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SELECTION OF *ATRIPLEX LENTIFORMIS* HOST PLANTS BY *HESPEROPSIS GRACIELAE* (LEPIDOPTERA: HESPERIIDAE)

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Abstract

We counted *Hesperopsis gracielae* (MacNeill) (Lepidoptera: Hesperiidae) eggs on *Atriplex lentiformis* (Torrey) S. Watson (Chenopodiaceae) plants on 3 dates during 2006-2007 next to the lower Colorado River in Cibola Valley, Arizona. The skipper has received conservation interest due to its restricted geographic range and apparent rarity. *Atriplex lentiformis*, the skipper's only known host species, is a large shrub capable of C_4 photosynthesis and N_2 fixation. We measured the size (canopy radius) and percent water of plants and the percent nitrogen of leaves. Percentages of water and nitrogen were partially correlated, whereas plant size was not partially correlated with the percentage of water or nitrogen. Skipper eggs were more likely to be present on shrubs with greater canopy radius, water content, or nitrogen concentration. Likelihood of egg presence also increased with plant size when percent nitrogen was controlled and increased with percent nitrogen when plant size was controlled. Numbers of eggs, adjusted for canopy radius, on shrubs with at least 1 egg were not related to the percentage of water or nitrogen. Ovipositing *H. gracielae* appear to select host plants when thresholds of plant size and water or nitrogen content are exceeded. These plant characteristics should be considered when surveying or restoring the skipper's habitat.

Key Words: Insecta, Chenopodiaceae, oviposition, canopy size, plant water, leaf nitrogen

Resumen

Los huevos de *Hesperopsis gracielae* (MacNeill) (Lepidoptera: Hesperiidae) sobre plantas de *Atriplex lentiformis* (Torrey) S. Watson (Chenopodiaceae) en 3 fechas durante los años 2006-2007 cercanas a la parte baja del Rio Colorado en Cibola Valley, Arizona fueron contados. Esta mariposa ha recibido interés en su conservación debido a su rango geográfico limitado y aparente rareza. *Atriplex lentiformis*, el único hospedero conocido de la mariposa, es un arbusto grande capaz de realizar la fotosíntesis de C_4 y la fijación de N_2. Nosotros medimos el tamaño del radio de la copa del arbusto, el porcentaje de agua de las plantas y el porcentaje de nitrógeno en las hojas. El porcentaje de agua y el nitrógeno estaban correlacionados parcialmente, mientras que el tamaño de la planta no estaba correlacionado con el porcentaje del agua y nitrógeno. Era más probable que los huevos de la mariposa estuvieran presentes en arbustos que tienen un mayor radio de la copa, contenido de agua y concentración de nitrógeno. La probabilidad de la presencia de huevos aumento en plantas mas grandes cuando el porcentaje de nitrógeno fue controlado y aumento con el porcentaje de nitrógeno cuando el tamaño de la planta fue controlado. El número de los huevos, ajustado por el radio de la copa, en arbustos con al menos 1 huevo no fue relacionado con el porcentaje de agua o nitrógeno. La mariposa, *H. gracielae* parece seleccionar la planta hospedera para ovipositar cuando se excede el umbral del tamaño de la planta y el contenido de agua o nitrógeno. Las características de esta planta deben de ser consideradas cuando se realiza un muestreo o trabajo en la restauración del hábitat de la mariposa.

MacNeill's sootywing, *Hesperopsis gracielae* (MacNeill) (= *Pholisora gracielae* MacNeill), is a small (wingspread 18-24 mm, MacNeill 1970) dark-brown skipper (Lepidoptera: Hesperiidae). It is found along the Colorado River downstream of the Grand Canyon and along the river's tributaries in Utah, Nevada, California, and Arizona (Austin & Austin 1980; Stanford 1980; Nelson & Andersen 1999). The skipper also occurs in Imperial County in southeast California (MacNeill 1970). *Hesperopsis gracielae* was described in 1970 from specimens collected in California south of Parker Dam (MacNeill 1970). Two flights of the sootywing occur during Apr and Jul to Oct (Emmel & Emmel 1973). Due to the skipper's rarity, it was granted the U.S. state conservation ranks (Master 1991) of S1 (critically imperiled) in Nevada, S1 or S3 (rare or uncommon but not imperiled) in California, and S? (not yet ranked) in Arizona.

