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Butterfly Feeding Preferences of *Lantana camara* Cultivars and *Lantana montevidensis* 'Weeping Lavender' in the Landscape and Nectar Characteristics[1]

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Abstract

In landscape studies conducted in 2002 and 2003, *Lantana camara* (L.) 'New Gold' and 'Radiation' were visited by native butterflies to a greater extent than the remaining eight lantana in the studies. Other lantana visited preferentially but not as consistently included *L. camara* 'White Doves', 'Firewagon', 'Confetti', and *Lantana montevidensis* (Spreng.) 'Weeping Lavender'. In general, the lowest visitation was experienced by *L. camara* 'Cherry' and 'Carlos'. Total visit duration by one randomly selected butterfly was greater for 'New Gold', 'Radiation', 'Firewagon', and 'White Doves' than the remaining lantana. Plant characteristics including inflorescence number, number of flowers per inflorescence, percentage of yellow flowers per inflorescence, growth index, flower morphology, and flower color characteristics differed among cultivars. Cultivar differences that consistently correlated with visitation preferences were inflorescence number in 2002 and 2003, flower number per inflorescence in 2003, percentage of yellow flowers per inflorescence in 2002 and 2003, and growth index in 2003. Flower lightness and flower chroma correlated sporadically with visitation in late September and October 2002 and 2003. Percentage light reflectance of flowers for the wavelengths of green, yellow, orange, and red correlated with visitation in 2003. Based on correlation analysis, the cultivar characteristics that did not contribute to visitation differences included inflorescence width, corolla width, and corolla tube length.

In a separate study conducted in 2003 using the same lantana as in the visitation study, nectar volume, carbohydrate composition, and sucrose and fructose concentrations differed among inflorescences. Of ten *Lantana* evaluated, 'Carlos' and 'Confetti had the largest inflorescence nectar volumes combined from nine flowers while 'New Gold', 'White Doves', and 'Weeping Lavender' had the smallest. The ratio of sucrose to hexose (fructose and glucose) in nectar from 'Weeping Lavender', 'White Doves', and 'New Gold' was greater than that of the remaining *Lantana*. The lowest ratios of sucrose to hexose were found for 'Irene', 'Hot Country', and 'Carlos', while similar to 'Cherry' and 'Radiation'. The sucrose to hexose ratio for recently opened inner flowers was double that of middle and outer flowers. Sucrose and total sugar concentrations were greatest in recently opened inner flowers compared to middle and outer flowers. While direct comparison to the 2002 and 2003 studies of butterfly visitation preferences was not possible due to experimental design, data trends suggest a possible relationship between sugar composition, inflorescence nectar production and visitation from native butterfly species.

Index words: Lepidoptera, visitation, inflorescence, light reflectance, sucrose, fructose, glucose.

Species used in this study: *Lantana camara* (L.) 'Carlos', 'Cherry', 'Confetti', 'Firewagon', 'Hot County', 'Irene', 'New Gold', 'Radiation', and 'White Doves; and *Lantana montevidensis* (Spreng.) 'Weeping Lavender'.

Significance to the Nursery Industry

Garden design to attract butterflies continues to be one of the most popular niches in gardening based on the subject's proliferation in popular press articles. The continued popularity of butterfly gardening with the general public has prompted the horticultural trade to market and sell many cultivated species as butterfly attractants for the landscape. Considerable knowledge exists regarding plant species that serve as important nectar sources for adult butterflies and effort has gone into further breeding of these plants. For *L. camara* alone, many cultivars exist, displaying an array of flower colors and growth habits. However, limited research has evaluated whether cultivars of a particular species or genus are equally attractive to butterflies. Based on the research performed in this study, *L. camara* 'New Gold' and 'Radiation' provide a consistent source of attraction to native butterfly species in the landscape. *L. camara* 'Cherry' and 'Carlos' fill a consumer niche with their lower growth habits and aesthetics; however, they were not consistently effective in attracting butterflies in the landscape.

This research provides guidance for *Lantana* hybridization specifically for butterfly attraction. Hybridization efforts should focus on the characteristics of inflorescence number, flower number per inflorescence, percentage of yellow flowers per inflorescence and overall plant size in developing *Lantana* for butterfly attraction. Inflorescence width, corolla width, and corolla tube length did not contribute to the observed preferences in visitation. Understanding the nectar characteristics of lantana could also help in efforts to improve butterfly attractiveness. While direct comparison to the research on butterfly visitation was not possible due to the experimental design, data trends suggest a relationship between sugar composition, total inflorescence nectar production and visitation from native butterfly species.

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Introduction

Lantana camara and *L. montevidensis* are shrubby aromatic perennials in USDA cold hardiness zones 8 to 10 and annuals in USDA zones 7 and colder. Native to tropical America, *L. camara* has naturalized in most suitable habitats of tropical and subtropical Africa, Asia, and Australia. *L. camara* can grow up to 1.8 m (6 ft) in height with an equal spread depending on cultivar. A native to South America, *L. montevidensis* is considered a groundcover or trailing lantana due to its low habit of 45 to 90 cm (18 to 36 in) in height with a spread of 1.8 m (6 ft) or more (11). Lantana flowers are typically small, multicolored and dense, flat-topped inflorescences to 4 cm (1.5 in) across. The corolla is a narrow tube with four short spreading lobes. *L. camara* flowers may be white to pink or lavender, yellow, orange or red, changing color over time, while flowers of *L. montevidensis* are white, lavender, or pink.

L. camara is a highly variable species with differences in flower size, shape and color; leaf size, pubescence and color; stem thorniness; growth rates; shade tolerance; toxicity to livestock; chromosome number and DNA content (30). Hybridization of the species began in the 18th century resulting in hundreds of named cultivars. Most of the cultivars and hybrids belong to the *L. camara* complex (4). Many new cultivars are available that exhibit various inflorescence colors, both solid and multi-colored, and a range of growth habits. One recent accomplishment in hybridization has been the introduction of sterile cultivars, including 'New Gold' and the Patriot series, which do not produce viable seed in nursery or landscape plantings (10). Flowering of lantana typically slows dramatically during seed production, detracting from the overall floral display; however, sterility allows flowering to continue.

