

Resource Abundance and Insect Herbivore Diversity on Woody Fabaceous Desert Plants

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ABSTRACT This study addresses four hypotheses that may account for differences in the number of insect herbivore species among plant species. These hypotheses are based on the assumption that insect diversity is a function of the number, quantity, and distribution of plant resources used by herbivores. The study investigated predictions that herbivore species richness will increase as a function of increasing the following: (1) host plant distribution over the landscape (host plant geographical distribution hypothesis), (2) host plant density within a habitat (resource concentration hypothesis), (3) size of individual plants (plant size hypothesis), or (4) abundance of resources (resource abundance hypothesis). We tested predictions from these hypotheses by examining the species richness of insect herbivores on five sympatric species of fabaceous plants that varied in their local dispersion of individual plants and plant architecture. Among these five species, plant geographical distribution varied threefold, density varied 38-fold, plant size and food resources available to insect herbivores varied \approx 100-fold. Plant geographical distribution, plant size, and the resource concentration hypotheses were not corroborated in this study. Resource abundance, measured as plant dry weight, accounted for the differences in number and abundance of insect species between host plant species. Leaf biomass accounted for 44.15% of the variation in number of insect herbivore species and 51.76% of the variation in abundance of insect herbivores using leaves as resources. Flower biomass accounted for 32.86% of the variation in the number of insect herbivore species using flowers. Therefore, plants that offered a greater quantity of resources, especially leaves and flowers, had greater species richness and abundance in insect herbivores.

KEY WORDS insect diversity, herbivory, plant size hypothesis, resource concentration hypothesis, resource abundance hypothesis

THE HOST PLANT represents a variable and heterogeneous resource affecting the distribution of insect herbivores. Aspects of the host plant that may influence insect distribution include the following: spatial and seasonal distribution (Tahvanainen and Root 1972; Root 1973; Thompson 1978; Bach 1980, 1984; Kareiva 1983; Aide 1991, 1993; Mopper and Simberloff 1995), size and growth form (Moran 1980, Bach 1981, Lawton 1983, Fernandes and Price 1988), nutritional quality and chemical defenses (White 1974, Coley 1983, Bryant et al. 1987, Waring and Cobb 1992). However, few studies have considered the role of resource abundance (quantity) on insect herbivore populations and communities (Hunter 1992, Ohgushi 1992).

Resource abundance, measured as the abundance of individual plants or plant parts or as plant biomass, is the main factor responsible for population oscillations of some eruptive moth and butterfly species that outbreak in temperate forests (White 1974, Myers and Campbell 1976, Thompson and Price 1977, Dempster

and Pollard 1981, Myers and Post 1981, Randall 1982, Dempster 1983). Egg density of a herbivorous lady beetle tracked that of its resources in different populations for five consecutive years despite heavy arthropod predation and other external disturbances, and resource abundance accounted for 66–98% of the population fluctuations observed (Ohgushi and Sawada 1985, Ohgushi 1992).

Although Hunter (1992) suggested that the abundance of resources represented an important factor in structuring insect herbivore communities, there have been very few studies conducted at the community level (Teragushi et al. 1981, Hunter 1987, Hunter and Wilmer 1989). Host plants with greater biomass can attract more insect species as illustrated by insect communities in Alaska and Ohio, where \approx 76% of the variation in number of insect herbivore species associated with two grass communities was attributed to plant biomass (Teragushi et al. 1981). Reducing the abundance of a plant part can affect an entire community of insects that depend on that resource (Hunter 1987, Hunter and Wilmer 1989).

