Notes On Phenological Patterns of Flowering and Flower-Feeding Beetles (Coleoptera: Chrysomelidae) in Two Clones of Cacao (Sterculiaceae: *Theobroma cacao* L.) in Costa Rica[1]

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ABSTRACT

For five successive years, freshly opened flowers and flowers damaged from feeding by chrysomelid beetles, chiefly *Colaspis* sp. and *Monolepta* sp. beetles (Coleoptera: Chrysomelidae) were measured for 35 mature trees each of two commercially-propagated clones ("Pound-7" and "UF-613") of *Theobroma cacao* Linnaeus (Sterculiaceae) at Finca Experimental La Lola in Costa Rica. The purpose of this study was to assess the relationship between temporal patterns of floral abundance, floral herbivory and beetle abundance in each cacao clone, and to evaluate the possible impact of floral herbivory in cacao on the potential for natural pollination. Although the abundance of flowers varied greatly at different times, total number of flowers produced was very similar between the two clones, as was the very low incidence (4-5% range) of floral herbivory for the entire study period. No positive correlations were found in either cacao clone between (1) abundance of flowers and beetles, (2) total flowers and the incidence of damaged flowers, or (3) the incidence of damaged flowers and the abundance of beetles. The observed very low numbers of *Colaspis* and *Monolepta* on all of 14 censuses, even though the former species was 2-4 times as numerous as the latter, may have precluded detecting a positive relationship between flowers and beetles. Yet the extent to which these beetles are specific to cacao flowers cannot be ascertained, even though both species were also occasionally found feeding on flowers of *Theobroma simiarum* Donn. Smith and *T. speciosum* Willd. at La Lola. Observed levels of both beetles and floral damage from their herbivory are too low to have a significant negative impact on natural pollination in *T. cacao* Because no noticeable differences were found between the two clones studied for the numbers of *Colaspis* and *Monolepta*, it is concluded that marked differences in floral pigmentation (reddish flowers in "UF-613" and whitish flowers in "Pound-7") did not influence floral feeding preferences by these beetle species for these clones.

COMPENDIO

En la Finca Experimental La Lola de Costa Rica, durante un período de cinco años, se hizo un estudio de las flores de 70 árboles maduros de *Theobroma cacao* Linnaeus (Sterculiaceae). De éstos, 35 eran del clon comercial Pound-7 y 35 del clon comercial UF-613. Se registró la abundancia de flores nuevas y de flores dañadas por los coleópteros, especialmente los *Colaspis* sp. y los *Monolepta* sp. (Coleoptera: Chrysomelidae). Este estudio busca calcular la relación entre la aparición y la abundancia de las flores, el grado de destrucción de las flores por los coleópteros herbívoros y la abundancia de éstos en cada clon de cacao. También se buscó evaluar la posible reducción en la polinización natural a causa de la destrucción de cierta cantidad de flores por los coléopteros herbívoros. La abundancia de las flores varió mucho. Sin embargo, ambos grupos de árboles produjeron cantidades casi iguales de flores. Los dos grupos mostraron baja destrucción de flores por los coleópteros herbívoros, constituyendo entre 4 y 5% duante los cinco años del estudio. No se encontró en ninguno de los clones correlación positiva entre los siguientes factores: 1) abundancia de flores y abundancia de coléopteros; 2) número total de flores y número total de flores dañadas; 3) número de flores dañadas y abundancia de coleópteros. El hecho de no haber observado correlación positiva entre las cantidades de flores y los coleópteros puede deberse al índice bajo de *Colaspis* y de *Monolepta* en los catorce recuentos que se hicieron; esto a pesar de que el número de *Colaspis* excedió el de *Monolepta* en dos a cuatro veces. No se puede afirmar hasta qué punto estos coleópteros limitan a las flores de cacao, aunque las dos especies en La Lola, también se alimentan ocasionalmente de flores de *Theobroma simiarum* Donn. Smith y de *T. speciosum* Willd. Las cantidades de coleópteros y de flores dañadas por coleópteros herbívoros son tan bajas que estos daños no representan un peligro para la polinización de *T. cacao*. Puesto que no hubo diferencia significativa entre el número de *Colaspis* y de *Monolepta* que se encontraron en los dos clones, se concluye que las diferencias de pigmentación de las flores (rojiza en UF-613 y blanuzca en Pound-7) no influyeron en las preferencias de estos coleópteros herbívoros.

