THE NATURAL HISTORY OF *TANAOSTIGMODES PITHECELLOBIAE* (HYMENOPTERA: TANAOSTIGMATIDAE), A GALL-MAKER ON BLACKBEAD (*PITHECELLOBIUM KEYENSE*)

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Abstract

Tanaostigmodes pithecellobiae LaSalle, a chalcidoid wasp, induces foliar galls on *Pithecellobium keyense* Britton ex Britton & Rose, a mimosoid legume native to South Florida. This paper provides the first description of the gall-maker's natural history: it is monophagous and multivoltine; its phenology varies with the season of gall initiation; and it is preyed upon by chalcidoid parasitoids and by an unusual microlepidopteran "gall-miner".

Key Words: insect gall-makers, cecidology, plant galls, gall-making wasps

Resumen

Tanaostigmoides pithecellobiae LaSalle es una avispa que induce la formación de agallas en hojas de *Pithecellobium keyense* Britton ex Britton y Rose, una planta leguminosa originaria del sur de la Florida. Este trabajo representa la primera descripción de la historia natural de este insecto. Esta especie es monófaga, multiovular y su fenología varía con las épocas de producción de agallas. Es parasitada y devorada por chalcicoides y por un microlepidóptero poco común que causa minas en las agallas.

Tanaostigmodes pithecellobiae LaSalle (Hymenoptera: Tanaostigmatidae) induces foliar galls on *Pithecellobium keyense* Britton ex Britton & Rose, blackbead, a mimosoid legume native to South Florida. The gall-maker was named and described in LaSalle's (l987) taxonomic revision of the New World Tanaostigmatidae, a small but well-circumscribed family of gall-making chalcidoids. It is indicative of the present state of knowledge of the Tanaostigmatidae that of the 74 New World species treated in LaSalle's monograph, two-thirds (49) were new to science. The present paper is among the first to characterize the biology of a tanaostigmatid.

Blackbead is an arborescent, evergreen shrub of the coastal scrub zone and of pineland and hammock margins (Tomlinson 1980). Its leaves are bipinnately compound, with four to eight leaflets in two pairs (Tomlinson 1980). The leaflets are elliptical to obovate, 4-5 cm long, and dark green and leathery at maturity. New growth is produced in recurrent flushes throughout the year, but appears least abundant during the dry season. During the initial stage of leaf development, which lasts about 1 week, opposite leaflets are oriented with their upper surfaces facing one another, leaving the lower surfaces exposed (personal observation).

The congeneric *P. unguis-cati* (L.) Benth., catsclaw, is also listed by LaSalle as a host species for *T. pithecellobiae.* Catsclaw closely resembles blackbead in leaf and flower morphology and occupies similar coastal habitats (Wunderlin 1998, Tomlinson 1980). Blackbead and catsclaw occur sympatrically in the Florida Keys, but their ranges diverge on the mainland. Blackbead occurs on the Atlantic Coast to Martin County, while catsclaw occurs on the Gulf Coast to Hillsborough County (Wunderlin et al. 1996, Isely 1990, Little 1978).

This paper establishes the host specificity of *T. pithecellobiae*, provides the first description of its natural history, and examines seasonal variation in gall density and patterns of development.

Materials and Methods

Host Specificity

Host-plant specificity was determined by a survey of 463 individuals of the two candidate species at nineteen sites in South Florida, extending from Key West to Sanibel Island on the Gulf coast and to Juno on the Atlantic coast. I examined blackbead and catsclaw plants in areas where they occurred together and in areas where one or the other was absent. Each plant surveyed was scrutinized for the presence of galls, and where galls were present I quantified gall density per plant by haphazardly censusing 100 leaflets. Per site gall density was estimated by calculating the mean percentage of galled leaflets based on all galled plants censused at a given site.

Natural History

Study site. The primary study site was the Deering Estate, part of the Metro-Dade Park system, in Miami, Fl. I monitored about 20 blackbead plants growing along the shoulders of a roadway through a coastal pine rockland/oak hammock established on Miami oolitic limestone. Average temperatures in Miami range between 10 and 32°C (Tomlinson 1980), with an annual average of ~23°C (Migliaccio 1987). Rainfall averages ~1500 mm per year, with about 70% of the annual precipitation occurring during the May-to-October rainy season (Migliaccio 1987).

