Oecologia (1989) 81:166–175

Oecologia

Interplant variation in creosotebush foliage characteristics and canopy arthropods

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Summary. We conducted a field study to test the hypothesis that creosotebush (*Larrea tridentata*) shrubs growing in naturally nutrient-rich sites had better quality foliage and supported greater populations of foliage arthropods than shrubs growing in nutrient-poor sites. Nutrient-rich sites had significantly higher concentrations of soil nitrogen than nutrient-poor sites. Multivariate analysis of variance revealed significant differences between high nutrient and low nutrient shrubs based on a number of structural and chemical characteristics measured. High nutrient shrubs were larger, had denser foliage, greater foliage production, higher concentrations of foliar nitrogen and water, and lower concentrations of foliar resin than low nutrient shrubs. Numbers of foliage arthropods, particularly herbivores and predators, were significantly higher on high nutrient shrubs. Shrub characteristics and foliage arthropod abundances varied considerably from shrub to shrub. Shrub characteristics representing shrub size, foliage density, foliage growth, and foliar nitrogen and water concentrations were positively correlated with arthropod abundances. Foliar resin concentrations were negatively correlated with foliage arthropod abundances. The positive relationship between creosotebush productivity and foliage arthropods is contradictory to the tenet that physiologically stressed plants provide better quality foliage to insect herbivores.

Key words: Desert shrubs – *Larrea tridentata* – Nitrogen – Plant-insect interactions – Phytophagous insects

Variation in host plant foliage quality to herbivores is often pronounced and recognized as a potentially important regulatory mechanism of insect populations on plants (Denno and McClure 1983). Insect populations are quite variable on desert shrubs (Hsiao and Kirkland 1973; Orians et al. 1977; Whitford and Creusere 1977), indicating potential variability in foliage quality, yet little is known about variation in foliage quality of desert shrubs to insects. Interactions between insects and the North American desert shrub, creosotebush (*Larrea tridentata*), are of particular interest because *Larrea* hosts a diverse and specialized insect fauna (Hurd and Linsley 1975; Schultz et al. 1977), *Larrea* foliage quality and foliage insect populations are highly variable in space and time (Mispagel 1974, 1978; Rhoades 1977; Schultz et al. 1977), and key concepts of early plant-insect interaction theory were derived from studies of creosotebush insects (Rhoades and Cates 1976; Rhoades 1979).

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Patterns and mechanisms of plant to plant variation in creosotebush foliage characteristics, and associated variation in assemblages of foliage arthropods are not well understood. Evidence from independent studies indicates that variation in foliar resin (Rhoades 1977) and nitrogen (Lightfoot and Whitford 1987) concentrations, and foliage substrate availability for cryptic background matching (Schultz et al. 1977), are important factors influencing spatial variation in foliage arthropod populations on creosotebush. However, none of the above studies examined plant to plant variation in chemical and structural characteristics of creosotebush in conjunction with variation in whole assemblages of associated arthropods.

In desert environments where water and nutrients are limiting to both producers and consumers (Crawford and Gosz 1982), plants with better than average access to water and nutrients should produce more biomass and nutrient rich foliage than less productive plants. Highly productive plants may be better or less defended from herbivores by defensive chemicals than less productive plants (Rhoades 1983). Our previous field experiment (Lightfoot and Whitford 1987) demonstrated that fertilized and watered creosotebush shrubs were more productive, had higher foliar nitrogen contents, and supported larger populations of foliage arthropods than unfertilized shrubs. Does such a positive relationship between shrub productivity, foliar nitrogen contents, and arthropod populations exist under natural unmanipulated field conditions? In unmanipulated creosotebush stands, some shrubs do appear to be more productive than others. Are those more productive shrubs better host plants to phytophagous insects, or do they have enhanced chemical defenses?

The research presented here examined relationships between natural levels of creosotebush productivity and densities of foliage arthropods. We conducted a field study to test the hypothesis that shrubs growing in naturally nutrient-enhanced sites support larger populations of foliage arthropods than shrubs growing in less productive sites. We also examined natural patterns of covariation between foliage arthropods and creosotebush shrub characteristics.

Methods

Study site

The investigation was conducted in the northern Chihuahuan Desert at the Jornada Long Term Ecological Research

Site, near Las Cruces, New Mexico. Field sampling was conducted during the late spring of 1985 and 1986.