INTRODUCTION

Several genera of chrysomelid beetles (Coleoptera: Chrysomelidae), including *Colaspis*, feed on the leaves of *Theobroma cacao* L. (Sterculiaceae) in the American tropics (3, 7, 11) Although some species of *Colaspis* are apparently host-specific for cacao and other tropical crops (4, 13), flower-feeding by these and other chrysomelids associated with cacao has not been previously reported In this paper I report the abundance of two species of

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chrysomelid beetles, *Colaspis* sp. (Eumolpinae) and *Monolepta* sp. (Galerycinae) feeding on the flowers of two commercially-propagated clones of cacao, "Pound-7" and "UF-613," in Costa Rica, as observed periodically over a five-year period, and in relation to flowering phenology in cacao trees. Although chrysomelid beetles associated with the flowers of other species of plants may be pollinators (6), the general perception that floral herbivory from these beetles can be detrimental (15) prompted the present study. My data, and observations of the association of these and other chrysomelids with other species of *Theobroma* at the study site, indicate a temporally persistent low-level population density of these floral herbivores on flowers, independently of flowering cycles in cacao.

MATERIALS AND METHODS

This study was conducted at Finca Experimental La Lola (35 m above sea level), near Siquirres (10° 06"N, 83°30'W), Limon Province, Costa Rica. At intermittent 3-5 month intervals between July 1982 and July 1987, the numbers of freshly-opened flowers and the numbers of beetles observed feeding on flowers were recorded individually for each of 35 trees of "Pound-7" and 35 trees of "UF-613" cacao in the Clonal Garden, La Lola. These two clones were chosen for study of beetle floral herbivory because the pigmentation of the flowers is markedly different between them: flowers of "Pound-7" are whitish, while those of "UF-613" are distinctly reddish. I was interested in determining whether or not beetles exhibited a definite feeding preference for flowers of one clone over the other, given this noticeable difference in color and other floral features between these clones (17). In terms of floral colors, these two clones represent two basic classes of flowers characteristic on many clones and varieties of commercially-propagated cacao throughout the world.

At each census of flowers and beetles, the same trees were examined, for a total of fifteen censuses within the five-year study period. Censuses of flowers and beetles were taken during both dry and rainy seasons over the five-year period, given the moderately dry period that occurs in February and March each year at La Lola (20). Occasional searches for beetles feeding on the leaves of cacao trees in the study area were also made to determine indirectly the apparent specificity of the adult stages for floral-feeding. I also opportunistically examined the flowers of other species of *Theobroma* growing in a "study garden" at La Lola for beetles, to determine if these insects were host-specific for *T. cacao* alone. Every attempt was made to count flowers and beetles exhaustively on all 70 trees. Censuses were usually performed from 0800-1200 h in sunny weather. A census consisted of walking between rows of cacao trees, stopping at each tree and examining open flowers for both beetles and traces of beetle-feeding damage to floral structures (Fig. 1). Given the small body length (4-5 mm) of the beetles found in flowers, it was often difficult to locate beetles in flowers in the upper branches of cacao trees, undoubtedly introducing some bias into the results. Yet this error was consistent for all trees studied. At various times during the study, voucher specimens of beetles were collected for taxonomic determination. Behavior of beetles other than feeding, such as mating (Fig. 1), were also noted. The number of flowers exhibiting noticeable signs of feeding damage (chewing damage) from beetles were also recorded. Based on observing the feeding behavior of beetles, it was possible to discern damage from their feeding even when they were not present. Notes were also made as to specific floral parts fed upon by beetles.

RESULTS

Feeding Behavior

Two species of Chrysomelidae (Coleoptera), *Colaspis* sp. and *Monolepta* sp. (M. sp. near *bipartita* Jacoby) were seen feeding on floral tissues on trees belonging to both clones (Fig. 1). Occasionally, an additional chrysomelid, *Sphinterophyta* (= *Chrysodi-*

