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STUDIES OF CECIDOMYIID MIDGES (DIPTERA: CECIDOMYIIDAE) AS COCOA POLLINATORS (*THEOBROMA CACAO* L.) IN CENTRAL AMERICA

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Abstract.—The role of cecidomyiids (Diptera: Cecidomyiidae) as floral visitors and pollinating agents of "cocoa," *Theobroma cacao* L. (Sterculiaceae), was examined in Costa Rica and, to a lesser degree, in Belize. Emphasis was placed on: (1) describing the mechanism of pollination, (2) determining the most abundant pollinating species, (3) estimates of adult population densities of midges in cocoa flowers, (4) confirmation of pollinating ability with the use of experimental field cages, (5) describing diurnal activity patterns of cecidomyiids in cocoa farms and in relation to similar patterns of anthesis in cocoa flowers, (6) description of communal roosting in spider webs by some species in cocoa farms, (7) observations on how midges interact with specific floral parts in cocoa, (8) estimates of seasonal changes in abundance of midges in cocoa flowers and in relation to annual flowering patterns of cocoa, and (9) determination of breeding microhabitats of cecidomyiids in cocoa farm habitats. By far the most abundant species in cocoa flowers at two localities in Costa Rica (Finca La Tigra and Finca Experimental La Lola) were *Clinodiplosis* sp. 1 and *Mycodiplosis* sp. 1, both new to science. Adults possess functional elongate mouthparts adapted for sucking liquids such as floral nectar, unusually long abdominal and leg hairs that trap cocoa pollen grains, very large compound eyes, and dusk-night-dawn activity patterns that match well the diurnal cycle of flower opening and pollination receptivity in cocoa. Female cecidomyiids are far more abundant as cocoa flower visitors than males, and both crawl inside enclosed floral parts associated with reproductive behavior in cocoa. The mechanism of pollination is similar to that described for ceratopogonids, but one major difference is the exploitation of the vivid yellow petal ligules as feeding sites by cecidomyiids, while these structures are largely ignored by ceratopogonids. Cecidomyiids feed at stomate-type nectaries lining petal ligules and the inner surfaces of petal hoods. Although as many as ten genera and 14 species of cecidomyiids occur in cocoa farms in Central America, only a few of these behave as consistent floral visitors to cocoa and related species of *Theobroma*. Cocoa flower-visiting forms are free-living with larval stages thriving in fungus-infected rotting organic debris, most of which is arboreal and includes: animal-generated holes in cocoa pods, rotting diseased cocoa pods and wilted cherelles, and epiphytic mosses. The observations of cecidomyiid densities being somewhat elevated in flowers during the drier months of the year may be due to either concentration of populations in shaded areas of cocoa or an actual increase in abundance at these times. Some cecidomyiids breed in the dry exocarp of rotting pods in trees during the dry season. Communal roosts in spider webs are re-used over several successive days as daytime resting sites for midges, probably as a predator (primarily anoles, mantids, and jumping spiders)-escape adaptation. The "pollinator reward syndrome" in cocoa and other *Theobroma* species is discussed from the standpoint of cecidomyiids, ceratopogonids, and wild bees as natural pollinating agents.

Several studies in different cocoa-growing regions (*Theobroma cacao* L.) of the world have concluded that tiny biting midges (Diptera: Ceratopogonidae) are the primary effective pollinators, although not exclusively so (e.g. Jones, 1912; Wellensiek, 1932; Cope, 1939; Billes, 1941; Posnette, 1942, 1944; Soetardi, 1950; Gnanaratnam, 1954; Van Der Knapp, 1955; Saunders, 1959; Walker, 1959; Dessart, 1961; Glendenning, 1962; Gorrez, 1962; Hernandez, 1965; Sampayan, 1966; Vello and Magalhaes, 1971; Edwards, 1973; De La Cruz and Soria, 1973; Kaufmann, 1973a, b, 1974, 1975a, b, c; Amponsah, 1972; Winder, 1972; 1977a, b, 1978a, b; Winder and Silva, 1975; Wirth and Waugh, 1976; Bystrak and Wirth, 1978; Young, 1982, 1983). Relative to the many genera and species of ceratopogonids suspected or proven to be effective pollinators of cocoa, several workers have noticed high abundances of similarly-sized cecidomyiid midges (Diptera: Cecidomyiidae) in cocoa farms, both in the New and Old World tropics (e.g. Privat, 1979; Winder, 1977c; Kaufmann, 1973b; Soria et al., 1980, 1981; Lucas, 1981), although the role of these midges in cocoa pollination is thought to be minimal (Winder, 1977b, 1978a). Yet Kaufmann (1937b), using experimental cages, demonstrated effective but low frequency pollinating activity of one species of cecidomyiid midge during the dry season in Africa, and subsequent studies using isotopes demonstrate that these midges transport cocoa pollen grains on their bodies in high frequency in some African farms (Decazy et al., 1980). Herein I present data indicating that several genera and species of Cecidomyiidae are effective cocoa pollinators in Central America, most notably in Costa Rica, and also summarize new ecological and behavioral information as related to the role of these midges as pollinators, and to their adaptation for breeding in cocoa farm habitats. I tentatively conclude that both ceratopogonids and cecidomyiids constitute one constellation of cocoa pollinators, but that other major pollinators (bees) have played equally important roles in the evolution of cocoa as a tropical rain forest tree species. Some studies have emphasized the role of small Diptera as effective, opportunistic pollinators of various plant species in shaded, moist forest habitats (e.g. Mesler et al., 1980; Levesque and Burger, 1982), environments that tend to accumulate high species density of Diptera (e.g. Vanhara, 1981), including cocoa farms (Bigger, 1981). Although it is generally maintained that Diptera are occasional pollinators (Percival, 1965; Kevan and Baker, 1983), several studies indicate more consistent associations with some plant species (Baumann, 1978; Vogel, 1978; Mesler et al., 1980; Gilbert, 1981; Steiner, 1983; Philbrick, 1983; Young, 1984a). With respect to *Theobroma* species (Sterculiaceae) overall, it may well be that Diptera are opportunistic "minor" pollinators that thrive best in moist, shaded habitats in the tropics, while "major" pollinators, ones coevolved with the floral structure and its associated physiology, are primarily wild bees (A. M. Young, in preparation) associated with *Theobroma* populations in more open, exposed habitats. Small flying insects such as tropical Cecidomyiidae are most active in shaded moist habitats (e.g. Mamaev, 1975; Fisher and Teetes, 1982; Barnes, 1930; Summers, 1975; Petralia et al., 1979; Shazli and Mostafa, 1980; Mogal et al., 1979; Kaufmann, 1973b) where they often exhibit marked diurnal cycles of activity (e.g. Shazli and Mostafa, 1980; Summers, 1975; Brewer, 1981; Brown and McGavin, 1982) and immature stages of free-living forms associated with fungi, molds, and rotting organic substrates such as leaf litter (e.g. Winder, 1977a; Gagné, 1977; Parnell, 1969). Because cecidomyiids and other allied dipterans often exhibit marked cycles in adult activity and breeding, both in the temperate zones and the tropics (e.g. Fontanilla-Barroga, 1962; Charlwood et al., 1982; Chiang, 1968; Kay, 1983), determination of potential roles in pollination of specific plant species such as cocoa has to be related to the known diurnal cycles of flower opening and anthesis (Wellensiek (1932) for cocoa). Because even decaying organic substrates can be limiting factors in the breeding structure of dipteran populations (e.g. Carpenter, 1983; Binns, 1980; Fallis and Snow, 1983; Siefert, 1980; Siefert and Barrera, 1981; Kaufmann, 1973b; Privat, 1979; Winder, 1977a), it is also necessary to determine whether or not cecidomyiids as cocoa pollinators breed within the cocoa farm environment, and this was done in the present studies. Although very few published reports indicate a possible role of cecidomyiids as pollinators (e.g. Soderstrom and Calderón, 1971), Winder (1977b) found cecidomyiids bearing cocoa pollen grains and also entering the petal hoods of cocoa flowers where they came into contact with viable pollen. Winder (1977b) suggests that the high abundance of these midges in cocoa farms indicates a possible role in cocoa pollination. Others, however, suggest that these midges are of negligible importance in cocoa pollination (e.g. Entwistle, 1972).

Localities and Study Methods

The following studies were conducted between 1978 and 1983 primarily at two localities on the Atlantic watershed of Costa Rica: (1) mechanism of pollination of cocoa by cecidomyiid midges and determination of most effective pollinating species; (2) breeding habits and life cycles of some species pollinating cocoa; (3) estimates of adult population densities in cocoa flowers at various times of the year; (4) experimental tests with cages to determine pollinating abilities of cecidomyiids; (5) estimation of overall cecidomyiid faunas associated with cocoa farms; (6) communal roosting habits of adult cecidomyiids in cocoa farms and relation to pollinating activity; (7) diurnal activity patterns of adult cecidomyiids in relation to cocoa tree flowering patterns and availability of possible pollination "rewards" in flowers. The greater portion of these studies were conducted at "Finca Experimental La Lola, near Siquirres (10°06'N, 83°30'W), Limon Province (see also Young (1983) for further desceiption of this site), and fewer studies at "Finca La Tigra," near La Virgen (10°23'N, 84°07'W), Heredia Province (see Young (1982) for additional information on this locality). In addition to these Costa Rican studies, I made preliminary surveys of adult cecidomyiids on cocoa flowers, and the larval microhabitats of some species, at the Hummingbird Hershey Cocoa Farm (approx. 17°08'N, 88°38'W), near Belmopan, Belize. Visits were made to all three localities during both wetter (rainy) and drier (dry) times (seasons) for one to three years. Because rainfall pattern has a marked influence on both the cycles of flowering in cocoa (e.g. Wellensiek, 1932; Alvim, 1977; Hutcheon, 1981;

