POLLINATORS OF *CHAPMANNIA FLORIDANA* (FABACEAE) AND THEIR FORAGING PREFERENCES

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ABSTRACT

The visitation rates of two major insect visitors, *Bombus impatiens* Cresson and *Augochloropsis* sp., of the Florida endemic plant species *Chapmannia floridana* Torrey & A. Gray, (Fabaceae); are determined for different microhabitats at the Archbold Biological Station in the summer of 1995. Significant differences in the total number of visits to each site were observed. Each pollinator species was found to visit different vegetation densities and sites with different frequencies. Relationships were also found between visitation rates and temperature and flower size. Variation in visitation rates did not significantly affect seed set in *C. floridana*. Disturbance did not seem to play a major role in determining visitation rates of either of the pollinators. Vegetation composition and flower density appear to be the best indicators of visitation rates to populations of this plant species.

Key Words: *Bombus impatiens*; *Augochloropsis*; Florida scrub; disturbance; pollination; foraging patterns; *Chapmannia floridana*

RESUMEN

Las tasas de visitación de los dos insectos visitantes principales, *Bombus impatiens* Cresson y *Augochloropsis* sp., de una planta endémica de Florida, *Chapmannia floridana* Torrey y & A. Gray (Fabaceae); fueron determinadas para los micro-habitats diferentes en la Estación Biológica Archbold en el verano de 1995. Se observaron diferencias apreciables entre los números de visitaciones totales en cada terreno. También había relaciones entre las tasas de visitación y la temperatura, y el tamaño de la flor. La variación en las tasas de visitación no mostró efecto apreciable en el número de semillas de *Chapmannia floridana*. El disturbio no fue importante para determinar las tasas de visitación de ningún polinizador. La composición de la vegetación y la densidad de las flores parecen ser los mejores indicadores de las tasas de visitación a poblaciones de esta especie de planta.

Many studies have shown that disturbance, both natural and human induced, can cause significant changes in the structure and dynamics of ecosystems. Some of the most obvious changes caused by habitat destruction or damage are changes in biodiversity, niche occupation, and animal feeding behavior (Armesto & Pickett 1985, Glitzenstein et al. 1986, Coffin & Lauenroth 1988, Foster & Zebryk 1993, Aizen & Feinsinger 1994). When disturbance is natural, occurring because of fire, storm damage, or landslides, biodiversity in an area tends to increase and niche occupations and animal feeding preferences remain unchanged (Armesto & Pickett 1985, Feinsinger et al. 1987). However, when areas are damaged by human activities such as grazing, agricultural development, and logging, drastic changes in species composition and foraging behavior are often observed (Brian 1959, Halpern 1988).

Despite the growing interest in the effects of human disturbance on ecosystems and on specific rare plants and animals, there are still many gaps in our understanding of how human disturbance affects the life history of these organisms and their interactions with each other. In this study, I examine the apparent success of the plant species *Chapmannia floridana* Torrey & A. Gray; (Fabaceae) in relation to the visitation rates of its major pollinators. I selected *C. floridana* for this study because of the differences in its population structure in disturbed and undisturbed areas. *C. floridana* is a very unusual Florida endemic scrub plant because of its success in disturbed areas. Most endemic plant species in central Florida are disappearing as central Florida scrub disappears. Undoubtedly, there are many factors that contribute to the success of *C. floridana* in disturbed areas. I was interested in determining if the differences in disturbed and undisturbed habitat and in population structures affect pollination services to this plant, possibly contributing to its success.

In this study, variation in pollinator composition and visitation rates to *C. floridana* were determined for six different sites varying in vegetation composition and disturbance. The effects of flower size and temperature on the pollinator composition visiting this plant were also determined (Cruzan et al. 1988). Information on the foraging behavior of this plant's pollinators can provide valuable information about how human and natural disturbance affects the relationship between *C floridana* and its pollinators.

Materials and Methods

Species description of *Chapmannia floridana:*

Chapmannia floridana is an endemic Florida herb ranging from Clay to Collier Counties in central Florida (Gunn, 1980). It can be found growing in open scrub, sandhills, and disturbed areas such as pastures and road sides. Little attention has been paid to *C. floridana* since its original description by Torrey and Gray in 1838. The information available about this species is minimal and often inconsistent (Gunn 1980). My greenhouse studies on this species suggested that selfing does not occur, but results were inconclusive and more study is needed. *C. floridana* is not thought to be a nitrogen fixer.

