

Population Dynamics and Prey-Predator/Parasite Relationships of Gall-Forming Thrips

S VARADARASAN and T N ANANTHAKRISHNAN
Entomology Research Institute, Loyola College, Madras 600034

(Received 28 November 1980)

Population periodicities of six species of gall-inhabiting thrips for a period of three years indicated that their abundance depends largely on the presence of young leaves. Factors influencing fluctuation of populations involve such biotic factors as (a) the inquiline predator, *Androthrips flavipes* Schmutz, on four of the gall-forming thrips, (b) the predatory anthocorid bug, *Montandoniola moraguesi* Puton on two of the gall thrips, and (c) the hymenopteran eulophid internal parasite, *Tetrastichus thripophonus* Waterson on one gall thrips, and the only abiotic factor, viz., heavy rainfall. In thrips-predator/parasite interactions, the efficient predatory inquiline, *A. flavipes*, though an important biotic factor in bringing about population fluctuations in the gall-maker, never outnumbers its prey population because of frequent cannibalism. It occurs in considerable numbers only within compact roll/rosette galls, while in less compact galls its number is damped down by the 'secondary predator', *M. moraguesi*. Though parasitization of the larvae of all the gall thrips is prevalent under laboratory conditions, the eulophid parasite, *T. thripophonus*, is recorded in nature only in galls inhabited by *Schedothrips orientalis* Ananthakrishnan, *Arrhenothrips ramakrishnae* Hood, and *Thilakothrips babuli* Ramakrishna.

Key Words: Gall thrips, Population dynamics, Predator/Parasite

Introduction

Information on the population dynamics of free-living Thysanoptera is considerable, compared with that on gall-inhabiting species, where the only available data pertains to *Gynaikothrips flavian-tennatus* Moulton in the galls of *Casearia tomentosa* Roxb. (Raman et al. 1978), *Aneurothrips priesneri* Bhatti inhabiting the galls of *Cordia obliqua* Willd.

(Ananthakrishnan & Swaminathan 1979) and *Gynaikothrips bengalensis* Ananthakrishnan and *Mesothrips jordani* Zimmerman within the galls of *Ficus bengalensis* Linn. (Muraleedharan et al., in press). An attempt is made at a comparative study of the population dynamics of the following six species of gall-forming thrips: *Arrhenothrips ramakrishnae*

(within leaf-fold galls of *Mimusops elengi* Linn., Sapotaceae), *Teuchothrips longus* (Schmutz) (within hypophyllous leaf-roll galls of *Pavetta hispidula* Linn., Rubiaceae), *Gynaikothrips flaviantennatus* (within epiphyllous leaf-roll galls of *Casearia tomentosa*, Samydaceae), *Schedothrips orientalis* (within epiphyllous leaf-roll galls of *Ventilago maderaspatana* Gaertn., Ramnaceae), *Crotonothrips dantahasta* (Ramakrishna) (within epiphyllous leaf roll galls of *Memecylon edule* Roxb., Melastomaceae, and *Thilakothrips babuli* (within rosette galls and inflorescence galls of *Acacia leucophloea* Willd., Mimosae). Analysis of populations, particularly in closed systems such as galls, naturally also involve interaction of host-predator/parasites. Information is provided on the predatory behaviour as well as predator-prey interactions of *Androthrips flavipes* Schmutz, a predatory inquiline very commonly present in most thrips galls, and the predatory anthocorid bug, *Montandoniola moraguesi* Puton, also inhabiting most thrips galls. Host-parasite interactions relating to *Tetrastichus thripophonus* Waterson (Eulophidae: Hymenoptera), a larval parasite attacking only three species of gall-forming thrips, *Schedothrips orientalis*, *Arrhenothrips ramakrishnae*, and *Thilakothrips babuli*, are also presented. Species of *Tetrastichus* are well known larval parasites of thrips and available information relates to this parasite affecting *Gynaikothrips ficorum* (Marchal), *G. uzeli* Zimmerman, *Liothrips urichi* Karny, *L. oleae* (Costa) and *L. setinodis* (Reuter) Lewis (1973). Ananthkrishnan and Swaminathan (1977) reported *Tetrastichus thripophonus* parasitizing the gall-forming thrips *Schedothrips orientalis*.

Materials and Methods

Galls were collected from different localities in and around Madras and according to the nature of the gall, were gently opened with fine needles and spread on a thermocole sheet to avoid crushing the immature stages. Individuals were tapped on to a white background and observations were made twice a month through random sampling of ten galls from the various host plants mentioned earlier, for a period of three years 1976–1979. Statistical analysis involving multiple regression and simple correlation was also done.

The predatory behaviour, efficiency, and life cycle of *Androthrips flavipes* were studied by rearing them in transparent plastic vials (8×2.5 cm; 5×2.5 cm). Eggs and immature stages of cecidogenous species were regularly provided as food.

Observations and Results

Population dynamics: Of the six gall-forming thrips studied, *Arrhenothrips ramakrishnae*, *Schedothrips orientalis*, and *Gynaikothrips flaviantennatus* forming galls on *Mimusops elengi*, *Ventilago maderaspatana*, *Casearia tomentosa* respectively were recorded every year of the three-year period with their population abundance occurring at 6–8, 3–6, and 4–9 months respectively (figures 1–3). Though *Teuchothrips longus* and *Crotonothrips dantahasta*, occur throughout the year, observations were made for only seven months, when they were in sufficient numbers, they being abundant only for 3–4 months (figures 5 & 6). *Thilakothrips babuli* on *Acacia leucophloea* was highly seasonal, inducing galls on the axillary buds (rosette galls) for about 45 days (May and June) and on the inflorescence (florete galls) for

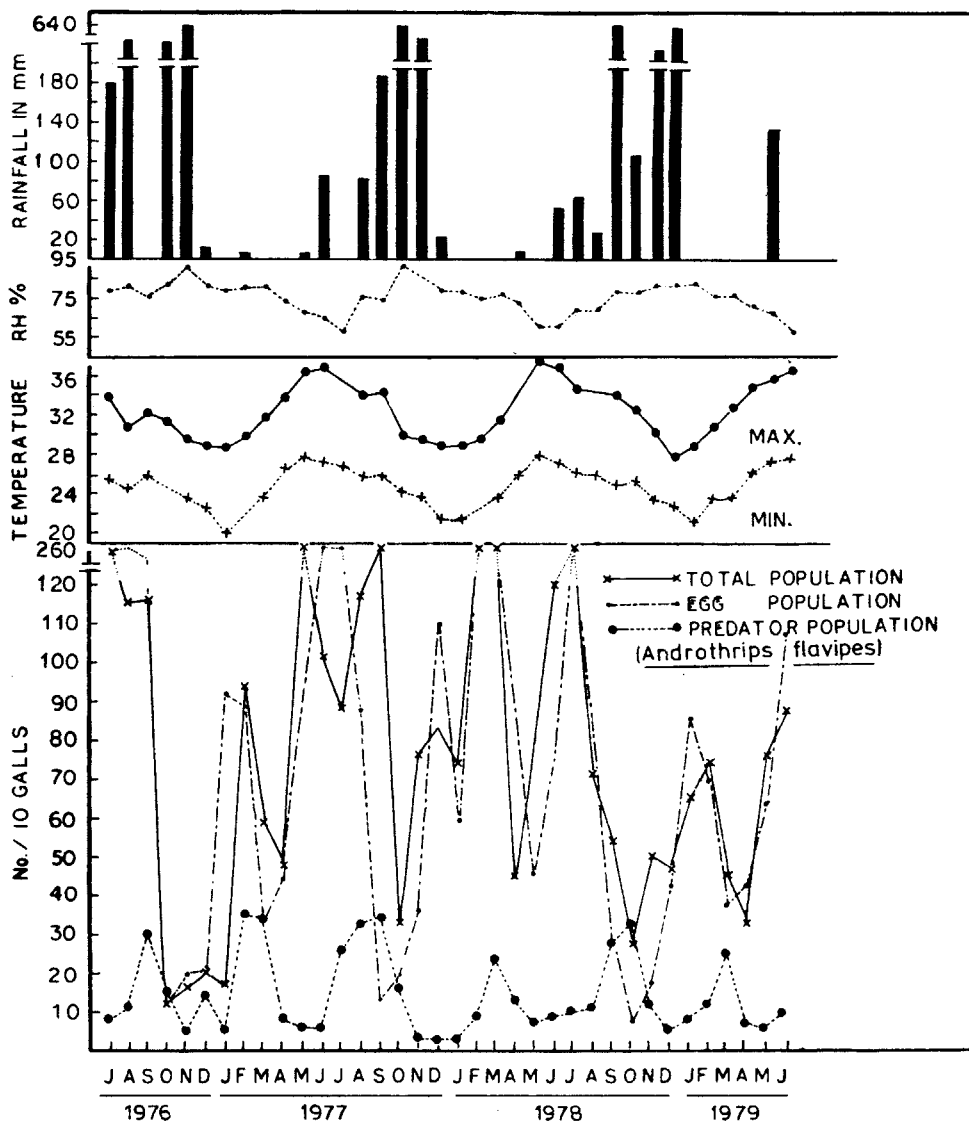


Figure 1 Population fluctuation of *Arrhenothrips ramakrishnae*

about twenty days (September). Rosette galls and inflorescence galls together were recorded for five months in a year and the population was abundant for 3 months (figure 4).