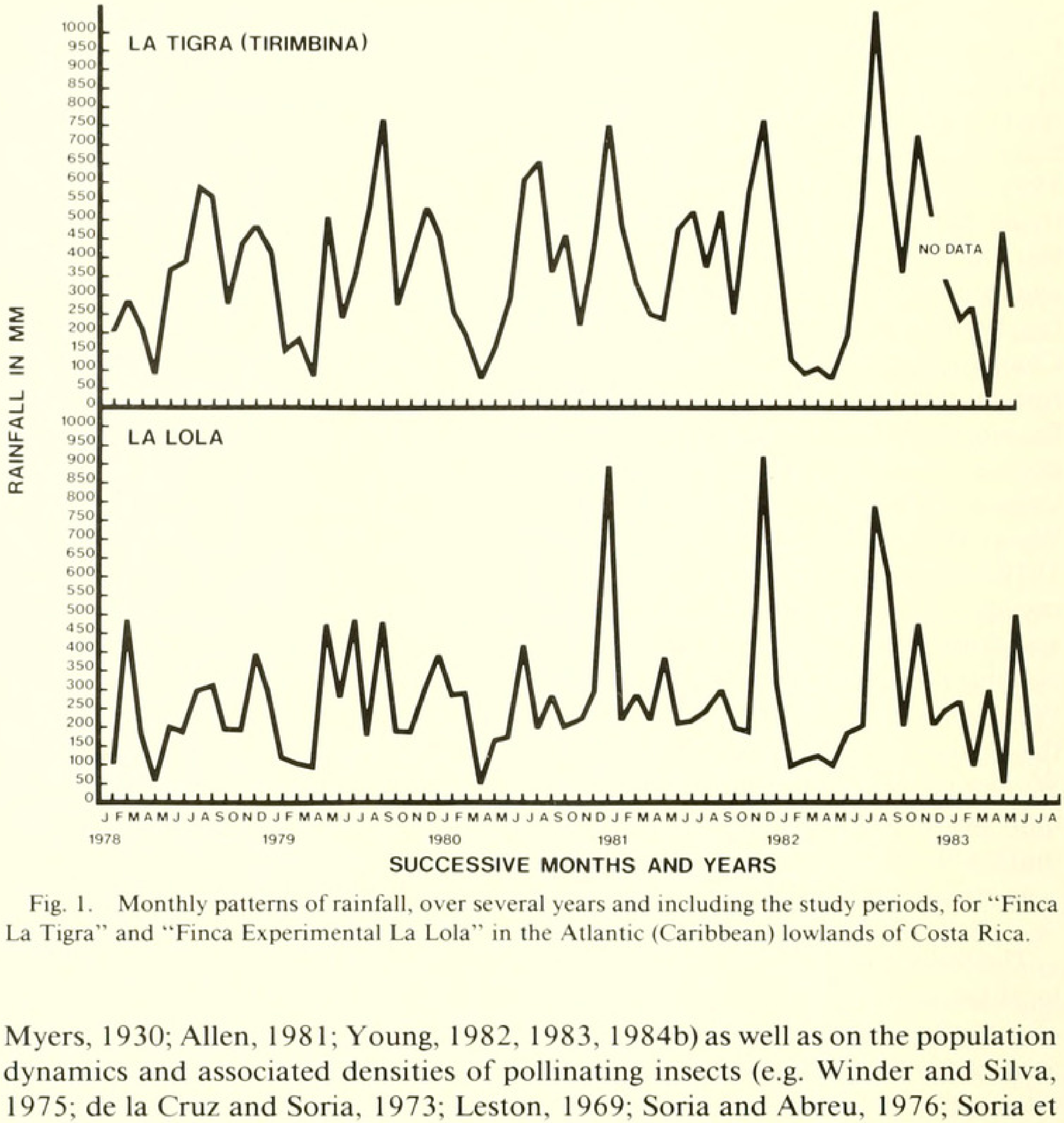

Fig. 1. Monthly patterns of rainfall, over several years and including the study periods, for "Finca La Tigra" and "Finca Experimental La Lola" in the Atlantic (Caribbean) lowlands of Costa Rica.

Myers, 1930; Allen, 1981; Young, 1982, 1983, 1984b) as well as on the population dynamics and associated densities of pollinating insects (e.g. Winder and Silva, 1975; de la Cruz and Soria, 1973; Leston, 1969; Soria and Abreu, 1976; Soria et al., 1981; Kaufmann, 1973b; Young, 1982, 1983, 1984a), monthly patterns of rainfall for "La Lola" and "La Tigra" are summarized here (Fig. 1).

The rainfall data (Fig. 1) encompass the periods of midge study at both localities, and it is apparent in the data from both localities that the driest times of the year are generally the months January through March, although the duration of reduced rainfall periods varies greatly from year to year. For the purposes of this paper, I assume that both localities have a short and irregular "dry season" ("veranillo") generally falling between January and March each year. Other studies (Young, 1982, 1983, 1984b) have shown that the dry season is a period of drastically reduced flowering in cocoa at these localities.

The study areas at La Lola include heavily-shaded cocoa, with the predominant shade tree being *Erythrina* sp. (Leguminosae), although other areas at the same locality have little shade. The La Lola studies included surveys of cecidomyiids in both the shaded (Area A) and unshaded (Area B) UF-29 cocoa studied in Young (1983) as well as a well-shaded clonal garden area with several clonal varieties (UF-677, UF-613, Pound-7, etc.). The La Tigra study area consisted of many varieties of cocoa planted beneath a thinned-out natural canopy of advanced secondary forest. At La Tigra there is a high incidence of rotting cherelles on cocoa trees while at La Lola these are removed quickly as they appear. In the La Tigra study area, many trees have sizable accumulations of epiphytic mosses and other epiphytes on the lower branches.

During both wetter and drier periods between 1978 and 1983, observations were made at both localities on the behavior of adult cecidomyiid midges at freshly-opened cocoa flowers at various hours of the day and night. Daylight transects through cocoa trees were taken by walking slowly and examining open flowers on each tree to determine the presence of cecidomyiids on or inside flowers. When a midge was encountered, it was scored as either "resting" motionless on an external portion of the flower, or as moving inside the flower. In the latter case, notes were kept on where the midge was located in the flower. Time of day was also recorded. These surveys generated a series of voucher specimens for those cecidomyiids actually found in contact with cocoa flowers. Other voucher series of cecidomyiids were obtained by collecting adult midges from communal roosts in spider webs in cocoa trees, and occasionally by rearing midges from larval samples.

Daylight observations at open cocoa flowers generally extended at intermittent intervals from 0600 to 1800 hours in both sunny and rainy weather, and nighttime samples from 1900 to 2300 and from 0400 to 0530 hours. Nighttime observations were aided by using red cellophane over a flashlight and occasionally by using a Night Vision infra-red viewing scope outfitted with a 50mm macrolens. Whenever midges were found moving inside flowers, detailed observations were made on this behavior. Additionally, behavior suggesting that midges were feeding on specific floral parts was followed up as much as possible. For example, early into the studies, I discovered that cecidomyiids (eventually determined to be *Mycodiplosis* sp. 1 and *Clinodiplosis* sp. 1) had their mouthparts embedded into the pliable, spongy tissue of the blade-like ligules extending from the petal hoods of cocoa flowers (see Cuatrecasas, 1964 for a detailed discussion of gross floral structure in cocoa), and when encountered in the field, observations were extended until the feeding stopped. Through brief observations at various times, I was able to determine how cecidomyiids interact with cocoa flowers and how this behavior relates to pollinating activity.

Opportunistically, immature stages of cecidomyiids breeding in cocoa farms were obtained by surveying rotting cherelles, arboreal and ground-cover leaf litter beneath cocoa trees, and by collecting repeated samples of epiphytic moss. The emphasis here was on obtaining a qualitative picture of breeding substrates rather than a quantitative sampling of population densities of immature stages. Collected breeding substrate samples were usually confined to tightly-shut large clear plastic bags to allow larvae to complete development and adults to eclose. Voucher series of larvae and adults were kept for determination studies. For all cecidomyiid voucher samples obtained, the insects were preserved in the field in vials of 70% ethanol and later shipped to the Insect Identification and Beneficial Insects Introduction Institute, ARS, USDA at Beltsville, Maryland for identification.

To estimate the densities of adult cecidomyiids in open cocoa flowers, I made repeated censuses of 70 mature trees, consisting of a mix of clonal varieties UF-677, UF-613, and Pound-7, in one of the clonal gardens at La Lola; the same set of trees was censused at various times of the year and data were also kept on the abundance of open flowers at each census for each tree. These censuses were usually taken at the same time of day each time (generally between 0900-1100 hours) and in both cloudy (overcast) and sunny weather. I attempted always to examine all open flowers within easy eye-viewing at each tree.

As these studies progressed, with the assistance of Raymond J. Gagné of the Systematic Entomology Laboratory, IIBIII, in Washington, D.C., it was possible to narrow down the number of genera and species of these midges most consistently found in cocoa flowers, and this allowed me to conduct some preliminary field tests with small experimental cages to determine the potential for these midges to pollinate cocoa. Such tests can only give a possible indication of pollinating activity, however, and the results may have little or nothing to do with whether or not these same species of midges actually pollinate cocoa under natural conditions. The bias and pitfalls of this sort associated with cage tests involving small flying insects as potential pollinators has been pointed out by Winder (1978a) in the case of cocoa. In the present field studies, small sleeves of fine-mesh silk bolting cloth (Tetkco Co., Elmsford, New York) were stretched over wire frames embedded into sections of branches on cocoa trees bearing lots of floral buds and open flowers. Details of this methodology are outlined in Young (1983). These tests were conducted at La Lola using the self-compatible UF-29 variety of cocoa, a condition that permitted confined insects such as cecidomyiids to fertilize confined flowers successfully without the need for cross-pollination with other varieties. A total of ten cage tests were conducted, five each at two different times during two successive rainy seasons (1981 and 1982); of the five cages used each time, three were "controls" having no midges introduced into them and the remaining two, experimentals. Experimental cages generally received anywhere from five to 30 cecidomyiids over a 1–3 day period, and the numbers of open flowers scored each day in all cages. Prior to initiation of these tests, all open flowers were removed from all cages and subsequently opening flowers were shielded by the bolting cloth from any possible external pollinating agents other than the confined cecidomyiids. Midges were usually introduced at different times of the day; sources of cecidomyiids included collections from open flowers and to a lesser extent from communal roosts. It was not always possible to determine the species of cecidomyiid used, although emphasis was placed on testing *Mycodiplosis* sp. 1 and *Clinodiplosis* sp. 1.

At two different dates at La Lola, I tagged the positions of several communal roost sites for adult cecidomyiids in a heavily-shaded area (the Area A of Young, 1983) of UF-29 cocoa trees to determine (1) the day-to-day changes in roosting habits and degree to which the same site is re-used over short periods of time (i.e. a succession of days), and (2) the diurnal patterns of roost formation and dissolution. I was also interested in determining which species of cecidomyiids participated in roosting behavior at La Lola, and which of these species were also visiting cocoa flowers and possibly exhibiting pollinating behavior. Several previous studies in the Neotropical Region have described the unusual phenomenon of cecidomyiids roosting communally in the silken webs of various species of spiders (Fig. 2), including both natural forest and cocoa farm habitats (e.g., Lahmann and Zuniga, 1981; Kaufmann, 1973b). As sometimes individual roosts on a given date contain more than one species of cecidomyiid (Dr. W. E. Eberhard,