Lantana is often listed as a butterfly attractant in popular press gardening articles and is a known source of nectar for feeding adult butterflies (35). There are many commercially available cultivars with flower colors of white, yellow, orange, red, pink, lavender, and purple, and growth habits from 0.7 m (2 ft) to greater than 1.8 m (6 ft). However, little scientific research has evaluated whether cultivars of lantana attract butterflies equally.

Butterflies can be highly selective in their choice of nectar plants, based on many factors, including color (7, 12, 15, 32, 33) and nectar guides (16), and sugar concentrations (8, 26, 27). Using *Lantana camara* 'Irene' and paper flowers, Weiss (34) documented naïve *Battus philenor* (pipevine swallowtails) spontaneously preferred yellow flowers. Previous research has shown that changes in corolla size and form during hybridization may disrupt or enhance morphological matches between flower and insect, affecting nectar accessibility and changing the pollinator species composition (6). In comparisons among *Consolida* sp. (larkspur) cultivars, Comba et al. (6) reported differences in nectar secretion associated with presence of a functional spur. In *Antirrhinum majus* (snapdragon), changes in flower morphology widened the range of insect species capable of foraging effectively on the flower. For *Viola* × *wittrockiana* (pansies), increased flower size was accompanied by an increase in nectar secretion, but not an increase in pollinator visitation. Comba speculated this was possibly due to pollinator difficulty manipulating the larger petals. In a field study of *Buddleia* sp. (butterfly bush) cultivars and butterfly visitation, glucose concentration and total nectar quantity varied greatly among cultivars while the ratio of glucose, fructose, and sucrose remained relatively consistent (7). For butterfly bush cultivars with relatively high amounts of sucrose-rich nectar, visitation was greatest for cultivars with red, pink, or lavender-pink flowers, suggesting butterfly visitation to butterfly bush was based on flower color and nectar qualities (7). Erhardt (9) demonstrated both sucrose to hexose and fructose to glucose ratios are important nectar characteristics to pipevine swallowtail visitation.

The objective of the study for feeding preferences was to evaluate nine *L. camara* cultivars and one *L. montedenvisis* cultivar for differences in visitation by native butterfly species. Additionally, *Lantana* were evaluated for differences in flower morphology, including inflorescence width, corolla width, corolla tube length, and flower number per inflorescence, overall plant size, flower color characteristics including flower lightness, chroma, and percentage reflectance in the visible spectrum. Differences in visitation and cultivar characteristics were then correlated in an attempt to identify the cultivar characteristics that contributed in part to the observed visitation preferences.

The objective of the subsequent study of nectar characteristics was to evaluate *L. camara* cultivars and *L. montevidensis* 'Weeping Lavender' for differences in nectar volume, sugar concentration and sugar composition. Additionally, flower location on an inflorescence (outer, middle, and inner positions), which corresponds to flower age in lantana, was studied for differences in nectar volume, sugar concentration and sugar composition.

Materials and Methods

Butterfly feeding preferences: Cultivar evaluations and butterfly visitation. On June 18, 2002, and June 4, 2003, *Lantana camara* cultivars 'New Gold', 'Irene', 'White Doves', 'Carlos', 'Firewagon', 'Cherry', 'Confetti', 'Hot Country', and 'Radiation' and *Lantana montevidensis* 'Weeping Lavender' in 3.8 liter (#1) containers (2002) and 0.95 liter (1 qt) (2003) containers were transplanted into a Marvyn sandy loam soil in field plots located in Auburn, AL. Soil analyses indicated a cation exchange capacity of 4.6 to 9.0 $cmol_c$/kg and pH of 5.0 to 5.5. Four similar but separate fields were installed. Each field contained four single plant replications per taxon planted 1.2 m (4 ft) on center and arranged in a completely randomized design. Before planting, existing site vegetation was eliminated with glyphosate, the soil disk-plowed to approximately 15 cm (6 in) and raked smooth. Planting beds were then mulched with approximately 7.6 cm (3 in) of ground/milled pine bark and hand weeded as needed throughout the study. Plants were drip irrigated at a rate of 3.8 liter/hour (1 gal/hour) for approximately eight hours weekly as needed. No additional fertilization was provided other than that contained in the growing substrate. Growing substrate consisted of a pine bark:sand (7:1 by vol) substrate amended per m^3 (yd^3) with 8.2 kg (13.8 lb) of Polyon 18–6–12 (Pursell Technologies Inc., Sylacauga, AL), 0.9 kg (1.5 lb) Micromax (The Scotts Company, Marysville, OH), and 3.0 kg (5.0 lb) dolomitic limestone.

Butterfly visitation data were collected between 1:00 pm and 2:00 pm on August 8 and 12, September 12, and October 11, 2002, and August 7 and 14, September 11 and 25, and October 23 and 30, 2003, by four to eight volunteers. Each single plant was observed for at least one minute and up to two minutes depending on duration of visits. Data included:

1) number of butterfly visitors — counted at the beginning and end of each observation and combined, 2) species of the butterfly visitors observed (data not shown), and 3) total duration of visit of one randomly selected butterfly during an observation. If the randomly selected butterfly continued visitation beyond one minute, observations were continued until visitation ended or up to a maximum of two minutes. Total visit duration was obtained by summing the total number of seconds the randomly selected butterfly fed on the plant during the one- to two-minute observation.

Nectar volume, carbohydrate composition and concentration. On May 4, 2003, rooted cuttings of *Lantana camara* 'Carlos', 'Cherry', 'Confetti', 'Firewagon', 'Hot Country', 'Irene', 'New Gold', 'Radiation', and 'White Doves' and *Lantana montevidensis* 'Weeping Lavender' were potted into 3.8 liter (#1) containers with the same growing medium as described previously.

Plants were initially grown outdoors in full sun under twice daily overhead irrigation, arranged in completely randomized design totaling 40 plants. On August 15, 2003, plants were moved into a double-poly greenhouse under natural light conditions to reduce environmental variability and facilitate data collection of nectar samples. Greenhouse vent and heat set points were 29C (85F) and 18C (65F). Plants were arranged in a completely randomized block design of four blocks on one greenhouse bench.