Gall-maker phenology. To determine gall-maker phenology, I followed the development from oviposition to gall-maker emergence of successive cohorts of galled leaflets. Between July l99l and March l993, I marked seven cohorts (designated I-VII) of newly galled leaflets. Each cohort consisted of at least 100 galled leaflets. I monitored four of these cohorts (I, II, V and VII) weekly from first emergence of the gall-maker to depletion of the cohort (with an 8 week gap in the case of cohort V). I have only partial data for cohorts III and IV, and cohort VI was destroyed by Hurricane Andrew (24 August 1992) prior to maturation.

Gall demographics. From November 1991 to March 1993, I periodically collected samples of 30 leaflets with mature galls for rearing in the lab. I set up 23 such samples, comprising 690 leaflets and approximately 5,000 galls. Each leaflet was maintained in its own 16 oz plastic container with a clear plastic lid for a minimum of 2 weeks. Moist tissue paper was kept in each container to maintain humidity. Temperature in the lab was approximately 20°C.

For each leaflet, I recorded the initial number of exited and unexited galls and marked the exited galls. I censused emerging wasps by species and sex and preserved voucher specimens of all wasps obtained. At the end of the rearing period, unexited galls were dissected and gall contents were recorded. M. E. Schauff of the U.S. Department of Agriculture (USDA) Agricultural Research Service/Systematic Entomology Laboratory provided species determinations.

I periodically collected additional leaflets with mature or immature galls for observation and dissection. Galled leaflets with leaf mines that encircled or invaded developing galls were also collected. I reared the caterpillars obtained from these "gall-mines" and sent larvae, pupae and moths to R. W. Hodges of the USDA Agricultural Research Service/Systematic Entomology Laboratory for identification.

Data Analysis

I constructed a phenology chart to show the duration of successive cohorts of galls and the timing of gall-maker emergence at the Deering Estate over a period of 22 months. To highlight seasonal variations in patterns of emergence, percent exited galls was plotted against the age of the galls (in weeks) for early, mid- and late season cohorts. To see if the proportion of emerging wasps per month differed statistically for early, mid- and late season cohorts, I used χ^2 contingency tables. Analysis of variance (ANOVA) was used to evaluate differences in gall density per cohort among early, mid- and late season cohorts.

To determine the statistical significance of the sex ratios for the wasps reared in the lab, I performed χ^2 goodness-of-fit tests.

All statistical tests were conducted using SAS version 6.1 (SAS Institute, 1990).

Results and Discussion

Tanaostigmodes pithecellobiae is monophagous (host- specific) and multivoltine. The phenology of gall-maker development varies seasonally and within a cohort. *T. pithecellobiae* is parasitized by at least two other chalcidoids and is preyed upon by an unusual "gall-mining" microlepidopteran.

Host Specificity

Eighty-two percent of the 266 blackbead plants censused between Key West and Juno had galls (Table 1). The percentage is even higher (96%) if the 30 blackbeads surveyed north of Boca Raton, on which no galls were found, are excluded. I found no galls on the 197 catsclaws censused between Big Pine Key and Sanibel Island.

In populations of blackbead containing galls, the mean percentage of galled leaflets per site (based on haphazard censuses of 100 leaflets per galled plant) varied from <10 to >40% (Table 1).

In addition to blackbead (*P. keyense*), LaSalle (1987) lists the sympatric catsclaw (*P. unguis-cati*) as a host plant for *T. pithecellobiae*. But LaSalle examined only museum specimens of *T. pithecellobiae* galls, and the congeneric putative host plants are often confused. From my survey of blackbead and catsclaw plants growing throughout most of their South Florida ranges, I conclude that only blackbead is a host for *T. pithecellobiae,* and that the gall-maker is therefore monophagous in the strictest sense (i.e., a single host-plant species).