Larvae of *H. gracielae* eat only *Atriplex lentiformis* (Torrey) S. Watson (Chenopodiaceae) leaves (MacNeill 1970). *Atriplex lentiformis* is a large (≤3 m high) blue- or grey-green, dome-shaped shrub that is wind pollinated, generally dioecious, and frequently found on floodplains where soils are saline and groundwater is available to roots (Turner et al. 1995). The plant assimilates carbon by the C_4 photosynthetic pathway (Laetsch 1968), permitting reduced rates of transpiration and water uptake and increasing adaptation to its hot, arid environment. *Atriplex lentiformis* also is capable of relatively-high rates of N_2 fixation by root-symbiotic bacteria (Malik et al. 1991).

Restoration of habitat and surveys for the sootywing would be improved by a clearer understanding of the skipper's oviposition and reproductive rate on different qualities of *A. lentiformis* plants. Two host-plant qualities that influence reproductive rates of insects are concentrations of water and nitrogen. Greater concentrations of these nutrients in plants generally increase the growth rate of lepidopteran larvae (Scriber 1984). Although insects are expected to distribute eggs in relation to plant quality, few studies have examined the influence of intraspecific host-plant variation on oviposition behavior (Bernays & Chapman 1994). Our objective was to examine the selection of *A. lentiformis* by ovipositing *H. gracielae* in relation to shrub size and water content and leaf nitrogen concentration. We examined 3 questions. (1) Are sizes and water and nitrogen contents of *A. lentiformis* shrubs interrelated? (2) Do these plant characteristics influence host-plant selection by sootywings? (3) Does intraspecific variation in host plants affect the presence of sootywing eggs on plants or numbers of eggs on selected plants?

Materials and Methods

The study site is located (33°17'N, 114°43'W; elevation 62 m) on the Colorado River floodplain in Cibola Valley, La Paz County, Arizona, 37 km south-southwest of Blythe, California. The site, within Cibola National Wildlife Refuge, contains irrigated farm fields converted to wildlife habitat and is bounded to the west by a remnant river oxbow and to the east by an excavated river channel. The surrounding floodplain is farmed or dominated by naturalized tamarisk, *Tamarix ramosissima* Ledebour or *Tamarix chinensis* Loureiro (Tamaricaceae), and bordered by Sonoran desert. Climate at Blythe is summarized as maximum temperatures averaging 42.5°C during Jul, minimum temperatures averaging 3.5°C during Dec, and rainfall averaging 97 mm yearly and occurring mostly during Dec-Mar and Aug-Sep (NOAA 2007).

Atriplex lentiformis shrubs along both sides of a dirt road were sampled for *H. gracielae* eggs. Percent covers of plant species bordering the road and measured with a tape were 47% for *A. lentiformis*, 28% for *Prosopis glandulosa* (L. Benson) M. Johnston (Fabaceae), 19% for *Pluchea sericea* (Nuttall) Coville (Asteraceae), 4% for *T. ramosissima*, 2% for *Baccharis sarothroides* A. Gray × *Baccharis emoryi* A. Gray (Asteraceae), and <1% for *Sesuvium verrucosum* Rafinesque (Aizoaceae) and *Sida rhombifolia* L. (Malvaceae). We recognized sootywing eggs by their spherical shape and heavily sculptured, ridged chorion (Fig. 71 Emmel & Emmel 1973) and reddish-brown color. Vouchers of adult *H. gracielae* were deposited at the Entomology Research Museum, University of California, Riverside.

