fertilized creosotebush plants.

The ability of certain sucking phytophagous insect taxa to exploit creosotebush foliage of high nitrogen content accounted for the decreased taxonomic diversity of foliage arthropods on fertilized plants. The densities and relative dominances of phytophagous mirid plant bugs (*Phytocoris vanduzeei* and *P. nigripubescens*) and thrips (*Thrips* sp.) increased on fertilized plants. These insects also were the most abundant taxa on unfertilized plants. A disproportionate increase in the densities of those few species indicates that they are better able than other phytophagous insects initially to exploit increased foliar quality of creosotebush. Prestidge (1982) demonstrated that nitrogen fertilization of a grassland community reduced overall species diversity of leafhoppers in a similar way due to the increased dominance of a few species. These findings are consistent with current community resource utilization theory, which predicts that resource enrichment should initially reduce overall species diversity (Rosenzweig 1971, Tilman 1982). Other plant fertilization experiments have demonstrated increased insect species diversity (Hurd and Wolf 1974, Kirchner 1977, Vince et al. 1981). Vince et al. (1981) concluded that nutrient enrichment of a *Spartina* community increased the evenness of phytophagous insect species abundances due to increased selective spider predation on a population of dominant delphacid plant bugs. Chew (1961) reported that spiders on creosotebush generally reject Hemiptera as prey, but accept Homoptera. This may explain why the numerous hunting crab spiders and jumping spiders on creosotebush did not depress increasing populations of *Phytocoris* plant bugs. Thrips were probably too small to be selectively preyed upon by spiders.

Other studies on creosotebush arthropods in the Chi-

huahuan, Sonoran, and Mojave deserts show a similar seasonal pattern of peak arthropod densities in the spring, low numbers in the mid-summer, and moderate increases in the late summer (Chew 1961, Mispagel 1974, Orians et al. 1977, Shultz et al. 1977, Whitford and Creusere 1977). Whitford and Creusere (1977) and Orians et al. (1977) related increases in foliage arthropod populations to increases in creosotebush productivity due to precipitation. Mispagel (1974) and Chew (1961) concluded that populations of foliage arthropods fluctuated in response to creosotebush production and to physiological adaptations to, or limitations by, seasonal temperatures. Seasonal temperatures appear to affect creosotebush foliage arthropod populations indirectly by regulating foliage quality, and may directly reduce numbers by surpassing the physiological tolerances of some species. Desiccation may be an important factor limiting the occurrence of phytophagous insects on plants (Strong et al. 1984). Neither the potential for nor the effects of desiccation on creosotebush arthropods are known.

The life cycles of many phytophagous insects are synchronous with host plant foliage production in the spring, when young, nutritious leaves are present. Such insects have been called early season feeders (Mattson 1980). The seasonal numbers of most phytophagous insects on creosotebush correspond to the temporal pattern of early season feeders. Although creosotebush is evergreen and produces new leaves throughout much of the year, the major annual pulse of productivity generally takes place in the spring (Barbour et al. 1977). Duisberg (1952) determined that creosotebush foliage (new and old leaves) sampled in the spring was higher in nitrogen content and lower in resin and NDGA (chemical antiherbivore compounds, see the section following) than foliage sampled in the summer.

Plant water status is known to have important effects on nitrogen availability to phytophagous insects. White (1969, 1974) proposed that increased foliar nitrogen content due to water stress is important in regulating populations of phytophagous insects. Short-term water stress also may decrease plant vigor, depressing chemical defenses and resulting in more available nitrogen to herbivores (Rhoades 1983). In contrast, increased foliar water content also is important to nitrogen utilization efficiencies of leaf-chewing phytophagous insects (Scriber 1977, 1978). Results from our experiment provide evidence that increased water status of creosotebush plants, in combination with increased foliar nitrogen content, benefited populations of phytophagous insects. Simulated rainfall alone did not affect numbers of insects nor foliar nitrogen content, but water and fertilizer treatments together resulted in significant increases in numbers of phytophagous insects in June. This positive water-nitrogen interaction effect on arthropod numbers may have resulted from higher foliar water contents increasing the nitrogen utilization efficiencies of phytophagous insects on fertilized plants.