Sampling design

Five plots, approximately 1 ha each and designated A through E, were selected randomly from a 1.0 by 0.5 km area within a creosotebush stand situated on a gradually sloping east-facing alluvial slope below the Dona Ana Mountains. Creosotebush was the dominant shrub in the area, associated with less abundant subshrubs and a variety of small annual forbs.

Thirty shrubs were selected for sampling from each of the five plots. To test for differences in foliage characteristics and arthropod densities between nutrient-rich and nutrient-poor shrubs, we selected 10 high nutrient shrubs and 10 low nutrient shrubs in each plot. Shrub nutrient status was determined on the basis of the relative size of leaf litter accumulations on the ground beneath shrub canopies.

Desert shrubs produce nutrient patches, such that horizontal and vertical gradients in soil nitrogen concentrations are greatest immediately under shrub canopies, decreasing toward open inter-shrub spaces (West and Klemmedson 1978; Crawford and Gosz 1982; Whitford 1986). In desert soils, nitrogen concentrations are correlated with soil organic matter content (Skujians 1981; Whitford et al. 1987), and accumulations of plant litter increase soil water infiltration (Elkins et al. 1986). Based on these facts, we assumed that creosotebush shrubs with large accumulations of subcanopy leaf litter were growing in soil with higher nitrogen and moisture conditions than shrubs with little leaf litter accumulations. Shrubs with large accumulations of leaf litter were likely to be nutrient-rich, or high nutrient shrubs. Shrubs with little ground surface litter accumulations were likely to be relatively low nutrient shrubs. Ten shrubs were also selected at random from each plot prior to selecting nutrient type shrubs, to provide us with measures of natural variability of shrub characteristics and foliage arthropods.

Soil nitrogen

Three 10 cm deep soil cores were taken from underneath the canopies of each of the shrubs in June of 1985. The soil was analyzed for total nitrogen using Kjeldahal digestion and colorametric analysis by autoanalyzer. Soil nitrogen measurements were used to test for differences in the content of nitrogen from surface soils of high and low nutrient shrubs.

Creosotebush characteristics

A modified point-quarter technique (Brower and Zar 1984) was used to assess patterns of shrub density on each of the five plots. Ten shrub characteristics were measured from each of the 150 tagged shrubs on the five plots. Three branches were sampled randomly from each shrub in an attempt to compensate for within-plant or branch to branch variability in foliage characteristics.

Branch growth increments. Three branch tips were selected randomly from each shrub, tagged with yarn, and marked with a permanent marking pen 4 cm below the terminal bud, on March 28, 1986. One month later, the distances from the pen marks to the terminal branch tips were measured.

Foliage weight. The same branch ends used for growth increment measurements were harvested from the shrubs on May 3. 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 weights of each branch tip, to the length, were used as measures of foliage weight or biomass of plant material (leaves, stems, 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 above measured branch ends.

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 Kjeldahal digestion and colorametric measurement by autoanalyzer.

Foliar resin content. On May 4, three additional randomly selected 5 cm branch tips were cut from each of the 150 shrubs. The branch tips were placed in coolers, taken to the lab, and fresh weighed. Foliar resin was then extracted from three combined branch tips per sample in ether, using the resin extraction method described by Rhoades (1977).

Shrub volume. Shrub height and diameter were measured for each of the 150 shrubs, in early May. From those dimensions, shrub volume was calculated using the mathematical formula for the volume of a circular cone ($V = r^2h/3$) (Ludwig et al. 1975).

Number of woody branches. The number of woody branches intersecting the horizontal plane of a 5 cm diameter plastic pipe at mid-shrub height were counted. The branches and foliage of creosotebush shrubs at the study site were oriented in a southeast direction (Neufeld et al. 1988), resulting in an asymmetrical arrangement of branches, so the pipe was placed on a northeast-southwest axis in each shrub.

Canopy density. A one-by-two-meter white board partitioned into a grid of 0.25 m squares was placed on one side of each shrub, and the shrub photographed from a perpendicular angle, from the opposite side. Canopy density was then visually estimated as the percentage of the board surface obscured by foliage cover. Foliage density was consistently measured on a northeast-southwest axis of each shrub.

Ground surface litter cover. In early May, a one-meter^2 PVC pipe grid, partitioned into four 0.5 m^2 quarters, was placed on the ground, centered under the foliage canopy of each shrub. Ground surface litter was mapped visually onto a diagram of the grid, from which total ground litter cover was measured.

Foliage arthropods

Foliage arthropods were sampled from each of the 150 shrubs on May 2, 1986. Three branches were selected randomly from each shrub and shaken into an insect sweep