We conducted a census of insect herbivores on five woody fabaceous plant species of the Sonoran desert to address four hypotheses concerning the species richness and abundance of insect herbivores between

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host plant species. The host plant geographical distribution hypothesis predicts that widespread plant species have a richer regional pool of insects and consequently usually have richer local communities because these are subsamplings of the regional pool (Ricklefs 1987, Cornell and Lawton 1992). The resource concentration hypothesis predicts that plants that occur in higher densities are more likely to be found by insect herbivores (Southwood 1961), and specialist herbivores tend to remain longer in these patches (Lewis and Waloff 1964, Root 1973). These conditions favor certain herbivore species that increase in abundance, reducing populations of other herbivore species and resulting in a decrease in insect species richness in that community (Murdoch et al. 1972, Root 1973). Therefore, one of the implications of the resource concentration hypothesis (Root 1973) is that low density stands with mixed plant species will show higher species richness when compared with high density stands of single species (Bach 1980). Consequently, we would expect plant density and insect species richness to be negatively correlated for a given host plant.

The plant size hypothesis suggests that larger plants can support more insect species when compared with smaller host plants because they are more likely to be found by the herbivore (Lawton 1983). The resource abundance hypothesis predicts that plants that offer more resources have the potential to support more species and greater abundances of insect herbivores (Teragushi et al. 1981, Hunter and Wilmer 1989, Ohgushi 1992, Hunter 1992). In this study we recognized two scales of resource quantity; we use plant density when referring to the number of individual plants existing in an area and resource abundance when referring to the amount of resources on individual plants.

Materials and Methods

Host Plant Taxa. We limited this study to the insect herbivore community on woody perennials in the family Fabaceae because of the following: (1) they were sympatric and thus we could rule out geographic differences in explaining insect species richness, (2) they provided a range of architectural characteristics from small shrubs to trees, and (3) they had a range of plant densities so that we expected an insect community response. Concomitantly, we assumed that they shared enough characteristics in their chemistry and nutritional quality that we could ascribe differences in insect communities to differences in architecture, size, density, or resource abundance. In addition, Fabaceae is one of the most speciose plant families in the Sonoran desert (Schreve 1951) and worldwide, enabling future comparisons with other insect communities on other leguminous host plant species. Five fabaceous species included in the study are found abundantly at our study site: two shrub species [*Acacia greggii* (Gray) (catclaw) and *Calliandra eriophylla* (Bentham)] and three tree species [*Prosopis velutina* (Woot) (mesquite), *Cercidium microphyllum* (Tor-

rey) (palo verde), and *Cercidium floridum* (Bentham) (blue palo verde)]. Four of these fabaceous host plants share similar phenologies with flowering and leaf flush occurring in May and fruit development occurring through June and July. *C. microphyllum* flowers in May, and leaf flush and fruiting occur in June (Schreve 1951).

Study Site. Our study site was located in Bureau of Land Management land near BumbleBee Ranch (34° N, 112° W), AZ, at 950 m in elevation above sea level. This elevation represents the northern-most distribution of the Sonoran desert. The study area encompassed ≈25 ha.

Sampling Insect Communities. Sampling of insect communities consisted of timed visual observations supplemented with sweep sampling. Visual surveys have been shown to be an effective and efficient method for censusing insect species richness and abundance on a variety of host plants including soybean (Mayse et al. 1978a, 1978b), *Heliconia* spp. (Seifert and Seifert 1976, 1979), *Pteridium aquilinum* (Kuhn) (Lawton 1982, 1983; Lawton and Gaston 1989), Apiaceae (Berenbaum 1981), Piperaceae (Marquis 1991), and Asteraceae (Root and Cappuccino 1992). The legumes included in this study easily lend themselves to visual sampling because of their open architecture and dissected foliage.

Visual censuses consisted of searching throughout all aboveground plant parts. Plant parts were categorized as leaves, stems, flowers, and fruits (pods). For each plant we recorded the presence of all herbivorous insects, excepting pollinators, their position on one of the above recognized plant parts, and whether they were feeding. Reference samples were obtained for all species recorded, adult insects were pinned and immature stages kept in 70% alcohol. Voucher specimens were deposited in the Entomology Museum at University of Arizona (2, 25, 27, 32, 43, 45, 55, 62–67, 69, 72–76, 79, 80, 82, 103, 104, 106, 108, 113, 118, 132, 138, 148, 149, 150, 151, 158–164, 166, 167, 171, 177, 178, 183, 202, 204, 221, 222, 224, 250, 251, 257, 258, 267–280, 291, 292, 294–305, 307–330).