However, increased foliar water content may not be advantageous to the nitrogen utilization efficiencies of sap-sucking insects (Raven 1983), which accounted for the significant interaction.

Variation in the availability of creosotebush nitrogen to herbivores

The availability of a resource to a consumer is a function of the abundance of that resource in the environment, and the accessibility of that resource to the consumer (Wiens 1984). The availability of foliar nitrogen to insects depends primarily upon the nitrogen content of leaf material, and the accessibility of that nitrogen to be used as food. Plant chemical defenses, such as toxins or digestion inhibitors, often limit the accessibility of plant nitrogen to phytophagous insects (Mattson 1980, Rhoades 1983). Schultz et al. (1977) concluded that plant chemical defenses, and spatial and temporal variations in those defenses, are the major limiting factors in creosotebush foliage as a food source to herbivores.

The leaves and terminal stems of creosotebush are coated with a resin composed largely of a protein complexing lignin, nordihydroguaiaretic acid (NDGA) (Mabry et al. 1977). NDGA acts as a herbivore digestion inhibitor, similar in function to tannins, and is an effective feeding deterrent to leaf-chewing insects (Rhoades 1977). However, we found that the majority of phytophagous insects on creosotebush were not leaf-chewers but sap-sucking insects. How the plant defense chemistry of creosotebush affects sap-sucking insects is not known, nor is it known how leaf resin affects the availability of nitrogen to modify the nutrient quality of creosotebush foliage to sap-sucking insects. Sap-sucking insects tap directly into xylem, phloem, or cell sap (Edwards and Wratten 1980, Raven 1983) and thus may avoid much of the NDGA on creosotebush leaf and stem surfaces by simply feeding through or around it, rather than consuming resin as leaf-chewers do.

In general, it is not clear if leaf-chewing and sap-sucking insects are affected in the same way or differently by variation in foliar nitrogen contents of their host plants. Sap-sucking insects are generally favored by increases in soluble nitrogen of their host plants (McClure 1983), they prefer plant parts with the highest levels of nitrogen (McNeill 1973, Horsfield 1977, Denno et al. 1980), and their population dynamics are greatly influenced by foliar nitrogen contents (van Emden and Bashford 1969, White 1969, Dixon 1970, Parry 1974, McClure 1980, Denno 1983). Herbivore protein digestion inhibitors such as tannins do not occur in the phloem or xylem sap that most sap-sucking insects feed upon, but are stored in specialized cells or vacuoles (Raven 1983), which are consumed by leaf-chewing insects. Diet selection and population dynamics of leaf-chewing insects appear to be strongly influenced by plant defense chemistry (Feeny 1970, Erickson and Feeny 1974, Chew 1975, Berenbaum

1983, Cates et al. 1983, Redak and Cates 1984). There also is evidence that plant nitrogen content is important in regulating populations of leaf-chewing phytophagous insects (Shaw and Little 1972, Kimmins 1971, Fox and Macauley 1977, Slansky and Feeny 1977, Myers and Post 1981), and that plant defense chemistry (probably toxins that do occur in plant sap [Raven 1983]) regulates sap-sucking insects (Edmunds and Alstad 1978, Whitham 1978, 1983).

The effects of host plant nitrogen fertilization on associated chewing or sucking phytophagous insects are also unclear. Rhoades (1983) concluded that the fertilization of host plants may result in decreased or increased success of associated phytophagous insects, depending upon the stress condition of the plants and the subsequent imbalance between host plant defenses and the proximate nutritional quality of the foliage. There is evidence that nitrogen fertilization of host plants does have negative effects on populations of chewing insects (Stark 1965, Smirnov and Bernier 1973, Auerbach and Strong 1981), and increases the success of both chewing (Rodriguez 1960, Shaw and Little 1972, Onuf et al. 1977, Slansky and Feeny 1977, Wiseman et al. 1973), and sucking (Rodriguez 1960, van Emden 1966, Leigh et al. 1970, Carrow and Betts 1973, McClure 1980, 1983, Vince et al. 1981) phytophagous insects.