Butterfly feeding preferences: Morphology. Flower morphology characteristics were determined in November 2002 and September 2003. One inflorescence at peak bloom was randomly selected from each plant for measurements. The inflorescence width was measured across the outermost edges of its flowers. One individual fully opened flower from the outer, middle, and inner locations on the randomly selected inflorescence was selected for corolla width and tube length measurement. Individual flowers were designated according to position on the inflorescence as either outer, middle, or inner flowers. Outer flowers included those in the outermost one to two rings on the inflorescence, while the inner flowers were the innermost, fully opened flowers and those in the adjacent ring. Middle flowers included those in the two or three rings between outer and inner flowers. The corolla width was measured from the flower's outermost edge across to the other edge at the widest point of the corolla. Corolla tube length was measured from the base of the tube upward to the point where individual petals were fused together at the opening. Flower number per inflorescence was determined in 2003 only. Morphological characteristics were measured in plants from one field in 2002 and each of the four fields in 2003.

Inflorescence number per plant was recorded when visitation data were collected in 2002 and 2003. Growth index, consisting of the sum of plant height, plant width at widest point, and width perpendicular to widest point, divided by three, were collected monthly in 2003.

Butterfly feeding preferences: Flower color qualification. Flower lightness, chroma, and percentage reflectance in the visible spectrum of 400 to 700 nanometers (nm) were quantified using a Minolta Spectrophotometer CM-2002 A (Minolta Camera Co., Ltd., Ramsey, NJ) on November 1, 2002, using plants from one field. One inflorescence at peak bloom was selected randomly from each plant for evaluation. An inflorescence was considered at peak bloom stage with three or fewer unopened flowers present in the center and retaining flowers in the outer ring of the inflorescence.

A lightness value of 100 represents white and a value of 0 represents black. Chroma values quantify the degree of color saturation with higher values representing more saturation. Percentage reflectance values were measured at intervals of 10 nanometers (nm) between 400 to 700 nm for a total of 30 values per sample. To facilitate data analyses of percentage reflectance values, the values were averaged across the wavelength range of each color to produce a single value. Wavelength ranges for each color include violet (400 to 435 nm), blue (436 to 500), green (501 to 565), yellow (566 to 590), orange (591 to 625), and red (626 to 700). Due to field observations of butterflies preferentially visiting yellow flowers on multi-colored inflorescences in the field, the percentage of yellow flowers per inflorescence was recorded in 2003. This was determined by dividing the number of yellow flowers per inflorescence by the total number of flowers present.

Nectar volume, carbohydrate composition and concentration: Nectar collection. On September 16 and October 10, 2003, one inflorescence at peak bloom was selected randomly from each plant. Peak bloom was characterized by three or less unopened flowers present in the center of the umbel and flowers retained in the outer ring. Individual flowers were designated according to position in the umbel as either outer, middle, or inner flowers which also corresponded with flower age. On a fully opened inflorescence, inner flowers being the most recently opened, or youngest, preceded by middle flowers, and outer flowers. Outer flowers included those in the outermost one to two rings of the umbel, while the inner flowers were the center and those in the adjacent ring. Middle flowers included those in the one to three rings between outer and inner flowers. Previous research by Weiss (34) documented the color change in *Lantana camara* 'Irene' occurring daily with flowers opening yellow, changing to pink the second, and deep magenta the third. Changed flowers remain fresh and are retained for several days on the inflorescence before senescence.

Individual flowers were removed and hand pressure of 14 lb/in^2 (984.3 g/cm^2), on average, was applied to the corolla tube forcing existing nectar through the basal opening. Hand pressure was determined using the Baseline® Hydraulic Pinch Gauge (Fabrication Enterprises, Inc., White Plains, NY). Nectar volumes were collected between 12:00 pm and 4:00 pm from three flowers from outer, middle, and inner positions on the inflorescence for a total of nine individual volume measurements per plant using calibrated micropipettes (3 and 5 µL Drummond Microcaps (Drummond Scientific Company, Broomall, PA)). Temperature, relative humidity, and light levels were recorded at the beginning and end of each block during data collection. On September 16, 2003, greenhouse temperatures during nectar sampling ranged from 26.7 to 30.0C (80 to 86F), relative humidity from 65 to 92%, and light levels from 103 to 591 µmol. On October 10, 2003, greenhouse temperatures ranged from 25.6 to 27.8C (78 to 82F), relative humidity of 92 to 95%, and light levels from 230 to 556 µmol. Total nectar volumes were calculated by combining the volumes from all nine flowers. Each nectar sample was added to an individual microcentrifuge tubes containing 25 µL of (ultrapure) water and stored at –80C.

Nectar volume, carbohydrate composition and concentration: Nectar sugar content. Nectar samples collected on September 16, 2003, were analyzed for fructose, glucose, and sucrose composition and concentration by high performance liquid chromatography (HPLC). The HPLC used included a Waters 501 HPLC pump (Waters Corporation, Milford, MA) for solvent delivery and a Waters Automated Gradient Controller injection system (Waters Corporation, Milford, MA) with a Refractive Index Detector HP 1047A refractometer (Hewlett Packard, Palto Alto, CA). Separation of carbohydrates was achieved using a Waters carbohydrate analysis column (3.9 × 300 mm, 125 Å, 10 µm). Operating conditions consisted of a flow rate of 2 mL/min and a run time of 15 min. An 85:15 acetonitrile:water solution was used as the mobile phase. Analysis was conducted with a Waters 745 Data Module (Waters Corporation, Milford, MA).

Experimental design and statistical analysis: *Butterfly feeding preferences.* Plants were arranged in a completely randomized design within each of the four fields. Data found to be similar using ANOVA between fields were pooled for analysis. Butterfly visitation data exhibited a Poisson distribution and a square root transformation was used to bring it closer to normality to meet Analysis of Variance (ANOVA) assumptions. Statistical software used for all data analysis was SAS (28). All data were subjected to ANOVA. Visitation data found to be similar between dates using ANOVA were combined accordingly for analyses.

Mean separation of visitation data was performed using Duncan's Multiple Range Test at the 10% level to avoid making Type II statistical errors (21), while mean separation of cultivar characteristics were tested similarly at the 5% level. Simple linear correlation (Pearson r) was used to determine the extent to which differences in visitation and plant characteristics, including inflorescence number, growth index, inflorescence width, corolla width and tube length, flower number per inflorescence, percentage yellow per inflorescence, and light reflectance in flowers in the visible spectrum were related.

Nectar volume, carbohydrate composition and concentration. Statistical software used for all data analysis was SAS (28). All data were subjected to ANOVA. Mean separation of total nectar volumes, sugar concentrations and sugar composition was performed using Duncan's Multiple Range Test at the 5% level.