We used a retrospective design (Agresti 1990) to ensure that approximate numbers of *A. lentiformis* plants with and without sootywing eggs were sampled. Separate plants >1 m tall were arbitrarily selected and examined for unhatched eggs by 2 persons for 10 min, by 1 person for 20 min, or until the entire shrub was searched. We counted eggs on each shrub. If an egg was not found, the nearest shrub that we previously observed being visited by sootywings was selected next for sampling. If at least 1 egg was found, we next sampled the nearest shrub that we had not observed being visited by sootywings. Two persons sampled 20 plants on 24 May 2006 and 12 plants on 29 Jun 2006, and 1 person sampled 7 plants on 5 Jun 2007. We measured (± 0.1 m) the height and minimum and maximum diameters of each sampled plant and calculated its average canopy-radius based on a hemisphere. We snipped eight 20 cm-long cuttings from the ends of branches around the circumference of each plant. Cuttings from each plant were combined and immediately weighed (± 0.5 g) with a 60-g capacity spring scale.

We reweighed branch cuttings from each *A. lentiformis* after drying 24 h at 100°C to calculate percent water. We estimated percent nitrogen of dried leaves from each plant by Kjeldahl digestion (Isaac & Johnson 1976). A 25-mg subsample of ground and sieved leaves was heated with a block digestor 1 h at 400°C in 7 mL of concentrated sulfuric acid, containing 4.2% selenous acid, and 3 mL of 30% hydrogen peroxide. Water was added to 50 mL, and the supernatant was diluted 1/10. We measured the ammonia concentration of the supernatant against standards by colorimetry with a segmented flow analyzer (OI Analytical, College Station, TX). We repeated the procedure on a second subsample of leaf tissue and averaged percentages of nitrogen between subsamples within plants.

Partial correlations between canopy radius, percent water, and leaf percent nitrogen (transformed 2 arcsin $[X/100]^{1/2}$) of *A. lentiformis* shrubs were calculated (Neter et al. 1996, SYSTAT version 10.2, Richmond, CA). We tested relationships between these 3 plant measurements and presence and absence of *H. gracielae* eggs with multiple logistic regression (Agresti 1990; Neter et al. 1996). Sampling date was included in the regressions as 2 indicator variables to account for differences in egg sampling and abundance. We evaluated regressions predicting egg presence based on significances ($P < 0.05$) of predictor variables and values of D, a logistic-regression analog of R^2 (Agresti 1990).

Dependences of egg abundance on the radius, percent water, and percent nitrogen of *A. lentiformis* shrubs supporting at least 1 sootywing egg were determined with sequential regressions (Graham 2003). Plants sampled on 24 May 2006 were analyzed separately, because they had higher water contents. We regressed numbers of eggs, transformed $(Y + 0.5)^{1/2}$, against canopy radius and calculated adjusted numbers of eggs by adding the residuals and mean. Numbers of eggs adjusted for canopy radius were regressed separately against plant percent water and leaf percent nitrogen. Regression of plants with eggs on 25 Jun 2006 and 5 Jun 2007 included an indicator variable for date.

RESULTS

We found different associations between canopy radius (1.6, 0.9-2.5 m [mean, range]), water content (63, 50-73%), and leaf nitrogen concentration (3.0 [back transformed], 1.5-4.7%) of *A. lentiformis* shrubs (n = 39) sampled for *H. gracielae* eggs. Percentages of water and nitrogen were positively correlated (partial $r = 0.44$; $t = 2.96$; $df = 36$; $P = 0.003$) when plant radius was controlled. This correlation is not due to confounding, because we estimated percent nitrogen in dried leaves. Shrubs high in water content usually contained high leaf nitrogen concentrations. We detected weak and non-significant correlations between plant radius and percent water (partial $r = 0.22$; $t = 1.36$; $df = 36$; $P = 0.091$), controlling for percent nitrogen, and between plant radius and leaf percent nitrogen (partial $r = 0.26$; $t = 1.59$; $df = 36$; $P = 0.061$), controlling for percent water. Neither water content nor nitrogen concentration was appreciably associated with sizes of shrubs.