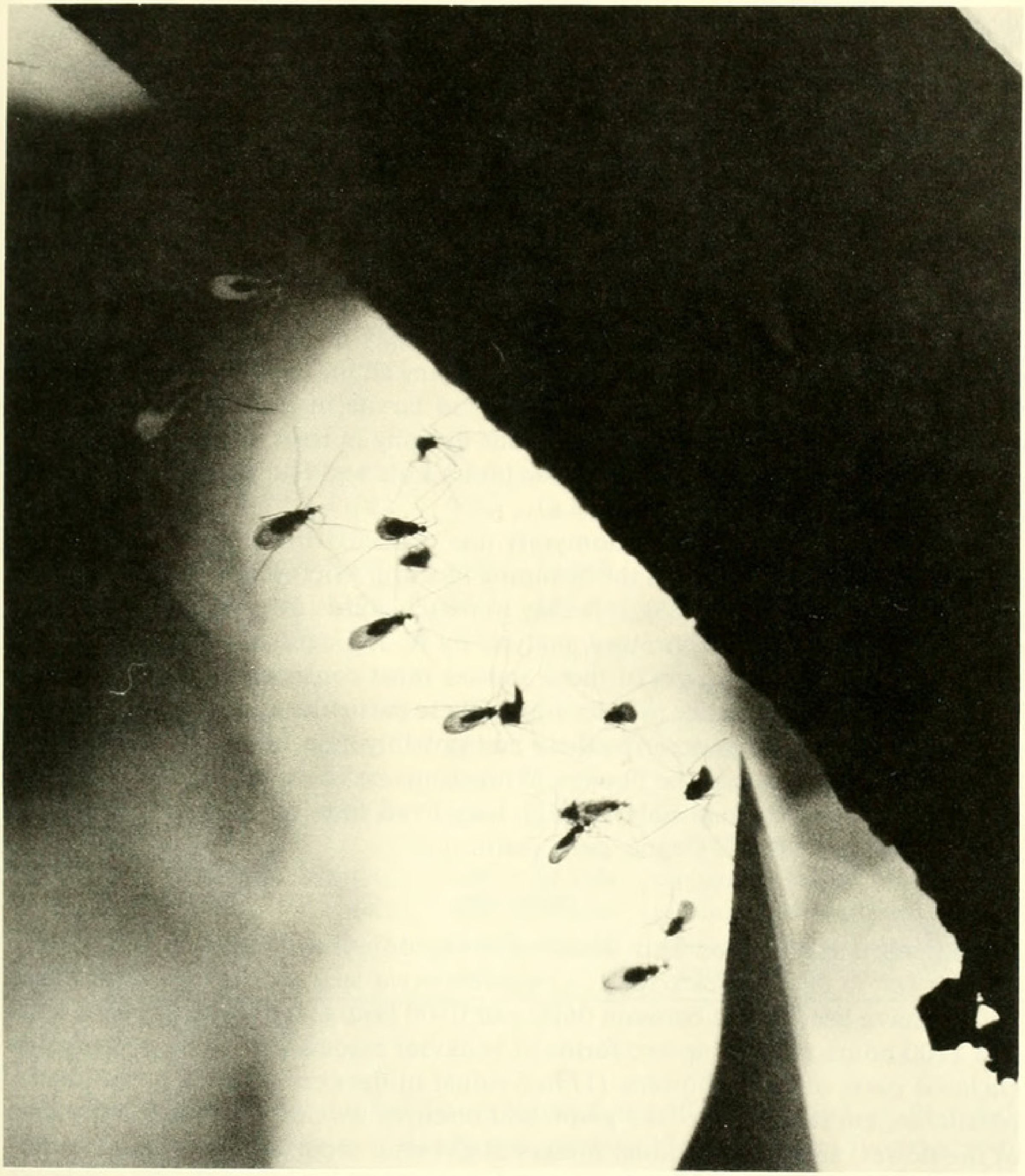

Fig. 2. Communal roosting aggregate of unidentified Cecidomyiidae in the Hummingbird Hershey Farm in Belize.

per. comm.), it was necessary to collect samples of midges from roosts at various dates to estimate the degree to which roosts in this particular case were monospecific in composition. Tagged roost sites were checked almost hourly and the number of midges in them counted and recorded. Particular emphasis was given to observing roost formation and dissolution as related to dawn and dusk. Observing roosts in this manner provided the opportunity to relate diurnal activity patterns of cecidomyiids to the diurnal cycle of flower opening and anthesis in cocoa. Only at the end of observation periods were samples taken of adults in roosts for determination purposes.

Although to be summarized in detail elsewhere (A. M. Young, in preparation), an experiment of setting out sticky squares of flypaper around open cocoa flowers at both La Lola and La Tigra and checking them for trapped flying insects at various times of the day and night, provided some additional information on diurnal activity patterns of cecidomyiids in the immediate vicinity of cocoa flowers. Relevant portions of these data are mentioned in this paper. The experiments involved placing several hundred such small squares (anchored on No. 3 insect pins) each time within a few mm of open cocoa flowers on 1–5 trees at each locality. Squares were then scored as to whether they were "occupied" by insects, what kinds, and time of the day.

Cecidomyiids surveyed at Hummingbird Hershey in Belize included the collections of larvae from rotting cherelles and rearing adults from these. Information was obtained on the locations of cecidomyiid larvae in these substrates. Also, collections of animal-damaged rotting pods hanging in trees were made to determine the presence of cecidomyiid larvae (at La Lola and Hummingbird Hershey) and to rear these to adulthood.

A small sample of adult cecidomyiids was collected from cocoa flowers and preserved dry to examine with the Scanning Electron Microscope for the presence of cocoa pollen (Taylor, 1965); it is easy to match grains from flowers with those collected from insects. Laboratory analysis by R. J. Gagné also included an examination of the mouthparts of those species most consistently found in cocoa flowers. This study was done to determine if these particular species had functional mouthparts and if so, to describe these and possibly associate with the observed behavior of the midges in the flowers. While some cecidomyiids possess vestigial mouthparts as adults (e.g. Ehler, 1982), long-lived free-living forms have functional mouthparts (R. J. Gagné, pers. comm.).

Results

Pollination Mechanism and Behavior.—Cecidomyiid midges, mostly *Mycodiplosis* sp. 1, *Clinodiplosis* sp. 1, *Coquillettomyia* sp., and *Aphodiplosis triangularis*, have been found between 0600 and 0700 hours, and again between 1500 and 2100 hours, exhibiting two forms of behavior associated with moving inside enclosed parts of cocoa flowers: (1) individual midges crawl along a staminode, parallel to, and adjacent to, the pistil, and oriented towards the basal ovary area of the flower, and (2) individual midges alight on a sepal, petal ligule, or exterior surface of a petal hood, and proceed to crawl inside the petal, often moving from one petal hood to the next and so on. For example, on 9 December 1982 at 0700 hours at La Lola, one female of *Clinodiplosis* sp. 1 landed at the tip of a staminode and crawled along it and rubbed against the pistil; examination of the pistil area after collecting the midge revealed a slight smear of several pollen grains. Sometimes a female remains motionless on petal ligules for several minutes to an hour beore moving. On 21 November 1981 at La Lola, one specimen (*Mycodiplosis* sp. 1) was discovered with mouthparts embedded into the distal surface tissue of a ligule at 1100 hours and was still there at 1500 hours. A male of the same species was seen crawling along a staminode at 0900 hours and with mouthparts clearly scraping against the staminode tissue, as if feeding. Another female *Clinodiplosis* sp. 1 alighted on the tip of a staminode at 0600 hours on 19 November 1981 at La Lola, stayed there for one minute, and then quickly crawled down the staminode to the ovary area of the flower; this cecidomyiid remained

Table 1. Adult cecidomyiid midge behavior in open flowers of *Theobroma cacao* as related to effective pollination.

Species	Sex	Date	Time	Locality	Description of Behavior Related to Pollination
Clinodiplosis sp. 1	female	9-XII-82	0700	La Lola	lands on tip of staminode and quickly crawls towards ovary, brushing against pistil
	female	9-XII-82	1630	La Lola	crawling in narrow space between staminodes and pistil
	female	11-XII-82	0730	La Lola	lands on floral petiole, crawls over to staminode and crawls along it and enters into inside of petal hood, exits few seconds later and enters a second petal hood
	female	12-III-82	2000	La Lola	captured while inside petal hood
Mycodiplosis sp. 1	female	11-XII-82	0730	La Lola	crawling along ligule towards petal hood opening
	female	13-XI-81	1600	La Lola	crawling around inside petal hood
	female	13-XI-81	1730	La Lola	perching on ligule and suddenly "flips" around and enters petal hood and moves around violently inside it and causes petal hood to momentarily change shape
	female	12-III-82	1700	La Lola	captured inside petal hood
	female	21-XI-81	0600	La Lola	crawling into petal hood
	female	21-XI-81	0630	La Lola	lands on outside of petal hood and crawls inside it
	female	9-XII-82	1630	La Lola	captured inside petal hood
	female	9-XII-82	1630	La Lola	captured inside petal hood
	female	9-XII-82	1645	La Lola	captured in narrow space between staminodes and pistil

on the ovary tissue for about four hours before flying off. While adult cecidomyiids are readily found resting on petal ligules, or upon dense mats of fungal growth (hyphae) covering squirrel or woodpecker-generated holes in cocoa pods (Fig. 3), of particular interest are those observations of these midges actually moving within confined spaces of the flower (Table 1). Midges hovering about cocoa flowers are sometimes captured as prey by the smaller nymphal instars of the mantid (Orthoptera) *Chaeteessa filata* (Burmeister) (Dictyoptera: Mantidae) which is abundant on branches of cocoa trees at La Lola (Fig. 3). One rainy season census (August 1983) of 70 adjacent trees at La Lola revealed that close to half (32 trees) had one individual of this mantid at 0900 hours in sunny weather, and that 20 of these individuals were nymphs and the remainder, adults (A. M. Young, unpubl. data). Various species of salticid and other spiders also capture these cecidomyiids routinely, and *Anolis* lizards, which are very abundant in Costa Rican cocoa farms, also feed upon them (A. M. Young, unpubl. obs., 1978–1983). Small dipterans sometimes comprise sizable portions of anole diets in the American tropics (e.g. Floyd and Jenssen, 1983).