C. floridana blooms between mid-April to early September. It is commonly found in large numbers in highly disturbed roadsides and pastures and in smaller numbers in undisturbed or burned habitat. Flowering individuals range in height from 20-101 cm and usually consist of 1 to 10 flowering stalks. Flowers are yellow-orange and range in size from 2.0-4.0 cm from top to the bottom and 0.9-4.0 cm horizontally across the petals. Flowers open at about 8:00 am early in the season and about 6:00 am later in the season. Flowers remain open from three to five hours for a single day, depending on air temperature and light conditions. I never observed flowers open after 10:30 am. Each flower produces one to four seeds in a legume covered with small viscid hairs (Gunn 1980).

Site description

I chose six sites for this study at the Archbold Biological Station in Highlands County, Florida. All sites were located in different micro-habitats (Table 1). Sites A, B, D, and E were 288 m^2 (12 m × 24 m) and sites C and F were 240 m^2 (12 m × 20 m). Each site was defined by its disturbance level and the density of *C. floridana* (Table 1). In this study, human disturbance was any area that had been grazed, plowed, bulldozed, or driven over extensively within the past 15 years. Burned sites were not considered disturbed since fire is a natural part of *C. floridana*'s environment. I was not able to find any high density-undisturbed sites or low density-disturbed sites.

TABLE 1. SITE DESCRIPTIONS USED FOR ANALYSIS OF FIELD EXPERIMENTS. MEAN NUMBER OF FLOWERS ARE BASED ON FLOWER COUNTS MADE ON DAYS WHEN OBSERVATIONS WERE MADE AT EACH SITE. DENSITY RATING REFERS TO THE DENSITY OF FLOWERING C. FLORIDANA.

Site	Mean # Flowers	Density Rating	Disturbance	Habitat Type	Major Vegetation
A	10	Medium	Disturbed	Damaged Scrub	Scrub oak, small herbaceous species
B	43	High	Disturbed	Former pasture	Legumes, weedy herbs, oaks, palmettos, grasses
C	175	High	Disturbed	Road side near a citrus orchard	Surrounded by oaks, weedy herbs, grass
D	3	Low	Undisturbed	Scrubby Flatwoods	Oaks, palmettos, and other Scrubby flatwoods
E	5	Low	Undisturbed	Southern Ridge Sandhill	Turkey oak, hickory, and pine, scrub oaks, palmettos, native herbs
F	13	Medium	Undisturbed	Rosemary Bald	Scrub rosemary, oaks, palmettos, and native herbs

Field Experiments

I observed pollination events in each of the six sites five days a week for all weeks between June 26 and July 28, 1995. Each morning I observed one of the six sites for 2 h. The exact time observations began and ended depended on weather conditions and when flowers began to close. This 2 h period encompassed the majority of the time these flowers were open and the sun was up.

Within a selected site, individual flowering *C. floridana* were observed for 10 minute intervals. In each observation period the number, type, and the time spent by insect visitors at flowers were recorded. I watched between 1 and 8 flowers at a time, depending on the orientation and distance of the plants from my observation point (~ 1 m from the nearest plant). All flowers on a selected plant were observed together. In low density sites, all flowering *C. floridana* were observed at the same time and in high density sites plants were selected arbitrarily. Different plants at high and medium density sites were selected throughout the summer of 1995.

Prior to each ten minute observation period, I recorded the air temperature. After observations were completed each day, the flower dimensions of all observed flowers were measured (Kearns & Inouye 1993), the number of flowers blooming during the observation period were counted, and the approximate vegetation cover in a 1 m radius around each *C. floridana* plant was determined. For vegetation cover I used five arbitrary catagories: 0%-15% (mostly open sand), 15%-30%, 30%-60%, 60%-80% and 80%-100% (the most dense vegetation). Seed set was determined several weeks after visitation observations.

Insect identifications were based on the insect collection at Archbold Biological Station. One time visitors were not always identified.

Statistical Analysis

Splus (MathSoft Inc., Seattle, WA), SAS (SAS Institute Inc., Cary, NC), and Statview (Abacus Concepts Inc., Berkley, CA) were used to analyze the data from this study. Because of the low number of visits of both species, visits by each species were considered independent of one another for all statistical tests. The low number of visits also made it necessary to use a Poisson regression (A Poisson regression is a regression based on a Poisson rather than normal distribution), an analysis of deviance based on a Poisson distribution and analysis of variance (ANOVA) were used to look at differences in pollinator visitation frequency (visitation rate of each species per 10 minute interval) (Snedecor & Cochran 1989). Visits by minor visitors were analyzed with a one-group t-test, and the average time spent on a flower by a visitor was analyzed with ANOVA.