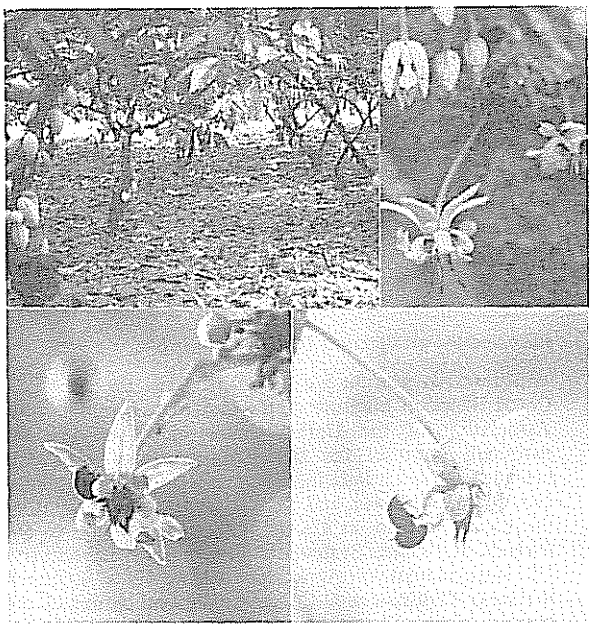

Fig 1. Clockwise, beginning in upper left corner: View through the "Pound-7" cacao trees in the clonal garden at La Lola; freshly-opened flowers of cacao; pair of copulating *Monolepta* beetles on a cacao flower at the study site; *Monolepta* beetle feeding on sepal of a cacao flower.

na) sp. (near *C. servula* Lefevre) (Eumolpinae) was found feeding on flowers, but clearly *Colaspis* and *Monolepta* dominated the samples of beetles found in flowers in this study. Although adults of both genera are about the same size, *Colaspis* beetles are reddish while *Monolepta* are metallic dark blue, greatly facilitating field censuses of both species. *Sphinterophyta* beetles are similar in size to the other species, but black and more roundish.

Both *Colaspis* and *Monolepta* adults feed heavily on these floral structures of *T. cacao*: sepals, petal ligules, petal pouches. Anthers and pollen sacs are sometimes completely destroyed on individual flowers, but staminodes and pistils are generally not fed upon. There appears to be no divergence in feeding chains between these beetle genera and species. Feeding by these beetles leaves characteristic evidence of chewing on partly-devoured structures such as sepals (Fig. 1). For petal ligules, petal pouches and sepals combined, a range of approximately 10% to 75% of the combined tissue surface area represented by these floral structures was destroyed per flower on a given census as a result of herbivory from these beetles. However, an estimated 60% of all flowers with damage from this herbivory on a given census date had approximately 25% of these floral tissues destroyed. Rarely were individual flowers found that had virtually all of these floral structures completely destroyed by these beetles, a feeding behavior clearly distinguishable from that of leaf-cutter ants, *Atta* spp. (Hymenoptera: Formicidae: Attinae).

An examination of approximately 500 flowers from each clone for the entire study period failed to turn up any chrysomelid larvae in flowers, and beetles were not found feeding on leaves of cacao trees. Feedings beetles are easily disturbed and fly off quickly or drop to the ground. Yet mating pairs of both *Colaspis* and *Monolepta* have been found in flowers (Fig. 1). Both single individuals and copulating pairs of *Monolepta* sp. near *bipartita* have also been found occasionally in the freshly opened flowers of *Theobroma simiarum* Donn. Smith and *T. speciosum* Willd. at La Lola during this study. A single individual of *Colaspis* sp. was found feeding on petals of *T. simiarum*.

Flowering Phenology and Beetle Abundance

Although the abundance of open flowers in both clones of *T. cacao* varied greatly among the various census periods, the shifts in abundance of both *Colaspis* and *Monolepta* did not follow the same pattern (Tables 1 and 2). Rainy months, such as July through November each year (20), tended to be periods of high flowering in both clones, although numbers of beetles on flowers were not always highest at these times. Even though *Colaspis* beetles were almost two

Table 1. Phenological patterns of flowering, floral damage from insect herbivory, and abundance of two species of floral-feeding Chrysomelidae (Coleopter), at widely scattered dates for a five-year period in a stand of "Pound-7" clone trees (N=35) of *Theobroma cacao* L. (Sterculiaceae) in Costa Rica.