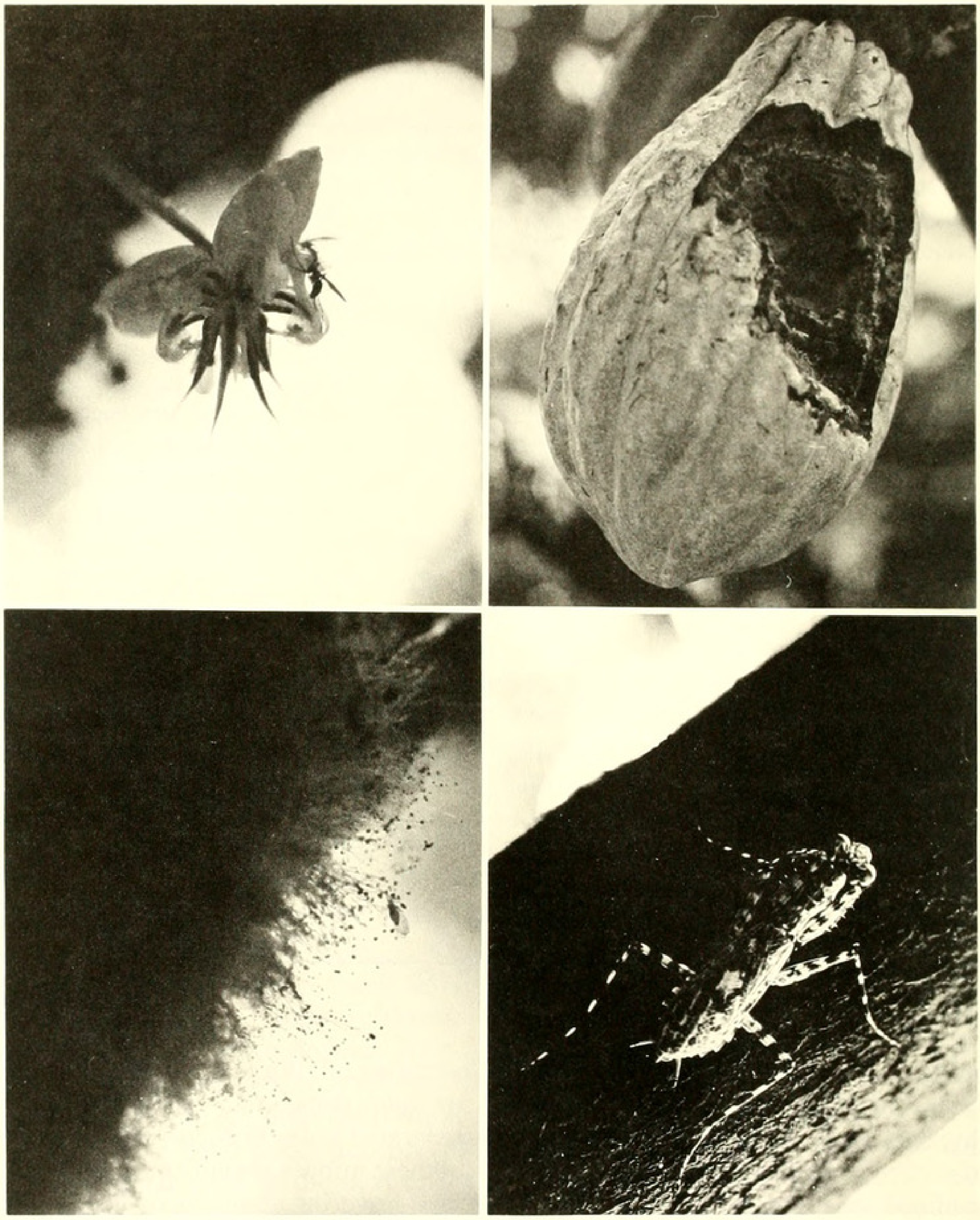

Fig. 3. Various aspects of cecidomyiid biology in Central American cocoa plantations. Clockwise, beginning in upper left photo: adult cecidomyiid perched on petal hood of cocoa flower during the daytime; squirrel-generated hole in cocoa pod, and filled with fungi and rotting pod tissues, a microhabitat where cecidomyiid larvae are found; the mantid *Chaeteessa filata* on branch of cocoa tree—in earlier nymphal stages, a predator on adult cecidomyiids; adult cecidomyiid perched in hyphae of fungi on hole in cocoa pod.

While more midges are seen resting on staminodes, petal hoods, and petal ligules of cocoa flowers than seen moving in them at both La Lola and La Tigra (Tables 2 and 3), I suspect that such a paucity of direct observations of midges pollinating flowers, or at least visiting flowers in such a manner so as to possibly pollinate them, is due to (1) my inability to find and record accurately all such instances at a given time of day, and (2) the very likely fact that only relatively few species of the total cecidomyiid faunas of cocoa farms are actually visiting cocoa flowers for the purpose of feeding or gaining some other reward. In the shaded understory conditions of cocoa farms cecidomyiids in general alight on light-colored objects. While the species most abundantly seen on or inside cocoa flowers fall within the body length range of 2–4 mm, the larger *Mycodiplosis* sp. 2, with variegated wings, is commonly found alighting in groups on the bottoms of large white-plastic cups used to simulate bromeliads (see Young, 1983). Thus it is necessary to distinguish between cecidomyiids that visit cocoa flowers for some purpose other than a resting place, namely for feeding. My observations suggest that forms such as *Clinodiplosis* sp. 1, *Mycodiplosis* sp. 1, *Coquillettomyia* sp. and *A. triangularis,* are the most likely pollinators of cocoa in Costa Rica. Of these, most of the observations on actively moving cecidomyiids inside cocoa flowers are of *Clinodiplosis* sp. 1 and *Mycodiplosis* sp. 1. Interestingly, females are far more abundant on or inside cocoa flowers than males for those genera and species found in greatest frequency associated with flowers (Tables 2 and 3). Examination of freshly-open flowers on other species of *Theobroma* trees growing adjacent to cocoa at La Lola and La Tigra also suggest that cecidomyiids are attracted to these flowers (Table 4), even though there is considerable difference in size, color, and three-dimensional design of the flowers among these species (see Cuatrecasas, 1964). Young et al. (1984) and M. Strand and A. M. Young (in preparation) also found considerable differences in the types of fragrance compounds among these species, although the general positioning of floral nectaries and other possible reward-generating structures is similar among these species. For the purposes of this paper, I tentatively conclude that *Clinodiplosis* sp. 1 and *Mycodiplosis* sp. 1 are the most frequent cecidomyiids visiting cocoa flowers at La Lola and La Tigra, and are the best candidates for being effective pollinating agents. Our totally new observations of adult cecidomyiids being attracted to the flowers of *Guazuma* (Sterculiaceae) at La Tigra add indirect evidence for the existence of a generalized pattern of associaiton of these cecidomyiids with sterculiaceous flowers in the American tropics (Table 4).

A good review of the mechanism of pollination in cocoa by ceratopogonid midges is given by Bystrak and Wirth (1978) and my observations with cecidomyiids suggest a very similar pattern of association with flowers. Basically I propose that cecidomyiids such as *Clinodiplosis* sp. 1 and *Mycodiplosis* sp. 1 pick up small numbers of viable cocoa pollen grains on long caudal hairs on the abdomen and elsewhere when midges crawl around inside petal hoods in the early morning and late afternoon. Pollen grains thus removed from the petal hoods are then smeared upon the pistil when pollen-bearing midges crawl along the narrow space between staminodes and pistil. Kaufmann (1973b) and Winder (1977b) both report smear-type pollination by cecidomyiids in Africa and Brazil, respectively.

Both *Clinodiplosis* sp. 1 and *Mycodiplosis* sp. 1 have well-developed compound eyes. While the mouthparts of both species possess no specialized adaptations for flower-feeding, both have elongate functional mouthparts adapted for sucking up fluids such as nectar in flowers (R. J. Gagné, pers. comm.). Interestingly members of both genera typically possess long hairs on the legs and abdomen (R. J. Gagné,

Table 2. The abundance of adult Cecidomyiidae on/in freshly-opened *Theobroma cacao* flowers[a] for five widely separated census dates[b] for 1000 flowers examined each date[c] at Finca Experimental La Lola, near Siquirres, Limon Province, Costa Rica.

Species	No. Occupied Flowers	No. Midges Resting on Flowers[d]			No. Crawling Inside Flowers[e]			Communal Roosts[f]		
		♀♀	♂♂	T	♀♀	♂♂	T	♀♀	♂♂	T
Clinodiplosis sp. 1	17/1000	13	0	13	5	0	5	0	0	0
Clinodiplosis sp. 2[g]	0/1000	—	—		—	—		8	7	15
Clinodiplosis sp. 3	0/1000	—	—		—	—		2	1	3
Mycodiplosis sp. 1[h]	63/1000	100	16	116	1	0	1	25	27	52
Mycodiplosis sp. 2	0/1000	—	—		—	—		10	0	10
Mycodiplosis sp. 3	0/1000	—	—		—	—		10	0	10
Coquillettomyia sp.[i]	0/1000	—	—		—	—		30	9	39
Lestodiplosis sp. 2	5/1000	2	5	7	—	—		0	0	0
Aphodiplosis triangularis	19/1000	30	18	48	—	—		0	0	0
Winnertzia sp.	4/1000	2	4	6	—	—		0	0	0
Ledomyia sp.	1/1000	1	0	1	—	—		0	0	0
Bremia sp.	2/1000	1	1	2	—	—		0	0	0
Trisopsis sp.	1/1000	1	0	1	—	—		0	0	0
Chrybaneura sp.	0/1000	—	—		—	—		0	5	5
Undet. Cecidomyiidae	6/1000	3	10	13	—	—		0	0	0

Total det. species: 14

Total det. species, individuals, and sex ratio on/in flowers, resp.: 9, 194, 150:44.

Total no. occupied flowers: 112/1000

Usual range of midge number/flower: 1–3

[a] Most censuses of flowers occurred between 0630–0900 hours and freshly-opened flowers were recognized by the horizontal orientation of the sepals.

[b] 18–23 Nov. 1981, 10–14 March 1982, 17–23 July 1982, 8–11 Dec. 1982, 12–15 March 1983.

[c] A total "pool" of approx. 1000 flowers was taken each date from usually 20–70 trees depending upon the time of the year and availability of flowers; tree varieties used were UF-677, UF-613, and Pound-7.

[d] Defined as one or more midges suspended motionless usually from staminodes, ligules, sepals or petal hoods of open flowers.

[e] Defined as a midge visibly seen crawling either between staminodes and pistil, or inside petal hood of freshly-open flower.

[f] Aggregates of several midges on spider webbing in trees; data combine one or more roosts.

[g] Tentatively named as new species *denotata* (R. J. Gagné, pers. comm.).

[h] Tentatively named as new species *ligulata* (R. J. Gagné, pers. comm.).

[i] Tentatively named as new species *obliqua* (R. J. Gagné, pers. comm.).

pers. comm.) and a preliminary SEM survey of wild-caught *Mycodiplosis* sp. 1 (N = 6 observed) revealed that one cecidomyiid had a cocoa pollen grain adhering to one caudal hair on the abdomen. While members of both genera occur worldwide, the particular species associated with cocoa flowers may have tropical distributions, and these species will soon be described by Gagné (in press).

Individual cecidomyiids approach an open cocoa flower with considerable "bobbing and weaving" flight paths around a flower. Seemingly healthy flowers are often passed by completely by cecidomyiids flying along branches in cocoa trees. The flies do not appear to "swarm" about open flowers in large numbers. But Cecidomyiidae sometimes swarm along branches in cocoa trees (i.e. 12 February 1981 at 1700 hours at La Lola) and with both sexes represented. *Winnertzia* sp. was found swarming (approx. 20 midges seen) at 1500 hours on 18 November

Table 3. The abundance of adult Cecidomyiidae on/in freshly-opened *Theobroma cacao* flowers[a] for six widely separated census dates[b] for 500–1000 flowers examined each date[c] at Finca La Tigra, near La Virgen, Heredia Province, Costa Rica.

Species	No. Occupied Flowers	No. Midges Resting on Flowers[d]			No. Crawling Inside Flowers[e]			Communal Roosts[f]		
		♀♀	♂♂	T	♀♀	♂♂	T	♀♀	♂♂	T
Clinodiplosis sp. 1	14/1000	23	0	23	—	—		—	—	
Mycodiplosis sp. 1[g]	18/1000	25	3	28	1	0	1	—	—	
Mycodiplosis sp. 2	3/1000	0	3	3	—	—		—	—	
Mycodiplosis sp. 4	1/500	0	1	1	—	—		—	—	
Coquillettomyia sp.[h]	2/1000	2	0	0	—	—		—	—	
Lestodiplosis sp. 1	2/1000	2	0	2	—	—		—	—	
Aphodiplosis triangularis	3/500	3	0	3	—	—		—	—	
Winnertzia sp.	1/500	1	0	1	—	—		—	—	
Ledomyia sp.	1/1000	1	0	1	—	—		—	—	
Cantarina sp.	2/1000	4	1	5	—	—		—	—	
Feltiella sp.	4/1000	3	3	6	—	—		—	—	
Undet. Cecidomyiidae	7/1000	?	?	9	—	—		—	—	

Total det. species: 11

Total det. species, individuals, and sex ratio on/in flowers, resp.: 11, 75, 64:11.

Total no. occupied flowers: 68/500–1000

Usual range of midge number/flower: 1–2

[a] Most censuses of midges in flowers occurred between 0630–0900 hours following an initial period of determining diurnal patterns of peak abundance, and freshly-opened flowers were readily recognized by the marked horizontal orientation of the sepals (which are more vertically positioned in older flowers).