Results

Pollinators

In this study, *C. floridana* flowers were commonly visited only by two types of bees: bumble bees, *Bombus impatiens* (Hymenoptera: Apidae; bumble bees), and several species of metallic green solitary bees in the genus *Augochloropsis* (Hymenoptera: Halictidae). These bees were usually observed ripping holes in the sides of the keel petals of the flowers and vibrating their wings to get pollen out of the floral tube. In a past study on *C. floridana* pollination, *Dialictus pilosus* (Smith) (Hymenoptera: Halictidae), a small solitary bee, was the only major insect visitor to this plant (Gunn et al. 1980). In my entire study, a single *Dialictus nymphalis* (Smith) was observed visiting a *C. floridana* flower and no *D. pilosus* were seen. The observed *Dialictus* sp. did not vibrate its wings to get pollen from the flower and it was too small to touch the stigma of these flowers.

Several minor insect visitors were observed foraging *C. floridana* flowers within my plots, including: *D. nymphalis*, *Geron vitripennis* Loew (Diptera: Bombyliidae) and *Copestylum barei* Loew (Diptera: Syrphidae), and several other unidentified bees and flies. In total, 15 of the 262 observed insect visits were by insects other than *B. impatiens* and *Augochloropsis* spp. Ten of these visits occurred at Site D, four at Site B, and one was observed visiting a single flower at Site F. No ants or beetles were observed visiting flowers, although several beetles were seen eating petals in the afternoon after the flowers were closed. Honey bees were seen foraging at other flowering species in all sites, but were never observed visiting *C. floridana*.

Results of Statistical Analysis

An analysis of deviance test (Snedecor & Cochran 1989) on the total number of insect visits to *C. floridana* flowers showed that the total number of insect visits was significantly different between site, bee type, temperature, percentage vegetation cover, and flower size as well as all interactions with bee type (all p-values ≤ 0.001 except for flower size which had a p-value of 0.0153). Specific effects were determined using a Poisson regression (Table 2).

A single group t-test indicated that there was no significant difference between the number of minor visitors visiting in each site or between disturbed and undisturbed sites. No significant differences (based on an ANOVA test) in the time spent by visitors foraging in 10 minute intervals were found for any variable. There were also no significant differences in seed set for any of the variables listed above.

TABLE 2. POISSON REGRESSION OF THE TOTAL NUMBER OF BEES OF BOTH SPECIES (B. IMPATIENS AND AUGOCHLOROPSIS SP.) VISITING C.FLORIDANA IN 10 MINUTE INTERVALS. NS INDICATES THAT THE EFFECT ON THE TOTAL NUMBER OF BEES VISITING WAS NOT SIGNIFICANT.

Variable	Coefficient	Standard Error	Z-value	P-value
Site A (intercept)	4.65	0.856	5.44	< 0.01
Site B	-0.667	0.287	-2.33	< 0.05
Site C	0.658	0.308	2.13	< 0.05
Site D	-1.43	0.473	-3.02	< 0.01
Site E	-0.561	0.359	-1.56	NS
Site F	-1.56	0.329	-4.75	< 0.01
Bee Type	-6.17	1.57	-3.94	< 0.01
Temperature	-0.237	0.0314	-7.53	< 0.01
60% Cover	-0.895	0.210	-4.27	< 0.01
30% Cover	0.963	0.216	4.45	< 0.01
15% Cover	0.0126	0.393	0.0321	NS
0% Cover	0.477	0.281	1.70	NS
Flower Area (cm^2)	0.614	0.0255	2.41	< 0.05
Site B vs. Bee Type	-1.12	0.724	-1.55	NS
Site C vs. Bee Type	-2.061	0.582	-3.54	< 0.01
Site D vs. Bee Type	1.103	0.767	1.44	NS
Site E vs. Bee Type	0.0650	0.551	0.118	NS
Site F vs. Bee Type	0.573	0.494	1.16	NS
Temp vs. Bee Type	0.242	0.0588	4.12	< 0.01
60% Cover vs. Bee Type	0.483	0.478	1.010	NS
30% Cover vs. Bee Type	-1.71	0.437	-3.920	< 0.01
15% Cover vs. Bee Type	-0.0444	0.894	-0.0496	NS
0% Cover vs. Bee Type	-0.264	0.445	-0.594	NS

