

BIOCONTROL OF CASSAVA MEALYBUGS IN THE RAINFOREST ZONE
OF GHANA

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DEDICATION

This work is dedicated to my parents, both of whom died during the short time I was away in pursuit of this course.

May their souls rest in peace.

GENERAL ABSTRACT

In the rainforest of Ghana, field surveys and monitoring of population levels of cassava mealybug and its exotic and indigenous natural enemies show very low densities on cassava tips. Mealybug hardly exceeds 40 per sampled tip or 100 per infested tip even during good periods (dry season) of its phenology. Mealybug infestation levels, as measured by proportion of plants showing damage (bunch top) and presence-absence of mealybugs on tips are below 20% of sampled tips out of a sample size of between 400 and 50 tips. Parasitoids, hyperparasitoids and predator densities are also low but correlated to the decline in mealybug densities and infestation levels. Increasing rainfall intensities (rainy season) give low mealybug population levels thus showing a possible mechanical impact. Field and laboratory simulated rain and wind confirm their mechanical impact on crawlers and second instars but having little or no effect on third and fourth instars.

Analysis of field data based on individual sampled tips of cassava, rather than on field means, gives a domed density-dependent relationship between the exotic parasitoid, E. lopezi and cassava mealybug. A positive density-dependent relationship exists for mealybug densities below 40 per tip and an inverse relationship develops with increasing host densities.

Indigenous predators show a slow but positive numerical response to host densities. Hyperparasitoids respond positively to increasing mummy (parasitoid) densities. Field means of natural enemies and host densities are erratic and do not show clearly density-dependent relationships as individual tips data have shown.

In field studies, the relative importance of the species of insects associated with mealybugs, reveal that more than 70% of all the insects are parasitoids and hyperparasitoids. Out of this proportion nearly 80% are the exotic parasitoid, E. lopezi.

Local predators, made up of basically coccinellids and cecidomyiids account for about 20% of fauna on heavily infested cassava tips. Peak densities of all fauna on cassava tips are recorded towards the end of the dry season and beginning of the rainy season.

Experimental evaluation of the efficiency of natural enemies involving their physical and chemical exclusion support conclusions that

they are efficient in controlling cassava mealybug and gives further indications of a sustained biological control of the pest in Ghana.

Very high aggregation indices for field populations of cassava mealybug obtained through Taylor's power law and Iwao's mean crowding statistics are used to develop and suggest binomial and enumerative sampling plans for the sampling of ^{the} low mealybug densities in the rainforest zone. At higher mealybug densities above 20 per tip both methods require nearly the same sample size for an acceptable degree of accuracy. However at low mealybug densities (<10 per tip) the enumerative plan offers the most practically reasonable sample size from an average size field.

The importance of ant attendance of cassava mealybugs is of significance in the rainforest zone. In a survey, almost 76% of cassava mealybug infested tips have ants in the forest whereas only 21% of tips have ants in the savannah zone though in both zones the same ant species are dominant.

Crematogaster sp. of ants showed preference for infested tips at edges of fields whereas Pheidole and Camponotus sp. prefer tips in open and inner fields.

Among the three dominant taxa, Crematogaster and Pheidole spp. usually build carton nests over mealybug colonies whereas Camponotus build soil nest over aphids on the weed Chromolaena = (Eupatorium) odorata. The first two are the most likely to influence the efficiency of natural enemies in the biocontrol of mealybugs.

There are significant differences in rates of parasitism in both field and exclusion experimental evaluations between tips with and without ants. At least 15% of reduction in parasitism is suggested to be the influence of ants on parasitism of cassava mealybugs.

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GENERAL INTRODUCTION

The cassava mealybug Phenacoccus manihoti Matile-Ferrero was accidentally introduced into Africa from South America where the crop, cassava, Manihot esculenta Crants (Euphorbiacea) also originated.

It is a serious pest of cassava which is an important source of carbohydrates (from roots) and proteins (from leaves) (Sylvestre, 1973; Hahn and Williams, 1973; Matile-Ferrero, 1977, 1978; Cook, 1982; Sylvestre and Arraudeau 1983). About 200 million people in Africa depend on cassava for greater parts of their calorific requirement (Hahn and Keyser, 1985). Damage inflicted by the cassava mealybug is conservatively estimated to be 80-100% (Anonymous, 1979), 10-100% (Herren and Lema, 1982), 54-84% (Nwanze, 1982), 80-100% (Korang-Amoakoh et al., 1987) and 55% (Schulthess, ^{et al} 1987).

The spread and occurrence of the cassava mealybug extends from Senegal in the extreme west across more than 30 countries to Mozambique in the extreme south-east of Africa, thus covering more than 90% of the cassava belt (Herren and Bennet, 1984; Herren et al., 1987; Neuenschwander et al., 1987, 1989) (See Fig. 1.1).

The ease and speed of spread of the new pest was made possible by the fact that its natural enemies did not accompany the accidental introduction. Indigenous natural enemies associated themselves with the new pest but could not efficiently reduce its population below economically damaging levels (Matile-Ferrero, 1977; PRONAM, 1978; Fabres and Matile-Ferrero, 1980; Iheagwam, 1981; Bousienguet, 1986). Therefore in the 1980s a classical biological control project was initiated against the new pest and in addition another introduced pest of cassava, the green mite, Mononychellus tanajoa Bondar sensu lato by the International Institute of Tropical Agriculture (IITA) based in Ibadan, Nigeria. The IITA, in collaboration with several international institutions and local agricultural and research institutions embarked on an Africa-wide Biological Control Program (ABCP) aimed at achieving a reasonable control at virtually no cost to peasant farmers and African governments which are facing serious economic problems (Herren, 1982).

To overcome the shortcomings of the collaborative control program due to lack of trained entomologists in African countries, the IITA included a training programme. Short term and long term training of

technicians and high calibre graduates up to PhD levels were initiated.

This thesis is composed of work sponsored and financed through a fellowship from IITA and contributes to the assessment of the efficiency of control agents, especially the exotic parasitoid, Epidinocarsis lopezi De Santis (Hymenoptera, Encyrtidae).

The two-year full-time research work was fully carried out in Ghana as a component of the Africa-wide Biological Control Program.

SECTION I

LITERATURE, BACKGROUND AND OBJECTIVES OF STUDY

CHAPTER 1

BACKGROUND AND LITERATURE REVIEW

Biological control, though a relatively new field of pest control, has received detailed or sometimes very lengthy literature reviews in theses and dissertations. To avoid repetition of generally known or well presented accounts of biological control, an attempt is made here to give only a concise summary of general principles and specifics only for cassava mealybug control.

Generally, biological control is the use of natural enemies (insects, mites, pathogens, etc.) for regulating pest populations below economic damaging levels.

The importance of natural enemies in pest population regulation has been demonstrated in many ways in which exotic or indigenous species have reduced pest populations to well below economic injury levels in many documented successful biological control attempts. In some cases total reduction of a pest to a non-pest status has resulted; in others, the impact of the beneficial species becomes the pivot around which a series of other procedures is organised and implemented (Stern et al., 1959; Debach et al., 1971; Caltagirone, 1981). In the broadest sense two approaches of biological control are explained here. Classical biological control, to which this work and discussions belong, is a regulation of pest population by exotic natural enemies that are imported for this purpose. Other than the importation of natural enemies for pest control, biological control involves the manipulation of local or exotic natural enemies by providing favourable conditions to enhance their effectiveness.

This tactic is much older than the one involving importation of species (Samways, 1981). Such an all-embracing approach operates on sound ecological principles. Biological control measures started in ancient China, where growers placed nests of the predatory ant, Oecophylla smaragdina (Hymenoptera: Formicidae) in citrus trees to control various leaf-feeding insects (Doutt, 1964). However, modern concepts of biological control were born with the dramatic success of the introduction of the predatory ladybird Rodolia cardinalis (Coleoptera: Coccinellidae) against the cottony-cushion scale, Icerya purchasi (Homoptera: Margarodidae) in California (Caltagirone, 1981).

Ever since more than 150 success cases with biological control have been achieved (Laing and Hamai, 1976; Clausen, 1978). In the case of cassava mealybug control in Africa with special reference to Ghana, all conventional control methods, especially screening of most potent agrochemicals, failed to deliver the required results. The only hopeful control option left for trial was breeding of resistant varieties of cassava and classical biological control since indigenous natural enemies failed to reduce pest population below economic damaging levels.

Another reason for the choice of classical biological control was the fact that the cost of agrochemicals, even if they were effective against mealybugs, was above the means of peasant farmers who produce more than 90% of cassava in Africa as a whole and Ghana in particular. Biological control therefore offered peasant farmers a control in which they contributed nothing to achieve and demanded no additional inputs from them.

1.1 CASSAVA INTRODUCTION, CULTIVATION, UTILISATION AND PRODUCTION CONSTRAINTS IN AFRICA

Cassava, Manihot esculenta Crantz is a dicotyledonous plant belonging to the family Euphorbiaceae. The origin of cassava is Latin America where it has been cultivated for over five thousand years. It was introduced into Africa between 300 and 400 years ago (Jennings, 1976; Leon, 1977; Lozano, 1977).

The Portuguese introduced cassava into the delta of the river Congo (Jones, 1959) and the new crop was quickly adopted into the traditional farming systems in different agro-ecological regions of Tropical Africa. By the beginning of the 19th century it had been effectively distributed throughout the tropics.

Colonial governments, such as the British, promoted cassava as a famine reserve crop in West Africa. Cassava is a long season crop (6-24 months or more) which is cultivated primarily for its edible enlarged roots (tubers), although the leaves are eaten for protein and vitamins in some parts of the tropics.

In Africa cassava is solely used as food for about two hundred million people and for livestock consumption, in contrast to Brazil where industrial alcohol is distilled from it (see Plate 1). In Ghana, cassava is more closely identified as a subsistence crop. As a subsistence crop



Plate 1 Cassava tubers (enlarged roots) in baskets going to be used solely for human consumption. Tubers were harvested from fields where studies were carried out at Koforidua in the rainforest of Ghana

par excellence, cassava is developing into the most important staple and commercial crop.

Its success in the varied and challenging agro-ecosystems of Africa is largely due to its hardiness, i.e. it produces economic yields under relatively marginal inputs, soils, rainfall conditions and adapts to diverse environmental conditions, withstanding dry periods of up to 4 or 5 months. It is particularly adapted to tropical soils and tolerates low pH and high aluminium levels.

The area devoted to cassava in Africa is far greater than the combined area in South America and Asia, yet Africa accounts for less than half of the world's production (Onwueme, 1978).

This is due to very low yields in Africa, hardly exceeding 10 tons per hectare, whereas under optimum conditions, but without irrigation, yields of 80 tonnes per hectare of fresh roots have been obtained (CIAT, 1979). Potential yields in Africa could be around 30-50 tonnes per hectare (Leuschner et al., 1980).

The major production constraints in Africa causing reduced or unstable yields of cassava are to a greater extent among other factors caused by a complex of pests and diseases that attack the crop. Weeds, poor soils and socio-economic factors also contribute to lower yields but are not considered in detail here. Cassava pests represent a wide range of arthropods, of which about 200 species were recorded most of which were minor pests (Bellotti and Schoonhoven, 1978).