Population abundance and fluctuation are brought about mainly by biotic factors like presence or absence of young

leaves, the predatory anthocorid bug, *Montandoniola moraguesi*, the inquiline predator, *Androthrips flavipes*, and the hymenopteran parasite, *Tetrastichus thripophorus*.

In all the cecidogenous thrips, gall-formation is a prerequisite for development and oviposition (Varadarasan 1979)

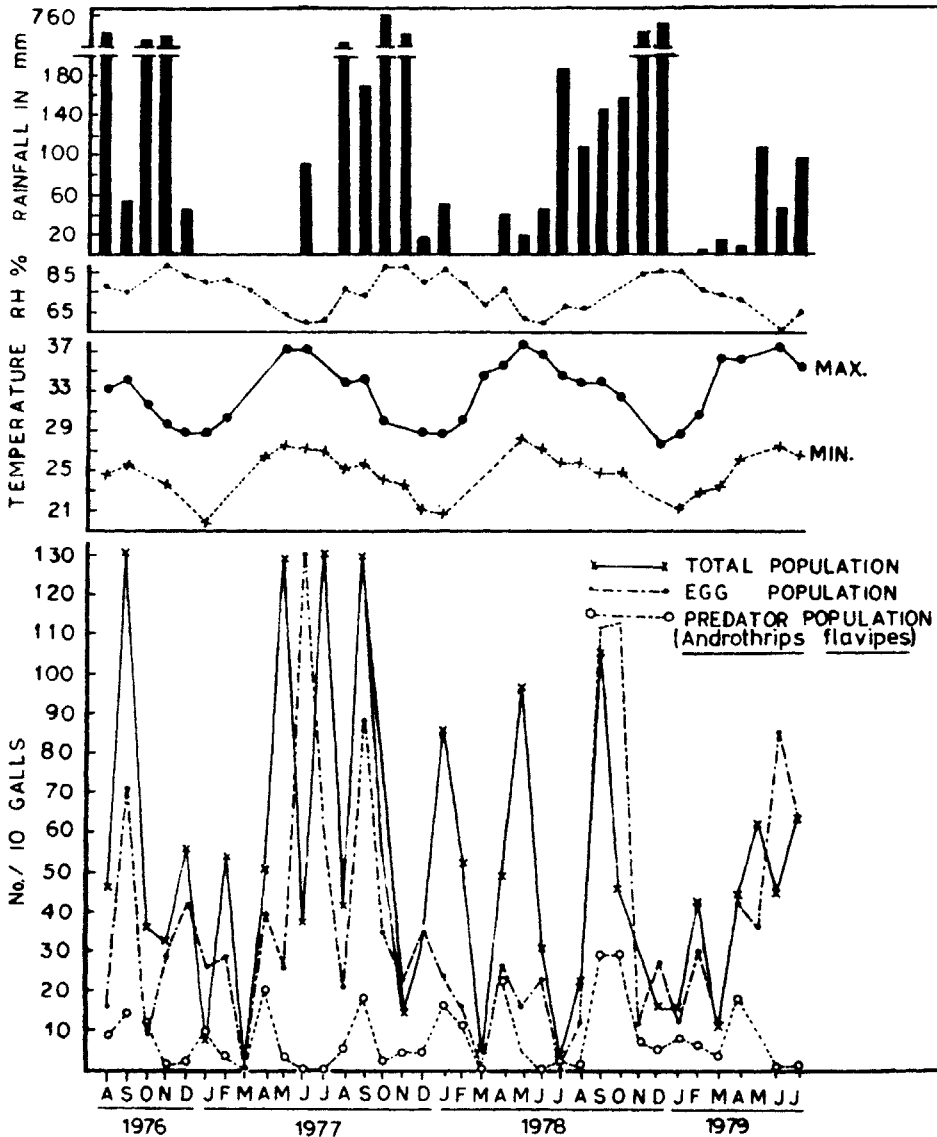


Figure 2 Population fluctuation of *Schedothrips orientalis*

They cause galls only in young, undifferentiated leaves and form a microhabitat of their own. The presence or absence of the latter is a major limiting factor in the abundance and fluctuation of gall thrips. Gall-forming thrips complete their life cycle within a month and this coincides with the monthly

production of young leaves on host plants, thus the emergence of adult thrips synchronizes with the formation of young leaf buds.

The gall-thrips *A. ramakrishnae*, *S. orientalis* and *G. flaviantennatus* occur throughout the year when the young leaves are also produced in large

numbers in their respective host plants. Young leaves are formed in *M. elengi* almost throughout the year, in *V. maderaspatana* for 6–8 months and in *C. tomentosa* for 4–9 months. The gall-makers occur in abundance for nearly 6–8, 3–6 and 4–9 months respectively. The presence of very few gall-making thrips during certain months in spite of the young leaf formation could be ascribed to various other biotic and abiotic factors. The population abundance of these gall-making thrips and the varying periods of young leaf formation on the respective host plants are shown in table 1.

Another important biotic factor that has a profound influence on the population of gall-making thrips is the number of predators/parasites or the combined effects of both. In the six gall-thrips studied, the inquiline predator, *A. flavipes*, the anthocorid bug, *M. moraguesi*, and the internal larval parasite, *T. thripophonus* act detrimentally on the populations at different periods. The presence of *A. flavipes* is found to be an important factor in population fluctuations both in *A. ramakrishnae* and *S. orientalis* (figures 1 & 2). Besides, the population of *S. orientalis* is found to be influenced by *T. thripophonus*, abundant

Table 1 Abundance of Young leaves in the host plants of the different gall thrips

Host Plant (Gall thrips)	Year	Periods of young leaf abundance
<i>Mimusops</i>	1976-77	July to Nov., Feb. to June
<i>elengi</i>	1977-78	July to Nov., Feb., Mar., May, June
(<i>Arrhenothrips</i> <i>ramakrishnae</i>)	1978-79	July to Feb., May, June
<i>Ventilago</i>	1976-77	Aug., Sept., Dec., Feb., Apr., May, June
<i>maderaspatana</i>	1977-78	Aug., Sept., Oct., Jan., Feb., May, June
(<i>Schedothrips</i> <i>orientalis</i>)	1978-79	Aug., Sept., Oct., Feb., May, June
<i>Casearia</i>	1976-77	Nov., Dec. to July, Oct.
<i>tomentosa</i>	1977-78	Nov., Dec. to July
(<i>Gynaikothrips</i> <i>flaviantennatus</i>)	1978-79	Jan. to July
<i>Pavetta</i>	1976-77	Nov., Dec., Jan., Feb., Aug., Oct.
<i>hispidula</i>	1977-78	Nov., Dec., Jan., Feb., Aug., Oct.
(<i>Teuchothrips</i> <i>longus</i>)	1978-79	Nov., Dec., Jan., Feb., Aug., Sept., Oct.
<i>Memecylon</i>	1976-77	Jan. to Mar.
<i>edule</i>	1977-78	Jan. to Mar.
(<i>Crotonothrips</i> <i>dantahasta</i>)	1978-79	Dec. to Mar.
<i>Acacia</i>	1977	May, June, Sept.
<i>leucophloea</i>	1978	May, June, Sept.
(<i>Thilakothrips</i> <i>babuli</i>)	1979	May, June, Sept.