[1]Null Deviance: 1304.3 on 1289 degrees of freedom
[2]Residual Deviance: 894.9 on 1267 degrees of freedom

For the Poisson regression shown in Table 2, the dependent variable is the number of bees visiting during a 10 min observation period. All main effects and interaction effects are compared to the values for Site A at 0°C (the assumed intercept for this model), 80-100% vegetation cover, and with a flower area of 1 cm^2. For all of the main effects, negative Z-values indicate that there were fewer total visits than expected. The significant negative Z-value for bee type indicates that there were significantly fewer *Augochloropsis* than expected. The negative Z-value for the temperature indicates that the number of total insect visits decreased as the temperature increased. The significant positive Z-value for flower area indicates that flowers with larger flower areas had significantly more insect visits than smaller flowers. For interaction effects, negative values indicate fewer *Augochloropsis* than expected. Positive values indicate fewer *B. impatiens* than expected. The significant negative interaction effect of bee type and temperature shows that as the temperature increased *B. impatiens* visitation decreased significantly, while the number of *Augochloropsis* visitation did not differ significantly according to temperature. The significance of the main temperature effect is due mainly to the change in the number of *B. impatiens* visiting flowers at higher temperatures.

The results of the Poisson regression also indicate that sites B, D, and F had significantly fewer total pollinator visits than expected. Site C had significantly more total visits than Site A but significantly fewer *Augochloropsis* visitors than expected (Table 2). The fitted means in Table 3 show differences between the number of visits to each site by *Augochloropsis* and *B. impatiens*. The mean number of *Augochloropsis* visits are lower than the mean number of *B. impatiens* visits at all sites except site D, a low density undisturbed site. The mean number of *B. impatiens* visiting is highest in the three disturbed sites A, B, and C.

Both bee types showed no vegetation preferences, although each type of bee was observed visiting significantly more frequently in certain vegetation covers. The Poisson analysis indicates a significantly lower number of visits by both species to areas of 60-80% vegetation cover and significantly more total visits to 30-60% vegetation cover but significantly fewer *Augochloropsis* visits indicating that the total increase in visitation in 30-60% vegetation cover was due to high visitation rates by *B. impatiens* (Table 4). An analysis of variance, type three sums of squares, indicates that there is a significant interaction effect of site and percentage vegetation on the number of total bee visits (p-value = 0.0056) and with the number of *B. impatiens* visits (p-value = 0.0001). The frequencies of visits by each bee type within each vegetation coverage are shown in Table 5.

Discussion

Both *B. impatiens* and *Augochloropsis* sp. exhibited complex foraging behavior while visiting *C. floridana* flowers. Statistical results indicate that both pollinators preferred larger flowers. This preference could indicate that the pollinators are using flower size to identify flowers with larger pollen or nectar rewards. The results also indicate that the number of bees visiting decreased significantly as temperature in-

Table 3. Mean Number Of Visitors Per Flower Based On All Observed Visits. Mean Flower Number Is The Mean Number Of C. Floridana Blooming In Each Site Each Day. The Visitation Means Are Low Due To The High Number Of Time Intervals Observed With No Visits.

		Bombus Impatiens			*Augochloropsis*		
Site	Mean Flower #	Mean	Std Dev	H	Mean	Std Dev	H
A	10	0.70	1.14	33	0.47	1.14	22
B	43	0.53	0.90	37	0.06	0.24	8
C	175	0.56	0.96	62	0.06	0.26	11
D	3	0.16	0.62	7	0.21	0.47	9
E	5	1.40	0.70	20	0.18	0.44	9
F	13	0.19	0.49	13	0.15	0.47	16

TABLE 4. MEAN NUMBER OF VISITS BY EACH MAJOR BEE SPECIES OBSERVED IN EACH PERCENTAGE VEGETATION COVERAGE FOR ALL SITES COMBINED.

	Bombus Impatiens			*Augochloropsis*			*Total*		
Veg Cover	Mean	Std Dev	N	Mean	Std Dev	N	Mean	Std Dev	N
0-15%	0.49	0.95	15	0.20	0.41	20	0.69	0.99	35
15-30%	0.25	0.50	6	0.07	0.26	11	0.69	1.05	17
30-60%	0.66	1.04	84	0.09	0.33	13	0.31	0.55	97
60-80%	0.20	0.38	15	0.07	0.49	5	0.75	1.12	20
80-100%	0.57	0.10	43	1.22	2.26	26	0.87	1.40	69

creased. It is likely that the bees' visitation rates decreased as flowers began to close later in the morning when temperatures were warmer and it is possible that floral rewards were depleted later in the morning.

