FIELD OBSERVATIONS ON HOST PLANT ASSOCIATIONS ENEMIES OF DIABROTICITE BEETLES (CHRYSOMELIDAE: LUPERINI) IN VERACRUZ, MEXICO

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RESUMEN

La asociación de diabroticinas con plantas hopederas fue observada en condiciones de campo (junio 1993 - agosto 1994). Los insectos adultos fueron colectados en cuatro localidades de dos zonas climáticas en el estado de Veracruz, México. La incidencia de parasitismo y depredación fue documentada. Diecisiete especies de diabroticina fueron encontradas. Las dos zonas climáticas difirieron en el número de especies presentes. Las *Acalymma* spp. fueron exclusivamente colectadas de cucurbitáceas silvestres y cultivadas, mientras que las *Diabrotica* spp. mostraron asociaciones con distintas plantas hospederas. El factor más importante que influyó en la presencia y abundancia de insectos fue el estado fenológico de la planta hospedera. El estado de floración y el número de flores de cucurbitáceas, determinó el número de insectos y la diversidad de especies. El parasitoide más abundante encontrado fue una mosca de la familia Tachinidae, *Celatoria compressa* Wulp. Se encontró parasitismo por nemátodos (Mermithidae) y hongos (Laboulbeniales). Depredación por varias especies de hemópteros (Reduviidae) y arañas (Oxyopidae) fue observada en varias ocasiones.
Palabras Clave: *Acalymma, Diabrotica, Celatoria*, Cucurbitaceae, *Laboulbenia*, Mermithidae.

ABSTRACT

Host plant associations of diabroticite beetles were observed under field conditions (June 1993-August 1994). Adult insects were sampled in four locations in two climatic zones in the state of Veracruz, Mexico. Incidence of parasitism and predation was recorded. Seventeen species of diabroticites were found. The two climatic zones differed in numbers of species present. *Acalymma* spp. were exclusively collected from cultivated and wild cucurbits, whereas *Diabrotica* spp. showed distinct host plant associations. The most important factor influencing insect presence and abundance was the phenological stage of the host plant. Flowering stage and number of flowers of cucurbits determined the number of insects and species diversity. The most abundant parasitoid encountered was a tachinid fly, *Celatoria compressa* Wulp. Parasitism by nematodes (Mermithidae) and fungi (Laboulbeniales) occurred. Predation by several hemipteran species (Reduviidae) and spiders (Oxyipidae) was observed at several occasions.
Key Words: *Acalymma, Diabrotica, Celatoria*, Cucurbitaceae, *Laboulbenia*, Mermithidae.

INTRODUCTION

Host plant breadth within groups of closely related insects can be highly variable (Scriber 1983, Scriber & Hainze 1987). Some species may be specialists on a certain species, genus or family, while others in the same genus feed on a wide variety of unrelated plant families (Singer 1983, Jermy 1984). Often the herbivore-plant association is mediated by plant secondary compounds (Ehrlich & Raven 1964, Jones *et al.* 1988, Spencer 1988).

An example of feeding specialization on different host plants in closely related herbivore species is the section diabroticites. The genera *Acalymma* and *Diabrotica* (Chrysomelidae: Luperini) are native to Mexico and Central America (Webster, 1895). The 338 described *Diabrotica* species are largely of neotropical origin (Wilcox 1972, Krysan & Smith 1987). For *Diabrotica*, data indicate that species in the *virgifera* group are univoltine and larvae are oligophagous on Poaceae. It has been proposed that the ancestor of the *virgifera* group developed as a specialist on the roots of certain grasses in central Mexico and moved with corn into northern temperate regions (Branson & Krysan 1981). Species in the *fucata* group are considered polyphagous and multivoltine, and their hypothesized original host plants are found in the Cucurbitaceae. According to current host plant descriptions, corn, peanuts, beans and cucurbits are their main cultivated hosts. The 19 described species in the genus *Acalymma* are oligophagous on cucurbits (Munroe & Smith 1979).

Diabroticites are abundant in subtropical and tropical regions of Mexico. Thirty one species of *Diabrotica* and 15 species of *Acalymma* are described from Mexico (Krysan & Smith 1987). There, the agronomic hosts of diabroticites are corn and beans. The areas with highest infestation rates are the major corn growing regions in central Mexico (Ayala-Orduño 1983). In the *virgifera* group *D. virgifera zeae* is the most important pest species in corn (Branson *et al.* 1982). *D. balteata* is the most economically important species in the *fucata* group. It attacks beans and can transmit bean wild mosaic virus and bean curly virus (Anaya *et al.* 1992). *A. blomorum* and *A. trivittatum* are described as pests in cultivated cucurbits (Anaya & Burgos 1990, Saunders *et al.* 1983).