The above evidence is difficult to evaluate because most studies examined either chewing or sucking insects, in relation to either plant nutrient content or plant defense chemistry. It is therefore impossible to compare chewing or sucking insects directly, nor is it possible to assess interaction effects between plant nutrients and defense chemistry. Investigations into the relationships between plant nutrients and defense chemistry and insect success (e.g., Slansky and Feeny 1977, Redak and Cates 1984) are needed for both chewing and sucking phytophagous insects.

An apparent dichotomy in the availability of foliar nitrogen to chewing and sucking phytophagous creosotebush insects may have been due to the effectiveness or ineffectiveness of plant chemical defenses as applied to different insect feeding mechanisms. Other factors such as insect behavior and habitat selection determine how insects respond to variable host plant resources. Insect morphological and behavioral predator avoidance attributes restrict some phytophagous insects to certain structural parts of the foliage (Price et al. 1980, Shultz 1983). The majority of monophagous insect taxa on creosotebush are remarkably cryptic on certain parts of the foliage (Shultz et al. 1977). Cryptic predator avoidance behavior is particularly pronounced among the leaf-chewing insects on creosotebush, such as caterpillars, walking sticks, and grasshoppers (Shultz et al. 1977). Cryptic behavior may limit chewing insects from moving to and exploiting rapidly increasing foliar nutrient quality, such as that resulting from our fertilization experiment. Small, fast-moving, sucking insects

such as mirid plant bugs and thrips have greater mobility to exploit variable foliage quality quicker than the larger, slower, chewing insects. Theoretically, highly mobile herbivores should be more likely to track variable foliage quality than relatively less mobile herbivores (Kareiva 1982). Mirids and other Hemiptera and Homoptera on creosotebush are also cryptic on the foliage, and probably select feeding sites that enhance concealment. The positive linear correlation between numbers of arthropods and foliage production was probably due to increased foliage density providing more and better habitat for many of those arthropods. However, the exponential increase in arthropods in relation to increased foliar nitrogen contents indicates that food quality was especially important for at least some of the dominant species of sap-sucking phytophagous insects.