[b] 11–24 March 1979, 1–4 Nov. 1980, 4–18 Feb. 1981, 12–17 Nov. 1981, 8–13 and 27–31 July 1982, and 2–6 March 1983.

[c] A total "pool" of usually 500–1000 flowers was taken as a sample each date from usually 20–50 trees in the same area (many mixed hybrid varieties of undetermined origin) depending upon the time of year and availability of fresh flowers; because cacao flowers drop off the trees within 24–48 hours after opening under most conditions, the occupancy data given in the table are expressed in terms of 500 or 1000 flowers, i.e., a single census.

[d] Defined as one or more midges suspended motionless usually from staminodes, ligules, sepals or petal hoods of open flowers.

[e] Defined as a midge seen actively crawling either between staminodes and pistil or inside petal hood (including entering and exiting) of freshly-opened flower.

[f] In the La Tigra study as compared to the La Lola study (Table 2), little attention was given to roosts.

[g,h] See species determinations given for same footnotes in Table 2.

1981 (La Lola) along a branch in a cocoa tree. *Micromya* sp. was found swarming about 5 cm above some rotting slices or discs of banana tree trunks (Young, 1983) (La Tigra, 26 July 1981).

Freshly-opened cocoa flowers between 0530 and 0700 hours are heavily visited by cecidomyiids, and these exhibit the potential pollinating behavior described above. While some of this activity may also occur in the pre-daylight hours of the dawn period, the rather compressed daylight period of cecidomyiid activity at dawn probably precedes the formation of communal roosts (see data below). While the basis for attraction to freshly-opened flowers awaits study, when three of the five petal hoods are surgically removed from flowers, cecidomyiids are found within a few minutes resting on various exposed floral parts: on 19 November 1981 at 0800, five were found perched on exposed anthers, petal ligule on one of the remaining petal hoods, and the tip of a staminode. Although the flower was deliberately damaged, this act did not lower attractiveness of the flower to potentially pollinating insects.

The results of a preliminary experimental study involving the confining of *Mycodiplosis* sp. 1 to experimental cages on flower-laden branches of cocoa trees at La Lola provide additional evidence that cecidomyiids can be cocoa pollinators, and confirms what others have concluded for other genera and species of these midges (Kaufmann, 1973b; Winder, 1977b). On 30 July 1981 a series of 14 such cages (2 experimentals and 12 controls) were set up (see Young (1983) for view of these cages) in the Area B study site of Young (1983) using UF-29 cocoa trees. One of the two experimental trees had 95 floral buds within the caged section of the branch and the second one had 23 buds at the time the test was initiated. The control trees had a range of about 30 to 100 floral buds at this time (these are tagged trees nos. 62, 63, 66, 76, 78, 79, 80 of Young, 1984b). The two experimental cages combined received a total of 33 cecidomyiids between 1–3 August 1981. By 10 August, one cherelle was well in evidence in one of the two experimental cages and no other cages had pods. The experiment was repeated on 12 March 1982 at La Lola, but this time in the Area A study site of UF-29 cocoa described in Young (1983). This time, however, I used only one control and one experimental cage, both on the same tree (tagged tree No. 15 of Young, 1984a). The confined area of the branch covered by the control cage had 64 floral buds while the experimental cage had 51 buds. A total of 39 individuals (mixed sexes) of what I judged to be *Clinodiplosis* sp. 1 were introduced into the experimental cage between 12–14 March. By 29 March three new cherelles were evident in the experimental cage and none in the control cage. In both tests, the cages were left in place on the trees until the final census (of pods) was taken.

Abundance Patterns of Cecidomyiids in Cocoa.—Typical adult abundance patterns in open cocoa flowers are readily seen from some data collected at La Lola (Area A of UF-29 cocoa in Young 1983) during March 1982: from a total of 70 flowering trees examined almost exhaustively, and representing a total pool of about 2000 open flowers, a total of 29 adult cecidomyiids were found perched on flowers, with a range of 1–2 per "occupied" flower and with five observations of three cecidomyiids on a single flower (and all observations made 1100 to 1300 hours in hot, sunny weather). During the March 1983 dry season at Hummingbird Hershey, a total of 39 cecidomyiids were counted from a total of 28 freshly-opened flowers at 1100–1200 hours on one date; total flower abundance on these trees just exceeded 5800 at this time (5880 open flowers). But unlike La Lola, these trees also had a total of 1586 pods, mostly cherelles, from natural pollination, whereas at La Lola pod numbers were less than 200 and the result largely of hand-pollination. The Hummingbird Hershey census area was well-shaded due primarily to self-shading cocoa trees, and an adjacent section of relatively little such shade yielded a total of 9 cecidomyiids found from a total sample of 3725 open flowers on an additional 70 trees. This area had a total of 245 cherelles. Generally, adult cecidomyiids are of very low density in open cocoa flowers, as also seen by some data from La Tigra: on 3 November 1980 at 1100 hours (hot, sunny day), a total of 20 flowering cocoa trees (mixed varieties) yielded a total of 640 open flowers ($\bar{x} \pm SD = 31.00 \pm 18.39$ flowers per tree for $N = 20$) and a total of 16 cecidomyiids ($\bar{x} \pm SD = 0.85 \pm 0.72$ per tree) from open flowers. Total abundance of cecidomyiids, i.e. all captured flying about flowers and landing on branches and leaves at this time was N = 69 or $\bar{x} \pm SD = 3.45 \pm 1.14$, a sample that undoubtedly included many non-pollinating species. An additional census at La Lola in March 1982 yielded a total of 54 cecidomyiids (28 female & 26 male) or $\bar{x} \pm SD = 1.42 \pm 0.77$ per tree and with a range of 1–4 per flower and 25 flowers with one cecidomyiid each, 6 with 2 each, 3 with 3 each, and one flower with 4 cecidomyiids each. Another census in the clonal garden area at La Lola in August 1983 revealed that nine of 70 trees had one or more cecidomyiids on or inside open cocoa flowers, and a total of 13, with 1–2 per "occupied" flower (5 female & 8 male); most of these appeared to be *Mycodiplosis* sp. 1. At this time, flowering was very low, with a range of about 0–5 open flowers per tree (N = 70 trees) and with slightly more than 50% of the trees with no flowers at all. In all censuses of cecidomyiids on flowers, virtually every specimen found was perched on one of the following floral parts: petal hood (abaxial surface), petal ligule, sepal, or staminode. All observations of specimens actually crawling inside flowers were limited to 0600–0800 hours (most observations) and 1600–1800 hours for daylight surveys taken. Other studies (Young, 1983; Young et al., 1984) indicate that cocoa flowers generally begin opening in the late afternoon and are fully open by 0400–0500 hours at both La Lola and La Tigra (see also the data of Wellensiek, 1932). Such a pattern is consistent with the early morning daylight activity period of cecidomyiids observed in the present study (Tables 1 and 4). Yet it is not uncommon to find large numbers of these midges perching motionless on open flowers at other times of the day. Casual observation indicated that midges were at least three times as abundant in this well-shaded area (Area A of Young, 1983) as contrasted with an unshaded area (Area B) at this time (dry season). Subsequent determinations indicated that most of the midges in all of these censuses were mixes of *Mycodiplosis* sp. 1, *Clinodiplosis* sp. 1, and *Coquillettomyia* sp. Differential partitioning of adult midges between shaded and sunny cocoa habitats at La Lola during the drier months was also demonstrated by an examination of aggregates of *Clinodiplosis* sp. 2 on the undersides of large plastic cups suspended from cocoa trees in both areas (see Young 1983 for details): on 13 March 1983 at 1400 hours, a total of 6 out of 20 such cups in Area A (shade) had a total of 51 midges with 5–16 per cup, while only one of 20 cups in Area B (sunny) had one midge. A 12 March 1982 census (i.e. one year earlier) of the same areas yielded a total of 56 midges from 7 "occupied" cups in the shaded area and none in the sunny area. During the drier months at La Tigra (such as March) typically many cecidomyiids are found on open cocoa and *Guazuma* flowers between 0600-0800 hours, but that after this time there is marked decline and virtual absence of specimens at flowers until much later in the day (near dusk). Such diurnal decline patterns are less pronounced during the rainy season for cocoa flowers.

Additional data on cecidomyiid abundance in cocoa flowers are seen in Table 2. A total of 12 genera and 16 species were collected in the La Lola studies, of which nine genera and species were found visiting cocoa flowers. A total of 116 individuals of *Mycodiplosis* sp. 1 (99 female & 17 male) on flowers (Table 2) represents about 60% of the total fauna of 193 determined midges) on flowers, followed by *A. triangularis* with about 20% of the fauna on flowers (N = 53 or 28 female & 25 male), and then by *Clinodiplosis* sp. 1 (all female) at about 6% of the total sample taken (Table 2). At La Tigra the most abundant species found

Table 4. Records of adult Cecidomyiidae in freshly-opened or open flowers of *Theobroma* species other than *cacao* at Finca Experimental La Lola and Finca La Tigra in Costa Rica.[a]

Midge Species	Date	Time of Day	Sex	Tree Species	Other Comments
			La Lola		
Clinodiplosis sp. 1	Feb. 1981	1600	male	*T. simiarum*	on staminode
	Mar. 1983	0800	male	*T. speciosum*	on ligule
	Mar. 1983	0700	male	*T. mammosum*	on ligule
Prodiplosis sp.	Feb. 1981	0700	1 female, 3 males	*T. simiarum*	on staminodes
Clinodiplosis sp. 4	Mar. 1983	0600	2 females, 1 male	*T. mammosum*	on staminode
Mycodiplosis sp. 1	Mar. 1983	1600	female	*T. silvestre*	on staminode
Bremia sp.	Mar. 1983	1700	female	*T. speciosum*	inside petal hood
	Mar. 1983	1700	male	*T. simiarum*	inside petal hood
Asynapta sp.	Mar. 1983	?	?	*T. mammosum*	on staminode
			La Tigra		
Clinodiplosis sp. 1	Mar. 1983	1000	—	*T. mammosum*	communal roost[b] of 18 (mixed sexes)
	Mar. 1983	0700	3 females	*Guazuma* sp.[c]	landing on open flowers
Bremia sp.	Mar. 1983	1000	—	*T. bicolor*	communal roost of approx. 400 (mixed sexes)[d]

[a] Examination of flowers made opportunistically on various days and not following a particular pattern.

[b] This roost was located on spider webbing between leaf petiole and branch and about 10 cm from nearest open flowers.

[c] Also Sterculiaceae.

[d] This roost located on webbing stretching across two leaves and about 15 cm from nearest open flowers.

in cocoa flowers (and also in *Guazuma* sp. flowers) was *Clinodiplosis* sp. 1 (23 of 44 or about 50%). Eight genera and 13 species were collected from flowers at La Tigra. At La Lola all five *Clinodiplosis* sp. 1 seen moving inside floral parts of cocoa were females as well as the two *Mycodiplosis* sp. 1 (Table 4). Several genera that were not found in cocoa flowers (Table 3) at all were found forming communal roosts in cocoa habitats. Caution is exercised in interpreting these patterns as the data are small. Some species, such as *A. triangularis,* while abundant in flowers, were never found in roosts (Table 3), but *Mycodiplosis* sp. 1, while common in flowers, also constituted about 69% of all cecidomyiids found in communal roosts (Table 3). In all studies, however, relative to abundance of open flowers, cecidomyiids are relatively rare in cocoa flowers in both rainy and dry seasons in Central America (Table 5). For the three most abundant species in the La Lola samples, namely, *Mycodiplosis* sp. 1, *A. triangularis,* and *Clinodiplosis* sp. 1 (in this order), a total of 122 individuals were collected on two different "dry" season dates and 66 on three wet season dates, even though the same number of trees was covered on all dates and samples were always taken at the same times of the day. For both seasons, all census dates, these three species constitute 188/194 or

Table 5. Estimates of population density of adult Cecidomyiidae on freshly-opened flowers[a] of *Theobroma cacao* in the La Lola (Costa Rica) and Hummingbird Hershey (Belize) cocoa farms in Central America.