At present, *T. pithecellobiae* is recorded only from Florida (LaSalle 1987). The distribution of its host plant is, however, complicated by taxonomic uncertainties. Long & Lakela (1976) list *P. keyense* as a South Florida endemic. Wunderlin et al. (1996) and Wunderlin (1998), using the same binomial, do not consider the taxon a Florida endemic, but fail to specify its range beyond Florida. Other authors (e.g., Little 1978, Tomlinson 1980, Isely 1990) refer to blackbead as *P. guadalupense* (Pers.) Chapm., with a distribution which includes the Yucatan peninsula and the West Indies. Further clarification of the degree of host specificity of *T. pithecellobiae* requires resolution of the taxonomic status and geographical distribution of its Florida host plant.

TABLE 1. A SURVEY OF 463 INDIVIDUALS OF BLACKBEAD AND CATSCLAW AT NINETEEN SITES FROM KEY WEST TO SANIBEL ISLAND ON THE GULF COAST AND TO JUNO ON THE ATLANTIC COAST. SHOWN ARE THE TOTAL NUMBER OF PLANTS CENSUSED AT EACH SITE; THE NUMBER OF EACH SPECIES CENSUSED; THE PERCENT OF INDIVIDUALS OF EACH SPECIES WITH GALLS; AND, FOR BLACKBEAD, THE MEAN PERCENT OF GALLED LEAFLETS PER SITE (BASED ON CENSUSES OF 100 LEAFLETS PER GALLED PLANT AT EACH SITE).

				Blackbead			Catsclaw	
Date	Site	Location	Total number plants surveyed	Number plants	% Plants with galled leaflets	Mean % galled leaflets per site	Number plants	% Plants with galled leaflets
12/31/91	Harry Harris Rd.	Key Largo	100	60	92	24.3 ± 18.8	40	0
12/31/91	Easement PP181	Key Largo	49	42	100	18.1 ± 9.7	7	0
12/31/91	Dynamite Docks	Key Largo	50	12	100	9.3 ± 5.7	38	0
12/31/91	Old SR 905	Key Largo	2	2	100	NA	0	0
06/10/92	Deering Estate	Miami	20	20	100	NA	0	0
06/26/93	Cactus Hammock	Big Pine Key	30	5	100	36.2 ± 13.97	25	0
06/26/93	Wilder Blvd.	No Name Key	10	10	100	25.9 ± 9.2	0	0
06/26/93	Blue Hole	Big Pine Key	10	10	100	42.3 ± 19.2	0	0
06/26/93	Roadway	Little Torch Key	10	10	90	13.4 ± 7.3	0	0
06/26/93	Roadway	Sugarloaf Key	10	10	100	19.4 ± 9.1	0	0
06/26/93	Little Hamaca Park	Key West	10	10	100	37.0 ± 13.9	0	0
07/17/93	Catsclaw Trail	Rookery Bay	36	0	0	NA	36	0
07/17/93	Delnor-Wiggins Pass	Naples	21	0	0	NA	21	0
07/17/93	Ding Darling NWR	Sanibel	30	0	0	NA	30	0
07/31/93	H. T. Birch State Park	Ft. Lauderdale	25	25	100	43.1 ± 13.0	0	0
07/31/93	Red Reef Park	Boca Raton	9	9	78	17.8 ± 19.9	0	0
07/31/93	Gumbo Limbo EnvCnt	Boca Raton	2	2	0	NA	0	0
07/31/93	MacArthur Beach SP	N. Palm Beach	19	19	0	NA	0	0
07/31/93	A1A N of Marcinski	Juno	20	20	0	NA	0	0
		Totals	463	266	82		197	0

The absence of *T. pithecellobiae* galls from the 30 blackbead plants surveyed north of Boca Raton suggests that the gall-maker may be excluded from the northernmost parts of its host plant's range.

Gall-maker Phenology

Tanaostigmodes pithecellobiae females oviposit on the lower surface of expanding leaflets within 1 week of bud break. One bladder of the encyrtiform egg is inserted beneath the lower epidermis of the rapidly growing young leaflet; the other bladder, connected to the first by a short stalk, remains on the leaflet surface for 1 or 2 days. Apparently the inserted bladder absorbs the contents of the external one, which disappears. Within a few days the eggs hatch and larval feeding begins.