In the dry season cassava in the tropics is attacked by insects and mites resulting in loss of leaves and shoots. The plant is capable of recovering from some minor attacks without the application of insecticides (Anon, 1978). Rodents and partridges attack edible roots. In Africa, the major pests species are the variegated grasshoppers Zonocerus variegatus L, red spider mite Oligonychus gossypii Zacher, white flies, Bemisia tabaci Gern which transmits mosaic virus, termites and of late, the destructive introduced cassava mealybug Phenacoccus manihoti and green spider mites Mononychellus tanajoa Bondar sensu lato (see Plate 2).

The constraint to cassava utilisation is expressed in high contents of cyanogenic glucosides in roots and leaves; the roots contain between 15 to 400 mg HCN per kg of fresh weight (Bruijn, 1973).



Plate 2 Tip of cassava covered by large colonies of mealybugs

This could result in chronic cyanide poisoning (Nestel, 1973). Cumulative effect of cyanide could lead to goitre development, cretinism, tropical ataxic neuropathy and diabetes. However, these could be avoided if cassava processing prior to consumption is thorough or adequate.

1.2 CASSAVA MEALYBUG

1.2.1 History of introduction and spread in Africa

In March, 1973, a new species of mealybug was reported causing severe damage to cassava on an experimental state farm near Brazzaville in Congo (Sylvestre, 1973; Matile-Ferrero, 1978). The same unknown species of mealybug was also found in farmers' fields in Kinshasha, Zaire (Hahn and Williams, 1973).

Within a short time the unknown mealybug species became the major pest on cassava causing severe yield losses (Herren, 1981; Nwanze, 1982; Sylvestre and Arraudeau, 1983).

In 1977, Matile-Ferrero named the parthenogenetic new mealybug species Phenacoccus manihoti.

From the point of its introduction in Congo and Zaire, the mealybug spread rapidly in the cassava belt of Africa. At present the pest has spread into 31 out of the 35 countries in the cassava belt of Africa (15°N to 20°S) according to reports (Fabres and Boussienguet, 1981; Nwanze, 1982; Herren and Lema, 1983; Herren, 1987, etc.). By December, 1985 the mealybug spread to the Rift Valley in Rwanda and the Northern and Copperbelt Provinces of Zambia. It then spread to Malawi, Burundi, Tanzania and Mozambique.

In West Africa it was first observed in 1976 in Gambia and in the Sine-Sahum Region of Senegal and then through Guinea Bisau and Western Mali.

In 1979 outbreaks of the new pest were observed in south-western Nigeria (Akinlosotu and Leuschner, 1981). The spread then moved west into Benin, Togo and eventually Ghana by late 1980. Cote d'Ivoire was invaded later. In 1985, Western Cameroon was also invaded. By 1986 and early 1987 the pest reached Sierra Leone, Liberia, Guinea-Conakry and since then continues to spread unabated.

1.2.2 BIOLOGY OF CASSAVA MEALYBUG AND DAMAGE INFLICTED ON CASSAVA BY ITS FEEDING

The cassava mealybug, Phenacoccus manihoti Matile-Ferrero (Hemiptera Pseudococcidae) was discovered and described in Africa as a neotropical species by Matile-Ferrero in the Congo in 1977.

This parthenogenetic species has a life cycle from egg to adult of 33 days at 27°C. It has 4 instar stages and a mean adult longevity of 20 days and an average fecundity of 440 eggs.

It reproduces throughout the year resulting in between 9 and 11 generations per year. Populations reach high peaks during dry seasons. Dispersal of the species is suspected to be passively carried out by winds (especially the crawlers) and by man on planting materials.

The mealybug is considered to be an indirect pest. Roots (tubers) which constitute the main source of food, are not attacked by the pest. However, severe bunch tops of leaves or complete loss of leaves are the result of mealybug attack. Photosynthesis is hampered and tuber yield losses result. Secondly, in places where cassava leaves are consumed as a source of protein and vitamins (e.g. Sierra Leone, Zaire/Congo, Madagascar), total leaf losses make the mealybug a direct pest.

Another very serious form of damage inflicted on cassava is the severe stunting of internodes on stems. It is suspected that as a sap-sucking insect, the mealybug injects toxins while feeding. This results in growth disturbances in cassava plant and eventually leads to stunting of internodes (Plate 3).

Stems with stunted internodes and sometimes crawlers of mealybugs become unsuitable for vegetative propagation. This form of propagation is the only one available to farmers. Therefore a severe attack from the pest usually threatens to wipe out the crop. The shortened internodes could also serve as refugia for crawlers who may bring about re-infestation of the shoots which come up from such stems. This requires an additional input of chemical for treating cuttings prior to planting, thus translating into an additional financial burden to the already poor peasant farmers and governments of African countries.



Plate 3 Damage inflicted on cassava stems by cassava mealybugs. Note the stunted internodes on stems. Such stems are unsuitable for vegetative propagation

A severe attack in Ghana resulted in total crop failures in dry savannan areas in Ghana (Korang-Amoakoh et al., 1987).

1.2.3 HISTORY OF CASSAVA MEALYBUG CONTROL IN AFRICA WITH SPECIAL REFERENCE TO GHANA

The initial shock-wave of the invasion of Africa and severe crop destruction by the new pest resulted in spontaneous trial and error methods of finding control.

The most widely resorted to control method in the majority of invaded African countries was the screening of several agrochemicals, some of which were potent and universally banned. However, control was not forthcoming. Each chemical spraying section was followed by a severe upsurge of mealybug populations and marked by human casualties as a result of neglect or inappropriate protection, or the abuse of one or more of the "dirty dozen". Cultural practices involving the mechanical nipping of infested tips and their subsequent burial or burning could not keep the pest at bay.

Internal quarantine restrictions on movement of infested materials were imposed but did not salvage the situation either (Korang-Amoakoh et al., 1987).

The best hope of achieving control was suggested by experts as an integrated approach involving classical biological control and a breeding programme for resistance to the new pest, a package which required huge financial and expertise resources (Herren et al., 1983).

Several African countries made requests for assistance to the International Institute of Tropical Agriculture (IITA), to the Food and Agriculture Organisation (FAO), USAID and other international organisations and donor agencies for the control of the new pest (Herren, 1987).

In 1980, IITA accepted the challenge and established the Africa-wide Biological Control Programme (ABCP) to play the leading role in the biological control of cassava mealybug and green spider mites.

A large scale survey for natural enemies was conducted by several institutions including the Commonwealth Institute of Biological Control (CIBC) in South America (Herren, 1982). Promising natural enemies were

identified, screened against diseases and hyperparasitoids in CIBC facilities in Britain and mass reared in IITA insectaries in Nigeria. Experimental release successes in Nigeria gave optimism for releases in many other African countries including Ghana (Herren and Lema, 1982; Lema et al., 1984; Hammond et al., 1987).

The most dramatic establishment and impact results were achieved with an encyrtid parasitoid, Epidinocarsis lopezi De Santis (Hymenoptera: Encyrtidae) (Plate 4).

At the present time the parasitoid has been recovered in several countries in Africa across several ecological zones, including places where it was not released (Sudan Savannah, Guinea Savannah, Sahel Savannah, Equatorial rainforest and Highlands). The speed of dispersal of E. lopezi in several countries was about 50 to 100km in one dry season (Herren et al., 1987). E. lopezi's dispersal rate is comparable to Trioxys pallidus Haliday, a parasitoid released against the walnut aphid in California. This parasitoid covered 130,000 km² within 2 years (van den Bosch et al., 1970). Some micro-hymenoptera dispersed at the rate of e.g. 170 km per season for Anaphoidea nitens Girault (Took, 1955), 100 km per year for Aphytis melinus Debach (De Bach and Argyriou, 1967), and for Cales noacki Howard dispersal rate was 10 km per year (O'Neill, 1973).

Though several biological control agents have been released in more countries or geographical regions than E. lopezi, e.g. Cryptolaemus montrouzieri Muls; on citrus mealybugs (Bartlett, 1978; Schuster et al., 1971; Sailer et al., 1984), the current distribution of the wasp is without precedent in Africa (see Greathead et al., 1971).

In March 1984, IITA and Ghana started a collaborative project on the biological control of cassava pests. Releases of E. lopezi and some exotic coccinellid predators e.g. Diomus spp., Hyperaspis etc. were carried out in a few locations in the Coastal savannah and transition zones. An exotic lacewing predator, Symphorobius was added to the released list in November, 1984.

In February and March, 1985, ground and experimental aerial releases were made in the Forest and Guinea savannah zones, thus completing a strategic coverage of all ecological zones in Ghana. Phytoseiid mites were also released against green mites which occur together with cassava

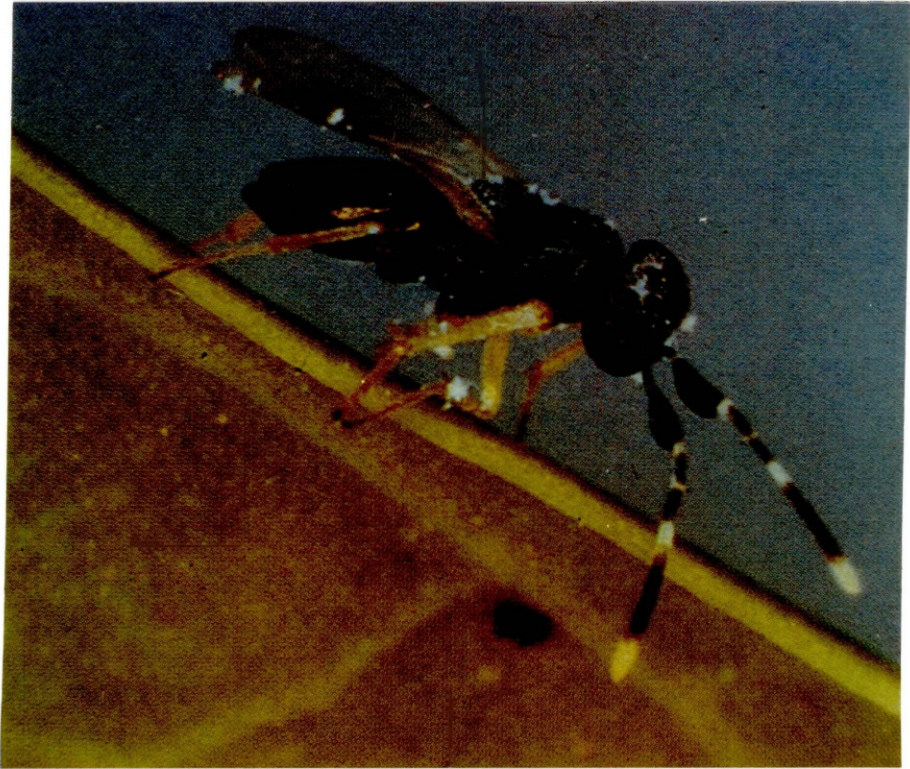


Plate 4 The introduced exotic parasitoid, *Epidinocarsis lopezi* De Santis
for the control of cassava mealybugs

mealybugs (see Table 1.1).

Impact assessment, monitoring of spread and surveys, revealed the establishment of the exotic parasitoid E. lopezi at all released sites a year after each release. None of the exotic predators was ever recovered in Ghana (Korang Amoakoh et al., 1987; Neuenschwander et al., 1989).