We found *H. gracielae* eggs on 23 of the 39 *A. lentiformis* shrubs sampled. We counted 35 eggs on 11 plants on 24 May 2006, 31 eggs on eight plants on 29 Jun 2006, and 16 eggs on four plants on 5 Jun 2007. Plant radius, plant percent water, and leaf percent nitrogen each were related to egg presence when separately considered (Table 1). The presence of eggs also was related simultaneously to plant radius and percent nitrogen. Shrubs were more likely to support at least 1 egg as canopy radius increased and nitrogen concentration was held constant and as nitrogen concentration increased and canopy radius was held constant (Fig. 1). For example, the odds of a shrub supporting at least 1 egg (= probability of eggs present/probability of eggs absent, see Neter et al. 1996) increased 104% (95% CI = 14-265%) as plant radius increased 0.2 m with percent nitrogen held constant. Similarly, the odds of a plant supporting at least 1 egg increased 104% (95% CI = 5.8-291%) as leaf nitrogen increased from 3.0 to 3.5% with plant radius held constant. The likelihood of egg presence also was related to plant water content when simultaneously considered with plant radius, whereas the latter was a weak and nonsignificant predictor (Table 1; Fig. 2). The odds of a shrub supporting at least 1 egg increased 83% (95% CI = 9.1-207%) with a two-percentage-point increase in percent water and shrub radius held constant. Variable likelihoods of egg presence are indicated by these large confidence intervals. Percent water also was related to egg presence when simultaneously considered with percent nitrogen. Nitrogen concentration likely did not significantly predict egg presence when con-

TABLE 1. MULTIPLE LOGISTIC REGRESSIONS OF PRESENCE OR ABSENCE OF *HESPEROPSIS GRACIELAE* EGGS ON *ATRIPLEX LENTIFORMIS* PLANTS AGAINST PLANT MEASUREMENTS.

No. of predictors	Plant measurement[1]	Partial $b \pm$ SE	t	df	P	D^2
1	canopy radius	3.95 ± 1.41	2.81	35	0.005	0.25
1	% water	36.8 ± 12.5	2.97	35	0.003	0.27
1	% nitrogen[3]	27.3 ± 10.3	2.64	35	0.008	0.21
2	canopy radius	2.95 ± 1.51	1.95	34	0.051	0.38
	% water	30.2 ± 13.2	2.29	34	0.022	
2	canopy radius	3.56 ± 1.49	2.40	34	0.017	0.36
	% nitrogen	25.6 ± 12.0	2.13	34	0.033	
2	% water	32.8 ± 14.7	2.24	34	0.025	0.33
	% nitrogen	17.3 ± 13.1	1.32	34	0.19	
3	canopy radius	3.08 ± 1.63	1.89	33	0.059	0.42
	% water	23.2 ± 14.3	1.62	33	0.11	
	% nitrogen	18.0 ± 14.2	1.27	33	0.20	

[1]Regressions include 2 indicator variables for sampling date.
[2]Analog of R^2.
[3]Measured in leaves, transformed 2 arcsin $(X/100)^{1/2}$.