Results and Discussion

Visitation observations. 'New Gold' had the greatest number of visitors followed by and similar to 'White Doves' in August and September 2002 (Table 1). The number of visits for the remaining cultivars ranged from 2.2 ('Radiation') to 0.4 ('Carlos'). 'New Gold' was visited for the longest total duration followed by and similar to 'White Doves' and 'Radiation'. Cultivars visited for the shortest total duration included 'Confetti', 'Cherry', and 'Carlos'.

In general, the number of butterflies visiting the fields increased overall in October 2002 compared to August and September and differences in preferences were observed. 'Radiation' and 'New Gold' were again two of the most visited cultivars in October, while similar to 'Hot Country'. Cultivars receiving the fewest visitors in October were 'Weeping Lavender' and 'Carlos' while similar to 'White

Table 1. Mean number of visitors and total visit duration to *L. camara* cultivars and *L. montevidensis* 'Weeping Lavender' on August 8 and 22, September 12, and October 11, 2002, and August 7 and 14, September 11 and 25, and October 23 and 30, 2003.

	2002			2003			
	Number of visitors[z,y]		Total visit duration (sec)[x]	Number of visitors[z,y]		Total visit duration (sec)[x]	
Species/Cultivar	Aug. 8 and 22 and Sept. 12[w]	Oct. 11	Aug. 8 and 22 and Sept. 12[w]	Aug. 7 and 14 and Sept. 11 and 25[u]	Oct. 23 and 30[t]	Aug. 7 and 14 and Sept. 11 and 25[u]	Oct. 23 and 30[t]
L. camara							
'Carlos'	0.4g[v]	0.8e	4d	0.5d[v]	0.4d	4d	7d
'Cherry'	0.9fg	3.2cd	7d	0.5d	0.7d	4d	14cd
'Confetti'	1.8bcd	3.4bcd	12d	0.8cd	3.1ab	8cd	33bc
'Firewagon'	1.7cde	2.3de	23bc	1.2bc	2.2bc	20ab	40ab
'Hot Country'	1.4def	4.7abc	13cd	0.6d	1.2cd	7cd	25bcd
'Irene'	1.0fg	2.6de	15cd	0.9cd	1.4cd	13bcd	28bc
'New Gold'	2.9a	5.1ab	34a	1.5ab	2.7ab	27a	38ab
'Radiation'	2.2bc	5.2a	28ab	1.2bc	3.6a	18b	55a
'White Doves'	2.4ab	2.6de	28ab	1.7a	1.2cd	17b	13cd
L. montevidensis							
'Weeping Lavender'	1.2ef	1.0e	13cd	1.2bc	3.4a	16bc	20bcd

[z]Total number of butterfly visitors were obtained by combining the number of individuals recorded at the beginning and end of each plant observation.

[y]Data exhibited a Poisson distribution and a square root transformation was used to bring data closer to normality to meet ANOVA assumptions; however, actual data is presented.

[x]Total visit duration in seconds for one randomly selected butterfly during each plant observation.

[w]Results from observations performed on August 8 and 22 and September 12, 2002, were similar according to ANOVA and therefore combined.

[v]Means within columns followed by the same letter are similar according to Duncan's Multiple Range Test, $\alpha = 0.10$.

[u]Results from observations performed on August 7 and 14 and September 11 and 25, 2003, were similar according to ANOVA and therefore combined.

[t]Results from observations performed on October 23 and 30, 2003, were similar according to ANOVA and therefore combined.

Table 2. Lepidoptera visitor demographic percentages (%), identified by family, and number of visitors documented throughout study in 2002 and 2003.

Family	2002				2003					
	Aug. 8	Aug. 22	Sept. 12	Oct. 11	Aug. 7	Aug. 14	Sept. 11	Sept. 25	Oct. 23	Oct. 30
Number of visitors	147	268	338	473	68	105	117	181	212	174
Hesperiidae	43	39	38	65	51	30	50	57	47	42
Pieridae	7	10	26	18	15	24	9	12	23	3
Nymphalidae	46	48	27	11	20	22	14	17	9	37
Heliconidae	4	2	2	4	10	18	27	7	17	7
Papilionidae	0	1	4	<1	4	2	0	4	0	0
Danaidae	0	0	3	<1	0	2	0	0	4	10
Other	0	0	<1	<1	0	2	0	3	0	0

Doves', 'Irene', and 'Firewagon'. Total visit duration was similar for all cultivars during October (data not shown).

In August and September 2003, 'White Doves' and 'New Gold' had the most visitors, while visitor numbers for 'Firewagon', 'Radiation', and 'Weeping Lavender' were similar to that of 'New Gold' (Table 1). Visitation was lowest for 'Cherry', 'Carlos', and 'Hot Country' while similar to 'Confetti' and 'Irene'. 'New Gold' was visited for the longest total duration, followed by and similar to 'Firewagon'. Of the remaining cultivars, visit duration was shortest for 'Cherry' and 'Carlos', while similar to 'Confetti' and 'Irene'.

In general, an overall increase in the number of visitors was observed in October 2003, which was similar to 2002. 'Radiation' had the greatest number of visitors, while similar to 'Weeping Lavender', 'Confetti', and 'New Gold' in October 2003 (Table 1). As previously observed in August and September, visitation was lowest to 'Cherry' and 'Carlos' although visitor numbers were similar to 'Hot Country', 'Irene', and 'White Doves'. 'Radiation' had the longest total visit duration with 'Firewagon', 'New Gold', and 'Confetti' being similar. Visit duration for 'Carlos' was the shortest of the remaining six cultivars but similar to 'Cherry', Hot Country', 'White Doves', and 'Weeping Lavender'.

In August and September 2002, butterfly species from the Lepidoptera families of Hesperiidae and Nymphalidae were similarly represented contributing to the documented visitation (Table 2) and the majority of the visiting population. In October, hesperids accounted for the majority of the visiting population with nymphalids and pierids contributing 10 and 17%, respectively. During this shift in demographics occurring in October, visitation increased for 'Radiation'. Additionally, inflorescence number for 'Radiation' was greater in October compared to the other cultivars, which corresponded to high visitation in October (Tables 1 and 3).

In August and September 2003, butterfly species from the Lepidoptera families of Hesperiidae and Nymphalidae contributed 30 to 57% and 14 to 22%, respectively, of the documented visitors (Table 2). In general, visitation from hesperids was higher than in 2002 with lower visitation from nymphalids species. In October, hesperid visitors remained fairly consistent with the earlier 2003 observations, while the visiting population of nymphalids increased to 37%.