The ecological relationship between diabroticite beetles and plants in the family Cucurbitaceae has been intensively studied (Chambliss & Jones 1966, Howe *et al.* 1976, Metcalf *et al.* 1982, Tallamy & Krischik 1989). The Cucurbitaceae is a neotropical family native to southern Mexico and Central America (Whitaker & Bemis 1965). Twenty-three genera of Cucurbitaceae and 37 species in the genus *Cucurbita* are described from the state of Veracruz, Mexico (Neé 1993). Although cucurbits are not considered to be host plants for some *Diabrotica* species (Krysan & Branson 1983, Krysan 1993), cucurbitacins (oxygenated tetracyclic

triterpenoids), bitter and toxic secondary compounds produced by the Cucurbitaceae are potent arrestants and phagostimulants for most species of diabroticites occurring in the United States (Metcalf & Lampman 1989). Cucurbitacins are sequestered by beetles and larvae that feed on cucurbitacin containing plants, and female beetles that ingest cucurbitacins produce bitter eggs (Ferguson *et al.* 1985, Anderson *et al.* 1988, Barbercheck *et al.* 1995). It has been hypothesized that beetles leave suitable hosts to seek bitter cucurbits because sequestered cucurbitacins may confer protection against predation by natural enemies. Experimental results have supported (Ferguson & Metcalf 1985) and challenged (Gould & Massey 1984, Brust & Barbercheck 1992, Eben 1995) this hypothesis. No reports exist to date on tests of the hypothesis of cucurbitacin feeding as defense under field conditions with naturally occurring diabroticites and natural enemies. Nor do there exist data on the diabroticite/Cucurbitaceae association in the habitat of origin of both partners of this chemically mediated plant/herbivore interaction.

Because the root feeding larval stage of *Acalymma* and *Diabrotica* is difficult to detect, effective control strategies have not yet been developed, and the main control tactic is intensive insecticide use. In the United States, there does not seem to exist any highly effective natural enemy of either the larval or adult stage. Reported natural enemies of adult diabroticites include tachinid flies *Celatoria diabroticae* Shimer (Sell 1915), *C. setosa* Coquillett and *Pseudomyothyria ancillus* Walker; the braconid wasp *Syrrhizus diabroticae* Gahan (Arnaud 1978, Krombein & Hurd 1979); and nematodes *Filipjevermis leipsandra* Poinar and Welch (Cuthbert 1968) and *Howardula benigna* Cobb (Fronk 1950). Rootworms are susceptible to infection by entomopathogenic nematodes in the genera *Heterorhabditis* and *Steinernema* and entomopathogenic fungi in the genera *Beauveria, Metarhizium*, and *Paecilomyces* (Jackson & Brooks 1989, Barbercheck unpubl. data). We expected to find a higher number of natural enemies in the native habitat, where diabroticites and cucurbits have had an evolutionary association in both natural and agricultural ecosystems (Metcalf 1979, 1986, Risch 1981).

The main goal of this study was to understand host plant associations of diabroticites in the native habitat. As an example for one of the possible areas of origin of this insect/plant interaction, we chose the state of Veracruz. The focus was on insect diversity and abundance on wild and cultivated cucurbits. The first objective was to detect if results from laboratory assays (Eben 1995) to determine degree of host-plant specialization were supported by field observations. The second objective was to assess the incidence of natural enemies on selected diabroticite/host plant combinations.

MATERIALS AND METODS

Study area. The main collection area was in the central part of the state of Veracruz, Mexico, in the vicinity of Xalapa (Fig. 1). Four locations were selected based on climatic differences. The locations were grouped into two distinct climatic and topographic zones (Table 1). Zone 1 included the warmer, lower altitude areas around the villages of Actopan and Apazapan. The natural vegetation is deciduous tropical lowland forest (Gomez-Pompa 1977). The climate is defined as "warm". Actopan is located to the east of Xalapa, and the coldest months occur from December to February, whereas the warmest occur between March and July. The highest rainfall occurs from June to July, and later again in September. The months from November to May are dry (10-40 mm). Apazapan is located to the west of Xalapa. There the warmer period lasts from April to October, while the months between November and March are colder and dry (10-50 mm). The coldest months occur from December to February. The highest rainfall occur from June to September (Soto & Garcia 1989). Corn, beans and cucurbits are cultivated in larger fields in both locations.

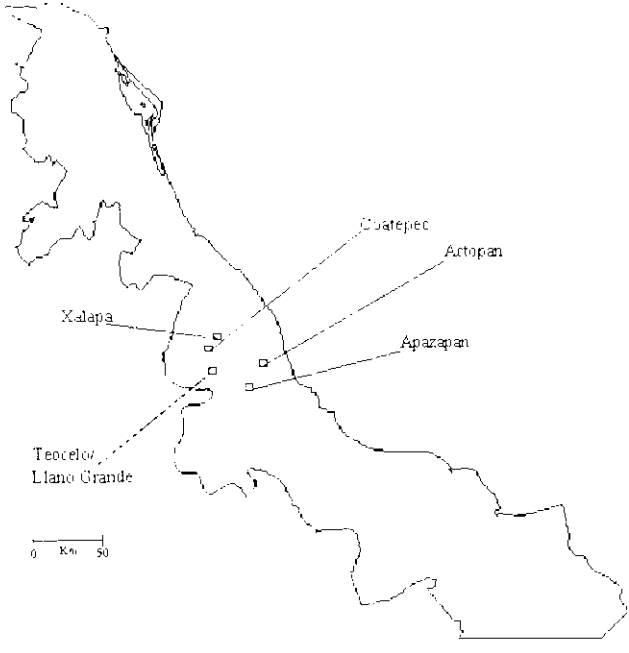

Figure 1
Map of the state of Veracruz, (Mexico) indicating collection sites.