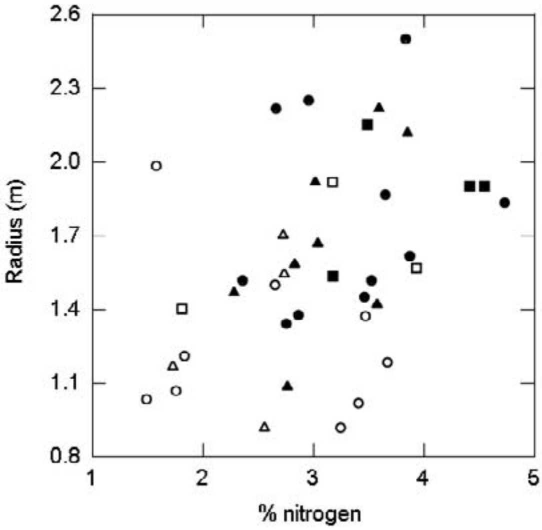

Fig. 1. Presence (solid symbols) and absence (open symbols) of *Hesperopsis gracielae* eggs on *Atriplex lentiformis* shrubs at Cibola Valley, Arizona, plotted as canopy radius vs. leaf percent nitrogen. Plants sampled on 24 May 2006 (circles), 29 Jun 2006 (triangles), and 5 Jun 2007 (squares). Some points slightly shifted to avoid overlap.

sidered with water content due to intercorrelation between the 2 plant measurements. Percentages of water and nitrogen also explained less variation in egg presence than other regressions with 2 predictors (Table 1), reinforcing the importance of plant size as a predictor of egg occurrence. Correlation between percentages of water and nitrogen, and weak associations between these concentrations and plant radius, likely prevented these measurements from significantly predicting egg presence when considered simultaneously.

Numbers of sootywing eggs (3.3 [back transformed], 1-8 eggs) on *A. lentiformis* shrubs with at least 1 egg were not dependent on plant size, water content, or nitrogen concentration. Egg abundance was not related to canopy radius on 24 May 2006 ($b = 0.66 \pm 0.37$ [SE]; $t = 1.79$; $df = 9$; $P = 0.11$) or on 29 Jun 2006 and 5 Jun 2007 ($b = 0.82 \pm 0.41$; $t = 1.99$; $df = 9$; $P = 0.078$). Egg numbers adjusted for canopy radius were not dependent on leaf percent nitrogen (Fig. 3) on 24 May 2006 ($b = 3.8 \pm 3.7$; $t = 1.03$; $df = 9$; $P = 0.33$) or on the later dates ($b = 5.0 \pm 3.2$; $t = 1.58$; $df = 10$; $P = 0.15$). Neither was plant percent water related to adjusted numbers of eggs (Fig. 4) on 24 May 2006 ($b = 7.9 \pm 6.3$; $t = 1.26$; $df = 9$; $P = 0.24$) or on 29 Jun 2006 and 5 Jun 2007 ($b = 5.3 \pm 3.0$; $t = 1.79$; $df = 10$; $P = 0.10$).

Discussion

Atriplex lentiformis shrubs sampled for sootywing eggs contained variable concentrations of leaf nitrogen despite their ability to fix atmospheric N_2. Performance of nitrogen fixing bacteria generally corresponds with conditions for

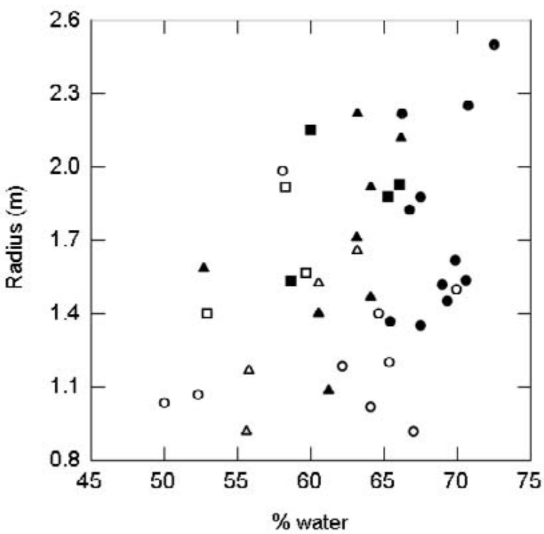

Fig. 2. Presence (solid symbols) and absence (open symbols) of *Hesperopsis gracielae* eggs on *Atriplex lentiformis* shrubs at Cibola Valley, Arizona, plotted as canopy radius vs. plant percent water. Shrubs sampled on 24 May 2006 (circles), 29 Jun 2006 (triangles), and 5 Jun 2007 (squares). Some points slightly shifted to avoid overlap.