Determination of Sampling Effort. We conducted a preliminary sampling in 1991 on all plant species to determine the appropriate time needed to visually search individual plants and obtain a representative sample of the insect community. We generated a species accumulation curve with the mean cumulative number of insect species found by minute on all plants sampled, until an asymptote in the number of new species found per individual plant was reached. The curve revealed that the asymptote was reached at a minimum survey time of 45 min per plant (Fig. 1a). If a new insect herbivore species was found at 45 min of searching, another 10 min was added to the search and this only ended after no new insect species were discovered after 10 min of continuous search.

For each sampling period we also employed an additional sampling method, which constituted beating five branches of each plant into a sweepnet to sample cryptic or very small species. The species that were found with this method and had not been re-

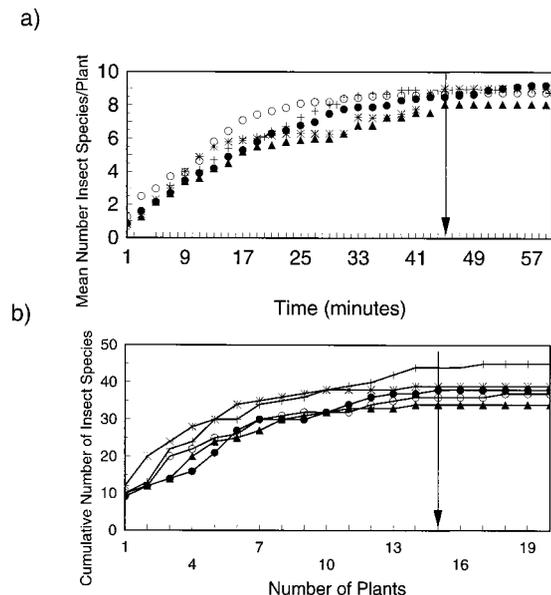


Fig. 1. Species accumulation curve representing the cumulative number of insect herbivore species encountered by sampling time (minutes) (a) and by number of plants sampled (b) for woody fabaceous plant species in the Sonoran Desert, AZ. The plant species are *C. microphyllum* (●), *C. floridum* (○), *P. velutina* (+), *A. greggii* (*), and *C. eriophylla* (▲).

corded by visual observation were added to the total number of species found per plant.

A second species accumulation curve was generated to determine the minimum number of individual plants required to obtain a representative sample for each of the host species. This species accumulation curve showed that an asymptote was reached (i.e., no new additional species found) at 15 plants regardless of the species (Fig. 1b).

According to the species accumulation curve, 15 individuals of each plant species constituted a representative sample of the insect communities on desert woody fabaceous plants. For the preliminary study in 1991 we sampled 15 plants of each plant species. This study provided information for a long-term community study on the insect species associated with these five desert fabaceous species on the Sonoran desert from 1991 to 1994. The current study presents data for the insect community on desert legumes for the year of 1994. We haphazardly sampled 20 individuals of each plant species to increase sample size for statistical analysis purposes. Insects were censused according to the method described above and measures of canopy volume were taken from each plant sampled (height × width × width).

Hypotheses Testing. We first determined the total number of insect herbivore species associated with each of the five legume species. The number of insect species associated with each legume species was compared by a chi-square test (Zar 1984). Nonparametric tests were used to test the plant geographical distri-

Table 1. Total number of insect herbivore species associated with the different resources of five woody fabaceous host plant species of the Sonoran Desert, AZ, for the summer of 1994

Plant species	Plant characteristics				
	Whole plant	Leaf	Flower	Pod	Stem
<i>C. microphyllum</i>	22	0	19	—	3
<i>C. floridum</i>	20	11	2	1	6
<i>P. velutina</i>	40	29	2	1	8
<i>A. greggii</i>	27	21	2	0	4
<i>C. eriophylla</i>	15	13	0	0	2

bution and resource concentration hypotheses because the data represented total insect richness, total area of plant distribution and mean density. The plant size and resource abundance hypotheses were analyzed by both nonparametric and parametric tests because we had measures for size and biomass for each of the 100 plant species studied. Parametric tests require larger sample sizes to meet the assumptions of normality and homoscedasticity of the data (Sokal and Rohlf 1984).