Table 1
Climatic zones of the four collection areas in the state of Veracruz

Location	Altitude (m)	Mean Annual Temp. (°C)	Total Annual Precipitation (mm)	Geographical location
Actopan	311	22-25	800-1000	19°30'N, 96°37'W
Apazapan	523	22-25	800-1200	19°20'N, 96°45'W
Coatepec	1252	18-20	2000-2500	19°27'N, 96°57'W
Teocelo-	1218	18-20	1500-2000	19°23'N, 96°58'W
Llano Grande	950			

Areas around Coatepec and Teocelo are situated in the cooler, higher altitude zone southwest of Xalapa (Zone 2). The natural vegetation type of this zone is cloud forest, and the climate is defined as "temperate, subhumid" with an annual mean temperature between 18-20°C. The rainy season lasts from the end of May until the beginning of October. Highest precipitation rates occur commonly in June and September and lowest (50-60 mm) from December to April. Coatepec is characterized by large coffee plantations with banana (*Musa paradisiaca* L., Musaceae) and *Inga jinicuil* Schltr. (Leguminosae) as shade trees. The coldest months are December through February, and the warmest May and June (Gomez & Soto 1990). In Teocelo temperatures are lowest between December and February, and highest between April and July (Gomez 1991, Medina & Soto 1991). The natural vegetation around Llano Grande is deciduous tropical lowland forest (Gomez-Pompa 1977). The climate type is "warm, humid" with summer rain and monsoon influence. Corn, cucurbits, beans and ornamental plants are cultivated in private gardens and smaller fields in both areas.

Host plants. The major host plants of diabroticites are cultivated and wild species in the family Cucurbitaceae. *Citrullus lanatus* (Thunb.) S. Matsum. & Nakei (common name: Sandía), *Cucumis melo* L. (Melón), *C. sativus* L. (Pepino), *Cucurbita argyrosperma* Huber ssp. *argyrosperma* (Pipian), *C. pepo* L. (Calabaza), *C. moschata* (Lam.) Poiret (Calabaza), *Sechium edule* (Jacq.) Sw. (Chayote), *Lagenaria siceraria* (Mol.) Standley (Tecomate), and *Luffa cylindrica* (L.) Roemer (Estropajo) are the main cultivated cucurbit species. *C. martinezii* L. Bailey (Morchete) and *Momordica charantia* L. (Melón de ratón) are the most abundant wild cucurbits in the collection areas.

Insects. All diabroticite beetles encountered in the described areas were collected. Species, number, sex and host plant were recorded. Insects were separated by species, and colonies were maintained in cages on zucchini (*C. pepo* L.) slices and dry diet (Branson *et al.* 1975) in the laboratory (26°C, 60% r.h., 12 h L: 12 h D)

at the Institute of Ecology, Xalapa, Veracruz. Insect identifications were confirmed by J.L. Krysan, USDA-ARS, Beltsville, Maryland. Voucher specimens were submitted to the museum collection at the Department of Entomology, North Carolina State University, Raleigh, NC, USA, and to the insect collection at the Institute of Ecology, Xalapa, Veracruz, Mexico.

Sampling. Adult diabroticite beetles were collected 1-2 times per week and location between June 1993 and August 1994. Preliminary surveys of diabroticites in the described locations resulted in successful sampling mainly on wild and cultivated cucurbits, corn and beans. In addition, associated plants, especially flowering ornamental plants, were searched. As diabroticites are mainly active between around 9 a.m. until about 12 a.m., collections were made during this time. Host plants and neighbouring vegetation were visually searched and beetles were collected with an aspirator. Cultivars in Actopan and Apazapan were searched for 30 min to 60 min by one or two collectors (quantifications are defined as beetle number per 30 min. collection time/collector/date). Wild hosts were searched for variable amounts of time depending on growth stage. Collecting seasons in each region were determined by host plant abundance.

Parasitoids and predators. Field collected diabroticites were inspected for external parasites under a binocular microscope. Dead insects removed from the cages were kept in petri dishes for observation of emergence of internal parasites. Predation in the field was recorded when observed and predator species were collected for later identification. Tachinidae were identified by Ken Ahlstrom, Dept. of Entomology, North Carolina State University, Mermithidae by Patricia Stock, Dept. of Nematology, University of California, Davis, and Laboulbeniales by Isabel Tavares, University Herbarium, University of California, Berkeley.

RESULTS

Insects. Seventeen species of diabroticites and one species of the genus *Gynandrobrotica* were found in the collection areas. Thirteen species were in the genus *Diabrotica* and four species in the genus *Acalymma* (Table 2). More diabroticite species were regularly encountered in the cooler locations in zone 2 than in the warmer zone 1 (Actopan: 7 species, Apazapan: 8 species, Coatepec: 14 species, Teocelo/Llano Grande: 14 species) (Table 2). The *Diabrotica fucata* group (nine species) was represented in both zones by a greater number of species than the *virgifera* group (three species). *D. curvilineata* was collected only twice, in Apazapan (1993) and in Llano Grande (1994). *D. bioculata, D. pulchella* and *D. circulata* were very rarely found (2-6 specimen each).

Table 2

Diabroticite species collected in climatic zone 1: A) Actopan, B) Apazapan and zone 2: C) Coatepec, D) Teocelo/Llano Grande. (+) common; (0) absent; (1 - 2) total number found during collecting seasons.