Inflorescence numbers, growth index, and color. In August 2002, 'New Gold' and 'White Doves' exhibited the greatest inflorescence numbers, which were greater than the remain-

Table 3. Mean inflorescence number collected on August 22, September 12, and October 11, 2002, and August 14, September 25, and October 30, 2003, growth indices collected on August 8, September 4, and October 30, 2003, and flowers per inflorescence collected on September 25, 2003, for *L. camara* cultivars and *L. montevidensis* 'Weeping Lavender'.

	Inflorescence number[z]						Growth index[y]			Flowers per inflorescence
	2002			2003			2003			2003
Species/Cultivar	Aug. 22	Sept. 12	Oct. 11	Aug. 14	Sept. 25	Oct. 30	Aug. 8	Sept. 4	Oct. 30	Sept. 25
L. camara										
'Carlos'	16h[x]	103d	87cd	2b[x]	6e	11c	18.9d	24.1e	32.3d	19d
'Cherry'	30g	130c	61d	4b	9e	36c	26.2cd	27.3e	31.5d	23bcd
'Confetti'	70d	130c	107c	4b	29de	77bc	38.2ab	54.8ab	87.6b	23bcd
'Firewagon'	54e	41ef	23f	8b	31de	71bc	38.0ab	53.8bc	92.4b	34a
'Hot Country'	35f	97d	68d	7b	14e	44c	32.5bc	41.8cd	63.9c	25bcd
'Irene'	26g	47ef	61d	6b	17e	39c	29.4c	40.4d	51.6cd	23cd
'New Gold'	160a	239a	190b	19a	77ab	247a	45.7a	58.5ab	105.0ab	29ab
'Radiation'	87cd	138c	199a	10b	46cd	131ab	39.7ab	57.8ab	99.9ab	29ab
'White Doves'	146ab	56e	58e	27a	96a	148a	45.5a	64.3ab	106.2ab	24bcd
L. montevidensis										
'Weeping Lavender'	119c	219b	92cd	26a	64bc	142a	42.4a	67.7a	119.1a	19d

[z]Inflorescences counted had at least five opened flowers.

[y]Growth index = (plant height + plant width at widest point + perpendicular width / 3).

[x]Means within columns and followed by the same letters are similar according to Duncan's Multiple Range Test, $\alpha = 0.05$.

Table 4. Lightness, chroma, and percentage yellow flowers per inflorescence for *L. camara* cultivars and *L. montevidensis* 'Weeping Lavender' collected on November 1, 2002.

Species/Cultivar	Lightness[z]			Chroma[z]			Yellow flowers per inflorescence[y] (%)
	Outer[x]	Middle	Inner	Outer	Middle	Inner	
L. camara							
'Carlos'	43g[w]	51g	60e	23e	25f	36f	20e
'Cherry'	41h	45i	63c	22f	27d	41e	6fg
'Confetti'	42f	52f	58g	26c	26e	33g	21de
'Firewagon'	45e	53e	59f	29b	36c	44b	15ef
'Hot Country'	42f	49h	60e	24de	26f	34g	10efg
'Irene'	42g	53ef	63d	24d	25f	39d	31cd
'New Gold'	65b	70b	66b	40a	41b	42c	100a
'Radiation'	46d	60c	62d	29b	42a	47a	46b
'White Doves'	77a	76a	75a	10g	13g	18h	35bc
L. montevidensis							
'Weeping Lavender'	53c	54d	58fg	25c	25f	17i	0g

[z]Lightness and chroma values quantified using the Minolta Spectrophotometer CM-2002. A lightness value of 100 represents white and a value of 0 represents black. Chroma values quantify the degree of color saturation with higher values representing more saturation.

[y]Percentage yellow flowers per inflorescence was calculated by dividing the number of yellow flowers by the total number of flowers per inflorescence of one fully opened inflorescence per plant.

[x]Floral characteristics were quantified for flowers in outer, middle, and inner locations of each inflorescence.

[w]Means within columns and followed by the same letters are similar according to Duncan's Multiple Range Test, $\alpha = 0.05$.

ing cultivars by 122 to 910% (Table 3). 'Irene', 'Cherry', and 'Carlos' exhibited the lowest number of inflorescences. Inflorescence numbers were greatest for 'New Gold' in September and 109 to 583% greater than the remaining cultivars. 'Radiation' exhibited the greatest number of inflorescences in October followed by 'New Gold'.

Throughout the 2003 data collections, inflorescence numbers for 'New Gold', 'White Doves', and 'Weeping Lavender' were greater than those of the remaining cultivars by 139 to 2245%, with the exception of 'Radiation' in October (Table 3). Inflorescence numbers among the remaining cultivars were mostly similar. Growth index for 'Weeping Lavender' was greatest throughout 2003, followed by and similar to 'New Gold', 'White Doves', and 'Radiation'. Growth indices were lowest for 'Carlos' and 'Cherry' throughout 2003 while similar to 'Irene' in October. In September 2003, 'Firewagon' had the greatest number of flowers per inflorescence with 34 flowers, similar to 'New Gold' and 'Radiation'.

Outer, middle, and inner lightness values collected in 2002 were greatest for 'White Doves' flowers, followed by 'New Gold' (Table 4). Cultivars exhibiting the lowest lightness values were 'Cherry', 'Irene', and 'Carlos' for outer flowers, 'Cherry', 'Hot Country', and 'Carlos' for middle flowers, and 'Confetti' and 'Weeping Lavender' for inner flowers. 'Radiation' exhibited the highest chroma or color saturation for inner and middle flowers, while 'New Gold'

Table 5. Percentage light reflectance[z] for visible spectrum wavelengths of green, yellow, orange and red for outer, middle, and inner flowers of *L. camara* and *L. montevidensis* cultivars determined in November 1, 2002.