To address the host plant geographical distribution hypothesis we obtained maps of the distributions of the five species of woody fabaceous desert plants from the atlas of the Sonoran Desert Plants (Turner et al. 1995) to estimate their geographic distribution. We correlated the total area of distribution of each plant species in square kilometers with the total number of insect herbivore species on those host plant species for the summer of 1994 by Rank Correlation test (Sokal and Rohlf 1984).

To address the resource concentration hypothesis we used three line transects (100 m long by 20 m wide) at least 1 km apart from each other to measure host plant density. To obtain density estimates for each plant species, all individuals of the five woody fabaceous species within the transect were counted (Table 1). Plant species density was estimated as the mean density of three transects and was correlated with total insect species richness for each of five leguminous plant species by the rank correlation test (Siegel and Castellan 1988).

To address the plant size hypothesis we correlated mean plant size (m³) of each plant species with its associated number of insect herbivore species by the rank correlation test (Siegel and Castellan 1988).

To address the resource abundance hypothesis, insect censuses were done on one representative branch of each plant that was sampled for insects by visual

Table 2. Total number of insect herbivore species in different feeding guilds associated with five woody fabaceous host plant species of the Sonoran Desert, AZ, for the summer of 1994

Plant species	Feeding guilds				
	Sucker	Chewer	Miner	Galler	Total
<i>C. microphyllum</i>	8	14	—	—	22
<i>C. floridum</i>	7	11	—	2	20
<i>P. velutina</i>	17	19	1	3	40
<i>A. greggii</i>	8	11	1	7	27
<i>C. eriophylla</i>	5	5	—	5	15

observation as described above for 10 min or until no new insect species was found. The branch was then marked and, after the census of the entire plant was completed, the branch was measured for its length and greatest width axis, collected in a plastic bag and the number of branches on the plant was estimated. Therefore, we had measures of insect species richness for a branch and also for the entire plant. Because of the small size of the shrub *C. eriophylla* the entire plant was collected after the insects had been counted and collected. These plants or branches were then taken to the laboratory and frozen. They were separated into the four different resource types: leaves, stems, flowers and fruits. These plant parts were then dried in an oven at 70°C for 32 h until they would lose no more water. We measured the dry weight for each type of plant part. The total number of insect herbivore species found on a specific resource was correlated with the mean dry weight (biomass) of that resource type, using the rank correlation test (Siegel and Castellan 1988).

Further analyses were conducted to evaluate the relationship between insect herbivore species richness and abundance, and the abundance of the resource at the individual plant level where all individual plants were pooled to enable comparisons with other studies. A great amount of variation was expected at this level, but if patterns were detected they must be strong. Data were analyzed by simple linear regressions and all data were transformed using a log transformation to meet the assumptions of the test (Sokal and Rohlf 1984).

Results

In total 108 insect herbivore species were sampled in the summer of 1994. Insect herbivore species used different plant parts (Table 1). The total number of herbivores differed significantly between leguminous species ($\chi^2 = 14.62$, $df = 4$, $P < 0.01$) with *P. velutina* supporting 40 insect species, *A. greggii* supporting 27, *C. microphyllum* and *C. floridum* supporting 22 and 20 insect species respectively, and finally *C. eriophylla* supporting 15 species (Table 1). The insect herbivores studied belonged to various feeding guilds including galling-insects, leaf-mining insects, and other free-feeding insects (Table 2). A total of 108 insect herbivore species was sampled in this system with $\approx 70\%$ of the insect species feeding on more than one plant species (Table 3). The remaining 30% of insect species fed only on one of the host plant species (Table 3). The total number of insect species found associated with each of the legume species was used to test the hypotheses below.