By February, 1986, the wasp had spread to virtually all major cassava growing areas in Ghana (Neuenschwander et al., 1989; Walker et al., 1985). The impact of the wasp was already showing as low mealybug populations and general improvements in cassava vegetation and yield became obvious (Korang-Amoakoh et al., 1987).

1.3 OBJECTIVES AND SCOPE OF THE STUDY

The major objective of this study was to assess or quantify the efficiency of natural enemies with special reference to the exotic parasitoid E. lopezi in the biological control of cassava mealybugs in Ghana. Hitherto, the assessment of the efficiency of natural enemies in the rainforest zone, ^{had} received little or no attention, though most cassava in Ghana is now grown in the rainforest zone instead of the dry coastal savannah where most studies have been done.

The ^{present} studies involve detailed population dynamic studies of the mealybug and its natural enemies, the effect of rains on the dynamics of populations and experimental evaluation studies involving exclusion of natural enemies to quantify their impact on mealybugs.

For the first time, an attempt is made to study ant-mealybug association and the influence of ants on the biological control programme.

The regulatory mechanism of mealybugs by natural enemies is related to theories of population regulation. As the most important abiotic factors, rain and wind, their impact on mealybugs in the field and simulation in the laboratory is also investigated.

Dispersion coefficients and patterns of distribution of mealybugs are discussed and sampling plans suggested on the bases of dispersion indices.

Fig. 1.1 Map of Africa showing the cassava belt, cassava mealybug distribution and expansion front (by courtesy of IITA)

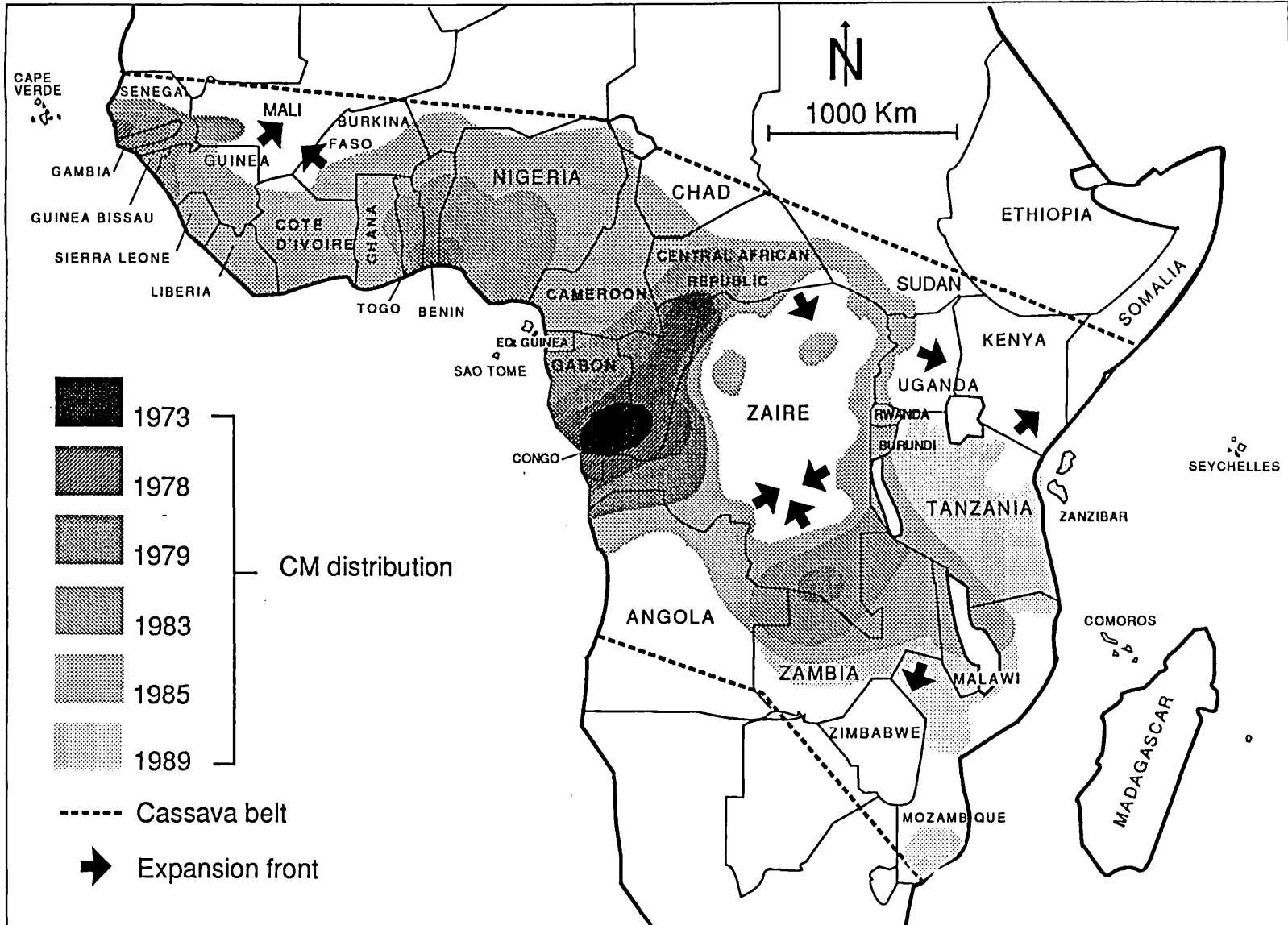


Table 1.1 Release and establishment of exotic beneficials in Ghana

Date of releases	Locality	Ecological zone	Numbers released	Date of post-release monitoring	Establishment/ remarks
<u>Epidinocarsis lopezi</u>					
14.03.84	Pokoase	C/S	1400	15.05.84	E
15.03.84	Sege	C/S	400	15.05.84	E
15.03.84	Ohawu	TR	50	15.05.84	E
22.11.84	Cape Coast	TR	140	21.12.85	E
22.11.84	Nsarfo Nkwanta	TR	435	21.12.85	E
23.11.84	Legon/Accra	TR	140	21.12.85	E
23.11.84	New Tafo	RF	90	21.12.85	E
23.11.84	Koforidua	RF	400	21.12.85	E
23.02.85	Bimbila*	G/S	8000	- .05.85	E
27.03.85	Kumasi*	RF	11200	- .04.85	E
<u>Coccinellid predators (Hyperaspis, Diomus sp)</u>					
14.03.84	Pokoase	C/S	150	15.05.84	NE
15.03.84	Sege	C/S	100	15.05.84	NE
15.03.84	Ohawu	TR	100	15.05.84	NE
<u>Lacewing predators (Sympherobius maculipennisⁿ)</u>					
23.02.85	Bimbila	G/S	250 ⁿ	15.05.84	NE
24.02.85	Techiman	TR	100	15.05.85	NE
<u>Phytoseiid mites (Neoseiulus idaeus, N. anonymus, T. limonicus)</u>					
20.03.85	Medie	TR	20000	15.05.85	NE
20.03.85	Pokoase	C/S	20000	15.05.85	NE
20.03.85	Agbozume*	C/S	20000	15.05.85	NE
27.03.85	Kumasi*	RF	30000	15.05.85	NE
04.03.86	Koforidua	RF	7000	24.05.87	NE
14.03.88	Banjiase	TR	40000	14.08.88	NE
18.04.89	Papase	C/S	20000	Not	-
15.05.89	Somanya	TR	30000	monitored yet	-

* Aerial releases
 C/S Coastal savannah
 RF Rain forest

E = Established
 NE = Not established
 TR = Transition zone
 G/S = Guinea Savannah.

SECTION II
FIELD STUDIES

CHAPTER 2

POPULATION DYNAMICS OF CASSAVA MEALYBUG PHENACOCCLUS MANIHOTI MAT-FERR ITS EXOTIC PARASITOID, EPIDINOCARSIS LOPEZI DE SANTIS AND INDIGENOUS PREDATORS IN GHANA: RAINFOREST AND COASTAL SAVANNAH ZONES COMPARED

2.0 ABSTRACT

Population densities of cassava mealybug, the exotic parasitoid E lopezi and local natural enemies were followed for twenty-four months in the rainforest and savannah zones of Ghana. Infestation and damage rates of cassava by the new pest were recorded and rates of parasitism and hyperparasitism were also followed for the same period. Rainfall intensities were related to mealybug densities.

Densities of mealybugs and natural enemies were very low. These hardly exceeded 30 per sampled tip and 100 per infested tip even during the dry season when population peaks were reached.

Rainfall was assessed to be a major abiotic factor since intensities negatively correlated with mealybug densities, suggesting a possible mechanical impact by rains on mealybugs. Rates of parasitism and hyperparasitism rarely exceeded 30%. Damage (bunch top) and infestation rates were below 20% except for the coastal savannah where they reached 50% at peak periods.

Ant attendance was observed to be a significant phenomenon on tips with mealybugs in the rainforest zone.

2.1 INTRODUCTION

The most serious pest problem which threatened to wipe out cassava in Africa was posed by accidentally introduced cassava pests, the cassava mealybug, Phenacoccus manihoti Matile-Ferrero (Homoptera: Pseudococcidae) and the cassava green mite Mononychellus tanajoa Bondar sensu lato (Acari: Tetranychidae) (Hahn and Williams, 1973).

Though over 200 species of insect pest have been recorded on cassava (Bellotti and Schoonhoven, 1978), only a few are pests of economic importance.

In Africa, the most important insect pest on cassava before the introduction of the new exotic pest mentioned above was the indigenous and cosmopolitan variegated grasshopper Zonocerus variegatus L

(Orthoptera: Pyrgomorphidae).

In Ghana cassava mealybug populations were several hundreds or a few thousands per infested tip over larger areas only two years after its observation in late 1980. The destruction of cassava by this single pest was so phenomenal and alarming that a big famine threat was imminent for a country like Ghana, the greater part of whose population live on cassava (Korang-Amoakoh et al., 1987).

In a control attempt, the South American monophagous parasitoid, Epidinocarsis lopezi De Santis (Hymenoptera: Encyrtidae) was released in Ghana in 1984 as part of the Africa-wide Biological Control Program of the International Institute of Tropical Agriculture. Since the parasitoid's introduction there have been notable improvements in cassava vegetation and a dramatic drop in mealybug populations. These observations were not quantified in detail in the rainforest in Ghana and many other countries in Africa prior to the study presented here.

The aims of this study were to assess population levels of cassava mealybug and its natural enemies in detailed phenology and population dynamic studies. Results are compared with the savannah zone, a few reported cases in other countries of Africa and discussed with theories on population regulation.

2.2 MATERIALS AND METHODS

2.2.1 Surveys and choice of fields for study

In August 1987 extensive surveys were conducted in two ecological zones in Ghana to locate suitable fields planted by farmers with local cassava varieties for an in-depth population dynamic study of the cassava mealybug and its associated fauna. Three locations in the rainforest zone and one in the savannah zone were chosen to conform to laid-down criteria, described as follows:

- a. Proximity of fields to meteorological stations to provide rainfall data
- b. Field size not below 0.5 ha to allow large sample size collection without considerably disturbing the ecology and microclimate.
- c. Harvest time of fields not below six months and/or proximity of similar age fields for continuity in case of earlier harvesting.