Census Date	Open Flowers		Flowers with Beetle Damage		%Flowers Damaged	*Colaspis* Beetles Feeding on Flowers			*Monolepta* Beetles Feeding on Flowers		
	T	X ± S.E.	T	X ± S.E.		T	X ± S.E.	%	T	X ± S.E.	%
16-VIII-82	684	16.56 ± 2.33	90	2.50±0.55	13.16	3	0.05±0.03	10.71	25	0.57±0.14	89.29
8-XII-82	1 205	26.77± 3.17	131	2.91±0.45	10.87	5	0.15±0.06	83.33	1	0.02±0.01	16.67
15-III-83	738	23.46± 5.03	48	1.71±0.34	6.50	8	0.25±0.11	88.89	1	0.02±0.01	11.11
4-VIII-83	2 666	66.65±10.89	43	1.10±0.22	1.61	4	0.13±0.06	100.00	0	–	–
6-XI-83	2 214	55.32± 6.07	94	2.35±0.39	4.25	5	0.15±0.06	62.50	3	0.05±0.03	37.50
12-III-84	856	21.94± 3.17	35	1.00±0.25	4.09	0	–	–	1	0.02±0.01	100.00
10-VIII-84	927	24.35± 2.88	79	2.08±0.47	8.52	10	0.25±0.01	58.82	7	0.02±0.08	41.18
16-XI-84	474	12.81± 1.55	103	2.86±0.56	21.73	16	0.45±0.13	69.57	7	0.20±0.08	30.43
7-III-85	148	4.93± 1.52	5	0.21±0.13	3.38	2	0.06±0.04	100.00	0	–	–
26-XIV-85	2 670	72.16±13.44	91	3.48±0.72	3.41	14	0.37±0.16	100.00	0	–	–
22-II-86	787	27.13± 4.97	35	1.31±0.34	4.45	0	–	–	0	–	–
28-VII-86	418	14.92± 2.45	48	1.71±0.34	11.48	2	0.06±0.04	100.00	0	–	–
10-XII-86	523	16.87± 2.97	8	0.34±0.13	1.53	0	–	–	0	–	–
2-III-87	72	32.06± 5.81	72	2.25±0.59	7.02	8	0.25±0.11	100.00	0	–	–
1-VII-87	1 519	47.46± 6.84	77	2.40±0.61	5.07	2	0.06±0.04	66.67	1	0.02±0.01	33.33
TOTAL	16 885		959			79			46		

Table 2. Phenological patterns of flowering, floral damage from insect herbivory, and abundance of two species of floral-feeding Chrysomelidae (Coleoptera), at widely scattered dats for a five-year period, in a stand of "UF-613" clone tress (N=35) of *Theobroma cacao* L. (Sterculiacea) in Costa Rica.

Census Date	Open Flowers		Flowers with Beetle Damage		%Flowers Damaged	*Colaspis* Beetles Feeding on Flowers			*Monolepta* Beetles Feeding on Flowers		
	T	X ± S.E.	T	X ± S.E.		T	X ± S.E.	%	T	X ± S.E.	%
16-VII-82	121	4.03± 1.01	14	0.37±0.16	11.57	3	0.05±0.03	75.00	1	0.02±0.01	25.00
8-XII-82	361	14.84± 2.63	76	3.24±0.68	21.05	1	0.02±0.01	100.00	0	–	–
15-III-83	855	29.37± 4.01	36	1.03±0.28	4.21	6	0.18±0.08	100.00	0	–	–
4-VIII-83	2 254	75.26±14.71	30	1.00±0.27	1.33	4	0.13±0.06	66.67	2	0.06±0.04	33.33
6-XI-83	1 829	60.95±8.66	67	2.23±0.52	3.66	4	0.13±0.06	80.00	1	0.02±0.01	20.00
12-III-84	1 081	34.87± 5.96	29	0.93±0.18	2.68	0	–	–	1	0.02±0.01	100.00
10-VIII-84	642	17.02± 2.90	58	1.65±0.35	9.03	7	0.20±0.08	38.89	11	0.31±0.09	61.11
16-XI-84	438	13.27± 1.94	86	2.60±0.62	19.63	15	0.45±0.19	75.00	5	0.15±0.06	20.00
7-III-85	931	26.60± 3.37	70	2.12±0.43	7.52	17	0.47±0.14	100.00	0	–	–
26-XIV-85	2 531	87.27±12.52	159	5.48±1.00	6.28	21	0.79±0.01	100.00	0	–	–
22-II-86	2 382	68.05± 7.76	53	1.55±0.34	2.23	0	–	–	0	–	–
28-VII-86	443	14.33± 1.98	19	0.63±0.18	4.29	2	0.06±0.04	100.00	0	–	–
10-XII-86	454	12.97± 2.33	8	0.24±0.11	1.76	0	–	–	0	–	–
2-III-87	1 412	38.16± 4.05	105	2.83±0.51	7.44	10	0.27±0.10	100.00	0	–	–
1-VII-87	2 438	67.72±10.23	83	2.17±0.52	3.40	1	0.02±0.01	100.00	0	–	–
TOTAL	18 172		893			91			21		