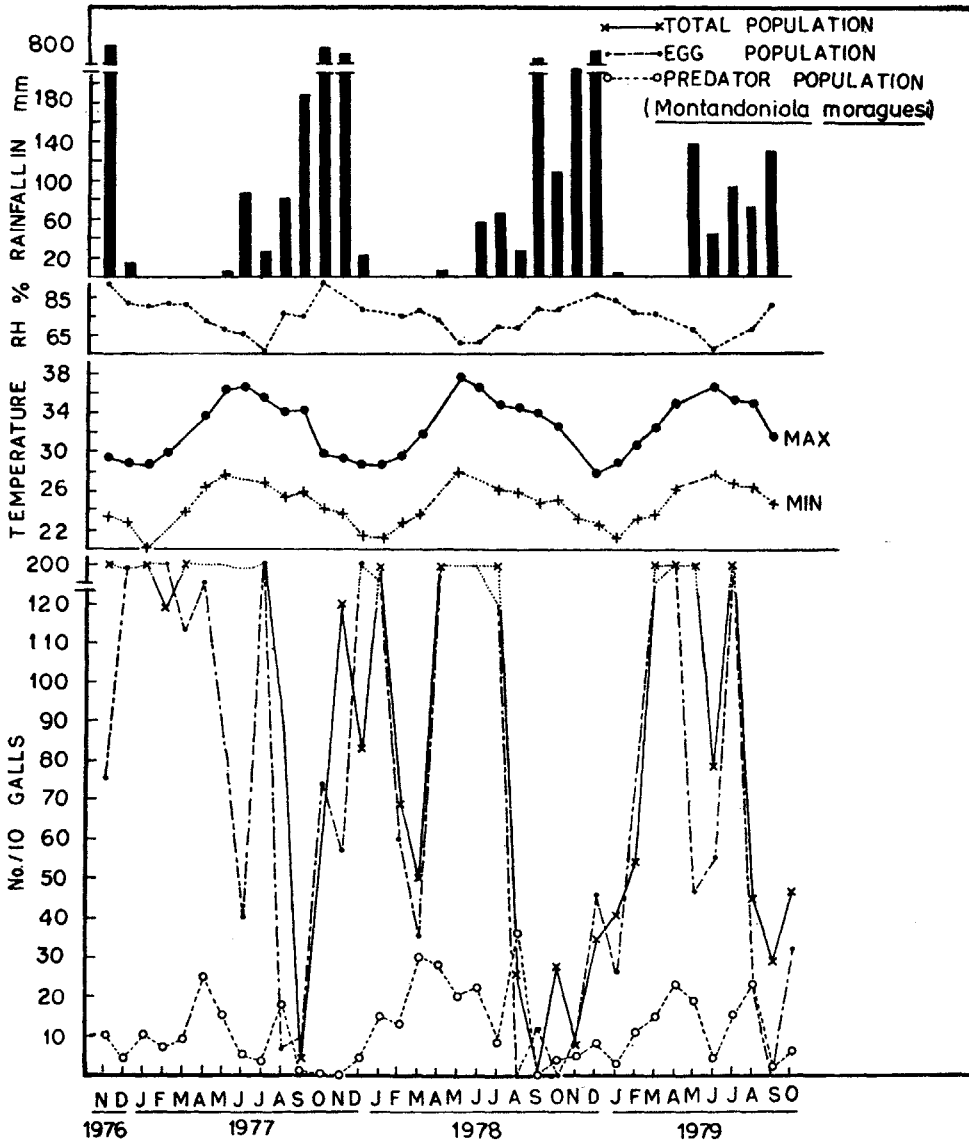


Figure 3 Population fluctuation of *Gynaikothrips flaviantennatus*

in November and February. Only the anthorcid bug appears to affect the population in *G. flaviantennatus*. This bug exhibits 2-3 peaks a year, each over 1-3 months (figure 3). It is thus evident that the abundance and peak populations

of the three gall-thrips are influenced by biotic factors.

The populations of *C. dantahasta* and *T. longus* on *M. edule* and *P. hispidula* were observed for seven months for population studies. Their absence for 5

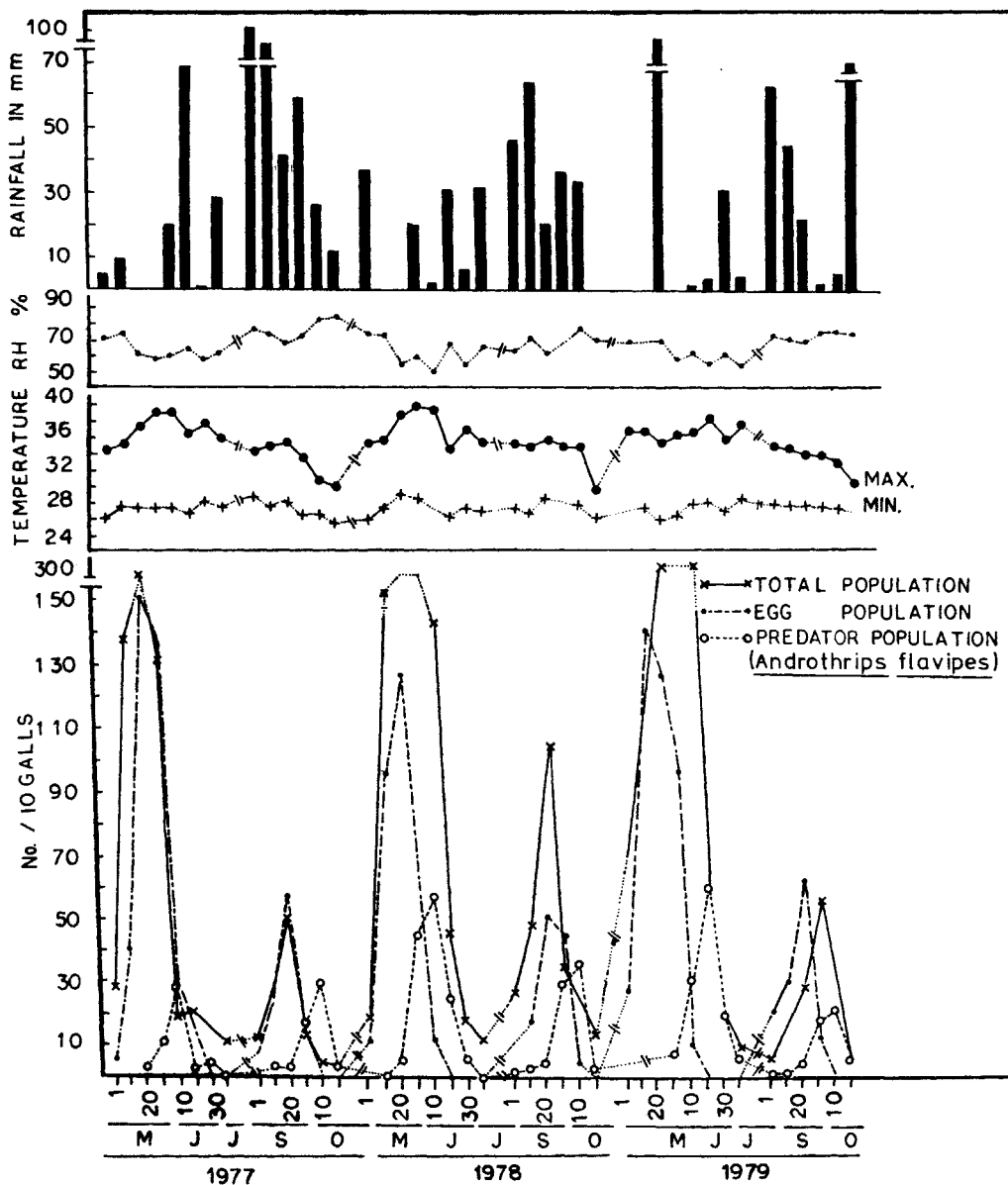


Figure 4 Population fluctuation of *Thilakothrips babuli*

months coincides well with the absence of new leaf formation in *M. edule* and *P. hispidula*. The few stargglers found during this period have abundant fat bodies and appear to be in a temporary diapause. When such thrips are provided

with young leaves, normally absent in that season, feeding and mating activities become evident and they reproduce normally. The population of *C. dantahasta* is affected by *A. flavipes* and that of *T. longus* by *M. moraguesi*. Unlike all