Gall development parallels leaflet development. It takes 8 to 10 weeks for leaflets to become dark green and leathery. During this time the galls develop from pimple-like eruptions on the upper surface of the leaflet to tumor-like swellings. Galls mature in about 10 weeks and do not change in physical appearance until emergence of the adult gall-maker (or one of its parasitoids). Gall-maker emergence begins only after 14 weeks (later for overwintering galls). Exited galls necrose and once all the galls are exited the leaflet abscises prematurely.

Since blackbead produces flushes of new growth throughout the rainy season, *T. pithecellobiae* is able to initiate several (overlapping) generations per year. A mass emergence of overwintering gall-makers may result in high densities of galls (per leaflet) on the first rainy season flush. Because of differential rates of gall-maker development within a cohort, emergences may be staggered to take advantage of the patchier availability of oviposition sites as the season progresses.

The time required for the development of insect gall-makers from oviposition to eclosion of the adult varies from a few days to over a year (Mani 1964) and may be prolonged by diapause (Mani 1964, Abrahamson and Weis 1987). *T. pithecellobiae* galls initiated in early or mid-season (March-July) may complete their emergence in as few as 14 weeks. Some mid-season wasps, as well as wasps oviposited late in the season, apparently undergo larval diapause and thus avoid emergence in the dry season when oviposition sites are unavailable.

Gall Demographics

Between February 1992 and March 1993, I reared 892 wasps from galls collected at the Deering Estate. Excluding 4 unidentified wasps of uncertain role, 65% were *T. pithecellobiae* and 35% were parasitoids belonging to 2 chalcidoid genera in the Eulophidae (Table 2). *Chrysonotomyia* sp. outnumbered *Aprostocetus* sp. by 2 to 1. Neither has been identified to species (M. E. Schauff personal communication). I obtained pupae of both parasitoid species from dissected galls and it appears that both are endoparasitoids on the later stages of gall-maker development.

Sex ratios of the gall-maker and its 2 major parasitoids showed a statistically significant 60:40 female bias (Table 2).

The only predator obtained was an undescribed microlepidopteran in the Cosmopterygidae (R. W. Hodges personal communication). The caterpillar mines into developing galls and consumes both gall tissue and the gall-maker, leaving only the upper and lower epidermis of the leaflet.

The "gall-mining" caterpillar is of interest both taxonomically—it may represent a new genus within the family Cosmopterygidae (Hodges personnel communication)—and ecologically. Mani (1964) recognized "cecidophages" (i.e., "gall-eaters") as a

TABLE 2. A SUMMARY OF WASPS REARED OVER A 13 MONTH PERIOD (FEBRUARY 1992 TO MARCH 1993) FROM GALLED LEAFLETS COLLECTED AT THE DEERING ESTATE, MIAMI. SEX RATIOS ARE SIGNIFICANTLY FEMALE-BIASED; SEX RATIOS AMONG THE THREE SPECIES DID NOT DIFFER. TOTAL PERCENT PARASITISM = 35.4%.

	Sex ratios				% of galls yielding each species
Species	Number females	Number males	Total number	% female	
T. pithecellobiae	345	231	576	59.9[1]	64.6
Chrysonotomyia sp.	126	90	216	58.3[2]	24.2
Aprostocetus sp.	61	39	100	61.0[3]	11.2
Totals	532	360	892	59.6[4]	100.0

[1] χ^2 (1) = 22.16, p < 0.01.
[2] χ^2 (1) = 5.67, p < 0.025.
[3] χ^2 (1) = 19.36, p < 0.01.
[4] χ^2 (2) = 0.246, p > 0.88.

"highly specialized group that feed either preferentially or obligatorily on galls". He singled out "cecidophagous insects [which] bore into the tissues of galls, eating the entire flesh [of the gall] and leaving only the outer skin in the form of an empty bag, inside of which they even pupate". Several microlepidoptera are mentioned by Mani as belonging to this category.