Species	A	B	C	D
Acalymma blomorum Munroe and Smith	+	+	+	+
A. fairmairei (Fabricius)	+	+	+	+
A. innubum (Fabricius)	+	+	+	+
A. trivittatum Mannerheim	0	+	+	+
Diabrotica fucata group				
D. balteata LeConte	+	+	+	+
D. biannularis Harold	0	1	+	+
D. bioculata Bowditch	0	1	+	+
D. circulata Harold	0	1	0	+
D. curvilineata Jacoby	0	1	0	1
D. dissimilis Jacoby	0	0	+	+
D. pulchella (Suffrian)	0	0	0	2
D. sexmaculata Baly	0	0	+	+
D. tibialis Baly	+	+	+	+
Diabrotica virgifera group				
D. porracea Harold	+	+	+	+
D. scutellata Baly	0	0	+	+
D. undecimpunctata duodecimnotata Harold	1	0	0	0
D. viridula (Fabricius)	+	+	+	+
Gynandrobrotica lepida (Say)	2	0	+	0

Insect abundance. All four *Acalymma* species were present throughout the year. *A. blomorum, A. fairmairei, D. balteata* and *D. scutellata* appeared to reach peak abundance in different months. *A. blomorum* were most abundant during the growing season of cultivated cucurbits (July-September), whereas *A. fairmairei* were most abundant in the winter months (January-March), during the growing season of *C. moschata. D. balteata* was collected in highest numbers from corn/cucurbit mixed-cultures during the summer months, and *D. scutellata* was only collected when *C. martinezii* bloomed (March/May-June/August). The most abundant species in all collection areas were *D. balteata* and *A. blomorum*. All other species were infrequently collected and conclusions on their seasonal occurrence could not be drawn.

Host plants. Insects were collected from a variety of different host plant families depending on locations and seasons. Main hosts visually searched for beetles were plants in the family Cucurbitaceae. *C. martinezii* was the most abundant wild cucurbit species. It was found mainly as a weed in coffee plantations, and occasionally along roadsides and fences in Coatepec and Teocelo/Llano Grande. The species was found only at one location in Actopan (June 1994) and was not

found in Apazapan. Wild *C. argyrosperma* subsp. *sororia* was found at only one location in Actopan (October 1993). Wild *Momordica charantia* was very abundant along roadsides and fences in Apazapan and less frequently in Actopan. It was not found in Coatepec and Teocelo/Llano Grande. Cultivated *C. pepo, C. moschata,* and *C. argyrosperma* subsp. *argyrosperma* were found in private gardens in Actopan and Coatepec, and in gardens as well as in larger agricultural fields in Apazapan and Teocelo. *Cucumis melo* and *C. sativus* were grown rarely in gardens, and only once (October 1993) in a larger field in Actopan. *Citrullus lanatus* was cultivated in agricultural fields in Actopan and Llano Grande. *Lagenaria siceraria* was found once in a field close to Llano Grande (September 1994). *Luffa cylindrica* was found throughout the year in all four locations along fences in villages and walls of houses, and *Sechium edule* was cultivated in larger areas in Actopan and Teocelo. Corn was grown in larger agricultural fields in Apazapan, Actopan, and Teocelo/Llano Grande. Beans were cultivated in Actopan and Apazapan, and peanuts were grown only in Apazapan.

Diabroticite-host plant associations. Diabroticites were found mostly when cucurbits where blooming. *Acalymma* spp. were present continuously throughout the collecting seasons and no *Acalymma* spp. was found on any other host except cucurbits. *Acalymma* spp. were found on cucurbits during all growth stages, but were most abundant during flowering. *Diabrotica* spp. were only found on cucurbits during the flowering stage. Main hosts in the family Cucurbitaceae were species in the genus *Cucurbita: C. argyrosperma* subsp. *argyrosperma, C. martinezii, C. pepo,* and *C. moschata. C. martinezii* was the only cucurbit species from which all diabroticites found in the collection areas could be sampled (Table 3). *A. blomorum, D. balteata,* and *Gynandrobrotica lepida* were collected on two occasions from a flowering *C. argyrosperma* subsp. *sororia* (Actopan, October 1993). On only one occasion were *D. balteata* and *A. blomorum* collected from *Momordica charantia* in (Apazapan, 248 flowers counted, 2 *D. balteata,* 11 *A. blomorum* collected). In this case, the plant was growing along a fence bordering a field with corn interplanted with *C. moschata,* where a high number of diabroticites were found. Diabroticites were not found on *Citrullus lanatus* (Actopan, April 1994; Llano Grande, July 1994).

Diabrotica spp. were collected on corn during two different growth stages of the host plant. Beetles fed on young corn (4-8 leaves) during early and mid whorl-stage and then again during the silk-stage. In the first stage, beetles were found on leaves and inside the whorl, and during the later silk-stage beetles were found feeding on silk and tassels. Species regularly found in corn were *D. balteata, D. tibialis, D. porracea,* and *D. viridula* (Table 3). Occasionally, *D. dissimilis, D. biannularis,* and *D. sexmaculata* were collected in corn. *D. bioculata, D. circulata,*

D. curvilineata, D. undecimpunctata duodecimnotata and *D. pulchella* were found in corn (Apazapan, Llano Grande). *D. scutellata* was found only once in corn (Llano Grande, July 1994).

D. balteata was the only species collected from foliage of young beans in Apazapan and Actopan. Plants were insecticide treated so at later growth stages no insects were found. Peanuts were also treated with insecticides and no beetles were collected at any time of the season.