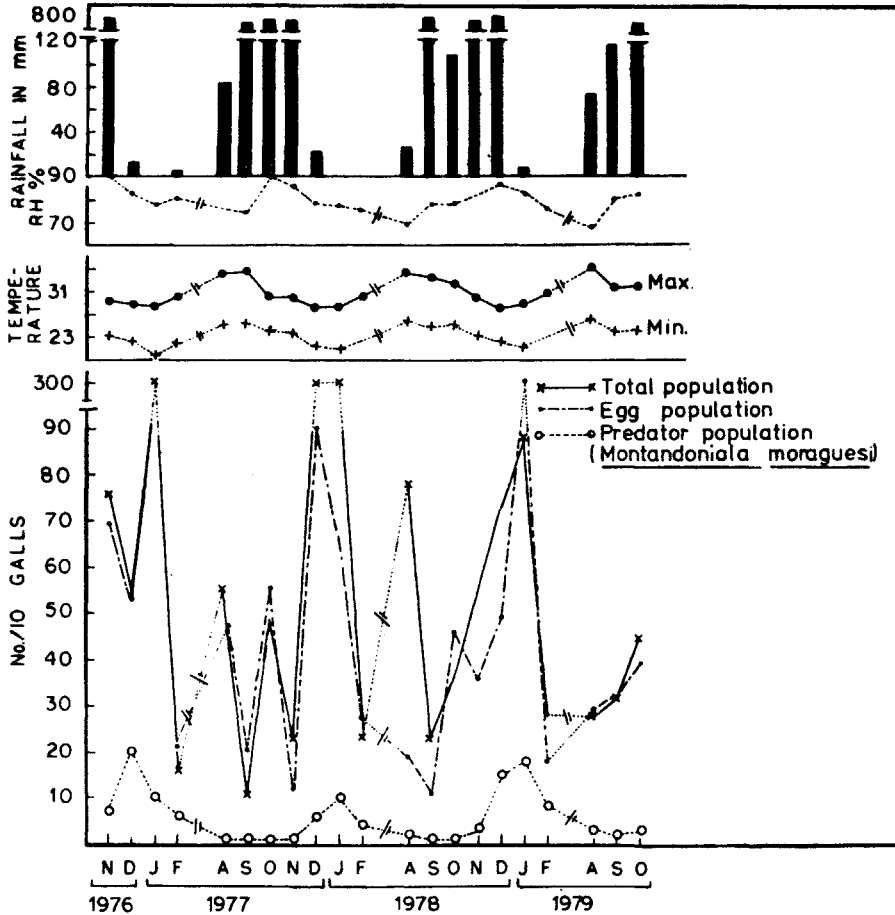


Figure 5 Population fluctuation of *Teucothrips longus*

the other previously mentioned gall thrips, the population abundance of *T. babuli* is restricted to only three months—two months in rosette galls and one in floret galls with 1–2 peaks in each habitat (figure 4). With the maturation, the rosette gall begins to dry up, and thrips population also dwindles, leaving behind very few apterous adults. These adults remain within the dry galls and diapause. With *Acacia* sprouting flower buds, the apterous adults leave the diapausing site and migrate to the flowers to form floret galls, in which

all polymorphic forms are established (Varadarasan 1979). Both in the rosette and floret galls, individuals of *T. babuli* are predated upon by *A. flavipes*, considerably decimating the population of the gall-maker (figure 4).

In the case of phytophagous insects, climatic factors normally influence their population indirectly by affecting the host plants. Earlier studies made by Harris et al. (1936) and Sakimura (1937) on *Thrips tabaci*, by Dev (1964) on tea thrips, and by Oettingen (1942) on *Aptinothrips rufus* have shown the

importance of abiotic factors like rainfall, temperature and humidity, and their adverse effect on these thrips populations. It may be emphasized that all this information pertains only to free-living thrips, which differ basically in their habitat from gall thrips. The latter live in a microhabitat of their own making, where the effects of the abiotic factors are totally different from those of free-living thrips. Hence an attempt is made to correlate the changes in gall-maker population with those in abiotic factors.

Analysis of the different ranges of abiotic factors like temperature, relative humidity, and rainfall taken over a three-year period, when the gall-maker populations were in abundance, indicates that the main visible effect on gall thrips population is produced by heavy rainfall

(figures 1-6). Though young leaves (the chief limiting factor) are available in plenty for gall formation, the cecidozoa seems unable to withstand the heavy downpour and suffers heavy mortality. Heavy rainfall (October-December) considerably brought down the population of *A. ramakrishnae* and *G. flaviantennatus* (figures 1 & 3), that of *S. orientalis* in October, November (1976, 1977), and December (1978) (figure 2), and of *T. longus* during October and November (figure 5). Table 2 however shows that moderate rainfall (120-200 mm) did not affect the populations very much. This is not surprising as several other studies Morison (1957) on *Aptinothrips rufus* (Gmelin); Lewis (1955) on *Euchaetothrips kroli* (Schille); Titschack (1969) on *Organothrips bianchi* (Hood) have shown

Table 2 The range of abiotic factors during the peak gall-maker populations

Thrips species	Year	Average temperature (°C)	Relative humidity (%)	Rainfall (in mm)
<i>Arrhenothrips ramakrishnae</i>	1976-77	25.9 to 31.9	63.5 to 76.5	0.5 to 370.0
	1977-78	24.9 to 32.9	54.0 to 80.5	1.0 to 496.0
	1978-79	25.0 to 32.5	61.0 to 73.0	0.1 to 264.0
<i>Schedothrips orientalis</i>	1976-77	25.0 to 31.3	58.0 to 75.5	10.5 to 49.0
	1977-78	24.2 to 33.1	61.0 to 83.0	19.8 to 171.3
	1978-79	29.5 to 32.0	60.5 to 68.0	95.0 to 146.9
<i>Gynaiokothrips flaviantennatus</i>	1976-77	24.25 to 31.9	57.0 to 77.0	0.5 to 36.4
	1977-78	24.9 to 32.8	62.0 to 80.5	1.3 to 496.1
	1978-79	28.1 to 31.1	66.0 to 72.0	1.0 to 136.0
<i>Teuchothrips longus</i>	1976-77	24.2 to 29.7	70.0 to 89.0	1.0 to 807.0
	1977-78	24.2 to 30.2	67.0 to 73.0	1.3 to 264.2
	1978-79	25.0 to 29.8	63.0 to 86.0	4.1 to 642.0
<i>Crotonothrips dantahasta</i>	1976-77	24.4 to 28.2	69.0 to 72.0	3.2 to 4.7
	1977-78	24.8 to 29.5	67.0 to 77.0	0 to 52.1
	1978-79	25.1 to 30.1	67.0 to 75.5	2.4 to 13.0
<i>Thilakothrips babuli</i>	1977	31.4 to 33.0	58.0 to 73.0	9.2 to 41.7
	1978	31.3 to 33.8	49.0 to 72.0	2.8 to 20.8
	1979	30.3 to 33.1	55.0 to 74.0	2.5 to 98.9

the ability of thrips to survive temporary submersion in water. The populations of *T. babuli* and *C. dantahasta* occur in abundance only during summer; hence rainfall has a negligible effect on them.

The effect of predator population (X_2), temperature (X_3), humidity (X_4), and rainfall (X_5) on the prey population (X_1) was studied through multiple regression analysis (table 3). This analysis helps to predict the prey (X_1) population at a given time if the values of other biotic and abiotic factors are known.

The correlation between prey population and each of the four variables, viz., predator, temperature, humidity, and rainfall, was examined through simple correlation. While there is a positive correlation with prey and predator in all cases, a low positive or a negative correlation is observed with prey and abiotic factors (table 4).

Prey-Predator/Parasite Interactions: Studies on the biology of the predators and the parasites are essential for the establishment of the interrelationships

between these organisms and the prey population. Muraleedharan and Ananthkrishnan (1971) and Ananthkrishnan and Swaminathan (1977) have discussed aspects of the behaviour of *M. moraguesi* and *T. thripophonus* respectively. Only the predatory nature of *A. flavipes* has so far been reported (Ananthkrishnan & Varadarasan 1977). An attempt is made to incorporate information on the biology of this inquiline to present a more complete picture of the prey-predator/parasite relationships. The relative abundance of the predators and parasites of the six gall thrips is shown in table 5.