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LITERATURE CITED

- Auerbach, M. J., and D. R. Strong. 1981. Nutritional ecology of *Heliconia* herbivores: experiments with plant fertilization and alternative hosts. *Ecological Monographs* 5:63-83.
- Barbour, M. G., G. L. Cunningham, W. C. Oechel, and S. A. Bamberg. 1977. Growth and development, form and function. Pages 48-91 in T. J. Mabry, J. H. Hunziker, and D. R. Difeo, Jr., editors. *Creosote bush: biology and chemistry of Larrea in New World deserts*. United States/International Biological Program Synthesis Series 6. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- Berenbaum, M. 1983. Coumarins and caterpillars: a case for coevolution. *Evolution* 37:163-179.
- Carrow, J. R., and R. E. Betts. 1973. Effects of different foliar-applied nitrogen fertilizers on balsam woolly aphid. *Canadian Journal of Forest Research* 3:122-139.
- Cates, R. G., R. A. Redak, and C. B. Henderson. 1983. Patterns in defensive natural product chemistry: Douglas-fir and western spruce budworm interactions. Pages 3-19 in P. A. Henderson, editor. *Plant resistance to insects*. American Chemical Society Symposium Series 208. American Chemical Society, Washington, D.C., USA.
- Chew, F. S. 1975. Coevolution of pierid butterflies and their cruciferous food plants. I. The relative quality of available resources. *Oecologia* (Berlin) 20:117-127.
- Chew, R. M. 1961. Ecology of the spiders of a desert community. *Journal of the New York Entomological Society* 69:5-41.
- Crawford, C. S. 1981. *Biology of desert invertebrates*. Springer-Verlag, Berlin, West Germany.
- Crawford, C. S., and J. R. Gosz. 1982. Desert ecosystems: their resources in space and time. *Environmental Conservation* 9:181-195.
- Cunningham, G. L., J. P. Syvertsen, J. F. Reynolds, and J. M. Willson. 1979. Some effects of soil-moisture availability on above-ground production and reproductive allocation in *Larrea tridentata* (DC) Cov. *Oecologia* (Berlin) 40:113-123.
- Denno, R. F. 1983. Tracking variable host plants in space and time. Pages 291-341 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- Denno, R. F., and M. S. McClure. 1983. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- Denno, R. F., M. J. Raupp, D. W. Tallamy, and C. F. Reichelderfer. 1980. Migration in heterogeneous environments: differences in habitat selection between wing-forms of the dimorphic planthopper *Prokelisia marginata* (Homoptera: Delphacidae). *Ecology* 61:859-867.
- Dixon, A. F. G. 1970. Quality and availability of food for a sycamore aphid population. *Symposium of the British Ecological Society* 10:271-287.
- Duisberg, P. C. 1952. Some relationships between xerophytism and the content of resin, nordihydroguaiaretic acid, and protein of *Larrea divaricata* Cav. *Plant Physiology* 27:769-777.
- Edmunds, G. F., Jr., and D. N. Alstad. 1978. Coevolution in insect herbivores and conifers. *Science* 199:941-945.
- Edwards, P. J., and S. D. Wratten. 1980. *Ecology of insect-plant interactions*. The Institute of Biology's Studies in Biology Number 121. Edward Arnold, London, England.
- Erickson, J. M., and P. P. Feeny. 1974. Sinigrin: a chemical barrier to the black swallowtail butterfly, *Papilio polyxenes*. *Ecology* 55:103-111.
- Ettershank, G., J. A. Ettershank, M. Bryant, and W. G. Whitford. 1978. Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. *Journal of Arid Environments* 1:135-139.
- Feeny, P. P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:656-681.
- Floret, C., R. Pontanier, and S. Rambal. 1982. Measurement and modelling of primary production and water use in a south Tunisian steppe. *Journal of Arid Environments* 5:77-90.
- Fox, L. R., and B. J. Macauley. 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. *Oecologia* (Berlin) 49:145-162.
- Hadley, N. D., and S. R. Szarek. 1981. Productivity of desert ecosystems: producer, consumer and decomposer organisms. *BioScience* 31:747-753.
- Horsfield, D. 1977. Relationship between feeding of *Phyllaenus spumarius* (L.) and the amino acid concentration in xylem sap. *Ecological Entomology* 2:259-266.
- Hsiao, T. S., and R. L. Kirkland. 1973. Demographic studies of sagebrush insects as functions of various environmental factors. United States/International Biological Program Desert Biome Research Memo 73(34):28.
- Hurd, L. E., and L. L. Wolf. 1974. Stability in relation to nutrient enrichment in arthropods of old-field successional ecosystems. *Ecological Monographs* 44:465-482.
- Hurd, P. D., Jr., and E. G. Linsley. 1975. Some insects other than bees associated with *Larrea tridentata* in the southwestern United States. *Proceedings of the Entomological Society of Washington* 77:100-121.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging. *Ecological Monographs* 52:261-282.
- Kimmins, J. P. 1971. Variation in the foliar amino acid composition of flowering and non-flowering balsam fir (*Abies balsamea* (L.) Mill) and white spruce (*Picea glauca* (Moench) Voss) in relation to outbreaks of the spruce budworm (*Choristoneura fumiferana* (Clem)). *Canadian Journal of Zoology* 49:1005-1011.