(on "Pound-7") or four times (on "UF-613") as abundant as *Monolepta* for all censuses combined (Tables 1 and 2), *Colaspis* abundance did not vary in accordance with floral abundance. The highest numbers of either *Colaspis* or *Monolepta* may occur even when floral numbers on both clones of *T. cacao* are low (Tables 1 and 2). For beetle abundances on flowers of both clones, there was no significant positive correlation between the abundance of beetles and flowers (Pearson's coefficients $r = 0.32$ and $r = 0.39$, both at $p > 0.02$). For all censuses of both clones of *T. cacao*, all but one indicated a greater abundance of *Colaspis* adult beetles over *Monolepta* (Tables 1 and 2). Although levels of flower damage from beetle herbivory varied greatly at different census of both clones of *T. cacao* (Tables 1 and 2), there was an absence of a significant positive correlation between total numbers of flowers and numbers of damaged flowers ($r = 0.28$, $p > 0.1$), and between numbers of damaged flowers and the combined abundances of beetles ($r = 0.35$ $p > 0.2$). For the entire study, only 5.69% of the open flowers of "Pound-7" and 4.91% of "UF-613" flowers of *T. cacao* were damaged by beetle herbivory.

DISCUSSION

These data indicate a consistently low level of abundance of two species of flower-feeding Chrysomelidae associated with the flowers of *T. cacao* at La Lola. Given the low numbers observed on flowers for both species of beetles, the data further suggest an absence of a definitive preference for association by either species with one or the other cacao clones examined. I therefore tentatively conclude that for these two particular clones, floral pigmentation differences between clones is not a factor selecting for floral feeding habits in *Colaspis* and *Monolepta* species associated with *T. cacao*. Low numbers of *Colaspis* and *Monolepta* were found in "Pherocon AM Sticky Traps" in the La Lola cacao plantation late in the rainy season (23). Little information is available on the biology of these beetles, although *Colaspis* species have been previously reported to be associated with *T. cacao* in Central America (4). Given the observed intermittent association of other chrysomelids such as *Sphintherophyta* with cacao flowers in my study, and the low density of beetles found in the flowers of other species of *Theobroma* planted at La Lola, the question of floral host specificity in these herbivorous species remains to be defined more clearly by further research studies.

The observed wide discrepancy between actual numbers of beetles censused and the incidence of floral damage at each census may reflect unobserved peak feeding by these insects at other times of the day-night cycle. A different species of *Monolepta* was observed to be active at night in visiting the flowers of *Syzygium cormiflorum* (F. Muell.) B.

Hyland (Myrtaceae) in Australian tropical rain forest (5). Flower-feeding in beetles in the present study may indicate an opportunistic habit in association with leaf-feeding as well, as known for many chrysomelids (21). Yet the observed absence of both *Colaspis* and *Monolepta* on leaves of *T. cacao* in my study, in spite of the opportunistic sampling program, may suggest a specialization for floral-feeding. Given what is generally known about the insect-mediated natural pollination of *T. cacao* at La Lola (8, 16, 22), it is likely that floral herbivory of cacao flowers by *Colaspis, Monolepta,* and other insects reduces the effectiveness of the floral attractant-reward system (24) and negatively impacts on pollination. Yet given the observed very low abundance of these insects in this study, such a negative effect on pollination is expected to be minimal. My study did not include a careful, systematic survey of insects feeding on flush leaves of *T. cacao,* which may be a preferred food resource for *Colaspis ornata* germar at Bahia, Brazil (3). Certainly the well-known association of *Colaspis* beetles with *T. cacao* would suggest a more generalized feeding association with this tree, especially in commercial plantations (7). Yet floral petals may possess suites of nutrients unavailable in leaf tissues, favoring a beetle-feeding association, as reported for other plant species (14). Seasonal and other temporal changes in the nutrient physiology of leaves and flowers may alter the feeding habits of chrysomelid beetles (10, 12, 18). Given what little is known about floral associations of chrysomelid beetles, it is unlikely that *Colaspis* and *Monolepta* on *T. cacao* function as pollinators (2, 6, 9).

Although in some chrysomelid-food plant associations the densities of beetles increase with the abundance (patch size) of the host (1, 19), the lack of a positive correlation between the abundance of flowers and abundance of beetles in the present study, notwithstanding the small sample sizes of beetles, suggests that other factors are regulating the abundance of *Colaspis* and *Monolepta* beetles in the La Lola cacao plantation. Very likely the populations of these beetles are widely dispersed over the entire cacao plantation, rather than confined to the small portion of *T. cacao* trees censused in this study.

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