Species/Cultivar	Green[y] (501 to 565 nm)			Yellow[y] (566 to 590 nm)			Orange[y] (591 to 625 nm)			Red[y] (626 to 700 nm)		
	Outer[x]	Middle	Inner	Outer	Middle	Inner	Outer	Middle	Inner	Outer	Middle	Inner
L. camara												
'Carlos'	9.6ef[w]	15.7de	28.5cd	11.1e	18.9e	31.7de	22.3d	32.9de	38.6ef	44.3cd	46.4b	46.1bc
'Cherry'	9.3ef	10.8f	32.4c	10.3e	13.1f	37.1c	20.0d	27.5f	44.6bcd	42.2d	48.4b	49.8ab
'Confetti'	9.1f	16.6de	24.2ef	10.6e	20.1de	28.2e	23.1d	34.6cd	39.8e	46.8bcd	48.9b	48.7abc
'Firewagon'	10.9de	18.3d	26.9de	13.6d	23.9d	35.6cd	27.1c	37.6c	42.5cde	45.3bcd	49.3b	47.2abc
'Hot Country'	9.1f	13.3ef	28.9cd	10.3e	16.7ef	31.9de	20.6d	31.7def	37.9ef	44.1cd	47.5b	44.0c
'Irene'	9.0f	16.9d	32.3c	10.3e	20.6de	35.6cd	21.0d	34.9cd	41.1de	44.9cd	48.6b	46.8bc
'New Gold'	37.1b	38.1b	38.5b	43.4b	44.5b	45.3b	45.3b	46.1b	47.1abc	46.2bcd	46.9b	47.9abc
'Radiation'	11.7d	26.9c	30.9cd	13.9d	32.6c	39.3c	28.8c	46.2b	47.8ab	50.3ab	55.4a	52.2a
'White Doves'	51.3a	50.9a	48.9a	52.6a	52.6a	50.4a	53.2a	53.1a	50.7a	53.8a	53.4a	51.0ab
L. montevidensis												
'Weeping Lavender'	15.6c	15.9de	21.4f	17.7c	18.1e	23.8f	28.9c	29.3ef	34.4f	49.2abc	48.5b	46.6bc

[z]Percentage light reflectance = calculation of the amount of light reflected by the sample at each wavelength interval (400–700 nm).

[y]Values were averaged across the wavelength range of each color to produce a single value for statistical analysis.

[x]Floral characteristics were quantified for flowers in outer, middle, and inner locations on each inflorescence. Outer flowers being located on the outermost and its adjacent ring of flowers on the inflorescence, the inner flowers were the innermost, fully opened flowers and those in the adjacent ring, and the middle flowers on the two to three rings located between outer and inner flowers.

[w]Means within columns and followed by the same letter are similar according to Duncan's Multiple Range Test, $\alpha = 0.05$.

outer flowers exhibited the most color saturation. Chroma values for 'White Doves' were the lowest of the cultivars for outer and middle flowers, while chroma values for 'Weeping Lavender' were lowest for inner flowers. 'New Gold' inflorescences exhibited the highest percentage of yellow flowers with 100% followed by 'Radiation' with 46%. The lowest percentage of yellow flowers was found in 'Weeping Lavender' and 'Cherry'.

Percentage light reflectance values of 'White Doves' outer, middle, and inner flowers were the highest of the ten cultivars in the green and yellow wavelengths (Table 5). Percentage reflectance values of 'White Doves' outer and middle flowers were the highest of the ten cultivars in the orange wavelengths while similar to 'New Gold' and 'Radiation' for inner flowers. The highest percentage reflectance values in the red wavelengths for outer flowers were found in 'White Doves' while similar to 'Radiation' and 'Weeping Lavender', 'White Doves' and 'Radiation' for middle flowers, and 'Radiation' for inner flowers while similar to 'White Doves', 'Cherry', 'Confetti', 'New Gold', and 'Firewagon'.

Differences were found among *Lantana* in flower morphology, including inflorescence width, corolla width, and corolla

Table 6. Probability value (P), Pearson's correlation coefficient (r), and number of observations (N) for simple linear correlation (Pearson r) of visitation[z] (unless noted otherwise) with inflorescence number, growth index, and percent yellow per inflorescence on August 8 and 22, September 12, and October 11, 2002, and August 7 and 14, September 11 and 25, and October 9 and 23, 2003, and combined visitation for 2002 observation dates and 2003 observation dates with flower number per inflorescence, green, yellow, orange, and red wavelengths.

	2002				2003					
	Aug. 8	Aug. 22	Sept. 12	Oct. 11	Aug. 7	Aug. 14	Sept. 11	Sept. 25	Oct. 9	Oct. 23
Inflorescence number										
P value[y]	—	<0.0001[y]	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
r value[x]	—	0.5026[x]	0.4595	0.2900	0.4589	0.6544	0.4631	0.5473	0.5354	0.5959
N value[w]	—	151[w]	154	147	117	156	76	117	108	77
Growth index										
P value	—	—	—	—	0.0014	<0.001	<0.0001	<0.0001	NS[v]	<0.0001
r value	—	—	—	—	0.2925	0.4008	0.4546	0.4142		0.6078
N value	—	—	—	—	116	116	75	114		80
Percentage yellow per inflorescence										
P value	0.0009	<0.0001	0.0247	0.0393	NS	NS	0.0014[t]	NS	0.0174[t]	0.0422
r value	0.2628	0.3185	0.1792	0.1690			0.3564		0.2194	0.2277
N value	157	154	157	149			78		117	80
	Combined visitation from Aug. 8 and 22, Sept. 12, and Oct. 11, 2002				Combined visitation from Aug. 7 and 14, Sept. 11 and 25, and Oct 9 and 23, 2003					
Flower number per inflorescence										
P value		NS					0.0070			
r value							0.3013			
N value							37			
Green (501 – 565 nm)										
P value		NS					0.0121[t]			
r value							0.4139			
N value							36			
Yellow (566 – 590 nm)										
P value		NS					0.0579			
r value							0.3189			
N value							36			
Orange (591 – 625 nm)										
P value		0.0575					0.0334			
r value		0.3289					0.3506			
N value		34					37			
Red (626 – 700 nm)										
P value		0.0271					0.0132[t]			
r value		0.3734					0.4091			
N value		35					36			

[z]Visitation = total number of butterfly visitors obtained by combining the number of individuals recorded at the beginning and end of each one to two minute plant observation.

[y]P value = probability value.

[x]r value = Pearson's correlation coefficient.

[w]N value = number of observations compared in the analysis.

[v]Nonsignificant.

[t]Values for correlation with duration of visit.

tube length (data not shown). However, based on correlation analyses these differences did not contribute to the observed preferences in butterfly visitation.