- Kirchner, T. B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology* **58**:1334-1344.
- Leigh, T. F., D. W. Grimes, H. Yomada, and D. Bassitt. 1970. Insects in cotton as affected by irrigation and fertilization practices. *California Agriculture* **24**:12-14.
- Ludwig, J. A., and W. G. Whitford. 1981. Short-term water and energy flow in arid ecosystems. Pages 271-299 in D. W. Goodall and R. A. Perry, editors. *Arid-land ecosystems*. International Biological Program Number 17. Cambridge University Press, Cambridge, England.
- Mabry, T. J., D. R. DiFeo, Jr., M. Sakakibara, C. F. Bohnsted, Jr., and D. Seigler. 1977. The natural products chemistry of *Larrea*. Pages 115-134 in T. J. Mabry, J. H. Hunziker, and D. R. Difeo, Jr., editors. *Creosote bush: biology and chemistry of Larrea in New World deserts*. United States/International Biological Program Synthesis Series 6. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen. *Annual Review of Ecology and Systematics* **11**: 119-161.
- McClure, M. S. 1980. Foliar nitrogen: a basis for host suitability for elongate hemlock scale, *Forinia externa* (Homoptera: Diaspididae). *Ecology* **61**:72-79.
- . 1983. Competition between herbivores and increased resource heterogeneity. Pages 125-153 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- McNeill, S. 1973. The dynamics of a population of *Leptoterna dolabrata* (Miridae) in relation to its food resources. *Journal of Animal Ecology* **42**:495-507.
- McNeill, S., and T. R. E. Southwood. 1978. The role of nitrogen in the development of insect-plant relationships. Pages 77-98 in J. B. Harborne, editor. *Biochemical aspects of plant and animal coevolution*. Academic Press, London, England.
- Mispagel, M. E. 1974. An ecological analysis of insect populations on *Larrea tridentata* in the Mojave Desert. Thesis. California State University, Long Beach, California, USA.
- Myers, J. H., and B. J. Post. 1981. Plant nitrogen and fluctuations of insect populations: a test with the cinnabar moth-tansy ragwort system. *Oecologia (Berlin)* **48**:151-156.
- Noy-Mier, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**: 25-51.
- Onuf, C. P. 1978. Nutritive value as a factor in plant-insect interactions with an emphasis on field studies. Pages 85-96 in G. G. Montgomery, editor. *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, D.C., USA.
- Onuf, C. P., J. M. Teal, and I. Valiela. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. *Ecology* **58**:514-526.
- Orians, G. H., R. G. Cates, M. A. Mares, J. Neff, D. F. Rhoades, M. L. Rosenzweig, B. B. Simpson, and C. S. Tomoff. 1977. Resource utilization systems. Pages 164-244 in G. H. Orians and O. T. Solbrig, editors. *Convergent evolution in warm deserts*. United States/International Biological Program Synthesis Series 3. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- Parry, W. H. 1974. The effect of nitrogen levels in Sitka spruce needles on the aphid *Elatobium abietinum* (Walker) populations in northeastern Scotland. *Oecologia (Berlin)* **15**:305-320.
- Penning de Vries, F. W. T., and M. A. Djiteye, editors. 1982. *La productivite des pasturages Saheliens*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Prestidge, R. A. 1982. The influence of nitrogenous fertilizer on grassland Auchenorrhyncha (Homoptera). *Journal of Applied Ecology* **19**:735-749.
- Price, P. W., E. E. Bouton, P. Gross, B. A. McPherson, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* **11**:41-65.
- Raven, J. A. 1983. Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Advances in Ecological Research* **13**:135-234.
- Redak, R. A., and R. G. Cates. 1984. Douglas-fir (*Pseudotsuga menziesii*)-spruce budworm (*Choristoneura occidentalis*) interactions: the effect of nutrition, chemical defenses, tissue phenology, and tree physical parameters on budworm success. *Oecologia (Berlin)* **62**:61-67.
- Reese, J. C. 1979. Interactions of allelochemicals with nutrients in herbivore food. Pages 304-326 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, New York, New York, USA.
- Rhoades, D. F. 1977. The antiherbivore chemistry of *Larrea*. Pages 135-175 in T. J. Mabry, J. H. Hunziker, and D. R. Difeo, Jr., editors. *Creosote bush: biology and chemistry of Larrea in New World deserts*. United States/International Biological Program Synthesis Series 6. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- . 1983. Herbivore population dynamics and plant chemistry. Pages 155-220 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- Rhoades, D. F., and R. G. Cates. 1976. Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry* **10**:168-213.
- Rodriguez, J. G. 1960. Nutrition of the host and reaction to pests. Pages 149-168 in L. P. Reitz, editor. *Biological and chemical control of plant and animal pests*. American Association for the Advancement of Science, Publication 61, Washington, D.C., USA.
- Romney, E. M., A. Wallace, and R. B. Hunter. 1978. Plant response to nitrogen fertilization in the northern Mojave Desert and its relationship to water manipulation. Pages 232-242 in N. E. West and J. J. Skujins, editors. *Nitrogen in desert ecosystems*. United States/International Biological Program Synthesis Series 9. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- Rosenthal, G. A., and D. H. Janzen, editors. 1979. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, New York, New York, USA.
- Rosenzweig, M. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**:385-387.
- SAS Institute. 1982. *SAS user's guide: statistics, 1982 edition*. SAS Institute, Cary, North Carolina, USA.
- Scriber, J. M. 1977. Limiting effects of low leaf-water content on the nitrogen utilization, energy budget, and larval growth of *Hyalophora cecropia* (Lepidoptera: Saturniidae). *Oecologia (Berlin)* **28**:269-287.
- . 1978. The effects of larval feeding specialization and plant growth form on the consumption and utilization of plant biomass and nitrogen: an ecological consideration. *Entomologia Experimentalis et Applicata* **24**:494-510.
- Shaw, G. G., and C. H. A. Little. 1972. Effect of high urea fertilization of balsam fir trees on spruce budworm development. Pages 589-597 in J. C. Rodriguez, editor. *Insect and mite nutrition*. North Holland, Amsterdam, The Netherlands.
- Shultz, J. C. 1983. Habitat selection and foraging tactics of caterpillars in heterogenous trees. Pages 61-90 in R. F. Denno and M. S. McClure, editors. *Variable plants and*