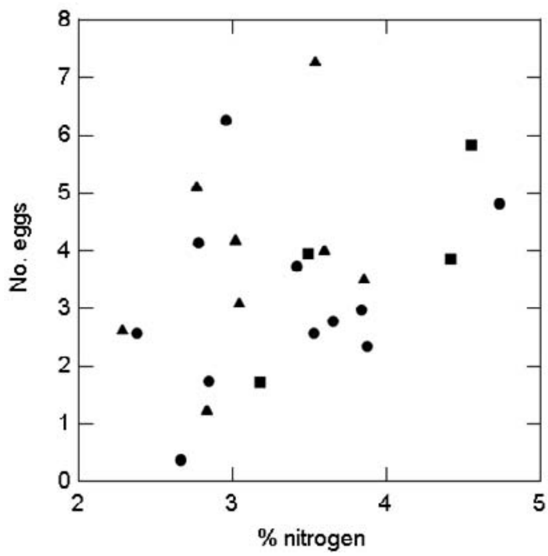

Fig. 3. Numbers of *Hesperopsis gracielae* eggs, transformed $(Y + 0.5)^{1/2}$, adjusted for canopy radius, and back transformed, plotted against leaf percent nitrogen of *Atriplex lentiformis* shrubs with ≥1 egg at Cibola Valley, Arizona. Plants sampled on 24 May 2006 (circles), 29 Jun 2006 (triangles), and 5 Jun 2007 (squares).

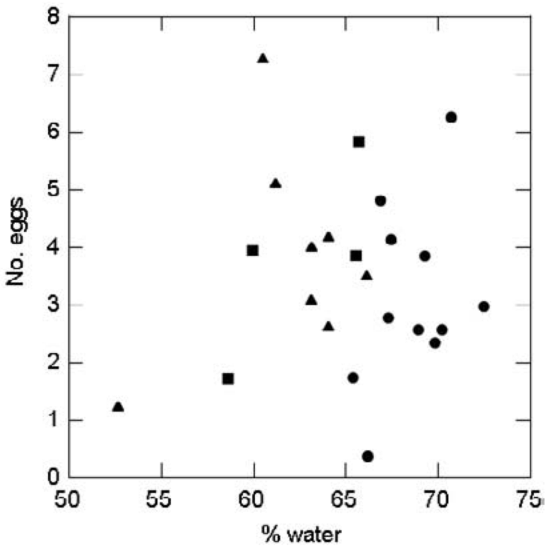

Fig. 4. Numbers of *Hesperopsis gracielae* eggs, transformed $(Y + 0.5)^{1/2}$, adjusted for canopy radius, and back transformed, plotted against percent water of *Atriplex lentiformis* shrubs with ≥1 egg at Cibola Valley, Arizona. Plants sampled on 24 May 2006 (circles), 29 Jun 2006 (triangles), and 5 Jun 2007 (squares).

plant growth (Mengel & Kirkby 2001). Soil moisture is especially important, as water stress reduces N_2 fixation by root symbionts and translocation of fixed nitrogen, as amino acids, from roots to leaves. Association between concentrations of water and leaf nitrogen in *A. lentiformis* likely was due to increased nitrogen fixation and translocation produced by increased soil moisture. Patchy soil moisture at our study site expectedly supported shrubs that varied in concentrations of water and nitrogen.

Presence or absence and numbers of *H. gracielae* eggs on *A. lentiformis* plants partly resulted from the oviposition behaviors of host plant finding and acceptance. Ovipositing females flying randomly would be more likely to encounter larger plants. Larger shrubs also may present greater visual or olfactory cues if females are attracted to host plants. *Hesperopsis gracielae*'s tendency to fly within shrubs (MacNeill 1970) may increase the likelihood of oviposition on large *A. lentiformis*. MacNeill's sootywings tolerate direct sunlight less than the smaller, sympatric lycaenid *Brephidium exilis* (Boisduval) (Wiesenborn 1999). Female sootywings may only oviposit on shrubs large enough to provide shade needed to limit body temperature.