Gall Season and Cohort Longevity

There was a distinct seasonality to gall-maker development as shown by the 7 cohorts monitored at Deering Estate over a 22 month period (Fig. 1). Gall season, the period of gall initiation and active development, corresponds roughly to the traditional South Florida rainy season (Chen and Gerber 1990), anticipating it by 2 months (March-April) during which mean precipitation increases from the November-Febru-

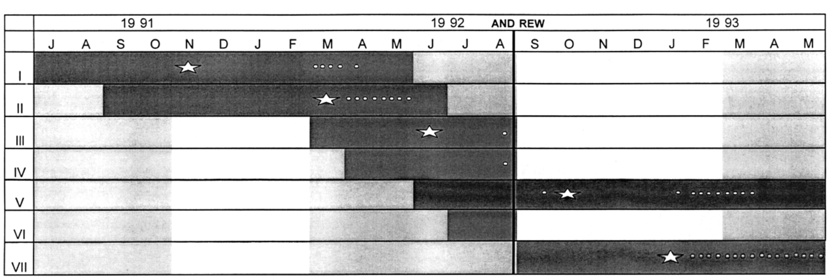

Fig. 1. A 22-month history of seven successive cohorts of galls at the Deering Estate, Miami (July 1991 to June 1993). Gall season (March to October) is indicated by stippled background. Width of horizontal bars indicates duration of cohort. Stars show first confirmed emergence of *T. pithecellobiae*; dots show weeks for which additional exits—either *T. pithecellobiae* or parasitoids—were recorded. Heavy vertical line represents Hurricane Andrew (August 24, 1992).

ary low. Within the gall season, I distinguish 3 periods: early (March-April), mid (May-July) and late (August-September). Each of the 7 cohorts was initiated during one of these three periods. Cohort VI was destroyed by Hurricane Andrew prior to maturation and is excluded from the following analysis.

The 2 early season cohorts, cohorts III (early March 1992) and IV (mid April 1992), showed first emergences in their 14th and 16th weeks, respectively (though for cohort IV, I do not have a confirmed gall-maker exit for that period) (Fig. 1). Data are not available for these 2 cohorts from mid June to late August. But on August 21, with only 18% of its original 1,195 galls present (80% of which were exited), cohort III had essentially completed its development within 24 weeks. Similarly, only 14% of cohort IV's original 1,141 galls remained on August 21, its 16th week, and of these 16% showed exit holes. It is likely that many (if not most) of these galls were exited before August 21 and their leaflets abscised. Further development of these cohorts was cut short by Hurricane Andrew.

The 2 mid season cohorts, cohorts I (mid-July 1991) and V (mid-June 1992), also produced gall-maker adults after 14 weeks, but emergence was discontinuous, with a hiatus during the dry season (Fig. 1). For cohort I there was a 12 week gap (November-February), after which emergences resumed and continued until April. Data are lacking for cohort V from November to early January, but I have records for weekly emergences from January to March (Fig. 2). Thus cohort V deviated from the pattern set