- herbivores in natural and managed systems. Academic Press, New York, New York, USA.
- Shultz, J. C., D. Otte, and F. Enders. 1977. *Larrea* as a habitat component for desert arthropods. Pages 176–206 in T. J. Mabry, J. H. Hunziker, and D. R. Difeo, Jr., editors. Creosote bush: biology and chemistry of *Larrea* in New World deserts. United States/International Biological Program Synthesis Series 6. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- Slansky, F., Jr., and P. Feeny. 1977. Stabilization of the rate of nitrogen accumulation by larvae of the cabbage butterfly on wild and cultivated food plants. *Ecological Monographs* **47**:209–228.
- Smirnov, W. A., and B. Bernier. 1973. Increased mortality of the Swain jackpine sawfly, and foliar nitrogen concentrations after urea fertilization. *Canadian Journal of Forest Research* **3**:112–121.
- Stark, R. W. 1965. Recent trends in forest entomology. *Annual Review of Entomology* **10**:303–324.
- Strong, D. R., Jr., J. H. Lawton, and T. R. E. Southwood. 1984. *Insects on plants: community patterns and mechanisms*. Harvard University Press, Cambridge, Massachusetts, USA.
- Tilman, D. 1982. Resource competition and community structure. *Monographs in Population Biology* **17**. Princeton University Press, Princeton, New Jersey, USA.
- van Emden, H. F. 1966. Studies on the relations of insect and host plant. III. A comparison of the reproduction of *Brevicoryne brassicae* and *Myzus persicae* (Hemiptera: Aphidae) on brussels sprout plants supplied with different rates of nitrogen and potassium. *Entomologia Experimentalis et Applicata* **9**:444–460.
- van Emden, H. F., and M. A. Bashford. 1969. A comparison of reproduction of *Brevicoryne brassicae* and *Myzus persicae* in relation to soluble nitrogen concentration and leaf age in brussels sprout plant. *Entomologia Experimentalis et Applicata* **12**:351–364.
- Vince, S. W., I. Valiela, and J. M. Teal. 1981. An experimental study of the structure of herbivorous insect communities in a salt marsh. *Ecology* **62**:1662–1678.
- West, N. E., and J. J. Skujins, editors. 1978. *Nitrogen in desert ecosystems*. United States/International Biological Program Synthesis Series 9. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania, USA.
- White, T. C. R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Oecologia* **50**:905–909.
- . 1974. A hypothesis to explain outbreaks of looper caterpillars with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. *Oecologia* (Berlin) **16**:279–301.
- . 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* (Berlin) **33**:71–86.
- Whitford, W. G., and F. M. Creusere. 1977. Seasonal and yearly fluctuations in Chihuahuan Desert lizard communities. *Herpetologica* **33**:54–65.
- Whitham, T. G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology* **59**:1164–1176.
- . 1983. Host manipulation of parasites: within-plant variation as a defense against rapidly evolving pests. Pages 15–41 in R. F. Denno and M. S. McClure, editors. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York, New York, USA.
- Wiens, J. A. 1984. Resource systems, populations, and communities. Pages 397–436 in P. W. Price, C. N. Slobodkin, and W. S. Gaud, editors. *A new ecology: novel approaches to interactive systems*. John Wiley and Sons, New York, New York, USA.
- Wiseman, B. R., D. B. Leuck, and W. W. McMillian. 1973. Effects of fertilizers on resistance of Antigua corn to fall armyworms and corn earworm. *Florida Entomologist* **56**:1–7.