Androthrips flavipes is associated with more than 15 thrips galls (Ananthkrishnan 1978). They always inhabit mature galls abundant in eggs and immature stages of the gall-makers. Their slender body in contrast to that of the gall-makers is adapted for swift movement. When let on a paraffin wax tray (Varadarasan 1979) they locate their prey through random searching recognising

Table 3 Multiple regression : Prey vs biotic and abiotic factors

* <i>Arrhenothrips ramakrishnae</i>	$(X_1 - 85.1380) = 0.4159 (X_2 - 14.4533) + 3.2508 (X_3 - 28.5903) - 0.8250 (X_4 - 72.3194) - 0.0500 (X_5 - 134.6833)$
* <i>Schedothrips orientalis</i>	$(X_1 - 56.9166) = 2.1404 (X_2 - 7.7770) - 4.1669 (X_3 - 28.8583) - 1.0113 (X_4 - 70.0833) + 0.0026 (X_5 - 146.211)$
* <i>Crotonothrips dantahasta</i>	$(X_1 - 45.0952) = 0.4383 (X_2 - 28.6190) - 2.5761 (X_3 - 28.7762) - 0.4441 (X_4 - 68.5) - 0.13736 (X_5 - 58.3238)$
** <i>Gynaikothrips flaviantennatus</i>	$(X_1 - 159.1944) = 4.5212 (X_2 - 11.555) - 27.0694 (X_3 - 28.6347) - 2.8669 (X_4 - 72.0411) + 0.5476 (X_5 - 132.9330)$
** <i>Teuchothrips longus</i>	$(X_1 - 63.3810) = -0.2419 (X_2 - 5.8571) - 20.6157 (X_3 - 27.2095) - 3.7025 (X_4 - 75.5) + 0.0259 (X_5 - 188.6809)$
* <i>Thilakothrips babuli</i>	$(X_1 - 76.5952) = -2.1685 (X_2 - 11.952) + 22.6920 (X_3 - 31.019) - 1.1029 (X_4 - 63.357) - 0.3624 (X_5 - 27.017)$

X_1 = Prey; X_2 = Predator; X_3 = Average temperature; X_4 = Relative humidity; X_5 = Rainfall

* Predator : *Androthrips flavipes*; ** Predator : *Montandoniola moraguesi*

Table 4 Simple correlation

	Prey vs Predator	Prey vs Average temperature	Prey vs Relative humidity	Prey vs Rainfall
	r_{12}	r_{13}	r_{14}	r_{15}
<i>Arrhenothrips*</i> <i>ramakrishnae</i>	0.1162	0.2322	- 0.2855	- 0.2956
<i>Schedothrips*</i> <i>orientalis</i>	0.2829	0.2995	- 0.2252	- 0.0434
<i>Gynaikothrips**</i> <i>flaviantennatus</i>	0.0314	0.2874	- 0.5130	- 0.1974
<i>Thilakothrips*</i> <i>babuli</i>	0.0862	0.3982	- 0.3446	- 0.2025
<i>Crotonothrips*</i> <i>dantahasta</i>	0.7666	- 0.4513	- 0.3797	- 0.2086
<i>Teuchothrips**</i> <i>longus</i>	0.3423	- 0.4771	- 0.1071	- 0.1667

* Predator: *Androthrips flavipes*

** Predator: *Montandoniola moraguesi*

Table 5 The relative abundance of predator/parasite associated with different gall thrips

Gall-maker	Predatory inquiline <i>Androthrips flavipes</i>	Anthocorid bug <i>Montandoniola moraguesi</i>	Internal parasite <i>Tetrastichus thripophonus</i>
<i>Arrhenothrips ramakrishnae</i>	* + + + + +	+	Trace
<i>Schedothrips orientalis</i>	+ + + + +	+	++
<i>Crotonothrips dantahasta</i>	+ + + + +	none	none
<i>Thilakothrips babuli</i>	+ + + +	none	Trace
<i>Gynaikothrips flaviantennatus</i>	+	+ + + + +	none
<i>Teuchothrips longus</i>	+ +	+ + + + +	none

* + = 5 individuals/10 galls

the prey only on closer approach or upon contact. Starved thrips sometimes fail to recognize a suitable prey even in close proximity. On locating a suitable prey, they usually stop long enough to empty the contents of the eggs or immature stages. *A. flavipes* are not very ferocious in their predatory habit and the larvae and the adult gall thrips easily deter them by a violent flicking of the abdomen, but the hungry predator always overcomes such a resistance.

The degree of incidence of *A. flavipes* varies in different galls (table 5). While they are numerous in the galls of *C. dantahasta*, *A. ramakrishnae*, *T. babuli* and *S. orientalis*, in the other two galls inhabited by *G. flaviantennatus* and *T. longus*, the anthocorid bugs are abundant and they have a detrimental effect on the inquiline predator also. The anthocorid bug may be called a 'secondary predator' (Holling 1968) as it feeds on the 'primary predator', namely *A. flavipes*. The latter occurs throughout the year, with two peaks of abundance in September–December and February–April (figures 1, 2, 4 & 6). *A. flavipes* population is high in the galls of *C. dantahasta* owing to the absence of the 'secondary predator', *M. moraguesi*. Since this secondary predator is abundant in the galls of *G. flaviantennatus* and *T. longus*, the predatory inquiline population is very low. But in the galls of *S. orientalis*, there is a considerable parasitization of the second instar larvae. *A. flavipes* population is, therefore, slightly lower than in the galls of *C. dantahasta* and *A. ramakrishnae*, but higher than in the galls of *G. flaviantennatus* and *T. longus* (table 5).

The first intruder into the thrips galls is invariably the inquiline predator which occupies mature galls having a full complement of eggs and immature stages

of these gall-makers. Since the inquiline predator has the shortest preoviposition period (Varadarasan 1979), it starts depositing eggs soon after entry into the galls, consuming by then about 1/10 of both the eggs and larvae of the gall-maker. The very few adults in the gall are not preferred because of its host resistance. The incubation period in this inquiline is short; the larvae emerge sooner from the eggs to find a ready source of food in the eggs and immature stages of the gall-maker. The fast rate of consumption soon depletes the prey food even before the inquiline reaches the non-feeding pupal stages. Being thus deprived of the normal food, the inquiline resorts to cannibalism, which is common in the galls studied. The cannibalistic behaviour of the inquiline predator is confirmed in the laboratory in three different sets of experiments by stopping the supply of food to this predator at various stages of their development.

In the first set, eggs, immature stages and adults of the gall thrips were regularly offered as food to *A. flavipes* from '0' day onwards including the larvae emerging from the eggs laid by such experimental adults till the completion of the adult stage. Eggs were laid regularly by the inquiline and the mortality rates of the eggs and emerging stages were found to be comparatively low (table 6A).

In the second set, food supply was stopped to experimental adults 5 days after the '0' day of emergence and to the larvae hatching from the eggs laid by such experimental adults. By this period the predatory adult female oviposited 8–12 eggs. In this experimental stage, the only sources of food available to the various stages of these insects were their own eggs, larvae, and adults. Under

such condition of acute food shortage, the emerging larvae not only fed on themselves but also on the eggs. Similarly, the adults not only fed on their own eggs and larvae but also on other adults. The mortality rate in this experiment was 100% (table 6B).

In the third set of experiments, food supply was stopped to the experimental adults 10 days after the '0' day of emergence and to the larvae hatching from the eggs laid by such experimental adults. The sources of food available to them after the 10-day period were their own eggs, larvae, pupae and adults. Nearly 60% of the eggs hatched and the larvae showed their cannibalistic behaviour. The mortality rate was 61–82% (table 6C). The cannibalistic pattern and the mortality rates of different stages of *A. flavipes* under experimental conditions are tabulated (table 6). An examination of shrunken cadaver of larvae and pupae revealed the complete absence of fluid, thus indicating that they had been fully sucked by their cannibalistic members.

This rules out the possibility of the death of these instars due to non-availability of food and starvation.

Analysis of the data, thus, shows that in spite of a regular supply of normal food, the inquiline resorts to cannibalism and the rate of mortality of immature stages is directly proportional to the total number of eggs laid (table 6A). In spite of their precocious development and high fecundity comparable to that of the gall-maker, the predatory inquiline fails to outnumber the gall-maker.