Census Dates	"Season"[b]	Total No. Open Flowers[c]	Range	$\bar{x} \pm SD$	Total No. Adult Midges	$\bar{x} \pm SD$	No. Midge Occupied Flowers	Percentage (%) Flower Occupancy
				La Lola				
21-VII-82	mid-rainy	650	0–53	9.81 ± 11.20	7	0.11 ± 0.36	6	0.92%
8-XII-82	late rainy	1577	0–75	22.52 ± 19.55	19	0.27 ± 1.25	7	0.44%
14-III-83	dry	1712	0–300	24.45 ± 41.45	61	0.77 ± 2.15	31	1.82%
5-VIII-83	mid-rainy	3278	1–178	38.24 ± 47.04	30	1.50 ± 1.87	14	0.42%
				Hummingbird Hershey				
22-III-83	dry	5880	10–108	73.50 ± 48.64	39	0.53 ± 1.09	28	0.47%

[a] For each locality, all of the data on both flowers and midges were taken always from the same set of mature and healthy cocoa trees. A total of N = 70 trees were sampled each time at each locality (in the case of La Lola for the repeated censuses). At La Lola, the tree sample was almost evenly divided among the clonal varieties of UF-677, Pound-7, and UF-613 (these rows being contingent), while at Hummingbird Hershey the 70 trees were of mixed undetermined varieties. Only freshly-opened flowers were examined for midges and only midges resting on or inside definite floral parts were counted.

[b] "Season" is considered here as a relative condition of "wetter" and "drier" periods as defined by available rainfall data (Fig. 1). As such, this condition changes considerably from year to year at each locality.

[c] For 21-VII-82 census at La Lola, 153/650 or 23.5% of open flowers with horizontal sepals, i.e., flowers freshly-opened that morning (as opposed to being 1-day old flowers); similar level for 8-XII-82; for 14-III-83 the 31 flowers occupied by cecidomyiids all but 4 with horizontal sepals and 36.1% of all flowers at this time with this condition of freshness. In Belize sample about 50% of all flowers with horizontal sepals.

about 97% of all cecidomyiids collected (Table 2). For La Tigra, only rainy season data (2 dates) are available.

The experimental studies using small flypaper squares to trap flying insects within the vicinity of open cocoa flowers and away from them (Table 6) revealed very low abundance of cecidomyiids in both day and night samples at La Lola during the rainy season. While the sample size is small, there is a slight trend towards finding more specimens in "experimental" sticky squares than in the "control" squares away from flowers (Table 6). Prior to these results, a total of 48 sticky squares distributed almost randomly among 15 trees (all Pound-7) at La Lola and within one area yielded two cecidomyiids (both *Mycodiplosis* sp. 1; females) captured in the traps between 1700 and 0700 hours (dusk-to-night-to-dawn) on 16 July 1982, and the same test repeated on the following evening produced one cecidomyiid of undetermined species designation. From 27 to 31 July 1982 similar tests conducted at La Tigra provided similar results: in one patch of four cocoa trees a total of 127 squares were placed around 60 open flowers at 1700 hours (27 July) and checked at 0730 the following day. A total of 18 squares had trapped flying insects (21) including one female *Clinodiplosis* sp. 1. A second test conducted with the same trees and same number of squares and flowers yielded no cecidomyiids for the period 0800 to 1700 hours (28 July) even though 49 other flying insects were trapped during this daytime census. Tentatively these findings taken together suggest that cecidomyiids are not abundantly active

Table 6. The occurrence of Cecidomyiidae versus other flying insects in small squares of sticky flypaper adjacent open cocoa flowers (experimentals) and on bare spots on branches (controls) in an area of typically-shaded Pound-7 variety cocoa trees in a clonal garden at Finca Experimental La Lola, Costa Rica.

Date Intervals	Time Range	Tree No.	No. Experi-mental Squares	No. Flowers Used	No. Control Squares (0 Flowers)	No. Squares with Trapped Insects	No. Cecido-myiids Trapped	Species
20 July	0630–1730	1	46	25	0	14/46	1	*Mycodiplosis* sp. 1
	(dawn–day–	2	22	20	0	5/22	2	*Mycodiplosis* sp. 1
	dusk)	3	0	0	30	3/30	0	(all females)
	Total trapped insects: 44 (all squares)							
20–21 July	1730–0630	1	46	25	0	15/46	1	*Clinodiplosis* sp. 1
	(dusk–night–		22	20	0	8/22	1	*Mycodiplosis* sp. 1
	dawn)		0	0	30	10/30		(both females)
	Total trapped insects: 40 (all squares)							
21–22 July	1730–0630	1	35	16	0	6/35	0	*Clinodiplosis* sp. 1
	(dusk–night–	2	10	6	0	5/10	2	(both females)
	dawn)	3	0	0	30	2/30	0	
		4 (new)	14	8	0	3/14	0	
	Total trapped insects: 15 (all squares)							

at cocoa flowers at any time of the day or night, assuming that the trapping method used is effective in capturing these insects, but that cecidomyiids are very likely active both at dawn and dusk at flowers.

Communal Roosts of Cecidomyiids in Cocoa.—When a total of nine different communal cecidomyiid roosts were followed in the shaded UF-29 cocoa at La Lola (Area A of Young, 1983) in November 1981, all but three roosts lasted at least five successive days in the same locations (usually in branch crotches or cherelle petiole-branch crotches) even though actual size (numbers of cecidomyiids) in each roost varies greatly from day to day. Roosts both increase and decrease in size over successive days. In one roost studied, a pattern of increase over three days was from 6 to 18 to 19, while the decline pattern of a second roost for the same period was 90 to 5 to 10. Roosting midges occupy small spider webs anchored to cocoa tree branches in shaded spots, and most roosts are within 0.1 to 3.0 m of the ground. Occasionally living spiders also occupy the webs used by roosting cecidomyiids; these include Theridiidae (possibly *Achaearenea* sp.) and *Leucauge* sp. (Araneidae). While most roosts at La Lola appear to consist of one primary species, one mixed-species roost of about 100 cecidomyiids collected at La Lola in March 1982 included 30 *Mycodiplosis* sp. 1 (15 female & 15 male), one *Mycodiplosis* sp. 2 (1 male), 10 *Coquillettomyia* sp. (8 female & 2 male), and *Feltiella* sp. (1 male). On a day to day basis, very large roosts, defined here as consisting of 100 or more midges at any one time, frequently break up into much smaller aggregates at the original roost site. As long as a web remains undamaged (by rain, wind, abrasions, etc.), midges may occupy the same web on several days. Cecidomyiids are most prevalent on roosts during daylight hours and vacate roosts at night; in clear sunny weather these frequently leave roosts by 1745 hours, as do those perching motionless on open cocoa flowers. On 20 November 1981 I witnessed the return of several cecidomyiids into a tagged roost site (web) at 0630 hours, and most roosts are formed between 0600-0700 hours each morning. Unless disturbed, the flies do not normally leave roosts in the daytime. The majority of specimens found in roosts appear to have much darker cuticles than many found on freshly-opened flowers in daylight hours, a condition suggesting that freshly-eclosed adult midges, particularly females (see Table 2), seek out cocoa flowers before entering into roost formations. On rainy, overcast days, dispersal from roosts may occur earlier in the afternoon, between 1700 and 1730 hours. Periods of heavy daytime rains do not disturb midges from roosts. During March 1982 in the shaded UF-29 cocoa habitat at La Lola, a total of 25 roosts were discovered among 50 cocoa trees, representing a total of 723 cecidomyiids (mostly *Mycodiplosis* sp. 1) with average roost size being $\bar{x} \pm SD = 28.92 \pm 31.21$ for a total of 18 trees having one or more roosts; the range in numbers of specimens per roost was 1–125 for a census at 1100 hours in hot, sunny weather. In the clonal garden area at La Lola in December 1982 (late rainy season) only three roosts were found on a total of 70 cocoa trees, with 20–40 cecidomyiids per roost; specimens were also scarce on open flowers at this time. Lowest roost densities in cocoa trees occur in the rainy season at La Lola. At Hummingbird Hershey during August 1981 (rainy season) a total of five roosts were found within a 10 by 10-meter area within Field Block 18, with range in midges being 25–150 at 0900 hours and all midges being *Coquillettomyia* sp. Mortality of roosting midges is probably low, but on 20 July 1982 at La Lola one roost of 25 specimens was totally encased in hyphal growths of fungi when discovered at 0900; the roost was found following an evening period of heavy cold rains. When the webbing of a roost site is destroyed, sometimes new webbing appears in the same spot a day or so later, and new webs are sometimes recolonized by midges. Earwigs scattering along branches in cocoa trees at La Lola (A. M. Young, in preparation) occasionally fall into webs with roosting cecidomyiids, and these quickly disperse in response to such disturbances. By following diurnal patterns of roost formation and dissolution, it was determined that roosting in cocoa cecidomyiids is a daytime behavior, and that they are active principally at dusk, night, and dawn (Table 7). Roosting cecidomyiids are not disturbed by actively hunting insect predators such as *Anolis* lizards and salticid spiders. The flies are most vulnerable to these predators when hovering above branches or landing on branches, leaves, and flowers. The exploitation of spider webs in cocoa trees may function to protect cecidomyiids from such predators at times of the day when these insects are largely inactive.

Cecidomyiid Midge Life Cycle Substrates.—Cocoa trees with branches covered with epiphytic mosses generally have many adult cecidomyiids flying about them during the early daylight morning hours. Most cocoa-associated cecidomyiids most likely breed close to the ground, colonizing various kinds of rotting organic materials for completion of the life cycle. Small areas within cocoa farms that consistently have high numbers of cherelles are also sites of sustained high adult population densities of cecidomyiids and ceratopogonids (A. M. Young, field obs. 1978–1983). At Hummingbird Hershey, a total of six large cocoa pods in various stages of rotting, and with large woodpecker-generated holes in them, yielded a total of 158 cecidomyiid larvae, with a range of 6-60, and for a total sample of 20 damaged pods (all but 4 150–180 mm long) examined (of which six had midge

Table 7. Comparative abundance of cecidomyiid midges (mostly *Mycodiplosis* sp. 1) in communal roosts[a] between day and night in one section of cocoa plantation[b] in Finca Experimental La Lola, near Siquirres, Limon Province, Costa Rica, during two different rainy season census periods.