- d. Fields cultivated to farmers variety widely grown in locality.
- e. The granting of fullest assurance and permission by farmer for use of field for study.
- f. Accessibility of roads or paths to fields.

In the rainforest zone suitable fields were located around the following towns or settlements:

1. Koforidua (Lat. 06°, 5'N; Long. 00°, 15'W; Altitude 167m above sea level)
2. New Tafo (Lat. 06°, 13'N; Long. 00°, 22'W; Altitude 198m above sea level)
3. Begoro (Lat. 06°, 23'N; Long. 00°, 23'W; Altitude 610m above sea level)

In the coastal savannah lowland one field was selected for comparison, at Kasoa near Accra.

Koforidua, with extremely large expanses of cassava fields, had four fields chosen in order to get a representative sample size from the location.

New Tafo and Begoro had two fields each due to much smaller and at times unsuitable fields.

Each field had cassava planted to less branching varieties (max. of two tips per stem), the most predominant if not unique in the locations studied. Cassava plants were haphazardly (no pattern) planted with an estimated average between plant distance of one meter. This gave an approximate crop density of 10,000 per hectare and therefore at least 5000 plants per 0.5 ha (i.e. the average size of fields chosen). The maximum of 100 tips sample size for each fortnight per field was considered appropriate to avoid upsetting the ecology and microclimate of fields.

2.2.2 Sampling procedure, dissection of tips and counting of insects

Selected fields described above were sampled fortnightly from late August 1987 to early August 1989.

Sampling procedure involved the in situ analysis of 100 regularly



Plate 5 A tip of cassava with mealybugs which is the sampling unit for study

* The percentage of current bunch top damage was assessed on 100 regularly chosen tips in each field. To avoid edge effects, counting of bunch tops was started on the third inner row and continued at 10 paces intervals according to the size of the field along several transect lines across the field in arbitrarily chosen directions referenced to trees on the horizon.

selected tips of cassava (the method is described in detail elsewhere, in *Hammond et al., 1987; *Neuenschwander and Hammond, 1988). Tips showing mealybug infestations were carefully broken within 10 cm from the apex over opened sampling bags to avoid the escape of associated insects (see Plate 5). Broken tips were put into sampling bags, sealed and taken to the laboratory for dissection. Mealybug stages II-IV, mummies and predators were counted. During sampling *percentage infestation and damage of cassava inflicted by mealybug (bunch top damage only) were recorded.

2.2.3 Rearing of mealybugs, mummies and predators

After counting insects on each tip, separated mummies (dead and hardened mealybug containing the parasitoid or its hyper) were kept, each in a gelatin capsule for emergence of adults, for identification purposes. The mealybugs which were still alive were reared in petri dishes on water leaf Talinum triangulare Jacq (Neuenschwander and Madojemu, 1986). Initial rearing on cassava succulent parts was discontinued due to high fungal contamination and unacceptable mealybug mortality. Larvae and pupae of coccinellids were also reared or kept for emergence. All insects collected were identified with low powered microscopy.

2.2.4 Calculation of densities of insects and rates of parasitism of cassava mealybugs

Due to low infestation rates, numbers of mealybugs, mummies of parasitoids etc. were pooled for each locality and divided by the sample size (including tips without mealybugs and mummies) to obtain field means. When uninfested tips were excluded, densities were expressed as numbers per infested tip.

Percentage parasitism and hyperparasitism were calculated according to equations (1) and (2), as follows:

$$\% \text{ Parasitism} = \frac{M}{CM (II-IV) + M} \times 100 \quad (1)$$

where M = Total mummies (parasitoids including hyperparasitoids)

CM = Total parasitisable mealybugs (stages II-IV)

$$\% \text{ Hyperparasitism} = \frac{H^*}{M} \times 100 \quad (2)$$

where H = Total hyperparasitoids

M = Total mummies (parasitoids including hyperparasitoids)

*Gregarious hyperparasitoids e.g. Chartocerus spp were divided by average number emerging from one mummy i.e. 2 for Chartocerus (Neuenschwander et al., 1987).

Field means were used for plotting phenology curves, where as means or weighted means were statistically analysed by ANOVA or t-test of regressions.

2.2.5 Weather data

Monthly rainfall data covering all months of the study period were obtained from stations of the Meteorological Services Department of Ghana at Koforidua, Cocoa Research Institute at New Tafo, Begoro and Accra. The data were related to the phenology curves by cursory comparison and by regression statistics of mealybug monthly densities against monthly rainfall in mm for locations studied. (See Appendices A1-A5 for full weather data for all locations.)

2.3 RESULTS

2.3.1 General phenology of cassava mealybug

Generally, mealybug populations were low at all locations throughout the study period. Densities were below 45 cassava mealybugs per sampled tip and 150 per infested tip for the highest infested location, i.e. the coastal savannah. Low infestation levels necessitated the pooling of field data for ^{the} four fields at Koforidua, 2 fields each for Begoro and New Tafo while the coastal savannah had only one field for comparison. Peak densities of mealybugs occurred in the dry season and lowest densities were recorded during the rainy season for all locations.

2.3.1.1 Phenology of cassava mealybug at Koforidua

The lowest and peak values of mealybugs per sampled tip were 0.4 and 8.4 (mean of 400 tips for each data point on curves) (Fig. 2.1A).

When uninfested tips were excluded from samples to reflect mealybug densities attracting calculated parasitisation rates, mealybug lowest and peak densities were 9 and 70 respectively (Fig. 2.5B). Lowest and peak values of mealybug densities occurred between April-October (rainy season) and November-March (dry season) respectively. (Compare Fig. 2.1A and Fig. 2.1C for influence of rain on mealybug densities.)

2.3.1.2 Phenology of mealybugs at Begoro

The lowest and peak densities of mealybugs were 0.2 and 8 per sampled tip (Fig. 2.2A) and 15 and 95 per infested tip (Fig. 2.6B) respectively. Low and peak densities occurred between April-October (rainy season) and November-March (dry season) respectively, just as at Koforidua (compare Fig. 2.2A with Fig. 2.2C).

2.3.1.3 Phenology of mealybugs at New Tafo

Apart from following the general rule of low mealybug numbers and seasonal density fluctuations, New Tafo was the only location where no mealybugs were encountered in fields by the general sampling procedure during the peak of the rainy season (June-July months). Peak densities were 15 mealybugs per sampled tip and 78 mealybugs per infested tip with zero as the lowest recorded density.

2.3.1.4 Phenology of mealybugs at Kasoa/Accra

As the only representative of the savannah zone, Kasoa/Accra differed from the other localities only by higher mealybug densities during the dry season. Peak density reached 45 mealybugs per sampled tip (Fig. 2.4A) and 130 mealybugs per infested tip (Fig. 2.8B).

2.3.2 General phenology of natural enemies

The greatest number (80%) of natural enemies of cassava mealybugs encountered at any location were the exotic parasitoid and its associated local hyperparasitoids. (Details of species and composition are given in Chapter 4 of Section II of this thesis.) Local predators constituted the remaining percentage.

Mummies representing the total of primary and hyperparasitoids, showed fluctuating densities but remained the dominant single mealybug mortality factor at all locations. Predator densities remained low. Fungal induced mortality was erratic, minor and negligible.

Fig. 2.1 Population dynamics of Phenacoccus manihoti (second to fourth instars) (A), its natural enemies, (mainly predators and mummies of parasitoids) (B), on average from 400 tips per fortnightly period at Koforidua in the rainforest of Ghana. Monthly rainfall totals in mm for Koforidua cover the study period (C)

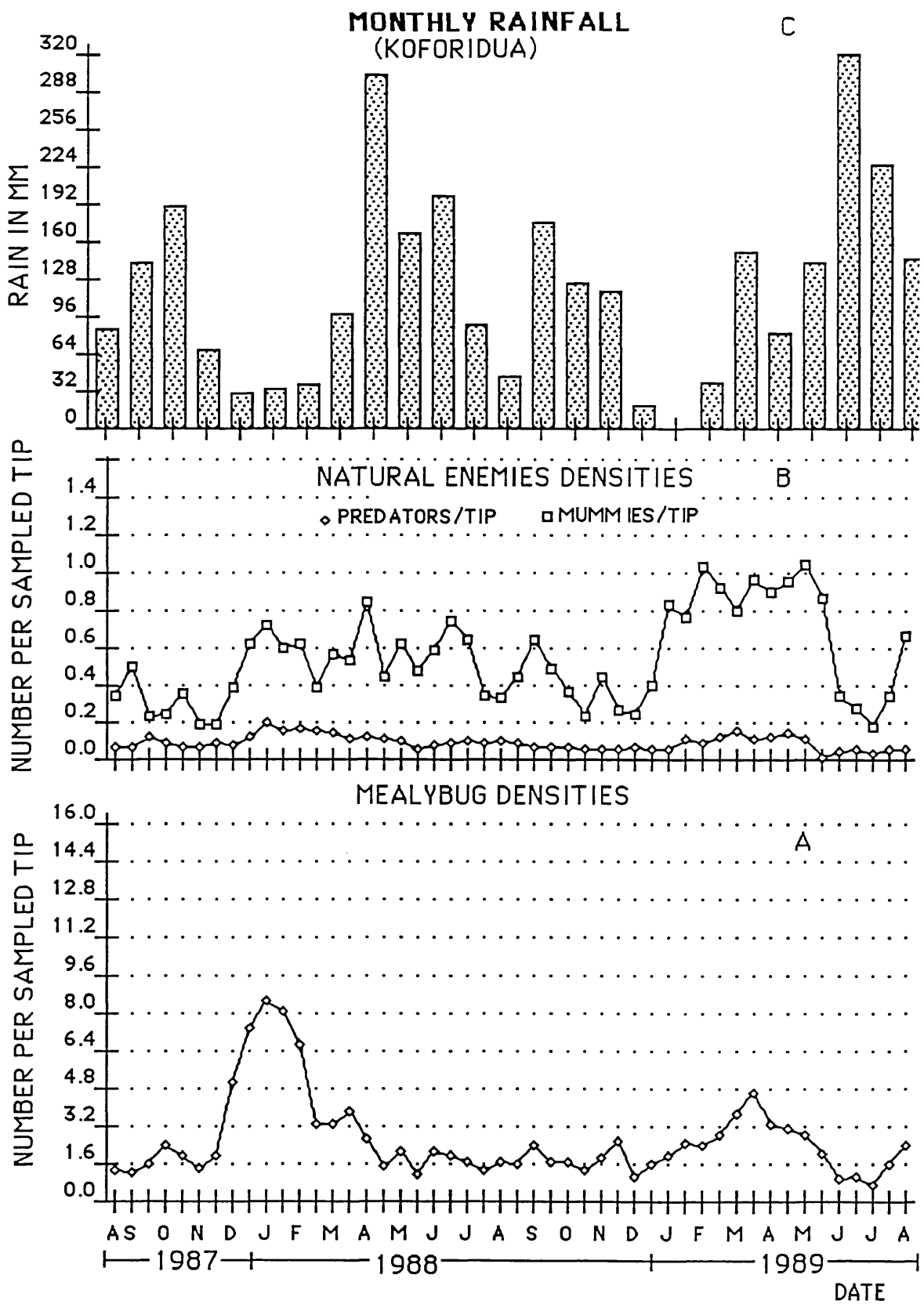
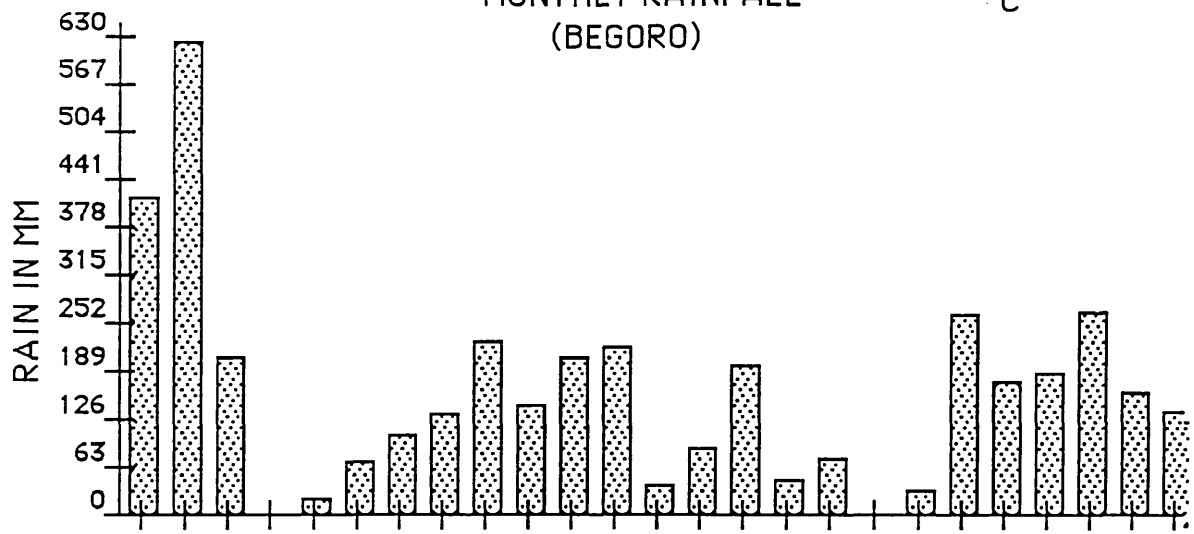