The bionomics of the anthocorid bug has been studied by Muraleedharan and Ananthakrishnan (1971) by providing *Gynaikothrips flaviantennatus*, the gall-forming species on *Casearia tomentosa*, as prey. Hence attention is focused here only on the abundance of this bug in the six galls. Table 5 shows its abundance in *C. tomentosa* and *P. hispidula* galls and to a certain extent in galls of *M. elengi* and *V. maderaspatana*. In the other two galls, viz, *A. leucophloea* and *M. edule* the anthocorid bug was never

Table 6 The cannibalistic pattern and the mortality rates of different stages of *Androthrips flavipes*

Food Supply	Total Number of					Natality %	Mortality %
	Eggs laid	Larvae emerged	Eggs predated	Immature stages predated	Adults emerged		
A. Food supplied throughout	25	19	2	3	16	36	64
	39	23	5	8	15	38	62
	56	31	8	12	19	34	66
B. Food supply stopped 5 days after emergence	12	1	10	—	—	—	100
	10	1	7	—	—	—	100
	9	1	8	—	—	—	100
C. Food supply stopped 10 days after emergence	28	22	2	14	8	28.5	61.5
	35	22	4	16	6	17.5	82.5
	41	24	3	13	11	26.8	73.8

recorded. It consumed 3–4 adult thrips/day up to 81–118 thrips during the entire life cycle (Muraleedharan & Ananthkrishnan 1971). The abundance of this bug drastically reduced the thrips populations.

The biology of the internal eulophid parasite has been studied earlier (Ananthkrishnan & Swaminathan 1977) and observations on the incidence of this parasite (table 5) indicate that a high incidence of the parasite occurs in *S. orientalis*. Very few individuals of this parasite were noted in *A. ramakrishnae* and *T. babuli*. In these two gall thrips, the larvae that were near the base or extremities of the galls appeared more prone to parasitic infection. This parasite was found to be effective in decimating the population of *S. orientalis*. As much as 20% parasitization was recorded when the thrips population was high. The remaining three gall-makers were never found to be parasitized under natural conditions though in the laboratory the adults of *T. thripophonus* readily oviposited on the gall-makers and completed the life cycle. Interestingly, the eulophid parasite also parasitizes the inquiline predator both under natural and laboratory conditions.

Discussion

There appears to be a distinct correlation between the population abundance of gall thrips and the production of young leaves on the host plants (table 1). Pruning of *P. hispidula* in May, when no young leaves are normally seen, produces enough young leaf primordia which became infested by *T. longus*. With such appearance of young leaves, the insect breaks its temporary diapause caused by the non-availability of food.

Though the abundance of gall-forming

thrips depends mostly on the availability of young leaves, which in turn depends on abiotic factors, many other biotic factors are also found to be detrimental to populations. The inquiline predator *Androthrips flavipes*, the anthocorid bug *Montandoniola moraguesi*, and the eulophid internal parasite *Tetrastichus thripophonus* are important in this respect. Although Lewis (1973) states that the effect of natural enemies, especially predator, on the size of field population of thrips is hardly noticeable, the predators and parasite are found to have a marked effect on the population of gall-forming thrips. The inquiline predator *A. flavipes* appears to be an important biotic factor in controlling the population of *C. dantahasta*, *S. orientalis*, *A. ramakrishnae* and *T. babuli* (figures 1, 2, 4 & 6). Statistical analysis with regard to prey-predator interactions shows a positive correlation in all the six species (table 4).

In general, the effect of predatory thrips on the size of the host population depends largely on the abundance and reproductive potentials of predator and prey (Lewis 1973). *A. flavipes* has a reproductive potential similar to that of the gall-forming thrips (Varadarasan 1979). But the population density is much lower than that of the gall-forming thrips, the prey-predator ratio being 1:20. A similar observation was made by Ananthkrishnan (1972) who reported that the inquiline species were always fewer than the gall-maker. The low ratio is due to cannibalism in the absence of normal food. A similar observation has been made in *Haplothrips subtilissimus* (Haliday), the individuals of which are usually crowded and the larvae become cannibalistic when the food source is scarce (Putman 1942). Moreover, in the

galls inhabited by *A. ramakrishnae* and *S. orientalis*, this inquiline predator is also attacked along with other gall-forming thrips by the secondary predator, *M. moraguesi*. The predatory inquiline leads a crowded life and the cannibalistic behaviour acts as an important factor in keeping down its own population.

Unlike the galls discussed earlier, the less compact roll galls of *C. tomentosa* and *P. hispidula* allow the entry of a larger secondary predator at an earlier stage. In *C. tomentosa* and *P. hispidula* the secondary predator steadily increases as the gall thrips population increases and statistical analysis also shows a positive correlation (table 4). In Hawaii, the bug *M. moraguesi* was introduced to control the Cuban laurel thrips, *Gynaikothrips ficorum*, and was found to be an efficient predator (Lewis 1973). Similarly, another species of anthocorid *Orius minutus* L., plays an important role in the population fluctuation of anthophilous Thysanoptera. The increase of thrips population is followed by a rise in anthocorid population, which in turn resulted in the decline of thrips population (Viswanathan & Ananthakrishnan 1974).

Apart from these predators, the eulophid parasite *T. thripophonus* also occurs on three gall-forming thrips. *A. ramakrishnae*, *T. babuli*, and *S. orientalis* (table 5). Of these *S. orientalis* is profoundly affected by the parasite as about 20% of the larvae are found to be parasitized. Similar examples of rapid changes in population density due to parasites are afforded by an eulophid *Thripoctenus brui*, a parasite on *Thrips tabaci* in Japan (Sakimura 1937). The population of this thrips, which gets well established during favourable seasons, is considerably reduced by *T. brui*. All these findings also agree with the present observations that in spite of the presence

of young leaves during favourable seasons the predators and the parasite cause a fluctuation in the population of gall thrips.

Abiotic factors normally influence the population of phytophagous insects indirectly by affecting the host plant. Since gall-forming thrips live in micro-habitat, the effect of abiotic factors is not profound. Observations showed that only heavy rainfall has a detrimental effect. The cecidozoa seem to be unable to withstand the choking effect of the rainfall and suffer heavy mortality. Seventy per cent of the population of *Thrips tabaci* Lindeman is washed off by heavy downpour (Harris et al. 1936). Similarly, larvae of the pear thrips *Taeniothrips inconsequens* (Uzel) from the leaves (Bailey 1934) and the larvae and adults of *Haplothrips verbasci* (Osborne) from the exposed sides of inflorescence of mullein (Shull 1911). Dev (1964) recorded the sudden decline of tea thrips, with the onset of monsoon. During the favourable months of November and December there is no population of *Anaphothrips sudanensis* (= *flavicinctus*) due to heavy rainfall (450–550 mm) (Ananthakrishnan & Jagadish 1967). All these examples confirm the detrimental effect of heavy rainfall on the population. Moderate rainfall does not, however, affect much of the gall thrips population (table 2). Thrips are known to survive long periods of submersion under water. *Aptinothrips rufus* (Gmelin) often lives on maritime grasses submerged twice daily by normal high tides (Morison 1957). Adults of *Euchaetothrips kroli* (Schille) can survive for at least four days in the leaf sheaths of *Glyceria* plants flooded by fresh water (Lewis 1973). Thus we find that in spite of the ability of thrips to survive temporary

immersion, they suffer high mortality under persistent rain.

The present investigation of the six gall thrips also reveals the complex relationship between the cecidozoa and predators/parasite. The inquiline predator *A. flavipes* is a facultative predator and occurs in more than fifteen thrips galls (Ananthkrishnan 1978). This predator was formerly regarded as a passive inquiline, feeding on gall tissues. Short-house (1973) also reported that the inquiline *Perclistus pirata* fed on gall of *Rosa acicularis* induced by a cynipid, *Diplolepis polita*. He believed that the feeding of the inquiline modified the gall-shape and that the inquiline destroyed the larvae of the gall-maker during oviposition. The distinctly predatory nature of *A. flavipes* on other gall-forming thrips has been established by Ananthkrishnan and Varadarasan (1977), who showed that the destruction of gall-forming thrips is due to the feeding of inquiline predator, *A. flavipes* on the eggs, immature stages and adults of the gall-maker. The predatory nature of the inquiline *Haplothrips inquilinus* Priesner has also been reported in gall thrips, viz., *Gynaikothrips uzeli* (Zimmerman) (on *Ficus* sp.), *Mesothrips claripennis* Moulton (on *Bladhia*), and *Gynaikothrips liliaceae* Moulton (on *Piper*) by Takahashi (1934). The inquiline predator *A. flavipes* is not a ferocious feeder and prefers to feed only on the eggs and immature stages of gall thrips, attacking the adults only when the eggs and immature stages are scarce. Similarly, Putman (1942) reports that *Haplothrips faueri* Hood fed mostly on the eggs of a tetranychid mite, *Panonychus ulmi*, feeding on the active stages of mites only when this became scarce.