Correlations. Correlation analyses identified cultivar characteristics evaluated that contributed in part to the observed differences in butterfly visitation. Cultivar differences that correlated with visitation preferences were inflorescence number in 2002 and 2003, flower number per inflorescence in 2003, growth indices in 2003, and percentage of yellow flowers per inflorescence in 2003 (Table 6). With all visitor numbers and visit duration combined for 2002 and 2003 separately, percentage light reflectance of flowers for the wavelengths of green, yellow, orange, and red (Table 6) correlated with visitation in 2003 and to a lesser extent for orange and red wavelengths in 2002.

Previous studies examining the relationship between pollinators and floral display characteristics have documented large floral displays may, in general, attract more pollinators (13, 18, 23). Using lantana flowers and two butterfly species, Weiss demonstrated larger floral displays received more visits and were visited from greater distances (33). In studies with nine species of *Labiatae* (mint family) and honeybee visitation, Dafni et al. (8) reported correlations between the number of open flowers per plant and the number of visiting honeybees with *Rosmarinus officinalis* (rosemary) and *Coridothymus capitatus* (conehead thyme). *Aster vimineus* (calico aster) undergoes a flower color change similar to lantana and displays both yellow and red flowers simultaneously. Niesenbaum et al. (24) demonstrated in *A. vimineus* that the yellow color phase was visited more than red with all pollinators. However, the retention of the red flowers contributed to a greater floral display which increased pollinator visitation rates.

Innate color preferences are documented for Lepidoptera genera and have been shown to differ between butterfly species. Weiss (33) demonstrated *Battus philenor* (pipevine swallowtail) preferred yellow on both paper and real flowers of *L. camara* 'Irene'. Weiss also found that additional foraging experience led to an even greater preference for yellow flowers. Other species-specific color preferences have been observed; *Papilio demoleus* (lime butterfly) for blue and purple (15), *Heliconius charitonius* (zebra longwing butterfly) for orange/red followed by blue/blue-green (31), and *Vanessa* species for yellow and blue (15). As previously mentioned, Culin (7) concluded flower color and nectar properties appear to influence visitation to butterfly bush cultivars. In several cultivars evaluated in our studies, flowers were yellow the day they opened and transitioned acropetally to either pink, magenta, orange, or red over time. Based on observations, 'New Gold', 'White Doves', and 'Weeping Lavender' demonstrated little to indiscernible color change as flowers aged. The percentage of yellow flowers per inflorescence correlated with visitation in both 2002 and 2003 (Table 6). Therefore, this characteristic appears to contribute in part to the observed visitation in our studies, in addition to inflorescence number, flower number per inflorescence, and overall plant size.

Our study identified 'White Doves', 'New Gold', and 'Radiation' (red wavelengths only) with consistently high percentage reflectance and these *Lantana*, in general, experienced high visitation (Table 1 and 5). A colored object reflects or transmits some wavelengths more readily than others. Objects which reflect all wavelengths equally will appear white to the eye. For colors, the dominant wavelength is the wavelength, or color, which appears to be most abundant.

Total inflorescence nectar volume and average nectar volume (data not shown) for outer, middle, and inner flowers differed among cultivars. 'Carlos' and 'Confetti' produced the largest volumes of total inflorescence nectar while 'New Gold', 'Weeping Lavender', and 'White Doves' produced the least (Table 7). Similar differences in nectar production among cultivars of a particular plant species are well documented and have been found for fruit (1) and vegetable (25, 29) species as well as ornamental plants (6). Karp et al. (17) found differences among cultivars of *Rubus arcticus* (arctic bramble) and speculated differences were due to intensity of flowering. They hypothesized a plant with a smaller number of flowers is spending less energy and nutrients for flowering; therefore, its flowers contain more nectar. In the 2002

Table 7. Mean total inflorescence nectar volumes[z] (µL) for outer, middle, and inner flowers (µL) of *Lantana* collected on September 16 and October 10, 2003[y], and nectar fructose and sucrose concentration (mg/mL), and ratio of sucrose to fructose and glucose for *Lantana* collected September 16, 2003.

Species/Cultivar	Total nectar volume (µL) Sept. 16 and Oct. 10[y]	Fructose (mg/mL)	Sucrose (mg/mL)	Ratio of sucrose to hexose (fructose + glucose)
L. camara				
'Carlos'	18.9a[x]	71.6abc[z]	35.6bcd	0.3c
'Cherry'	13.3bc	50.5abc	54.4bcd	0.8bc
'Confetti'	18.5a	47.4abc	85.2abcd	1.0b
'Firewagon'	11.0bc	86.6a	105.7ab	1.0b
'Hot Country'	13.2bc	73.6ab	40.7bcd	0.3c
'Irene'	14.3b	54.2abc	24.3d	0.3c
'New Gold'	4.5d	37.7bc	102.9abc	1.7a
'Radiation'	10.6c	35.1bc	27.7cd	0.8bc
'White Doves'	6.3d	30.1bc	95.9abcd	2.0a
L. montevidensis				
'Weeping Lavender'	5.5d	34.2bc	142.6a	2.2a

[z]Total nectar volume calculated by combining nectar volumes from nine flowers per inflorescence (three flowers each from outer, middle, and inner inflorescence locations).

[y]Results from September 16 and October 10, 2003, were statistically similar according to ANOVA and therefore combined.

[x]Means within columns followed by different letters are different according to Duncan's Multiple Range Test, $\alpha = 0.05$.

and 2003 landscape evaluations, inflorescence numbers were quantified in August, September, and October of 2002 and 2003 (Table 3). A possible relationship between lantana cultivars' inflorescence numbers and total nectar volume was observed when data from these two studies were compared separately. Cultivars in the 2002 and 2003 landscape evaluations consistently exhibiting the lowest mean inflorescence numbers were 'Carlos' (ranging from 2 to 103), 'Cherry' (4 to 130), and 'Irene' (6 to 61). Total inflorescence nectar volumes for 'Carlos', 'Cherry', and 'Irene' were among the greatest recorded in our study. However, these cultivars experienced the lowest butterfly visitation. 'New Gold' generally had the greatest inflorescence numbers ranging from 19 to 247 at times similar to 'White Doves' (27 to 148) , 'Weeping Lavender' (26 to 219), and 'Radiation' (10 to 199). Total inflorescence nectar volumes were lowest for these cultivars and overall, these cultivars experienced the greatest butterfly visitation.