Fig. 2.2 Population dynamics of Phenacoccus manihoti (second to fourth instars) (A), its natural enemies (mainly predators and mummies of parasitoids) (B), on average per tip from 200 tips per fortnightly sampling period at Begoro in the rainforest zone of Ghana. Monthly rainfall totals in mm for Begoro cover the study period (C)

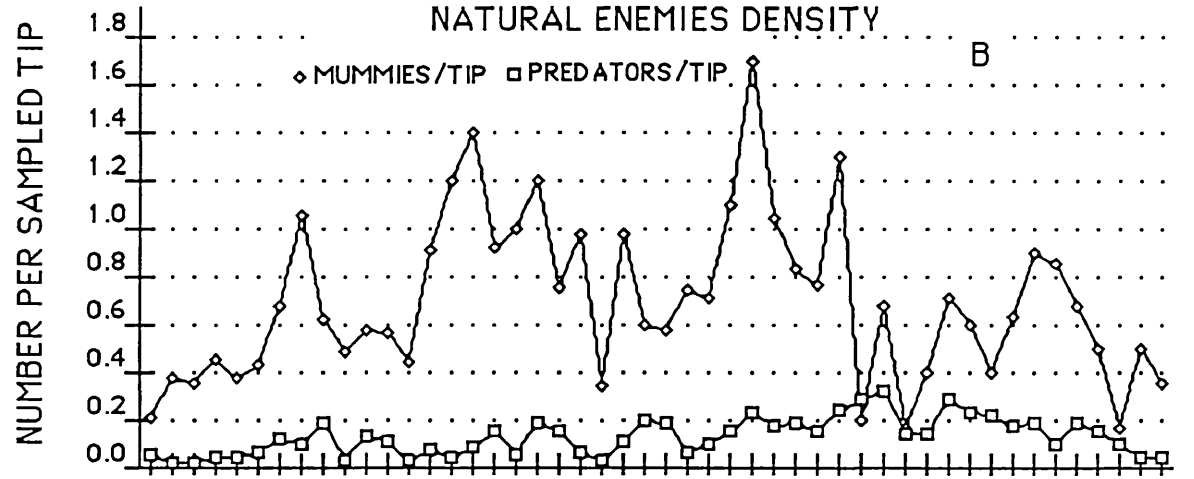
MONTHLY RAINFALL
(BEGORO)

C



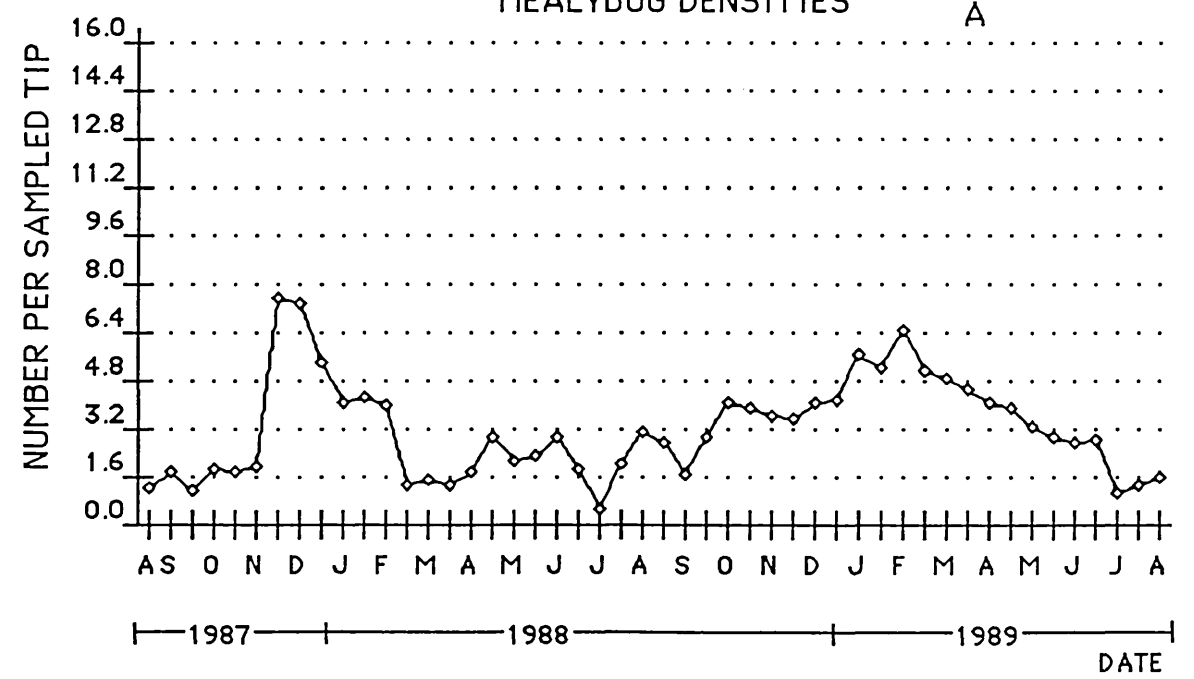
NATURAL ENEMIES DENSITY

B



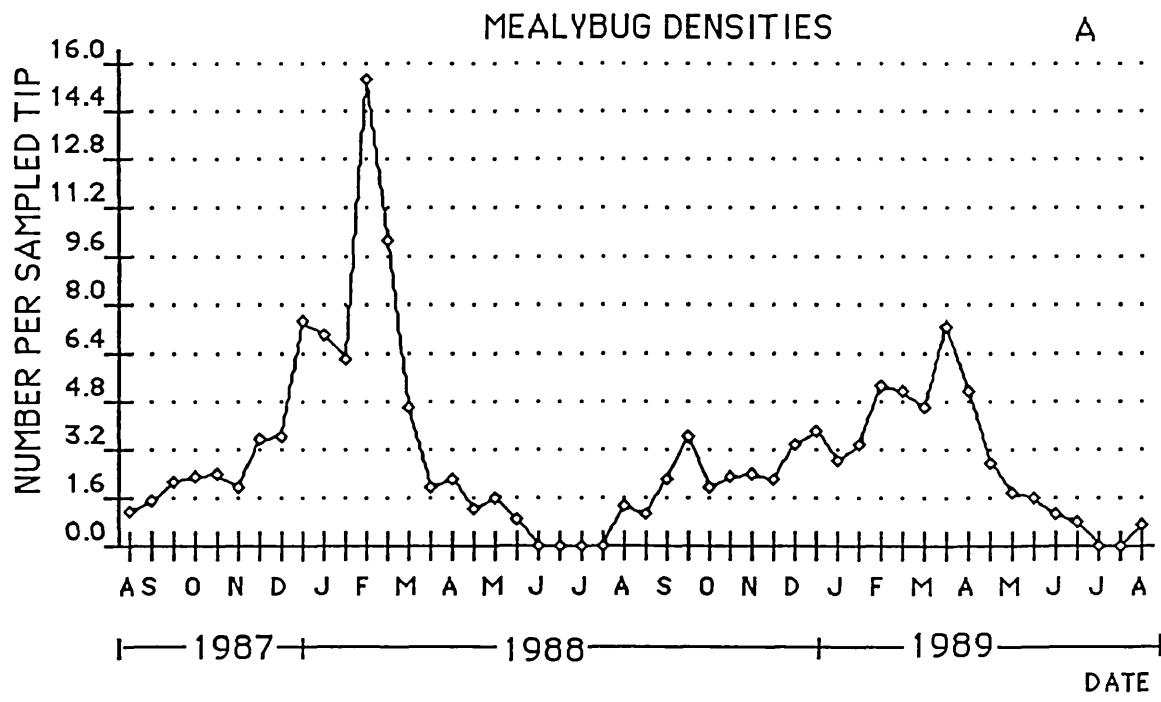
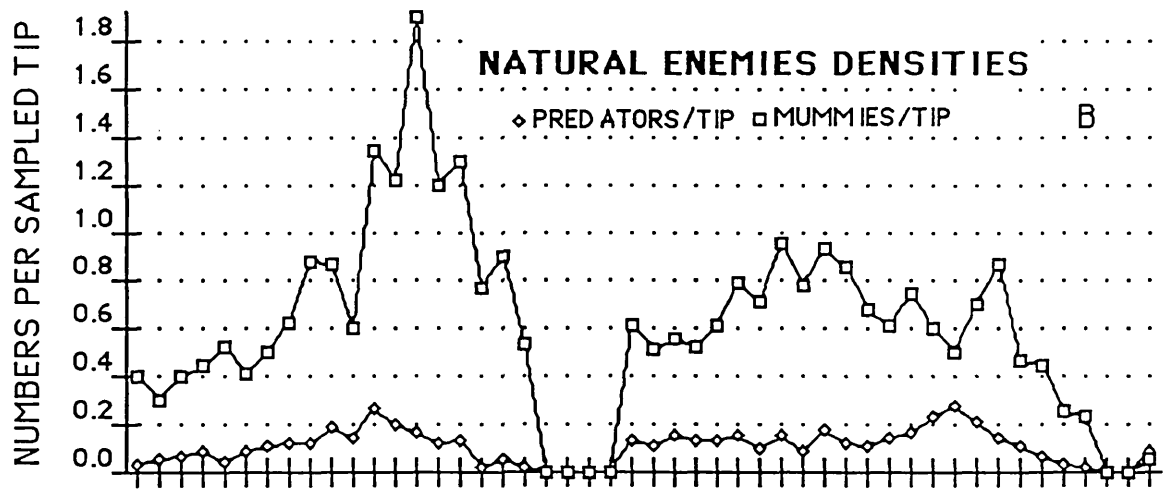
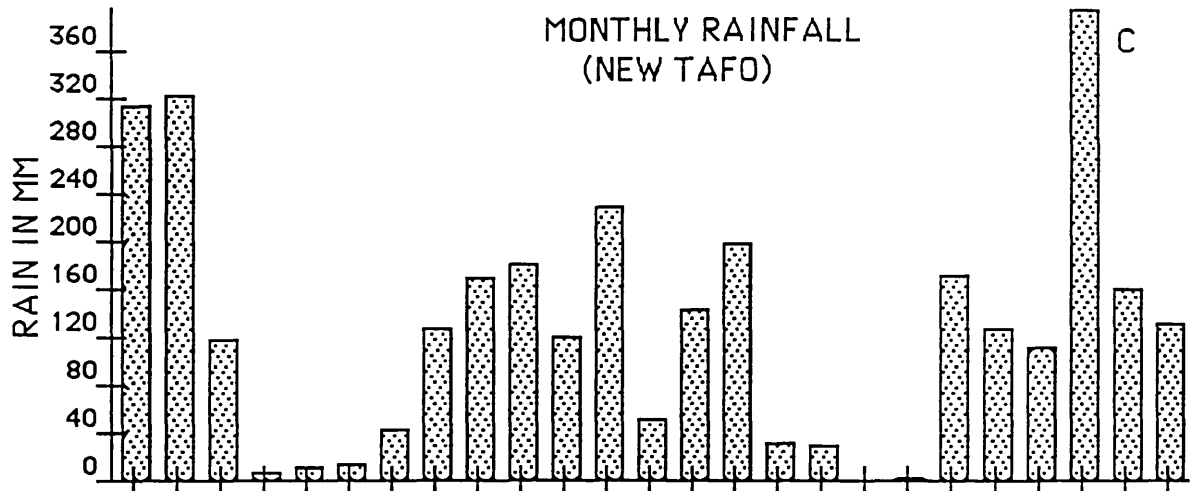
MEALYBUG DENSITIES