APPENDIX

Common arthropod taxa of three major trophic groups sampled from the foliage of creosotebush. Taxa are from all dates and treatments combined. Specificity of taxa to creosotebush is indicated in parentheses following the names.*

Herbivores	Predators
Sucking	
Hemiptera	Araneida
Miridae	Thomisidae
<i>Phytocoris vanduzeei</i> Reuter (S)	<i>Misumenops coloradensis</i> Gertsch (G)
<i>P. nigripubescentis</i> Knight (S)	<i>M. celer</i> (Hentz) (G)
<i>Parthenicus covilleae</i> Van Duzee (S)	Salticidae
Pentatomidae	<i>Sassacus papenhoei</i> Peckham (G)
<i>Dendrocoris contaminatus</i> Uhler (S)	Coleoptera
Homoptera	Coccinellidae
Issidae	<i>Hyperaspis</i> spp. (G)
<i>Hysteroptera unum</i> Ball (S)	Hemiptera
Membracidae	Reduviidae
<i>Multareis cornutus</i> Ball (S)	<i>Zelus socius</i> Uhler (G)
<i>Multareoides digitatus</i> (Van Duzee) (S)	Dictyoptera
Cicadellidae	Mantidae
<i>Spathanus accuminatus</i> (Baker) (?)	<i>Stagmomantis limbata</i> (Hahn) (G)
<i>S. nigricollis</i> (Ball) (?)	Omnivores
<i>Idiocerus</i> spp. (?)	Hymenoptera
Coccidae	Formicidae
<i>Tachardiella larreae</i> (Comstock) (S)	<i>Crematogaster larreae</i> Buren (S)
Thysanoptera	<i>Forelius foetidus</i> (Buckley) (G)
Thripidae	<i>F. pruinosis</i> (Roger) (G)
<i>Thrips</i> spp. (G)	
Chewing	
Coleoptera	
Curculionidae	
<i>Ophriastes</i> spp. (?)	
Orthoptera	
Acrididae	
<i>Boottetix argentatus</i> Bruner (S)	
Phasmatodea	
Phasmatidae	
<i>Diapheromera covilleae</i> (R&H) (S)	
Lepidoptera	
Geometridae	
<i>Synglochis perumbraria</i> Hulst	

* (S) = creosotebush specialists, restricted to *Larrea tridentata*; (G) = generalists, occur on other plants in addition to *Larrea*; (?) = unknown host plant specificity.