Although the total number of insects visiting each site varied significantly for all but one site, only site C had a significantly different number of *Augochloropsis* visiting. Site C had the greatest number of flowering *C. floridana* and was a highly disturbed site on the edge of a citrus orchard. The high number of *B. impatiens* visiting this site could have been related to the larger number of flowers at site C (Table 3), proximity to other flower sources, or the presence of near by nests. The low number of *Augochloropsis* forging at this site could have been caused by overwhelming competition from the abundant *B. impatiens* at this site.

The amount of vegetation cover most often visited by each type of pollinator did not follow a pattern except when considered in connection with the sites. Vegetation preferences of *Augochloropsis* sp. were not related to sites dominated by a particular vegetation coverage while *B. impatiens* visits were (Tables 4 and 5).

There was no clear indication from this study that the foraging patterns of *C. floridana*'s pollinators were directly affected by the level of human disturbance in the area. Seed set levels did not differ significantly between sites, indicating that despite the significant difference in pollinator visitation between sites, all populations observed in this study were receiving similar pollination services. *Bombus impatiens* were observed visiting sites A, B, and C more frequently than in the undisturbed sites, but this was not a significant difference. *Augochloropsis* was found visiting most frequently in disturbed site A and least frequently at the other two disturbed sites B and

TABLE 5. THE FREQUENCY OF CHAPMANNIA FLORIDANA OBSERVED IN EACH SITE IN EACH VEGETATION COVER.

Vegetation Cover	Site A	Site B	Site C	Site D	Site E	Site F
0-15%	9	4	30	59	12	0
15-30%	1	0	170	30	0	0
30-60%	0	39	49	42	26	39
60-80%	0	0	0	0	0	76
80-100%	33	0	0	21	12	20

C (Table 3). Sites B and C had the highest flowering densities and high visitation rates by *B. impatiens* indicating that competition may play a role in the visitation rates of *Augochloropsis* to this plant. Site A was bordered on three sides by undisturbed habitat which may have contributed to the visitation rates of *Augochloropsis*.

The visitation rates of these pollinators were undoubtedly affected by factors not determined in this study. From the data collected, the factors that appear to play the greatest role in determining visitation rates to *C. floridana* are temperature, flower size, and flowering density. Although disturbance does not seem to strongly affect the pollinator visitation rates or resulting seed set in this plant, the higher numbers of flowers in disturbed areas clearly attract more pollinators than the low density undisturbed populations do. This relationship between flowering density and visitation rate may be important to the reproductive success of this plant species in the long term or at least in years with fewer pollinators.

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References Cited

Aizen, M. A., and P. Feinsinger. 1994. Forest fragmentation, pollination, plant reproduction in a chaco dry forest, Argentina. Ecol. 75: 330-351

Armesto, J. J., and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant communities: impacts on species richness and abundance. Ecol. 66: 230-240.

Brian, A. D. 1959. Differences in the flowers visited by four species of bumble-bees and their causes. J. Animal Ecol. 26: 71-98.

Coffin, D. P., and W. K. Lauenroth. 1988. The effects of disturbance size and frequency on a shortgrass plant community. Ecol. 69: 1609-1617.

Cruzan, M. B., P. R. Neal, and M. F. Wilson. 1988. Floral display in phyla-incisa consequences for male and female reproductive success. Evolution 42: 505-515.

Feinsinger, P., J. H. Beach, Y. B. Linhart, W. H. Busby, and G. Murray. 1987. Disturbance, pollinator predictability, and pollination success among Costa Rican cloud forest plants. Ecol. 68: 1297-1305.

Foster, D. R., and T. M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a Tsuga-dominated forest in New England. Ecol. 74: 982-998.

Glitzenstein, J. S., P. A. Harcombe, and D. R. Streng. 1986. Disturbance, succession, and maintenance of species diversity in an east Texas forest. Ecological Monographs 56: 243-258.

Gunn, C. R., E. M. Norman, and J. S. Lassetter. 1980. *Chapmannia floridana* Torrey and Gray (Fabaceae). Brittonia 32: 178-185.

Halpern, C. B. 1988. Early successional pathways and the resistance of forest communities. Ecology, 69: 1703-1715.

Kearns, C. A., and D. W. Inouye. 1993. Techniques for pollination biology. The University Press of Colorado. Niwot, CO.

Snedecor, G. W., and W. G. Cochran. 1989. Statisitcal Methods: Eighth edition. Iowa State University Press, Ames.