The area of plant geographic distribution was not correlated with the total number of insect herbivore species on each host plant species ($r_s = -0.3$, $P > 0.1$) (Table 4). Therefore, widespread plant species such as *A. greggii*, *C. microphyllum*, and *C. floridum* did not necessarily have richer local insect species richness when compared with plant species with more restricted distribution such as *P. velutina*. The re-

Table 3. Total numbers and percentages of generalist and specialist insect herbivore species associated with five woody fabaceous host plant species of the Sonoran Desert, AZ, for the summer of 1994

Plant species	Insect feeding habits	
	Generalist (%)	Specialist (%)
<i>C. microphyllum</i>	17 (77.3)	5 (22.7)
<i>C. floridum</i>	16 (80)	4 (20)
<i>P. velutina</i>	24 (60)	16 (40)
<i>A. greggii</i>	20 (74)	7 (26)
<i>C. eriophylla</i>	14 (93)	1 (7)
All insect herbivores	75 (69.5)	33 (30.5)

source concentration hypothesis was not corroborated because the total number of insect herbivore species associated with each host plant species was not correlated with its mean plant density (log) (abundance per 2,000 m²) ($r_s = -0.6$; $P > 0.1$) (Tables 1 and 4). The plant size hypothesis was not corroborated because the total number of insect herbivore species on each woody fabaceous plant species was not correlated with mean plant size (log) (m³) ($r_s = 0.3$; $P > 0.1$) (Tables 1 and 4). Therefore, species with larger canopy volumes did not support more insect herbivore species. The only significant correlation obtained between these variables was that between mean plant size and mean plant dry weight ($Rho = 0.69$; $n = 73$, $P < 0.01$) (Table 4). No significant correlations were obtained between plant density and plant geographical distribution ($r_s = 0.35$; $P > 0.1$), plant density and plant size ($r_s = -0.85$; $P > 0.1$), and plant size and geographical distribution ($r_s = 0.2$; $P > 0.1$).

Total herbivore species richness on each plant species was not correlated with mean plant dry weight (biomass) (log) (g), suggesting that insects were not responding to the total amount of biomass available on a plant species ($r_s = 0.6$; $P > 0.1$) (Tables 1 and 5). When host plant resources were broken down into different types of resource—flowers, fruits, leaves, and stems—and correlated with the number of insect species that used those resources, most correlations were significant, except for that of fruits and its herbivore species richness (leaves, $r_s = 0.9$; $P < 0.05$; stems, $r_s = 0.9$; $P < 0.05$; flowers, $r_s = 0.9$; $P < 0.05$; fruits, $r_s = 0.78$; $P > 0.1$) (Tables 1 and 5).

Similarly, for all plant species and all individuals pooled, leaf biomass accounted for 44.16% of the variation in the number of insect herbivore species that used leaves for all five legume species ($F = 29.25$; $df = 1, 37$; $r^2 = 0.4416$; $P < 0.0001$; $Y = 0.28 + 0.16 X$). Flower biomass accounted for 32.86% of the variation in the number of insect species associated with flowers ($F = 10.769$; $df = 1, 22$; $r^2 = 0.3286$; $P < 0.0001$; $Y = 0.067 + 0.22 X$). Stem and pod biomass were not correlated with the number of insect species associated with these resources, respectively (stem, $F = 1.78$; $df = 1, 12$; $P > 0.21$; pod, $F = 0.005$; $df = 1, 9$; $P > 0.94$) (Fig. 2).