Table 3

Host plant associations of diabroticites (in order of frequency) from selected areas in Veracruz, Mexico. Insects were only rarely found on plant species in parentheses.

SPECIES	HOST PLANTS
Acalymma spp.	
A. blomorum	*Cucurbita argyrosperma, C. pepo, C. moschata, C. martinezii (C. sororia, Sechium sedule, Momordica charantia)*
A. fairmairei	*C. martinezii, C. moschata, C. argyrosperma, C. pepo (Sechium sedule)*
A. innubum	*C. moschata, C. argyrosperma C. pepo, C. martinezii*
Diabrotica fucata group	
D. balteata	*C. argyrosperma, C. pepo, Zea mays, C. moschata, C. martinezii, Phaseolus vulgaris, Beta vulgaris (C. sororia, Luffa cylindrica, M. charantia, Hibiscus rosa-sinensis)*
D. biannularis	*C. martinezii, C. argyrosperma, C. pepo, C. moschata, B. vulgaris, Brugmansia candida (Ipomoea wolcottiana, L. cylindrica)*
D. bioculata	*C. martinezii, B. vulgaris (B. candida, H. rosa-sinensis)*
D. circulata	*Z. mays (2x)*
D. curvilineata	*Z. mays (2x)*
D. dissimilis	*C. martinezii, C. moschata, B. candida, I. wolcottiana, H. rosa-sinensis*
D. pulchella	*Z. mays (3x)*
D. sexmaculata	*C. martinezii, B. vulgaris, C. moschata, I. wolcottiana, H. rosa-sinensis*
D. tibialis	*C. martinezii, C. pepo, Z. mays, B. vulgaris, C. moschata, C. argyrosperma (H. rosa-sinensis)*
virgifera group	
D. scutellata	*C. martinezii (C. pepo, Z. mays)*
D. porracea	*Z. mays, C. martinezii (C. pepo, C. moschata, B. candida, H. rosa-sinensis)*
D. viridula	*Z. mays, C. argyrosperma, C. martinezii (C. pepo, C. moschata, H. rosa-sinensis)*

Several diabroticite species showed distinct host plant associations (Table 3). *D. scutellata* was almost exclusively collected from wild, bitter *C. martinezii*. It was collected once from *C. pepo* in Llano Grande and Coatepec, and once from corn in Llano Grande. *Gyandrobrotica lepida* was collected from *C. martinezii* in Coatepec and once from *C. argyrosperma* subsp. *sororia* in Actopan. On *C. martinezii* in the pre-bloom stage (Jan.-March) only *A. blomorum* and *A. fairmairei* were found. During the flowering period *D. scutellata* was the dominant species on *C. martinezii*. It was almost exclusively found in flowers and in highest numbers

in male flowers. *A. innubum* was occasionally (5 times) collected from *C. martinezii* flowers, and all *Diabrotica* spp. were regularly found in low numbers on flowering plants of this cucurbit species.

Diabroticites were commonly encountered on a variety of other plant families. In vegetable gardens in Coatepec and Llano Grande *D. balteata, D. tibialis, D. sexmaculata, D. biannularis*, and *D. bioculata* were collected from *Beta vulgaris* L. (Chenopodiaceae). *D. sexmaculata, D. dissimilis, D. biannularis, D. bioculata*, and *D. porracea* were regularly found in the flowers of *Hibiscus rosa-sinensis* L. (Malvaceae), *Brugmansia candida* Pers. (Solanaceae) and *Ipomoea wolcottiana* Rose (Convolvulaceae) (Table 3).

Differences in species composition and abundance could be found in Apazapan in corn and *C. argyrosperma* subsp. *argyrosperma* monocultures and corn/*C. argyrosperma* bicultures throughout the growing seasons 1993 and 1994 (Table 4), and close to Llano Grande in 1994. In corn monocultures only *Diabrotica* spp. were found (12.IV.- 25.VII.94). *D. balteata* were most abundant, *D. viridula* was regularly collected, while *D. porracea* and *D. tibialis* were only occasionally found. In cucurbit monocultures, a variety of *Diabrotica* spp. and *Acalymma* spp. were collected, but *Acalymma* were found in higher numbers than *Diabrotica* throughout the season (29.VI.-30.VII.94). *A. blomorum* and *D. balteata* were the most abundant species. Numbers of *A. blomorum* (50-72 beetles/sampling date) were 5-7 times higher than *D. balteata* (7-11 beetles/sampling date). Between 1-5 specimen of *A. innubum, A. fairmairei, A. trivittatum* and *D. viridula* were collected at each date. In corn/*C. argyrosperma* bicultures in Apazapan where the cucurbit was more abundant than corn, both genera occurred, but *Acalymma* were more numerous than *Diabrotica*. Again, *A. blomorum* was the most abundant species (60-173 beetles/sampling date), followed by *D. balteata* (5-33 beetles/sampling date). *A. innubum* (4-27 beetles/date) and *D. viridula* (1-4 beetles/date) were regularly collected, whereas *D. biannularis, D. porracea* and *D. tibialis* were only occasionally collected (1-3 beetles/date).