		0700 to 1700 hrs ("Day")		1800 to 0600 hrs ("Night")	
Day	No. Roosts Present	Range in Roost Size	Max. No. Midges Seen in Roosts/Day	Range in Roost Size	Max. No. Midges Seen in Roosts/Day
		18–22 November 1981 ("late rainy")			
1	5	2–6	26	0	—
2	9	2–110	131	0–10	10
3	9	2–18	47	0	—
4	9	1–22	73	0–16	16
5	9	0–34	34	0	—
Total midge "observations":[c] 341					
$\bar{x} \pm$ SD (N = 5 days): 68.20 ± 54.85					
		16–22 July 1982 ("mid-rainy")			
1	5	10–45	109	0	—
2	7	1–20	67	0	—
3	14	2–150	517	0	—
4	15	2–60	217	0	—
5	15	1–88	251	0	135
6	17	7–51	322	0	—
7	17	2–53	293	0	—
Total midge "observations":[c] 1776					
$\bar{x} \pm$ SD (N = 7 days): 253.71 ± 148.70					

[a] Roosts were discovered and positions tagged with small, yellow plastic tags (numbered); most roosts in spider webbing draped between branches or pods and branches in cocoa trees.
[b] Well-shaded "habitat" of UF-29 cocoa—the "Area A" of Young (1983).
[c] Defined as the total number of midges obtained by summing the "maximum number seen" figures in the table.

larvae), the average abundance was $\bar{x} \pm$ SD = 7.85 ± 17.52 midges per pod (23–24 March 1983 census). Within a given pod having larvae, larvae are distributed in a patchy fashion. Larvae occur in both moist and dry exocarp as well as on moist rotting seeds inside pods. Shaded areas of cocoa have many rotting cherelles and tend to have more roosts of cecidomyiids than exposed areas. Pockets of several larvae frequently occur inside pods. At Hummingbird Hershey in March 1983, I witnessed several instances of female cecidomyiids perched on rotting pods in cocoa trees, and with the terminal tips of swollen abdomens (perhaps filled with mature eggs) probing the pod surface as if determining an egg-placement site. Larvae clustered in pockets in pods may reflect a clustered egg-laying habit in cecidomyiids. A hanging pod at La Lola in March 1982 and having a large squirrel-generated hole in it was blanketed with the hyphae of various fungi (*Fusarium*, *Phytophthora*, and *Thielaviopsis* sp.) and several adult cecidomyiids (*Clinodiplosis* sp. 1 and several undetermined ones as well) having swollen abdomens were perched in the fungal growth (Fig. 3). When the pod was collected and opened, many larvae of *Clinodiplosis* sp. 1 were found inside, within the rotting tissues exposed by the wound in the pod wall. Prior to collecting, adults on the fungus remained there for several hours, and adults were also present the next day as well. *Clinodiplosis* larvae make audible clicking sounds and jump several centimeters when disturbed. Various genera and species of cecidomyiids dwelling in cocoa farms in Central America undergo their life cycles in a range of rotting organic debris (Table 8). Samples of epiphytic moss from cocoa trees brought into the laboratory (Milwaukee) exhibit a gradual day-to-day emergence of *Mycodiplosis* sp. 1 adults: a sample collected in November 1981 at La Tigra generated 3 adults on 28 December 1981, and one each on 7, 8, 11 and 12 January 1982, and with all emergences occurring 0700–1000 hours under laboratory conditions. Both *Mycodiplosis* and *Clinodiplosis* species are known to be fungus-feeders in the larval stages and none are predatory or gall-makers (R. J. Gagné, pers. comm.). Cocoa farm habitats appear to be suitable for breeding in cecidomyiids, some of which may be cocoa pollinators (Table 8).

Discussion

Other studies have indicated that some Cecidomyiidae are pollinating agents of cocoa in both the New and Old World humid tropics (Kaufmann, 1973b; Winder, 1977b, 1978a), although the general conclusion has been that these midges are only incidental or fortuitous cocoa pollinators (e.g. Entwistle, 1972; Winder, 1978a). The present findings indicate that a few species of cecidomyiids, such as *Clinodiplosis* sp. 1 and *Mycodiplosis* sp. 1, are natural pollinators of cocoa in Central America, and several species also visit the flowers of other *Theobroma* species. The observed mechanism of pollination of cocoa by cecidomyiids in Costa Rica did not appear to include the "wing vibration" syndrome of several specimens in one flower as observed by Kaufmann (1973b) in Ghana. Rather, pollination appeared to be largely limited to the movements of individual cecidomyiids through enclosed reproductive floral parts in the present study.

In general the mode of cocoa pollination by cecidomyiids in Costa Rica matches well the typical pollination system involving ceratopogonid midges (e.g., see the review in Entwistle (1972) and in Bystrak and Wirth (1978) with these notable differences: (1) cecidomiids tend to carry fewer pollen grains than ceratopogonids (as also noted by Winder, 1977b), (2) cecidomyiids are mostly active in cocoa flowers at dawn, dusk, and at night while ceratopogonids are generally most active in the later daylight hours of the morning (e.g. Fontanilla-Barroga, 1962; Soria et al., 1980), and (3) cecidomyiids exhibit apparent feeding behavior at the fleshy petal ligules in areas filled with stomate-type nectaries (see Young et al., 1984) whereas this floral part is largely ignored by ceratopogonids; such feeding in cecidomyiids generally precedes the movement of midges into the enclosed reproductive parts of the cocoa flower, and might therefore be a prerequisite to actual pollination by cecidomyiids. Decazy et al. (1980) found many cocoa pollen grains adhering to the cuticle of cecidomyiids in South Cameroon, and determined that these midges often fly up to 35 meters and can therefore serve as cross-pollinating agents. Winder (1977b) also noted pollen grains in the cuticle of cecidomyiids in Brazil and Privat (1979) describes the movement of cecidomyiids in the petal hoods of cocoa flowers in Costa Rica. The question of whether or not this interaction is fortuitous awaits further study, given the general conclusion that dipterans are generalist floral visitors (e.g. Percival, 1965; Faegri and Pijl, 1971; Kevan and Baker, 1983). Yet some field studies indicate a more specialized role of some dipterans as pollinators (e.g. Baumann, 1978; Vogel, 1978; Mesler et

Table 8. Rearing records for Cecidomyiidae in some Central American cocoa farms.

Species	Locality	Rearing Conditions
Mycodiplosis sp. 1	La Tigra (Costa Rica)	10 from larvae on moss on trunk of tree in forest adjacent to cocoa; July–August, November 1981
	La Lola (Costa Rica)	1 from larva in experiment rotting disc (slice) of banana tree trunk (Young, 1983), March 1983
Mycodiplosis sp. 2	La Tigra (Costa Rica)	4 from larvae in ground-cover rotting cocoa leaf litter; July 1982
Clinodiplosis sp. 1	La Tigra (Costa Rica)	9 from larvae in arboreal plastic cup (artificial bromeliad) filled with rotting cocoa leaves (Young, 1982) and from moss on trunk of tree in forest adjacent to cocoa; Dec. 1978, Nov. 1981 and March 1983
	La Lola (Costa Rica)	30 larvae in squirrel-generated wound in ripe cocoa pod in tree (with pod hole covered with hyphae of various fungi); March 1982
	Hummingbird Hershey (Belize)	8 larvae just beneath dry exocarp layer of hanging cocoa pod destroyed by black pod rot; March 1983
Clinodiplosis sp. 3	La Lola (Costa Rica)	1 from larva in arboreal plastic cup (artificial bromeliad) filled with rotting cocoa leaves (Young, 1983); February 1981
Coquillettomyia sp.	La Lola (Costa Rica)	1 from larva in arboreal plastic cup (artificial bromeliad) filled with rotting cocoa leaves (Young 1983); August 1981
Micromyia sp.	La Lola (Costa Rica)	2 from larvae in experimental rotting discs (slices) of banana tree trunk (Young, 1983); July 1981
	La Tigra (Costa Rica)	1 from larva in arboreal plastic cup (artificial bromeliad) filled with rotting cocoa leaves; December 1978
Ledomyia sp.	La Tigra (Costa Rica)	1 from larva in ground-cover rotting cocoa leaf litter and 2 from larvae in arboreal plastic cup (artificial bromeliad) filled with rotting cocoa leaves; Dec. 1978 and March 1979
Lestodiplosis sp.	La Tigra (Costa Rica)	1 from larva in ground-cover rotting cocoa leaf litter; March 1979
Porricondylia sp.	La Tigra (Costa Rica)	2 from larvae in ground-cover rotting cocoa leaf-litter; December 1978
Camptomyia sp.	Hummingbird Hershey (Belize)	12 larvae in both wetter and drier portions of exocarp galleries in 3 arboreal rotting cocoa pods; March 1983
Resseliella sp.	Hummingbird Hershey (Belize)	10 larvae inside woodpecker-generated gouge or hole in arboreal cocoa pod in early stages of rotting cycle; March 1983
Undet. Cecidomyiidi	La Lola (Costa Rica)	5 larvae in squirrel-generated wound in ripe cocoa pod in tree (with pod hole covered with hyphae of various fungi); March 1982

al., 1980). The presence of functional elongate mouthparts and exceptionally long hairs on the legs and abdomen of *Clinodiplosis* and *Mycodiplosis*, and the observed apparent feeding by these midges on petal ligules and other floral parts involved in the reproductive biology of cocoa, point to a specialized association with flowers. Both Kaufmann (1973b) and Winder (1977b) observed cecidomyiids inside petal hoods of cocoa flowers in Ghana and Brazil, respectively, and related this behavior to pollination. Other genera of these midges formed the basis of their studies. Patterns of feeding on nectar and pollen by some Diptera may vary within a group of closely related species and may be expressed in terms of divergence in mouthpart structure (e.g. Gilbert, 1981). Although there exist some extensive records of life cycle associations in Neotropical Cecidomyiidae (Gagné, 1968, 1977), a pollination association with cocoa has not been emphasized in great detail (with the exceptions of Kaufmann, 1973b and Winder, 1977b). The observed heavily skewed abundance of female midges in cocoa flowers suggests a possible feeding association somehow linked to the reproductive physiology of these midges. But Kaufmann (1973b) found a 1:1 sex ratio in *Parallelodiplosis triangularis* (Cecidomyiidae) in cocoa flowers in Ghana, and the females were sexually mature. Pollen-feeding by female *Heliconius* butterflies is an adaptation for acquiring some amino acids essential for egg development (Gilbert, 1972). Female cecidomyiids in cocoa farms may seek out flowers for pollen or nectar, and then proceed to breed in nearby microhabitats such as epiphytic mosses and rotting cocoa pods still on the trees. In some studies of mosquitoes, there are good correlations in females between breeding sites and feeding sites from the previous evening (e.g. Kay, 1983). While Baker et al. (1953) noted associations of cecidomyiids with predaceous larval stages feeding on mealybugs associated with cocoa and other *Theobroma* in Brazil, free-living non-predaceous forms such as species found as adults in cocoa flowers may have larval stages associated with these trees in a different way: larvae are found in the rotting tissues of either animal-damaged or diseased pods still on the trees. *Toxomyia*, a genus evolutionarily close to *Mycodiplosis*, has larval stages associated with rust spores on leaves in the West Indies (Parnell, 1969). Unlike the association of other cecidomyiids with the flowers of grasses in the American tropics (Soderstrom and Calderón, 1971), larval stages of cocoa-pollinating cecidomyiids have not been found in the flowers. Kaufmann (1937b) in her Ghana studies has reported larvae of cocoa-associated cecidomyiids in flowers.