A



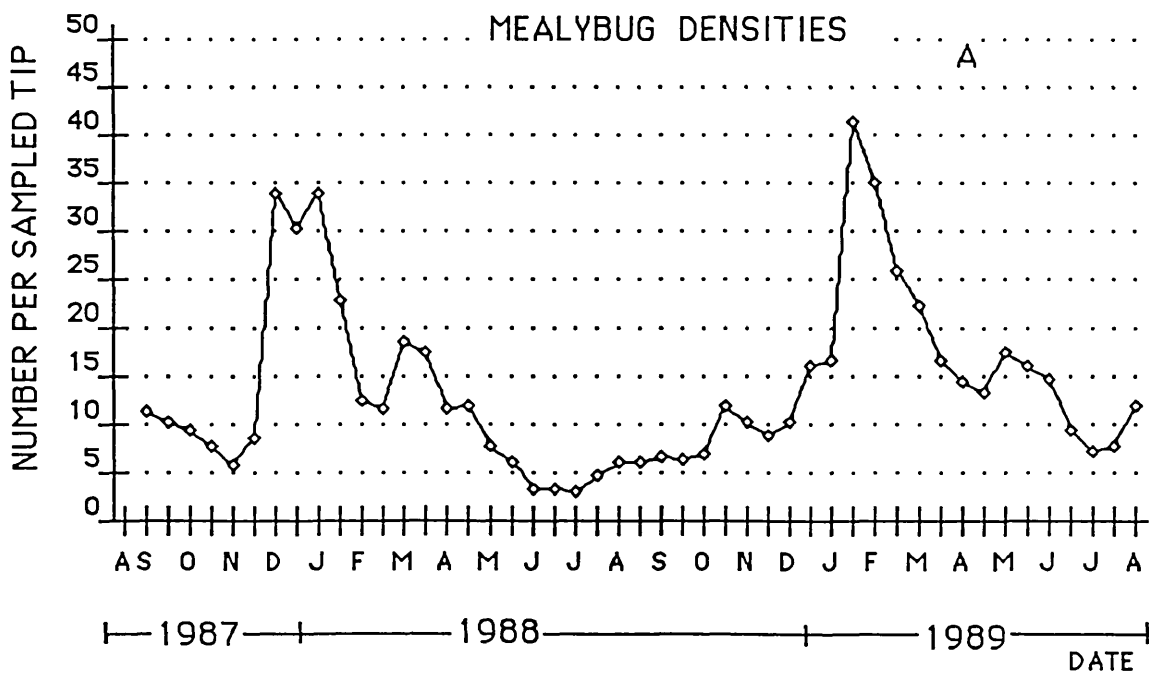
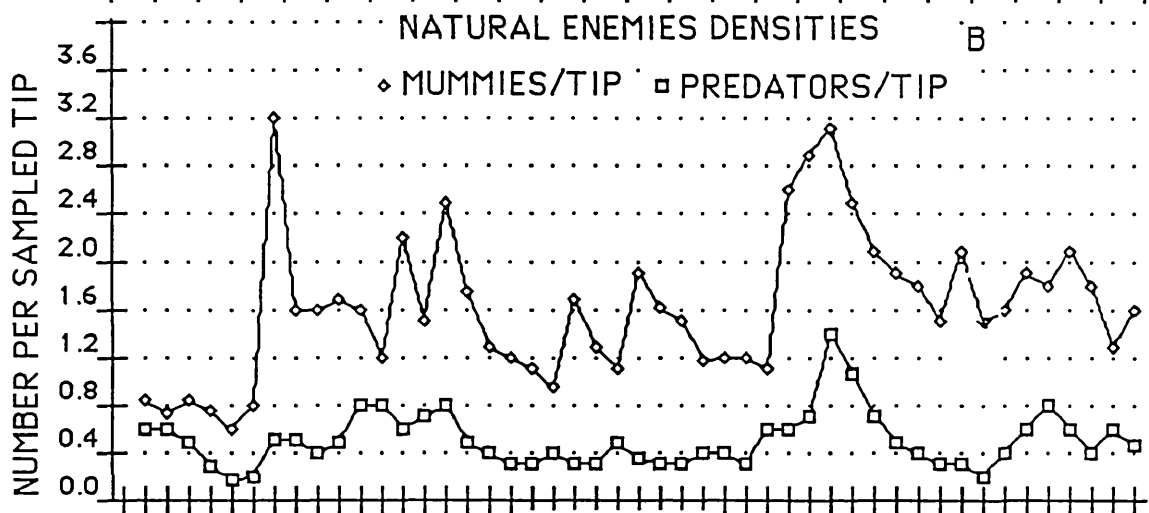
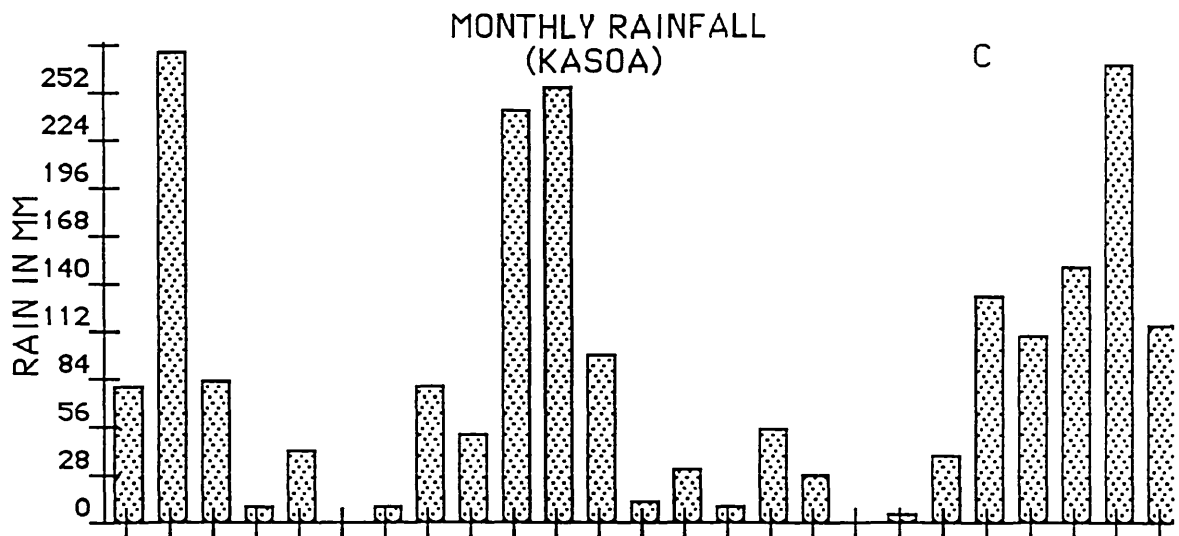
1987 | 1988 | 1989 | DATE

Fig. 2.3 Population dynamics of Phenacoccus manihoti (II-IV instars) (A), its natural enemies (mainly predators and mummies of parasitoids) (B), on average per tip from 200 tips per fortnightly sampling period at New Tafo in the rainforest of Ghana. Monthly rainfall totals in mm for New Tafo cover the study period (C).



1987 1988 1989 DATE

Fig. 2.4 Population dynamics of Phenacoccus manihoti (II-IV instars) (A), its natural enemies (mainly predators and mummies of parasitoids) (B), on average per tip from 100 tips per fortnightly sampling period at Kasoa/Accra in the coastal savannah of Ghana. Monthly rainfall totals in mm for Kasoa/Accra cover the study period (C).



2.3.2.1 Phenology of natural enemies at Koforidua

Parasitoid mummy densities fluctuated between 0.2 and 1.0 per sampled tip. Phenology curves showed rather irregular peaks and falls at times corresponding to high and low mealybug densities. No clear rain influence could be visually detected. Predators per sampled tip hardly exceeded 0.2 at peaks. The curve also showed erratic increases and falls (Fig. 2.1B).

2.3.2.2 Phenology of natural enemies at Begoro

Parasitoid mummies were between 0.2 to 1.7 per sampled tip. The phenology curve showed slight variation from all other locations. Strangely, peaks occurred during low mealybug densities indicating an inverse relationship. This presented the only example of a trend away from a positive density-dependence relationship between the parasitoid and mealybugs. Predator densities rarely exceeded 0.2 and showed no remarkable increases during mealybug peaks (Fig. 2.2B).

2.3.2.3 Phenology of natural enemies at New Tafo

Mummy densities showed peaks corresponding to mealybug peaks with some slight delay. Apart from no mealybug on sampled cassava tips for the months of June and July, and also no mummies for the same period, densities of mummies rarely exceeded 0.2 and 1.9 per sampled tip for the other months. Predator densities remained low and seldom exceeded 0.2 per sampled tip. However, slight increases corresponded with mealybug peak densities (Fig. 2.3B).