In the corn/cucurbit bicultures in another location close to Apazapan, where corn and *C. argyrosperma* were present in about equal numbers, insect species composition and numbers were determined by the different growth stages of the two host plants (Table 4). At the beginning of the field season (late May), during the early whorl-stage of corn, *Diabrotica* spp., especially *D. balteata*, were most abundant. Later, during the silk-stage of corn and the blooming of the cucurbit (29.VII.94) *Acalymma* spp. became more abundant and *A. blomorum* dominated the community until the end of the cucurbit flowering season (6.IX.94). A similar situation could be observed in a corn/*C. moschata* biculture close to Llano Grande. The number of *A. blomorum* increased during the collection period (26.VII.94: 29 individuals, 29.VII.94: 67 ind., 4.VIII.94: 102 ind.) and decreased at the end of

the flowering season of the cucurbit (11.VIII.94: 22 ind.), whereas the numbers of *D. balteata* steadily decreased during the same time (26.VII.94: 15 individuals, 29.VII.94: 9 ind., 4.VIII.94: 4 ind., 11.VIII.94: 2 ind.).

Table 4

Diabroticite species collected in a corn/*C. argyrosperma* biculture in Apazapan (30 min, 1 collector, 1994).

Species	12.VII	16.VII	20.VII	25.VII	30.VII	3.VIII	6.IX
D. balteata	140	132	31	19	19	8	5
D. viridula	14	14	6	-	8	7	3
D. porracea	-	-	1	2	-	-	5
D. tibialis	-	-	1	-	-	-	1
A. blomorum	25	34	39	44	72	62	38
A. innubum	2	3	1	1	2	2	1
A. trivittatum	-	11	5	-	9	12	17
A. fairmairei	-	-	-	-	-	-	1

Parasitoids and predators. The main parasitoid found from all diabroticite species commonly encountered was a tachinid fly, *Celatoria compressa* Wulp (Diptera: Tachinidae). The species was found to parasitize the four *Acalymma* spp. as well as the three species in the *virgifera* group, and *D. balteata* and *D. tibialis* in the *fucata* group. Most of the tachinids were collected from the laboratory colonies when already in the pupal stage. The newly emerged *C. compressa* larvae were white, and turned quickly into dark brown pupae (pers. observ.). After 9 days (*D. balteata, D. scutellata*) to 12 days (*A. fairmairei*) adult flies emerged. Body size of insect host and parasitoid pupae and adults was positively correlated (Fig. 2). Parasitoid abundance was low (*A. faimairei* 2.7%, *A. blomorum* 1.0%, *D. balteata* 4.0%, *D. scutellata* 10.2%, *D. tibialis* 11.1%; as percentage of total number of insects collected), but parasitized insects were continuously encountered throughout the collecting period.

Nematodes in the family Mermithidae were found in two specimens of *A. fairmairei* and one specimen of *D. balteata* collected in Apazapan, and in another *D. balteata* specimen from Llano Grande. All nematodes were in the postparasitic stage and could only be identified to the genus level. *D. balteata* was parasitized by *Hexamermis* sp. The mermithid found in the second specimen could not be identified due to its morphological stage. *A. fairmairei* collected in Apazapan contained three mermithids in a multiple parasitism. Two specimens of *Hexamermis* sp. and one *Agamermis* sp. were found in a single insect. A multiple parasitism with different mermithid species has not previously been described in terrestrial insects (P. Stock, pers. comm.).

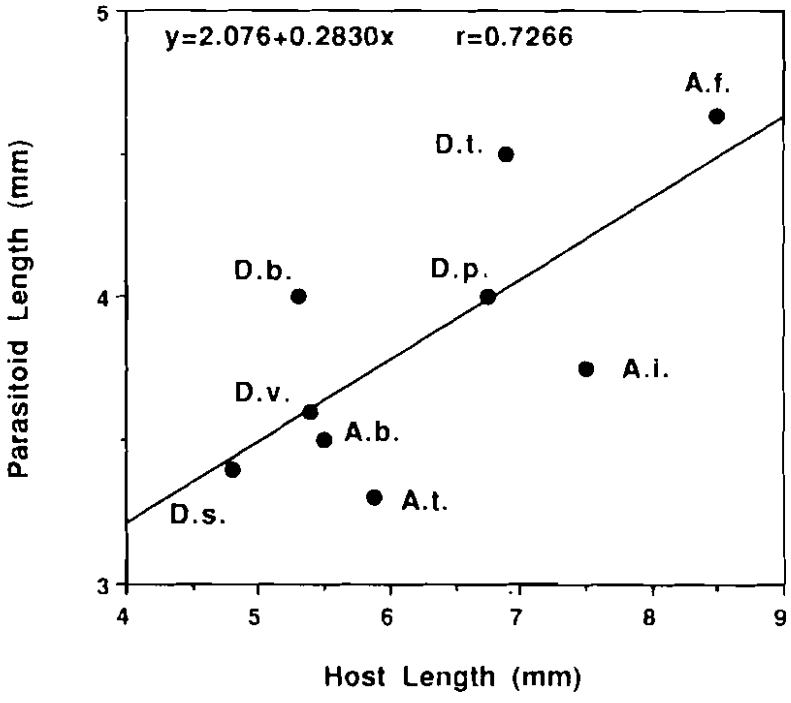

Figure 2

Correlation of mean host size (mm) and mean parasitoid size (mm) for 9 species of *Acalymma* and *Diabrotica* parasitized by the tachinid parasitoid *Celatoria compressa* (*A.f.* = *Acalymma fairmairei*, *A.b.* = *A. blomorum*, *A.i.* = *A. innubum*, *A.t.* = *A. trivittatum*, *D.b.* = *Diabrotica balteata*, *D.p.* = *D. porracea*, *D.s.* = *D. scutellata*, *D.t.* = *D. tibialis*, *D.v.* = *D. viridula*)