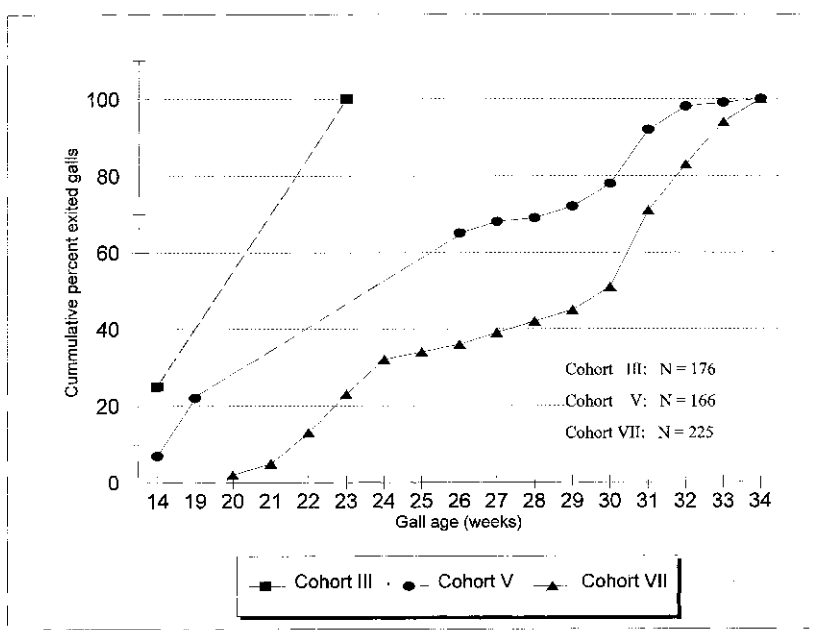

Fig. 2. Seasonal variation in patterns of gall-maker emergence. A comparison of the seasonal variation in patterns of gall-maker emergence among early (III), mid- (V) and late (VII) season cohorts of galls at the Deering Estate, Miami. Percent exited galls based on total number of exited galls recorded. Dotted lines for cohorts III and V indicate weeks for which data are unavailable. Cohort III galls were initiated about 1 March 1992; cohort V galls initiated about 10 July 1992; cohort VII galls initiated about 1 September 1992.

by cohort I by yielding gall-makers during the dry season. For both cohorts gall-maker emergence extended over a period from 14 to 32+ weeks.

The two late season cohorts, cohorts II (mid- September 1991) and VII (early September 1992), were both initiated within 8 weeks of the onset of the dry season (Fig. 1). Cohort II yielded wasps only after 21 weeks, while cohort VII began to show exits at week 20 (Fig. 2). Both cohorts produced continuous weekly emergences at least through their 30th weeks. In both cases gall-maker emergence was delayed by the onset of the dry season. However, cohort VII wasps began to emerge in January 1993, about 2 months earlier than cohort II wasps had emerged the previous year.

The earlier emergences of cohort V and cohort VII gall-makers compared to the corresponding cohorts of the previous year correlate with higher temperatures (Fig. 3) and greater rainfall (Fig. 4) in January 1993 compared to January 1992.

Seasonal Variation in Patterns of Development and Gall Density

Comparison of early, mid-, and late season cohorts revealed distinctly different seasonal patterns of emergence (Fig. 2). Cohort III gall-makers developed more rapidly than cohort V or cohort VII gall-makers, as measured by the proportion of exited galls per month for the three cohorts ($\chi^2(2) = 528.2$, $p < 0.001$). Gall densities, the mean number of galls per leaflet, also varied with the season, being significantly greater for early season than for either mid- or late season galls (Table 3).

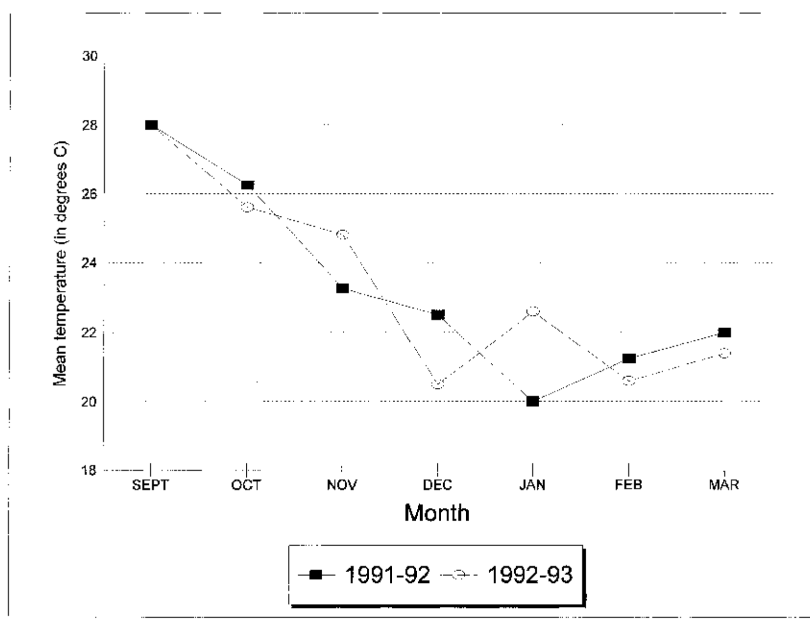

Fig. 3. A comparison of average monthly temperatures in °C for South Dade County for the winter of 1991-92 versus 1992-93. The sharp increase in monthly average temperature for January 1993 compared to January 1992 corresponded to the early emergence of overwintering gall-makers in cohorts V and VII. Temperature averages computed from data collected in Homestead and supplied by the U.S. Weather Service.