Leaf biomass accounted for 51.47% of the variation in the abundance of insects associated with the five legume species pooled ($F = 39.23$; $df = 1, 37$; $r^2 =$

Table 4. Mean dry weight (g) (\pm SE), mean volume (m^3) (\pm SE), mean density (plants/2,000 m^3) (\pm SE) and total area of geographical distribution (km^2) of five woody fabaceous host plant species of the Sonoran Desert, AZ, for the summer of 1994

Plant species	Plant characteristics			
	Dry wt	Size	Density	Geographical distribution
<i>C. microphyllum</i>	2,212.49 (\pm 889.8)	10.50 (\pm 1.82)	32 (\pm 12.7)	451,089.09
<i>C. floridum</i>	3,440.41 (\pm 638.4)	20.56 (\pm 2.24)	9 (\pm 8.0)	433,282.95
<i>P. velutina</i>	5,209.60 (\pm 1,238.0)	17.59 (\pm 3.08)	8 (\pm 4.4)	267,092.22
<i>A. greggii</i>	417.36 (\pm 65.0)	4.14 (\pm 1.26)	45 (\pm 15.7)	629,150.59
<i>C. eriophylla</i>	19.63 (\pm 3.6)	0.024 (\pm 0.006)	305 (\pm 141.8)	356,122.97

0.5147; $P < 0.0001$; $Y = 0.177 + 0.3455 X$) (Fig. 3). Flower, stem and pod biomass were not correlated with the abundance of insects associated with each of these resource types respectively (flower: $F = 1.32$; $df = 1, 23$; $P > 0.26$; stem: $F = 0.87$; $df = 1, 12$; $P > 0.37$; pods: $F = 0.59$; $df = 1, 12$; $P > 0.48$).

Discussion

The number of insect herbivore species associated with five desert leguminous species differed between host plant species. Most plants with more widespread geographical distribution did not necessarily harbor more insect species when compared with less widespread species. The host plant *P. velutina* had the narrowest distribution of all five plant species but harbored the greatest number of insect herbivore species. *A. greggii* had the widest distribution and the second greatest number of insect species associated, with no clear pattern being evident for the other host plant species. Although, many studies have shown that plants with a more widespread distribution will have more insect species associated at the local level (Southwood 1961, Lawton and Schröder 1977, Strong and Levin 1979), geographical distribution alone did not account for most of the variation in the number of insect herbivore species associated with their host plants in other studies (Lawton and Price 1979, Fernandes and Price 1988).

After Root (1973) proposed the resource concentration hypothesis several studies in controlled agricultural systems evaluated the role of plant density on insect species richness and abundance. A general conclusion from these studies is that mixed stands with low plant density contain more insect species (Lewis and Waloff 1964, Murdoch et al. 1972, Root 1973, Thompson 1978, Bach 1980). A major question is whether predictions derived from agricultural studies can be extrapolated to natural systems. Therefore, we

predicted that plants that occurred in denser patches should have fewer insect species associated than those that occurred in lower density patches. We did not obtain a significant correlation between mean plant density and total number of insect herbivore species on legumes. Although *P. velutina* had the lowest mean plant density and the highest number of insect herbivore species associated, as predicted by the plant density hypothesis, other plant species such as *A. greggii*, *C. microphyllum*, and *C. floridum* showed variable patterns of insect richness and plant density (Table 1).

Although the plant geographical distribution and the plant density hypotheses relate to different scales of plant distribution over the landscape they both relate to plant abundance but on a regional and local scale, respectively. Neither was corroborated by this study.

The number of insect herbivore species did not seem to be influenced by growth form because the shrub *A. greggii* had more insect species associated than the tree species, *C. microphyllum* and *C. floridum* (Table 2). Although more complex growth forms such as trees provided more structural resources for colonization by insect species when compared with less complex plant forms such as shrubs and herbs (Lawton and Schröder 1977, Price 1977, Strong and Levin 1979, Moran 1980, Neuvonen and Niemelä 1981, Niemelä et al. 1982, Fowler 1985) some studies have shown that species richness of herbivorous insects can be greater on shrubs than on trees (Fernandes and Price 1988, 1991). In fact, the extensive study by Fernandes and Price (1988) did not support the area of geographical distribution and growth form hypotheses among others and concluded that galling insect richness was determined by the hygrothermal harshness of the environment. Galling species being more speciose in environments under greater hygrothermal stress (dry environments), whereas free feeding in-