External parasitic fungi of the order Laboulbeniales were found on several occasions on *A. fairmairei* collected from *C. argyrosperma* ssp. *argyrosperma* (Actopan) and *C. martinezii* (Coatepec), once on *D. viridula* (*C. moschata*, Llano Grande), and *A. blomorum* (*C. moschata*, Llano Grande). The species has been identified as *Laboulbenia diabroticae* Thaxter. It demonstrated morphological variations which might be due to the different locations where it was collected (I. Tavares, pers. comm.).

On one occasion an *A. blomorum* specimen parasitized with *Beauveria bassiana* (Balsamo) Vuillemin (pers. observ.) was found on a *C. moschata* leaf in Llano Grande.

Predation on adult diabroticites was observed several times in the field. In Apazapan and Llano Grande, a Green Lynx spider (Oxyopidae: *Oxyopes salticus*) was observed preying on *D. balteata* and *A. blomorum*, respectively (pers. observ.). Three predatory hemipteran species of the family Reduviidae were

observed in Apazapan, Teocelo and Llano Grande capturing and feeding on *D. balteata, D. viridula* and *A. blomorum* (pers. observ.). Observations of prey captures by spiders and hemipterans were made in corn/*C. moschata*, corn/*C. argyrosperma* subsp. *argyrosperma* biculture (six occasions) and on *C. martinezii* (three occasions).

DISCUSSION

The number of diabroticite species present varied by climatic regions. A greater number was found in the temperate, higher altitude regions with greater rainfall. The driest months in the temperate zone locations still have an average rainfall of more than 50 mm, whereas the driest months in the warmer regions only receive about 10-20 mm rainfall monthly. The long dry period in these areas restricts the growing season of the main hosts of diabroticites to July through September. Multivoltine species in the genus *Acalymma* and in the *Diabrotica fucata* group cannot complete several generations per year under such conditions, because soil moisture and host plant abundance are not sufficient throughout the major part of the year. In both locations, Actopan and Apazapan, only the highly polyphagous *D. balteata* and *D. tibialis* represented the *fucata* group. Both species can complete their life cycle on a wide variety of host plants in different families and do not depend on the presence of their main cultivated hosts (Saba 1970, Branson & Krysan 1987).

The large number of species in the *Diabrotica fucata* group described for the tropics (Wilcox 1972) was represented by nine species compared to four species in the *virgifera* group. The univoltine *virgifera* group was represented by four species in Veracruz. Only two species, *D. porracea* and *D. viridula* were collected in all regions throughout the year. The diapausing stage is maybe the adult, because both species were collected continuously but in very low numbers from flowering ornamental plants (*Brugmansia candida, Hibiscus rosa-sinensis, Rosa* spp.) during the winter. Higher numbers were collected only during the corn growth season. This observation provides further support for the idea that the major reason for univoltism in mono/oligophagous insects might be the seasonal abundance of host plants (Branson & Krysan 1981, Krysan 1993).

Some patterns could be detected for the host plant associations of several diabroticite species. *D. scutellata* was collected only during the flowering season of its major host plant, *Cucurbita martinezii*. This species seemed to be the most host specific diabroticite found in the sampling areas in Veracruz. It reached highest numbers during the flowering season of *C. martinezii*. It could not be collected during other times of the year nor was it present in the warmer regions (Zone 1) where *C. martinezii* was not found. As a supposedly univoltine species,

(J.L. Krysan, pers. comm.) its life cycle might be synchronized with the growth season of its major host. *C. martinezii* had different peak flowering time during the two collecting seasons. In 1993, flowers were found between January and June, and in 1994, between May and October. Further research is necessary to understand if this has any implications for the biology of *D. scutellata*.

D. balteata was collected in highest numbers during the growth season of corn and the flowering season of cultivated cucurbits. The presence of larger populations of *Diabrotica* spp. with overlapping generations in corn in the reproductive stage was also reported by Rodriguez & Magallanes (1994) for the states of Tamaulipas and Veracruz (Mexico). Negative impact of dryness and cold have been demonstrated for diabroticites (Saba 1970, Brust & House 1990). In addition to host plant seasonal abundance, the climatic conditions in the warmer and drier regions in Veracruz might restrict beetle abundance and diversity.

Several species in the *fucata* group were not found in cultivated cucurbits. *D. bioculata, D. circulata, D. curvilineata* and *D. pulchella* were collected from corn, swiss chard (*Beta vulgaris*) and ornamental plants (*Hibiscus rosa-sinensis, Rosa* spp.), but only *D. bioculata* was encountered frequently enough to allow any conclusions as to its host plant associations. *D. biannularis, D. dissimilis and D. sexmaculata* were found on cultivated cucurbits and on other host plants from different families, and can be considered generalists as adults.

All four *Acalymma* spp. found in the collection areas were encountered throughout the year in cultivated cucurbits, but their peak abundance was correlated with the flowering period. *A. blomorum* was the most abundant species in all sampling areas. The high numbers found throughout the year are evidence for its multivoltinism.