There is an abundant data base indicating that small-bodied midges such as cecidomyiids are largely limited in activity to moist forest habitats or to times of the day and evening when ambient conditions are moist and cool (e.g. Fisher and Teetes, 1982; Barnes, 1930; Summers, 1975; Shazli and Mostafa, 1980; Brewer, 1981; Vanhara, 1981; Brown and McGavin, 1982; Charlwood et al., 1982; Lumsden, 1952; Willmer, 1982). My data indicate a strongly crepuscular and nocturnal activity pattern of cocoa-pollinating cecidomyiids, as determined from surveys of midges in cocoa flowers, and by observing roosting habits in some species. Kaufmann (1973b) noted similar diurnal activity patterns for cocoa-associated cecidomyiids in Ghanian cocoa farms, and at least one tropical study indicates that *Toxomyia* (a genus close to *Mycodiplosis*) adults emerge in the late afternoon and early evening from their pupae (Parnell, 1969). Lucas (1981) reported cecidomyiids laden with cocoa pollen grains being collected at or before 0700 hours in cocoa farms in the Ivory Coast, and Decazy et al. (1980), using radio-isotopes as midge markers, determined two peaks of cecidomyiid activity in cocoa plantations in South Cameroon as 0730–0930 and 1630–1830 hours. In general cocoa flowers begin to open in the late afternoon, and gradually open all night and are fully open by 0500 hours (e.g. Wellensiek, 1932; Sampayan, 1966; Gorrez, 1962; Soetardi, 1950). Although Sampayan (1966) concludes that anther dehiscence in cocoa flowers peaks between 0600-1000 hours and stigma receptivity to pollen between 1000–1300 hours in the Philippines, similar data from Costa Rica (La Lola) indicates pollen-release throughout most of the day and night, and greatest fertilization of flowers in the early and mid-morning hours (Young et al., 1984). Given these data and the observed activity patterns of cecidomyiids in the Costa Rican studies, I propose, tentatively, that these midges pick up viable cocoa pollen grains during their dusk and evening activity periods, and deposit pollen on stigmas and pistils primarily in the dawn hours (e.g. 0530–0700 hours). Thus cocoa flowers behaviorally function as males during most of the day and evening following anthesis, and as females in the dawn hours, even though the flowers are morphologically and physiologically hemaphroditic (e.g. Walker, 1959). Differential rates of sexual maturation in male and female floral parts in relation to pollinator behavior have been noted in other plant species exhibiting synchronized flowering (e.g. Philbrick, 1983; Essig, 1971; Gibbs et al., 1977).

The habit of some cocoa flower cecidomyiids forming roosting aggregates in spider webs on cocoa trees may assist in the concentration of midges near floral rewards. Although such roosts in the present study were found to contain about equal numbers of male and female midges, Kaufmann (1973b) noted twice as many females as males in Ghanian cecidomyiids in cocoa. As in the present study, Kaufmann (1973b) also noted dissolution of roosts in the evening and the formation of roosts in the daylight hours. Although not yet determined, roosting behavior in cecidomyiids may function primarily to conceal midges from predators that forage on the trunks and branches of cocoa trees (see also Lahmann and Zuniga, 1981) as they apparently have little or no function in mating behavior (Sivinski and Stowe, 1980). As in the present study, Kaufmann (1973b) too noted that midges often roost in spider-occupied webs, suggesting little threat of predation from these animals. By far, the greatest densities of midge predators in cocoa trees are seen in *Anolis* lizards and the mantid *Chaeteessa filata*. Dipterans are known to be a major component of the diet in *Anolis* (e.g. Floyd and Jenssen, 1983), and the high densities of these lizards in cocoa habitats like La Lola (see Andrews, 1979) suggests that considerable selection pressure is operating for effective predator defense behavior in small-bodied flying insects in the same habitats. Aggregative behavior has been long known to be one form of protection against predators in invertebrate animals (Allee and Rosenthal, 1949 and several included references). The observation that the same sites (webs) tend to be reused over several successive days suggests a social organization associated with roosting cecidomyiid species in cocoa habitats. Roosting in these midges, with daily recruitment of new individuals in some instances, may represent a form of "local enhancement" to advertise optimal resources within the cocoa habitat (e.g. Ward and Zahari, 1973). Because reproductive effort (i.e. numbers of eggs deposited in the environment per unit area) in forest-dwelling dipterans can be relatively high (e.g. Fallis and Snow, 1983), predators may selectively forage on numerically-abundant species such as cecidomyiids. The high turnover in organic rotting materials in cocoa farms very likely promotes the maintenance of cecidomyiid breeding populations, unlike closed laboratory systems in which enforced migrations can sometimes occur in response to contamination arising from high population densities, as shown for some fungus-dwelling Sciaridae (Binns, 1980). Preferential egg-laying behavior in cecidomyiids may allow midges to exploit a range of different microhabitats, both terrestrial and arboreal, as a means of resource partitioning as shown for other dipterans in the tropics (e.g. Siefert, 1980; Siefert and Barrera, 1981; Gagné, 1968, 1977; Carpenter, 1983; Winder, 1978b and many included references). A major component of the evolutionary association of Cecidomyiidae with cocoa trees may include the exploitation of arboreal breeding microhabitats routinely found in *T. cacao* populations in the American tropics, namely, rotting holes in cocoa pods made by animals such as squirrels and woodpeckers, and epiphytic mosses.

Various studies have shown that cocoa-pollinating Ceratopogonidae exhibit wide fluctuations in population structure correlating well with seasonal patterns of rainfall (e.g. Soria and Abreu, 1976). While the drier months of the year at Costa Rican cocoa-growing localities such as La Tigra and La Lola tend to be times of reduced levels of flowering in cocoa trees (e.g. Young, 1982, 1983, 1984b) the preliminary data on abundance of adult cecidomyiids given in the present paper suggest an increase in abundance during the drier months. These data were not gathered in such a way so as to distinguish between greater abundance being an artifact of sampling, i.e. in which areas of cocoa sampled in the dry season tended to have greater accumulations of midges, or an actual indication of greater absolute abundance in populations at these times. But Kaufmann (1973b) determined that cecidomyiids were more abundant in cocoa flowers during the dry season in Ghana. If the observed high densities of these midges during the drier periods is a real biological effect and not an artifact of small sample size, and if it represents a concentration of these insects into moist pockets of cocoa, there is expected to be an increased dispersion of the populations during the rainy months. Flowering tends to be greater in the wetter months at the Costa Rican localities studied (Young, 1984b) and there will be a greater floral reward for pollinators over larger areas of cocoa habitats. Because the egg-to-adult developmental time in some free-living tropical cecidomyiids is only about ten days (e.g. Parnell, 1969), many overlapping generations can occur each year. During the drier months, these midges may exploit dry substrates as breeding sites as shown by the discovery of larvae in relatively dry exocarp of cocoa pods in the dry season at Hummingbird Hershey. Particularly during the drier months, small-bodied Diptera may accumulate in the more shaded areas of cocoa farms in response to thermal and moisture stress, and shaded areas of cocoa habitats tend to have a greater diversity of Diptera than sunny habitats (Bigger, 1981; Gibbs and Leston, 1970; Young, 1983). Seasonally-related changes in the spatial distribution and abundance of moist or wet microhabitats used by Cecidomyiidae and other Diptera in the tropics result in changes in the availability of adult insects in breeding populations (e.g. McLachlan and Cantrell, 1980). Levels of natural pollination in cocoa are determined in part by the ways in which seasonal changes in rainfall influence population cycles in natural pollinators (De la Cruz and Soria, 1973). Times of the year in which flowering is highest and synchronous within a population of a tropical tree species are also times of greatest abundance of pollinators at flowers, since more pollinators are attracted to more intense floral displays (e.g. Augspurger, 1981).

Although it was determined, by light microscopy, that cocoa flowers possess nectary-like structures on specific floral parts (Stejskal, 1969), recent studies using scanning electron microscopy reveal stomate-type nectaries on petal ligules and on the inner surfaces of petal hoods in these flowers (Young et al., 1984). These nectaries have diameters suitable to accommodate the sucking mouthparts of cecidomyiids such as *Clinodiplosis* sp. 1, *Mycodiplosis* sp. 1, *Coquillettomyia* sp., and *Aphodiplosis triangularis*. The surface of the floral ovary is blanketed with peg-like glandular structures (Stejskal, 1969; Young et al., 1984) of unknown function, but perhaps an additional component of the "pollinator reward syndrome" of *Theobroma* flowers (Young et al., 1984). Cecidomyiids and ceratopogonids, as well as wild bees (Young et al., 1984), may visit cocoa flowers and those of other *Theobroma* for both pollen and nectar as floral rewards. A fragrance-producing ring of glandular structures located between the sepals and petals of *Theobroma* flowers, and greatly reduced in faintly-scented cocoa flowers (Young et al., 1984), may constitute the mechanism by which floral visitors are attracted to flowers. Once inside petal hoods, cecidomyiids often follow the pigmented "nectar guides" leading towards the basal area of the flower, and they are perhaps also following a fragrance being produced by the basal glandular ring, albeit faint in cocoa. Similar behavior, resulting in pollination, has been noted for certain species of fungus gnats associated with *Asarum* (Vogel, 1978).

Elsewhere (Young et al., 1984) the hypothesis is advanced that the basic floral design in *Theobroma* may have originally evolved as a bee-pollination system as most species of the genus have colorful flowers with strong pleasant fragrances, two conditions reduced in *T. cacao*. It is suggested that *T. cacao* which thrives well in cool, moist shaded forest understories, even in its natural state (Allen, 1981), has evolutionarily replaced bees with Diptera as frequent natural pollinators (Young et al., 1984). While some wild bees, such as *Trigona jaty* (Hymenoptera: Apoidea: Meliponinae) may not directly pollinate cocoa flowers (Soria, 1975; Young, 1981), such heavy-bodied insects may sufficiently jostle pollen loose from anther sacs to facilitate eventual contact with small midges crawling through petal hoods. Pollen grains frequently lodge on the inner surface of petal hoods, adjacent to the anthers they enclose (Young et al., 1984). In the closely related genus *Herrania*, pollen grains adhering to the side of petal hoods are picked up by phorid flies, the natural pollinators (Young, 1984c). Still other kinds of small-bodied wild bees may directly pollinate cocoa flowers (e.g. Kaufmann, 1975c). In Costa Rica, wild bees tend to forage primarily on cocoa flowers in the sunlit upper portions of cocoa trees, while midges (cecidomyiids and ceratopogonids) are more commonly encountered on shaded, lower branches (A. M. Young, unpubl. data). In some plant species, both dipterans and bees jointly contribute to the overall reproductive success in populations (e.g. Motten et al., 1981). When bee-pollinated plant species occur in cool, moist environments, generalized or specialist flies tend to replace bees as routine pollinating agents (e.g. Levesque and Burger, 1982; Anderson and Beare, 1983). In the American tropics, some tree species such as *Hevea* possess specialized associations between flowers and their midge pollinators (Steiner, 1983), and it is sometimes necessary to view a plant species as having both "major" and "minor" sets of pollinators, often belonging to very different taxa (Lewis and Zenger, 1983). Wild bees and midges (Ceratopogonidae and Cecidomyiidae) may comprise such a constellation of pollinator sets in *Theobroma* and other Sterculiaceae.

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