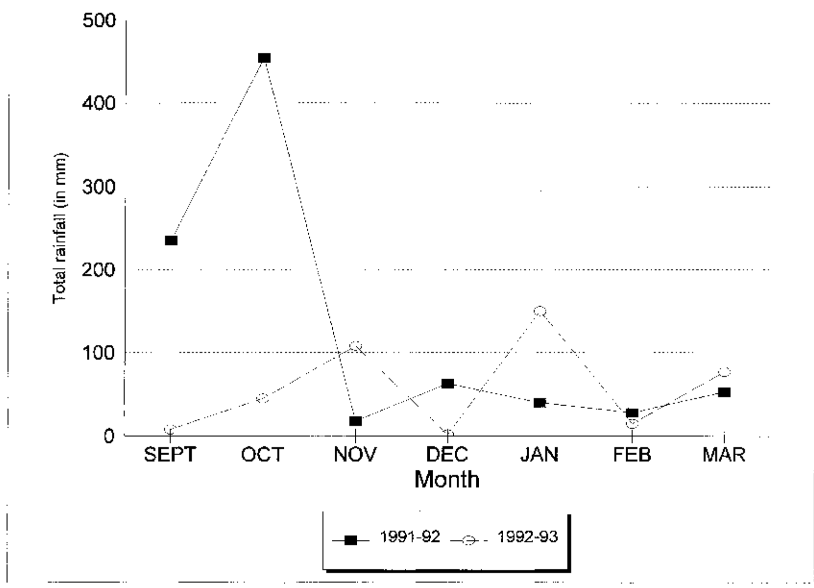

Fig. 4. A comparison of total monthly rainfall in mm for South Dade County for the winter of 1991-92 versus 1992-93. The sharp increase in rainfall for January 1993 compared to January 1992 corresponded to the early emergence of overwintering gall-makers in cohorts V and VII. Rainfall totals computed from data collected in Homestead and supplied by the U.S. Weather Service.

Gall densities and patterns of gall-maker emergence varied among early, mid- and late season cohorts. Early season cohorts had statistically greater gall densities (per leaflet) and completed development more rapidly than either mid- or late season cohorts (Table 3, Fig. 2). Greater gall densities per leaflet early in the season were related to the mass emergence of overwintering wasps.

TABLE 3: A COMPARISON OF THE MEAN NUMBER OF GALLS PER LEAFLET FOR EARLY (III), MID- (V), AND LATE (VII) SEASON COHORTS OF GALLS AT THE DEERING ESTATE. THE MEAN NUMBER OF GALLS PER LEAFLET WAS SIGNIFICANTLY GREATER FOR EARLY SEASON COHORT III THAN FOR MID-SEASON COHORT V OR LATE SEASON COHORT VII.

Cohort	Number galled leaflets	Mean number galls/leaflet[1]
III	106	11.23 ± 16.4
V	91	5.5 ± 4.5
VII	93	4.2 ± 2.8

[1]$F(2, 287) = 13.34$, $p < 0.001$.

Emergence schedules were protracted in mid- and late season cohorts compared to early season cohorts. Most early season wasps emerged within 24 weeks, with the first emergences at 14 weeks (Fig. 2). Some mid-season wasps also emerged in 14 weeks, but some overwintered and resumed emergence over a period from 26 to 32 weeks. No wasps emerged in 14 weeks in either of the two late season cohorts. Emergences began only after 20 weeks for cohort II and 21 weeks for cohort VII, and for both cohorts emergences continued for more than 30 weeks.

Insect gall-makers co-opt host plant resources and are thus dependent on the availability of those resources (Hovanitz 1959, Abrahamson & Weis 1987, Hori 1992). Seasonal variation in patterns of gall-maker development on blackbead are undoubtedly related to plant resource allocation which varies from wet to dry season. Within-cohort variations may be due to environmental stimuli, condition of the host plant, gall density per leaflet, per leaf, or per plant, or some combination of these factors.

Comparison of *T. pithecellobiae*'s phenology to that of other gall-making tanaostigmatids is precluded for lack of information on other species. A non-gall-making tanaostigmatid from India, *T. cajaninae* LaSalle, ecloses in less than three weeks (Lateef et al. 1985).

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