Table 5. Mean dry weight (g) (\pm SE) of plant resources of five woody fabaceous host plant species of the Sonoran Desert, AZ, for the summer of 1994

Plant species	Dry wt				
	Plant	Leaf	Flower	Pod	Stem
<i>C. microphyllum</i>	2,219.49 (\pm 889.8)	32.32 (\pm 3.81)	200.25 (\pm 39.21)	—	1,979.92 (\pm 300)
<i>C. floridum</i>	3,440.41 (\pm 638.4)	94.14 (\pm 27.9)	71.28 (\pm 27.5)	14.14 (\pm 3.0)	3,133.61 (\pm 786.4)
<i>P. velutina</i>	5,209.60 (\pm 1,238.0)	1,401.62 (\pm 232.5)	55.00 (\pm 10.3)	24.00 (\pm 0)	3,728.98 (\pm 1,223.5)
<i>A. greggii</i>	417.36 (\pm 65.0)	271.81 (\pm 109.9)	66.74 (\pm 42.0)	6.30 (\pm 1.34)	72.51 (\pm 11.4)
<i>C. eriophylla</i>	19.63 (\pm 3.6)	4.82 (\pm 0.95)	0.25 (\pm 0.07)	0.41 (\pm 0.06)	14.15 (\pm 2.77)

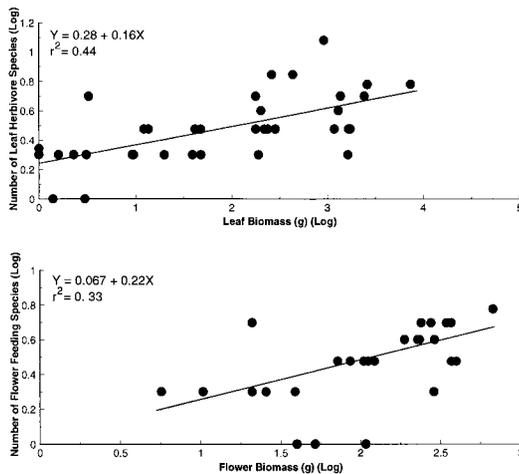


Fig. 2. Simple linear regressions between leaf and flower biomass against number of leaf feeding insect species and flower feeding insect species, for all data pooled for five woody fabaceous legumes of the Sonoran Desert (*C. microphyllum*, *C. floridum*, *P. velutina*, *A. greggii*, and *C. eriophylla*).

sects would be more speciose in more moist environments.

Mean plant size did not have a significant effect on the number of insect herbivore species associated with host plant species. Mean plant size was not correlated with insect species richness on the five host plants. Some studies have found a significant correlation between plant size and number of herbivores (Moran 1980, Neuvonen and Niemelä 1981), but size effects were not as clear in at least one other study where size was correlated with leaf form (Lawton and Price 1979). In the current study, plant size was correlated with plant biomass (dry weight), which had greater biological meaning than plant size alone.

The host plant *C. eriophylla* was the species with the smallest amount of resources available, whereas *P. velutina* had the greatest amount of resources. The amount of a particular resource accounted for a significant amount of the variation observed in herbivore species richness and overall herbivore abundance. Although four of the host plant species had all four types

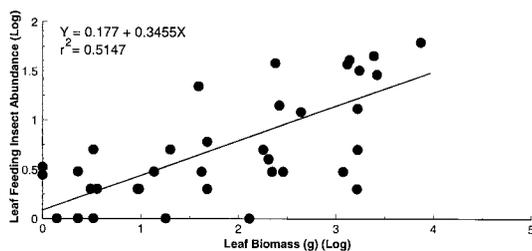


Fig. 3. Simple linear regression between leaf biomass against the abundance of leaf feeding insects for all data pooled for five woody fabaceous legumes of the Sonoran Desert (*C. microphyllum*, *C. floridum*, *P. velutina*, *A. greggii*, and *C. eriophylla*).

of resources available, nevertheless, they supported different number of insect species. Therefore, we conclude that the differences observed in the number of insect species associated with the different host plants was not caused by the types of resources present but simply by the amounts of resources present, especially of leaves. For most plant species the major resource available to herbivores was leaves, but for *C. microphyllum* the major resource available was flowers, and not surprisingly these resources supported the greatest number and abundance of insect herbivore species.