2.3.2.4 Phenology of natural enemies at Kasoa/Accra (coastal savannah)

Densities of up to 3.2 mummies per sampled tip were reached at Kasoa/Accra. The lowest mummy density was 0.5 per sampled tip. Predators' phenology curve showed similarity to that of the rainforest zone. However, densities went up to 1.4 per tip and rarely fell below 0.2 per tip. The relative higher predator density in the savannah could be due to higher mealybug densities in this zone (Fig. 2.4B).

2.3.3 General rates of parasitism, hyperparasitism, infestation and damage to cassava by mealybugs

Generally, rates of parasitism and hyperparasitism, infestation and

damage of cassava by mealybugs were all ~~very~~ low for all locations in both the rainforest and savannah zones. Parasitism and hyperparasitism rarely exceeded 30%. However, these low rates were not reflected in an expected high density of mealybugs. Infested tips had no more than 100 mealybugs (only a few tips had more than 100 mealybugs) on individual tips. Hyperparasitism rarely exceeded rates of parasitism indicating a good trend. Rates of infestation and damage (only bunch top) of cassava inflicted by mealybugs were below 30% except for the coastal savannah zone where infestation rates occasionally went up to 50% of sampled tips.

2.3.3.1 Rates of parasitism, hyperparasitism infestation and damage to cassava by mealybugs at Koforidua

The lowest and peak rates of parasitism were 14% and 38% respectively. The lowest parasitism rates were recorded at mealybug peak densities. Rates of hyperparasitism showed a similar trend but increased with higher mummy densities reaching a peak rate of 35% (Fig. 2.5C). Infestation and damage inflicted by mealybugs were between 5 and 15% of sampled tips (Fig. 2.5A).

2.3.3.2 Rates of parasitism, hyperparasitism infestation and damage to cassava by mealybugs at Begoro

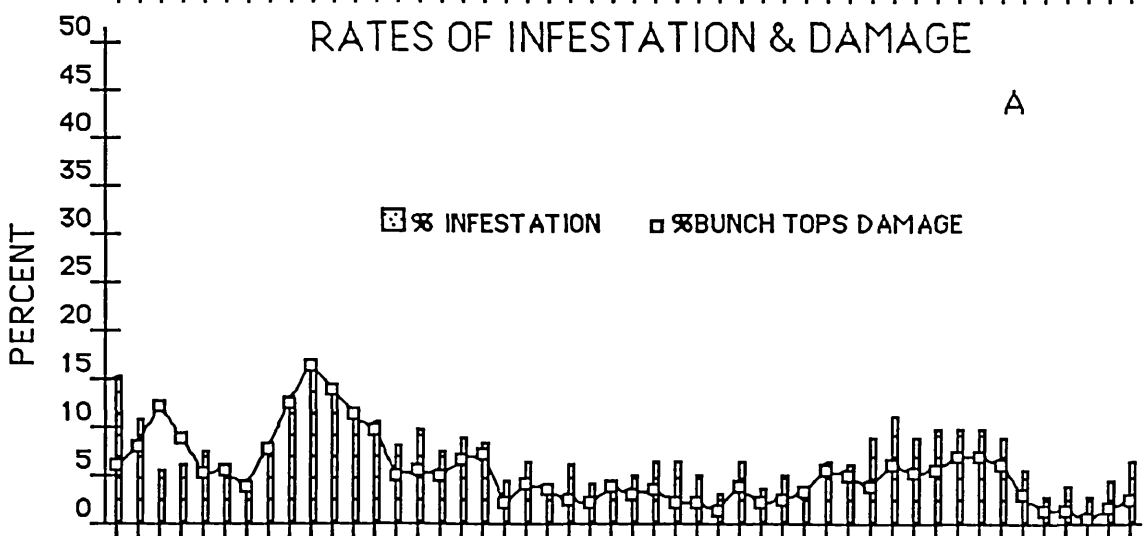
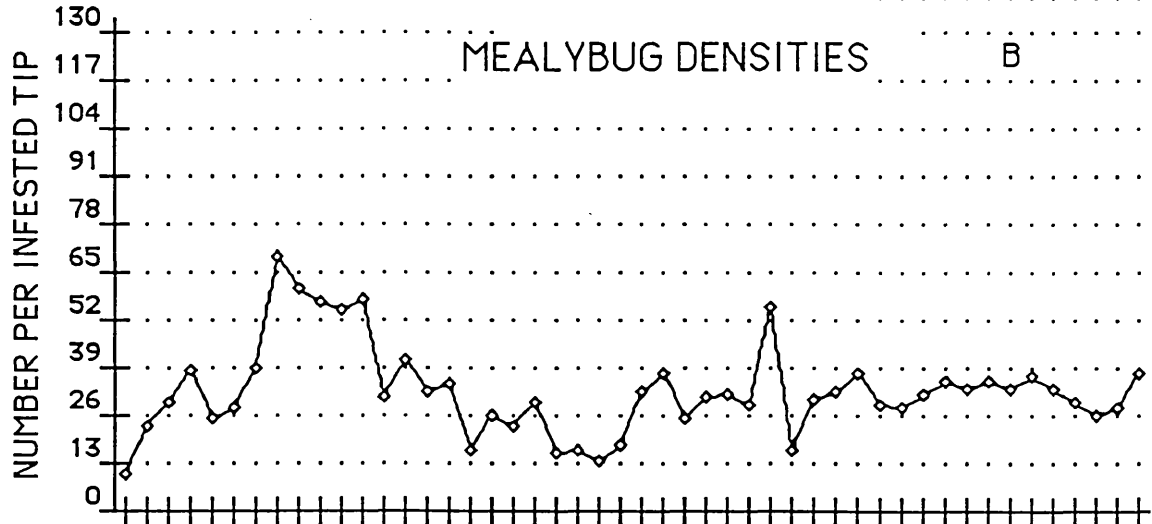
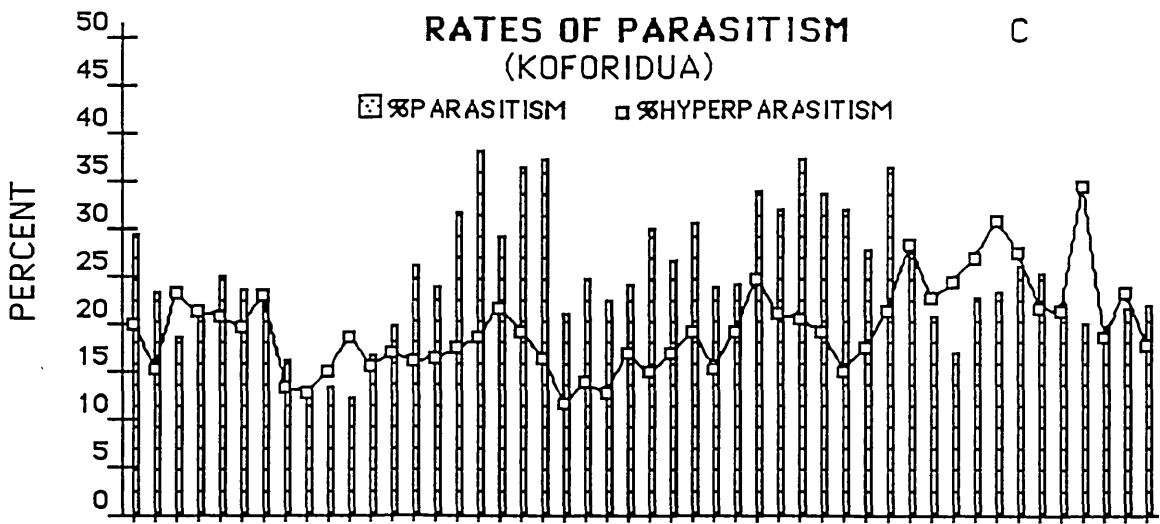
The lowest and peak values of parasitism rates were 4% and 38% respectively. Hyperparasitism also showed a similar trend but a much better density-dependence relationship in relation to parasitism (Fig. 2.6C).

Begoro had the lowest infestation and damage rates of all the locations. These were well below 10% at all times coupled with low mealybug densities per infested tip. This could be a reason for the relatively uniform parasitism rates observed (Fig. 2.6A).

2.3.3.3 Rates of parasitism, hyperparasitism infestation and damage to cassava by mealybugs at New Tafo

Parasitism varied between 0, when there were no mealybugs in June and July, to 8% for the next lowest level, to 45% on a few occasions. Hyperparasitism showed levels of peaks of 35%. It however failed to drop at low parasitisation rates, as observed for other localities. This was an exception but not the rule and may be explained by the nearness of

Fig. 2.5 Cassava mealybugs infestation and bunch top damage symptoms as a proportion of 400 sampled tips (A), mealybug densities on infested tips producing the damage (B) and rates of parasitism and hyperparasitism (C) at Koforidua in the rainforest zone of Ghana



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Fig. 2.6 Cassava mealybugs infestation and bunch top damage symptoms as a proportion of 200 sampled tips (A), mealybug densities on infested tips producing the damage (B) and rates of parasitism and hyperparasitism (C) at Begoro in the rainforest zone of Ghana