Selection by *H. gracielae* of host plants with greater water and nitrogen contents agrees with experimental evidence that development rates of lepidopteran larvae generally increase on plants with higher concentrations of these nutrients (Scriber 1984) and the concept that phytophagous insects place eggs on plants that maximize offspring growth, survival, and fecundity (Jaenike 1978; Thompson & Pellmyr 1991). Water is especially critical to sootywing larvae due to their arid environment, and greater nitrogen contents in insects (7-14% of dry mass) than in plants (0.03-7.0%) require insect herbivores to concentrate this element (Mattson 1980). An example of a butterfly ovipositing on plants in relation to host nitrogen content and suitability for larvae is provided by the nymphalid *Heliconius erato* (F.) (Kerpel et al. 2006). Confined *H. erato* females placed more eggs on shoots from *Passiflora suberosa* (Passifloraceae) grown in nitrogen-rich soil that increased leaf nitrogen content (from 2.4 to 3.9%) and shortened larval development time (from 21 to 19 d). More rapid development increases larval survival by reducing exposure to predators and parasites (Rhoades 1983).

Water and nitrogen contents of *A. lentiformis* appeared to dichotomously affect oviposition by *H. gracielae*. Shrubs low in water or nitrogen were not found or accepted as hosts, whereas shrubs high in these nutrients received variable numbers of eggs. This observation suggests that concentrations of plant nutrients exceed a threshold before acceptance by female sootywings. Ovipositing insects are hypothesized to accept host plants when plant stimuli exceed thresholds that are influenced by each insect's physiological state (Miller & Strickler 1984). For example, females of the nymphalid butterfly *Euphydras editha* Boisduval placed on various plant species accepted less-preferred hosts as more time elapsed since the previous oviposition (Singer 1982). In nature, the rarity of suitable hosts would influence the frequency of oviposition and the threshold of plant acceptance (Jaenike 1978). Oviposition by a population of sootywings, each with a different physiological state, would tend to obscure the water and nitrogen concentrations stimulating host-plant acceptance.

Female *H. gracielae* may use visual and chemical cues to find and discriminate *A. lentiformis*. Chlorophyll concentrations in leaves are associated with leaf nitrogen contents and affect plant color. Colors of plant models influenced landing and oviposition by *Eurema hecabe* (L.) (Pieridae) butterflies (Hirota & Kato 2001). Nutrient concentrations in leaves also may affect plant volatiles that influence host finding by olfactory cues and leaf-surface compounds that influence host acceptance by contact chemoreception. Oviposition by the moth *Cochlyis hospes* Walsingham (Cochylidae) on green floral foam was stimulated by moisture and by volatiles and contact-chemicals extracted from leaves and bracts of its host plant, sunflower (Barker 1997).

Preserving or creating habitat to increase populations of *H. gracielae* should provide large *A. lentiformis* with high contents of water and leaf nitrogen. Female sootywings oviposited on all shrubs in our sampling that exceeded 1.6 m in mean radius, 64% in water content, and 3.2% in leaf nitrogen. Moisture appears to be the most important soil nutrient because it affects concentrations of plant water and leaf nitrogen. Measuring plant water content also provides an easy method for estimating levels of leaf nitrogen in *A. lentiformis*. Rates of N_2 fixation and levels of leaf nitrogen may be influenced by other soil nutrients, especially phosphate and potassium (Mengel & Kirkby 2001). Plant water and nitrogen concentrations partly explain the apparent rarity of *H. gracielae* compared with *A. lentiformis* throughout the skipper's range. Soil moisture levels adequate for shrub growth may be inadequate, or asynchronous with sootywing oviposition due to intermittent rainfall or changing groundwater depth, for host plant finding and acceptance.

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