Interestingly, all species regularly collected were found on wild, bitter *C. martinezii* during the flowering period. In laboratory experiments testing the host breadth of 11 species of mexican diabroticites in the genera *Acalymma* and *Diabrotica, D. balteata* and the three species in the *virigifera* group (*D. porracea, D. scutellata, D. viridula*) preferred leaves of non-cucurbit hosts (corn and beans) over a cultivated cucurbit (*C. pepo*). *D. dissimilis, D. tibialis*, and *D. sexmaculata* preferred the cucurbit host over the non-cucurbits. In a second test series including a bitter cucurbit in the choice tests, the presence of the bitter cucurbits altered host preferences and all species fed significantly more from the bitter cucurbit host (Eben 1995). Since not all of the diabroticite species tested in bioassays and observed in the field accepted the cultivated cucurbits as hosts, but without exception all of them were collected from bitter *C. martinezii* in the field or preferred the bitter cucurbit as host in feeding assays, the secondary compounds typically produced in wild species of the genus *Cucurbita*, the

cucurbitacins, seem to influence to some extent the association of the Mexican diabroticites tested and observed with plants in the genus *Cucurbita* (Eben 1995).

To date *Celatoria diabroticae* Shimer and *C. crawii* Coquillett are the only tachinid parasitoid mentioned for *Diabrotica* spp. (Chittenden 1905, Sell 1915, Gordon *et al.* 1987) and *A. vittatum* (Walton 1914). In our field surveys of parasitoids and natural enemies of diabroticites, we found that *Diabrotica* spp. had a higher parasitism rate (4-11%) by *Celatoria compressa* (Diptera: Tachinidae) than *Acalymma* spp. (1-2.7%). Ferguson *et al.* (1985) reported that 100% from *A. vittatum* adults collected in the field contained cucurbitacin accumulated by feeding on bitter cucurbit hosts. Only 20% of all *Diabrotica* spp. collected in the same area accumulated cucurbitacin. The low parasitism rate of *A. blomorum* found in our surveys compared to the higher rates in *Diabrotica* spp. may provide an indication for the putative function of cucurbitacins as defense chemicals for adapted herbivores (Ferguson & Metcalf 1985). Further research is necessary to confirm accumulation of cucurbitacins in field collected insects and to find a potential correlation of quantities of cucurbitacins and incidence of parasitism. Our survey is the first report of *C. compressa* as parasitoid of diabroticites.

Laboulbenia diabroticae Thaxter (Ascomycetes: Laboulbeniales) was found on *A. faimairei, A. blomorum* and *D. viridula* (Tavares 1985). It has so far been described only from *A. fairmairei*. The presence of the fungus could not be related to a certain host plant, but it was mainly found on *A. fairmairei* collected from *C. moschata* and *C. martinezii*.

Parasitism of field collected *A. fairmairei* and *D. balteata* by mermithid nematodes of the genera *Hexamermis* and *Agamermis* has also not been previously described. Nickle *et al.* (1984) reported a *Hexamermis* spp. from a Peruvian *Diabrotica* spp. where over 50% of the collected adult beetles were parasitized. We found only three specimens parasitized during the first year of sampling in Veracruz (1993). A common mermithid parasite in *D. balteata* in the United States is *Filipjevimermis leipsandra* (Cuthbert 1968, Poinar 1968, Elsey 1989). The identification of *Agamermis* spp. from *A. fairmairei* is the first report of a nematode in this genus from a diabroticite.

Incidence of predation was low. Spiders and predator y hemipterans of the family Reduviidae were observed preying on *D. balteata* and *A. blomorum* in corn and *C. martinezii*. Risch (1981) reported similar observations from corn fields in Costa Rica.

The observational data presented support the hypothesis that the association of diabroticites with Cucurbitaceae is mediated by cucurbitacins in the host plants. A number of species were not commonly found on cultivated cucurbits but were regularly collected from wild bitter *C. martinezii*. The ecological implications of this interactions remain unclear. The patterns of host plant associations observed in

the areas sampled show different degrees of intensity of the association of diabroticites with cucurbits which was also found in laboratory feeding choice assays (Eben 1995). Some species (*Acalymma* spp., *D. balteata, D. biannularis, D. tibialis*) were found on all cucurbits, others (*D. dissimils, D. porracea, D. scutellata, D. sexmaculata*) only on certain cucurbit species. Furthermore diabroticites seem to be more closely associated with cucurbits in the genus *Cucurbita*. Species in the genera *Lagenaria, Luffa*, and *Momordica* were not regular hosts despite their production of cucurbitacins and other terpenoids (Rehm *et al.* 1957). This observation did not support the hypothesis that cucurbitacins are mediator of the associations between Cucurbitaceae and diabroticites. There may be another factor as important as cucurbitacins for the acceptance of cucurbits as hosts by diabroticites, for example shape and color of flowers or floral odors. The broadening of the host range of *Diabrotica* spp. might be a more recent change as has been proposed for *Diabrotica* species currently distributed in the United States (Branson & Krysan 1981, Krysan 1993). Since all Mexican diabroticites observed and tested in bioassays showed an association with bitter *Cucurbita* spp., even if cucurbits are not their main hosts, further experimental studies to detect suitability of different host plants for the development of larvae and reproductive efficacy of adults are necessary to understand current changes that may be occurring in host ranges and to reveal the ecological importance of cucurbitacins.

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