Predatory activity of the inquiline is recorded in all the six gall thrips studied.

The abundance of this predator is dependent on the presence of the secondary predator, anthocorid bug, *M. moraguesi*. *A. flavipes* is more abundant in the galls of *M. edule*, *V. maderaspatana*, *A. leucophloea*, and *M. elengi* than in *C. tomentosa* and *P. hispidula*. This abundance can be attributed to the absence of the secondary predator or the presence of very few of them (table 5). Further, the slender-bodied swift moving inquiline is adapted for easy penetration into the more compact roll/rosette type of galls of *V. maderaspatana*, *M. edule*, and *A. leucophloea*, where the large-bodied anthocorid bug is unable to enter freely. But the galls of *C. tomentosa* and *P. hispidula* have less compact folds that facilitate the entry of the secondary predator *M. moraguesi*, which in turn brings down considerably the number of inquiline thrips.

In all the different types of more compact roll/rosette galls, where the inquiline is found in abundance, there is a distinct correlation between the primary predator, *A. flavipes*, and the gall-forming thrips. Compared to the gall-makers, the inquiline predators are swift movers, facilitating prey capture. Though they are adapted for a predatory life, they never use their forelegs during feeding. A similar behaviour has been reported in swift-moving predatory *Haplothrips subtilissimus* Haliday which also never uses the forelegs for prey capture (Putman 1942). Prey location in *A. flavipes* is only at random when it comes into contact with the prey thigmotatically. But the predator has ample opportunities to locate and feed on the gall-makers as the predator and the prey are confined to a small space within the gall.

A. flavipes exhibits many other features characteristic of a truly efficient

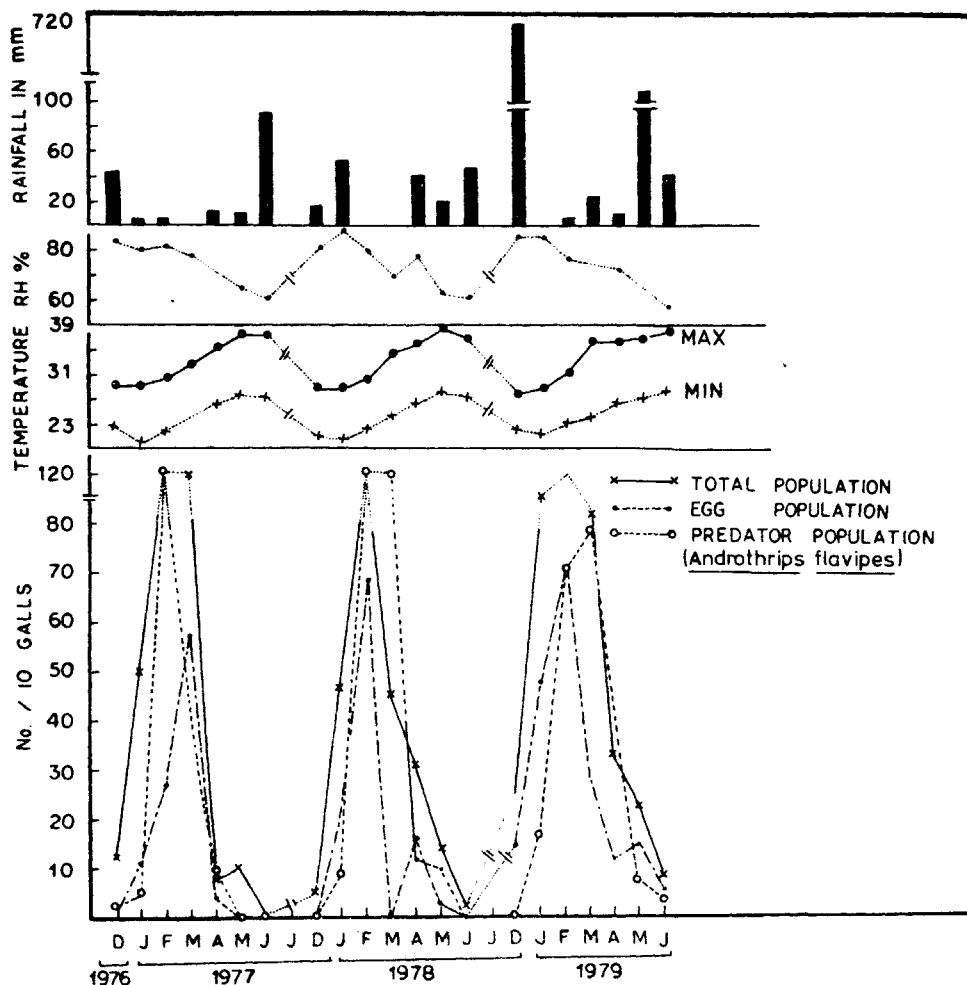


Figure 6 Population fluctuation of *Crotonothrips dantahasta*

predator. When compared with the gall-forming thrips this inquiline has the shortest life cycle—a prime requisite for a successful predator (Ananthakrishnan & Varadarasan 1977). Besides, it lays its eggs inside the gall, between or near the egg clusters of gall-makers, thus ensuring a ready source of food for the newly emerging young ones. In spite of its true predatory nature, *A. flavipes* never outnumbers its prey population (figures 1, 2 & 4). Even in the galls of *M. edule*,

where the population slightly outnumbers that of the prey *C. dantahasta*, there is an abrupt fall within fifteen days (figure 6). The ratio of the predator and the gall-maker was always 1:20. This may be attributed to cannibalistic behaviour. Cannibalism appears to be common among several predatory thrips. Loan and Holdaway (1955) reported the cannibalistic behaviour in the larvae of *Haplothrips leucanthemi* (Schrank) in the absence of regular food supply.

Similarly, the predatory *Haplothrips subtilissimus*, which is usually crowded, resorts to cannibalism when the food is scarce (Putman 1942). Overcrowding is also one of the reasons for cannibalistic behaviour, as in predatory adults and larvae of *Scolothrips sexmaculatus* (Pergande) (Bailey 1939). *Haplothrips faueri* feed occasionally on their own eggs and pupae when confined in cages (Macphee 1953). Thus, both scarcity of food and overcrowding appear to induce cannibalism in predatory thrips.

The inquiline *A. flavipes* normally inhabits and oviposits in galls that abound in eggs and immature stages of the prey thrips. By the time their larvae pupate, they have already devoured almost 80% of the prey population. The remaining larval stages and the newly emerged adults of the inquiline, which remain crowded within the same gall, are now deprived of their normal food and readily resort to cannibalism. Food and overcrowding, however are not the only reasons for cannibalism in *A. flavipes*. Table 6A shows that there is nearly 60% mortality even when they are provided with regular and normal food. The cannibalistic nature seems inherent in the predatory *Scolothrips sexmaculatus*; the post-teneral adults and larval stages feed on prepupa, pupa and smaller larvae of their own species even when their prey-mites, adults and eggs of Tetranychids are abundant (Pamella & William 1977). Thus it is evident that the cannibalistic behaviour of *A. flavipes* is due not only to the scarcity of food and overcrowding but also to their inherent tendency for cannibalism.

Morison (1958) and Varley and Gradwell (1960) are of the opinion that most predatory thrips are unlikely to be the

key factor in limiting the prey population. They suggest that the slow breeding and the smaller number of the predators could be decisive. The present study reveals however that the inquiline *A. flavipes* breeds much faster than its prey thrips and plays a key role in limiting the population of the latter. As already shown, the presence of fewer individuals of the predator in the gall community is due to the inherent cannibalistic behaviour, besides food scarcity and overcrowding.