Resource abundance accounted for 76% of the variation on the number of insect species associated with two grass communities in Alaska and Ohio (Teragushi et al. 1981). In the current study, resource abundance measured as plant biomass of leaves, flowers, and fruits were correlated— $r_s = 0.9$ —to the number of insect herbivore species associated to each resource type. Resource abundance measured as plant biomass of leaves for all individuals pooled accounted for 44.16% of the variation in the number of insect herbivore species associated. Flower biomass accounted for 32.86% of the variation of insect herbivore species associated with flowers. Although less than half of the variation in species richness is accounted for by the resources present on a host plant, the potential of resource abundance as an important host plant characteristic in affecting insect herbivore species richness can no longer be ignored.

The pattern improved when resource abundance was regressed against total insect abundance. Biomass of leaves accounted for 51.47% of the variation in the abundance of insects using leaves as resources. Resource abundance has also accounted for 66–98% of the variation of the abundance of a herbivorous lady-beetle (Ohgushi and Sawada 1985, Ohgushi 1992) and has been correlated to the densities of other insect herbivores (White 1974, Myers and Campbell 1976, Dempster and Pollard 1981, Myers and Post 1981, Randall 1982, Dempster 1983).

The effect of resource abundance on a community of insect herbivores will be greater if most herbivores are generalists and are able to choose a host-plant species that offers more resources in detriment of another that offers less resources. Approximately 70% of the insect herbivores studied in this desert legume system were generalists (oligophagous or polyphagous), whereas 30% were specialists. This means that 30% of the insects were bound to their plant species independently of the abundance of resources available on that host-plant species. The other 70% of insect herbivore species had the potential to evaluate the abundance of resources, select, and move between host plant species. The insect community found associated with the desert legumes studied included free-feeding and concealed feeders such as galling insects and leaf-mining insects. Many of the galling-insect species, and leaf-mining insects to a lesser extent, are thought to be specialists on their host plants. Therefore, we conclude that only generalist insect herbivore species will be capable of responding to differences in

resource abundance between host-plant species and not specialist insects such as galling-insects.

The results of this study show that the abundance of resources can be more important in determining the species richness than the types of resources available. In addition, the positive correlations obtained between the number of insect species using the different resource types—leaves, flowers, or stems—suggest that an increase in the availability of any resource results in an increase in the number and abundance of insect species associated with a plant species. Although more resource types suggest that there are more structural niches available for colonization, we have to acknowledge that most insect species known use leaves as a resource and that an increase in the biomass of leaves available can attract more insect species than a similar increase in the dry weight of stems. Therefore, if a shrub has greater dry weight of leaves when compared with a tree it will have more insect species associated. This also suggests a difference in the architecture of these plants where the leaves in the *A. greggii* shrub would be closer together when compared with the palo verde trees where leaves are spaced apart. This tighter packing of leaves in *A. greggii* may provide cooler and moister shelters for insects. This could also explain why *A. greggii*, a shrub, had more insect species than the two *Cercidium* species which are trees.

Therefore, our data corroborate the resource abundance hypothesis and suggest that its role on insect herbivore communities is much more important and widespread than believed. We suggest that insect herbivore species respond to the relative amount of key resources within a host plant, and not plant size per se or the amount of available resources in an area such as in the geographical distribution of a plant or plant density. Even if resources are abundant in a small area, they apparently do not harbor the expected number of herbivores if key resources are distributed among small plants. The spatial and temporal distribution of resources within a host plant is the critical variable. This herbivore response to the “packaging” of plant biomass in a plant population accounts for major differences in insect species richness and abundance among host plant species.

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