Nectar concentration and composition. Analysis of sugar composition in the nectar indicated the presence of sucrose, glucose, and fructose. Research first conducted in the 1950s documented that most nectar contains the disaccharide sucrose and monosaccharides glucose and fructose in detectible amounts (3). Cultivar differences were found for fructose and sucrose concentrations (Table 7), while the glucose concentration was similar among cultivars (data not shown). The fructose concentration was greatest for 'Firewagon', followed by and similar to 'Hot Country', 'Carlos', 'Irene', and 'Confetti' ranging from 73.6 to 47.4 mg/ml. Sucrose concentration was greatest for 'Weeping Lavender' followed by and similar to 'Firewagon', 'New Gold', 'White Doves', and 'Confetti'. Sugar concentrations in nectar may be affected by environmental conditions influencing nectar production and evaporation (3). Due to the sample size and variability, the data presented for fructose and sucrose concentrations was insufficient to reject the null hypothesis for equal means.

Baker and Baker (2) distinguished nectar with sucrose/hexose ratios of more than 0.99 as 'sucrose-dominant', those with 0.50 to 0.99 as 'sucrose-rich', those with 0.10 to 0.49 as 'hexose-rich', and those with less than 0.10 as 'hexose-dominant'. The ratio of sucrose/hexose differed among cultivars with 'Weeping Lavender' having the highest ratio of 2.2 followed by and similar to 'White Doves' and 'New Gold'. Of the ten cultivars evaluated five are considered sucrose-dominant including 'Weeping Lavender', 'White Doves', 'New Gold', 'Confetti', and 'Firewagon'. The lowest sucrose/hexose ratios were found in 'Carlos', 'Hot Country', and 'Irene' which are considered hexose-rich. Although some research has concluded the sucrose/hexose ratio remains largely constant within species (3, 18), other studies have found differences among cultivars or within a species similar to our results. Mayer et al. (22) found that sugar ratios in crabapple and apple cultivars varied widely with sucrose levels being the most variable in studies evaluating honey bee foraging behavior and apple cultivars. In comparing *Buddleia* cultivars' nectar characteristics, Culin (7) reported 10 of the 13 cultivars evaluated had two to three times more sucrose than either glucose or fructose, with the remaining three having only slightly more sucrose. Nectar sugar concentration and composition differed among watermelon cultivars and the study concluded sugar concentration in nectar may be partially responsible for the differences among watermelon cultivar attractiveness to honey bees (34). During the 2002 and 2003 lantana landscape evaluations, 'New Gold' and 'Radiation' were consistently visited by butterflies more than the remaining eight cultivars in the study. Other cultivars visited preferentially, but not as consistently, were 'White Doves', 'Firewagon', and 'Weeping Lavender'. The cultivars visited preferentially in the landscape evaluation exhibited sucrose/hexose ratios in nectar of 1.0 or greater in this study, with the exception of 'Radiation' with 0.8. In general, 'Carlos' and 'Cherry' experienced the least butterfly visitation in the landscape and exhibited sucrose/hexose ratios of 0.3 and 0.8, respectively.

Table 8. Nectar sucrose concentration (mg/mL), total sugar concentration (mg/mL), and ratio of sucrose to hexose (fructose + glucose) for outer, middle, and inner flowers collected September 16, 2003.

Flower location	Sucrose (mg/mL)	Total sugar concentration (mg/mL)	Ratio of sucrose to hexose (fructose + glucose)
Outer[z]	43.0b[y]	125.1b	0.8b
Middle	53.1b	149.1b	0.8b
Inner	120.2a	207.9a	1.6a

[z]Means for outer, middle, and inner flower locations calculated from all *Lantana* species and cultivars in study.

[y]Means within columns followed by different letters are different according to Duncan's Multiple Range Test, $\alpha = 0.05$.

Nectar characteristics differed similarly among flower location on the inflorescence (outer, middle, or inner) for all cultivars (Table 8). The sucrose concentration of nectar collected from inner flowers was more than double that of outer or middle flowers. Total sugar concentration (fructose, glucose, and sucrose combined) found in inner flowers was 207.9 mg/ml compared to 125.1 and 149.1 mg/ml in outer and middle flowers, respectively. Additionally, the sucrose/hexose ratio for inner flower nectar was double that of outer and middle flowers. During landscape evaluations of lantana cultivars and butterfly visitation in 2002 and 2003, butterflies were observed preferentially visiting inner yellow flowers on multi-colored inflorescences (5). Based on the analytical results, nectar characteristics of inner flowers differ from those of outer and middle flowers similarly among cultivars and inflorescence color schemes (multi-colored vs. single colored). Similar results were found comparing nectar constituents of orange and yellow flowers of *Pyrostegia venusta* (flame vine) where orange flowers are characterized by higher sucrose content, higher total nectar production, and higher amino acid content per volume (14). In research with three butterfly species, Rusterhold (26) and Erhardt (9) found that butterflies clearly discriminate between three main nectar sugars with a hierarchy of preferences generally of sucrose over fructose over glucose. For honeybee visitation, Kumar and Gupta (20) concluded the preference of honeybees for one onion species over others was partially related to the higher sugar content in nectar.

In summary, the butterfly visitation study demonstrates native butterfly visitation differs between cultivars of *L. camara* and *L. montevidensis*. In general, *L. camara* 'New Gold' and 'Radiation' were visited by native butterflies to a greater extent than the remaining eight lantana in the studies. The lowest visitation was experienced by *L. camara* 'Cherry'

and 'Carlos'. Cultivar characteristics that contribute in part to these differences are associated with the overall floral display and inflorescence colors and distribution.

The study of nectar characteristics demonstrates nectar volume and sugar concentration and composition differ among lantana cultivars. Additionally, in general the nectar concentration and composition differed with flower location within an inflorescence for the cultivars evaluated with inner, most recently opened flowers having a higher sugar concentration and a higher sucrose:hexose ratio than previously opened, outer and middle flowers. The landscape evaluations documented butterflies visit lantana cultivars preferentially in the landscape and based on the observations prefer inner flowers over others in the inflorescence (5). Due to the experimental design of this study, butterfly visitation to lantana cultivars in the landscape and nectar characteristics were not subjected to correlation analysis. However, data trends suggest a relationship between sugar composition, total inflorescence nectar production and visitation from native butterfly species.

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