The anthocorid bug *M. moraguesi* is also found to be an important facultative predator in four of the six thrips galls studied. Muraleedharan and Ananthakrishnan (1971) recorded this species in 12 thrips galls. Carayon and Ramade (1962), while providing a brief account of their predatory habit and their geographical distribution, indicate their thrips prey in Europe. The occurrence of *M. moraguesi* is restricted to the galls of *Casearia tomentosa*, *Pavetta hispidula*, and *Mimusops elengi* (table 5). Interestingly these thrips galls are less compact, facilitating the entry of the comparatively large-bodied anthocorid bug. They are also recorded in the more compact roll galls of *Ventilago maderaspatana*, but the predator gains entry into such galls only after they become senescent and less compact. They consume more gall-forming thrips than the inquiline and act as the most detrimental factor in checking the population of gall thrips. The abundance of this bug in *C. tomentosa* and *P. hispidula* has a deleterious effect, and reduces the population considerably (figures 3 & 4). The anthocorid bug can be called a 'secondary predator' (Holling 1968), since it feeds on the inquiline predator, besides feeding on other gall-forming thrips.

The eulophid internal parasite *T. thripophonus* is also found to influence the gall thrips population. It is parasitic on various thrips like *Liothrips lavreti* (Mason), *Liothrips urichi* Karny, *Gynaikothrips uzeli*, Zimmerman (Burks 1934), and *Gynaikothrips ficorum* (Marchal), (Wolcott 1948). In the present study, this parasite was found in abundance only on *Schedothrips orientalis* and very few on *A. ramakrishnae* and *T. babuli*. On *Teuchothrips longus*, *Crotonothrips dantahasta*, and *Gynaikothrips flaviantennatus* this parasite is never found. Under laboratory conditions successful parasitization of the second larvae of all the six gall-forming thrips as well as the inquiline predator indicate the parasitic potency. They are more abundant in *V. maderaspatana* galls, parasitizing as much as 20% of the *Schedothrips orientalis* populations. Parasitization of *A. ramakrishnae* is res-

tricted to individuals at the base of galls, which are the only places where this parasite can come into contact with the prey thrips. On *T. babuli* parasitization is observed only in the outer whorls of the rosette galls of *A. leucophloea*, the prey being found in good numbers in the inner whorls also. In spite of the ability of this eulophid to parasitize all the gall thrips in laboratory, it is totally lacking in the galls induced by *Crotonothrips dantahasta*, *Teuchothrips longus* and *Gynaikothrips flaviantennatus*, and the reason for the absence of parasitization of these three gall thrips in natural conditions appears enigmatic.

Acknowledgements

The authors thank Mr B Chandrasekhar, Department of Statistics, Loyola College, Madras, for his assistance in population analysis.

References

- Ananthakrishnan T N 1972 Further studies on Indian gall thrips II; *Marcellia* 37 3-20
- 1978 Thrips galls and gall thrips; *Zool. Sur. India. Tech. Monogr* 1 1-69
- and Jagadish A 1967 On some species of the genus *Liothrips* Uzel from India; *Bull. Ent. Madras* 8 1-13
- and Swaminathan S 1977 Host-parasite and host-predator interactions in the gall thrips *Schedothrips orientalis* Ann. (Tubulifera: Thysanoptera); *Entomon.* 2 247-251
- 1979 On the population trends of *Aneurothrips priesneri* Bhatti (Insecta: Thysanoptera) from the leaf galls of *Cordia obliqua*; *Bull. Zool. Sur. India* 2 91-94
- and Varadarasan S 1977 *Androthrips flavipes* Schmutz (Insecta: Thysanoptera) a predatory inquiline in thrips galls; *Entomon.* 2 105-107
- Bailey S F 1934 Factors influencing pear thrips abundance and effectiveness of cultural control; *J. econ. Ent.* 27 879-884
- 1939 The six spotted thrips *Scolothrips sexmaculatus* (Perg.); *J. econ. Ent.* 32 43
- * Burks B D 1934 The North American parasitic wasps of the genus *Tetrastichus*. A contribution to biological control of insect pests; *Proc. U.S. Nat. Mus.* 93 505-608
- Carayon J and Ramade F 1962 Note sur la presence en France et en Italie *doniola moraguesi* (Put.) avec quelques observations sur cet Heteroptere Anthocoridae; *Bull. Soc. Ent. Fr.* 67 207-211
- Dev H N 1964 Preliminary studies on the biology of the Assam thrips *Scirtothrips dorsalis* Hood on tea; *Indian J. Ent.* 26 184-194
- Harris H M, Drake C J and Tate H D 1936 Observations on the onion thrips; *Iowa Coll. J. Sci.* 10 155-172
- Holling C S 1968 Tactics of a predator; *Insect abundance, Ed. Symposia of the Royal Entomological Society of London No. 4*
- Lewis T 1955 Two interesting British records of Thysanoptera; *J. Soc. Br. Ent.* 5 110-113

- 1973 *Thrips: Their Biology, Ecology and Economic Importance* (London: Academic Press) 340 pp
- Loan C and Holdaway F G 1955 Biology of the red clover thrips *Haplothrips niger* (Osborn); *Can. Ent.* **87** 210-219
- Macphee A W 1953 The influence of spray programs on the fauna of apple orchards in Nova Scotia V. The Predaceous thrips *Haplothrips faurei* Hood; *Can. Ent.* **85** 33-40
- Morison G D 1957 A review of British glasshouse Thysanoptera; *Trans. R. ent. Soc. Lond.* **109** 467-534
- 1958 The Thysanoptera of Kew Gardens; *Kew Bull.* **2** 295-301
- Muraleedharan N and Ananthakrishnan T N 1971 Bionomics of *Montandoniola moraguesi* (Puton) (Heteroptera: Anthocoridae) a predator on gall thrips; *Bull. Ent.* **12** 4-10
- Pramanik N K and Sengupta C K Observations on the population fluctuations of two species of gall thrips (Tubulifera; Thysanoptera); *Bull. Zool. Sur. India*. In press
- Oettingen H von 1942 Die Thysanoptera des Norddeutschen Grasslands; *Ent. Beih. Berl. Dahlem.* **9** 79-141
- Pamella C and William W Allen 1977 Life table and feeding habits of *Scolothrips sexmaculatus*; Anan; *Entomol. Soc. Am.* **70** 11-16
- Putman W L 1942 Notes on the predaceous thrips *Haplothrips subtilissimus* Hal. and *Aeolothrips melaleucus* Hal; *Can. Ent.* **74** 37-43
- Raman A, Ananthakrishnan T N and Swaminathan S 1978 On the simple leaf galls of *Casearia tomentosa* Roxb. (Samydaceae) induced by *Gynaikothrips flaviantennatus* Moulton (Thysanoptera: Phlaeothripidae); *Proc. Indian Acad. Sci.* **B87** 231-242
- Sakimura K 1937 On the bionomics of *Thripocatenus brui* Vuillet a parasite on *Thrips tabaci* Lind. in Japan (II); *Kontyu* **11** 410-424
- Shorthouse J D 1973 The insect community associated with rose galls of *Diplolepis polita* (Cynipidae, Hymenoptera); *Quaest. Ent.* **9** 58-98
- Shull A F 1911 Thysanoptera (and Orthoptera). In a biological survey of the sand dune region on the south shore of Saginaw Bay, Michigan (Ruthuen, A-G. Ed.); *Publs. Mich. Geol. Biol. Sur.* **24** 177-216
- Takahashi R 1934 Association of different species of thrips in their galls; *Bot. Zool. Tokyo.* **2** 1827-1836
- Titschack E 1969 Der *Tarothrips*, ein neues Schadinsekt in Deutschland sonderdr; *Anz. Schadlingsk. Pflschutz.* **42** 1-6
- Varadarasan S 1979 Bioecological Investigation on some gall-inhabiting Thysanoptera (Insecta: Arthropoda), Ph.D. thesis, Madras University
- Varley G C and Gradwell G R 1960 Key factors in population studies; *J. Anim. Ecol.* **29** 299-401
- Viswanathan T R and Ananthakrishnan T N 1974 Population fluctuation of 3 species of Anthophilous Thysanoptera in relation to the numerical response of their predator, *Orius minutus* L. (Anthocoridae: Hemiptera); *Curr. Sci.* **43** 19-20
- *Wolcot G N 1948 The insects of Puerto Rico; *J. Agric. Univ. Puerto Rico* **32** 975 pp

*Original not referred.