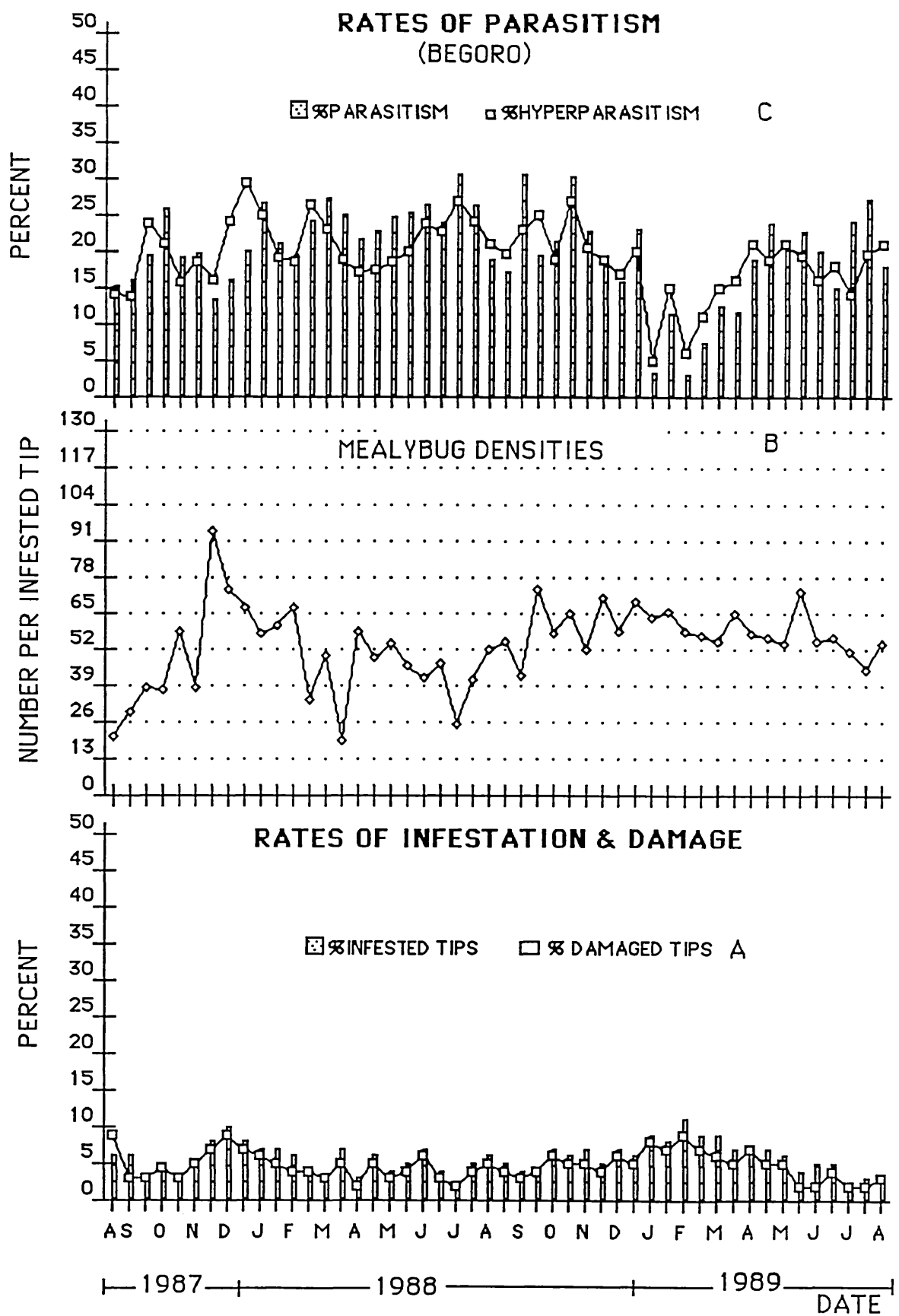


Fig. 2.7 Cassava mealybugs infestation and bunch top damage symptoms as a proportion of 200 sampled tips (A), mealybug densities on infested tips producing the damage (B) and rates of parasitism and hyperparasitism (C) at New Tafo in the rainforest zone of Ghana

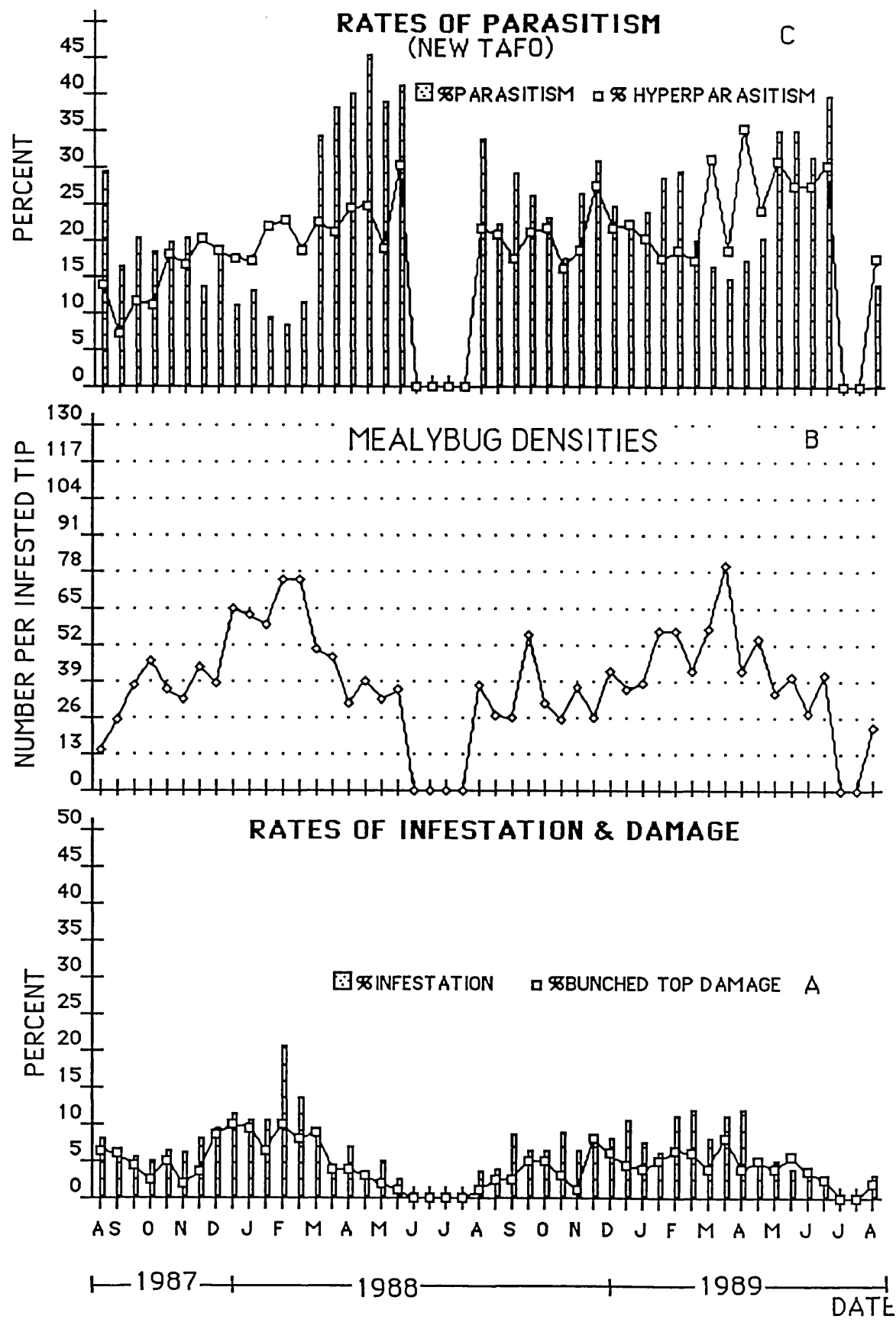
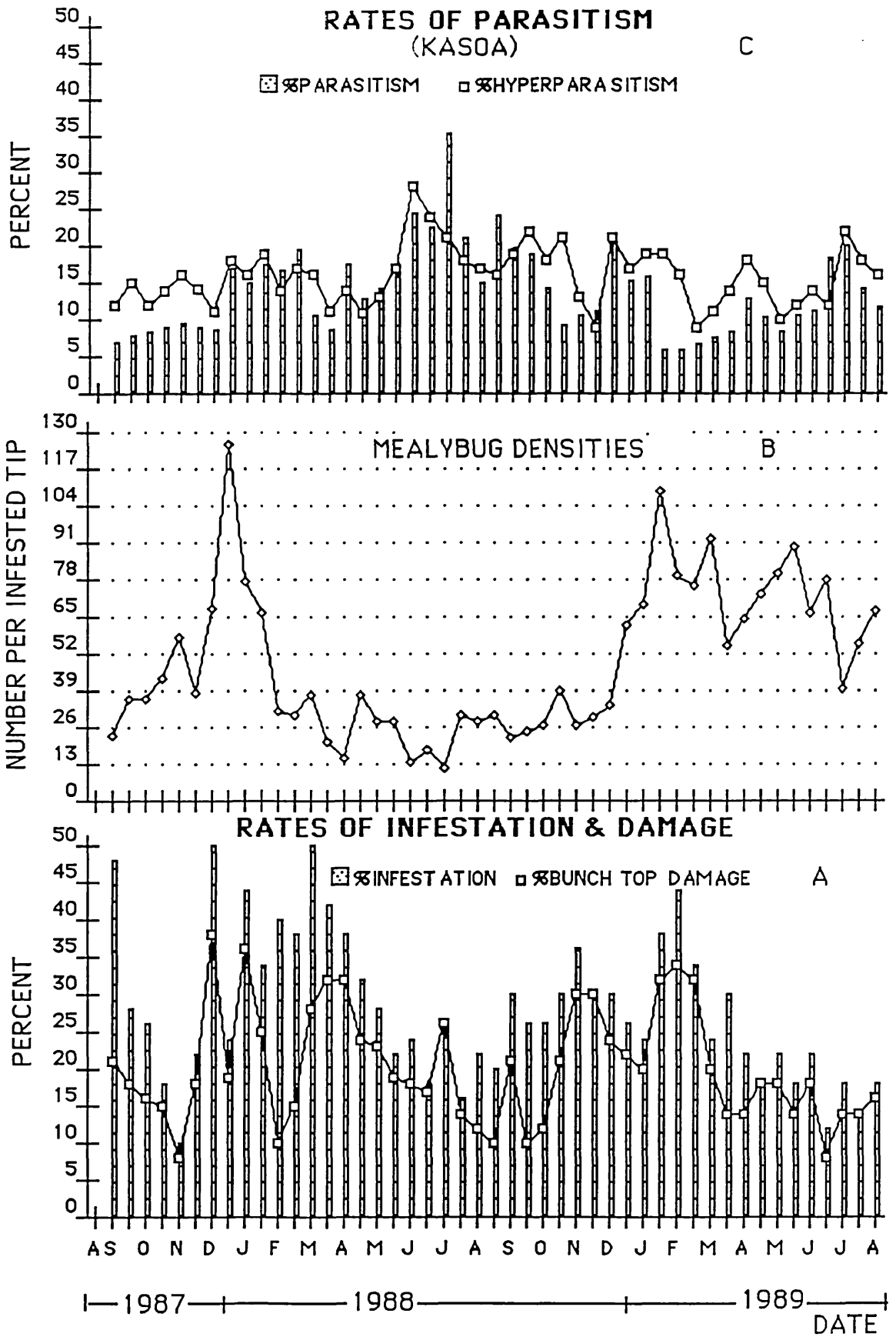


Fig. 2.8 Cassava mealybugs infestation and bunch top damage symptoms as a proportion of 100 sampled tips (A), mealybug densities on infested tips producing the damage (B) and rates of parasitism and hyperparasitism (C) at Kasoa/Accra in the coastal savannah of Ghana



predominant cocoa farms with a lot of mealybug species from where hyperparasites could easily transfer to mummies with E. lopezi at all times in cassava fields. The fields were usually surrounded by large cocoa farms (Fig. 2.7C).

Infestation and damage rates fluctuated between 0 and 10% reaching 20% only once throughout the period of study (Fig. 2.7A).

2.3.3.4 Rates of parasitism, hyperparasitism infestation and damage to cassava by mealybugs at Kasoa/Accra (coastal savannah)

Parasitism and hyperparasitism rates were between 5% and 25% reaching 35% only on one occasion. On many occasions hyperparasitism exceeded rates of parasitism, however fluctuations corresponded well to each other indicating a positive density-dependence relationship (Fig. 2.8C). Infestation and damage rates ranged between 10% and 50% (Fig. 2.8A).

2.3.4 Relationship between rain intensities and cassava mealybug intensities

Phenology curves and monthly rainfall intensities for all locations suggest that peak mealybug densities, coincide with dry months (October-March) and lowest densities with the rainy season (April-November). Natural enemy phenology followed the same pattern in relation to rainfall.

However, some phenology curves are too erratic in relation to rainfall. Peak densities do not always correspond with the driest months but show some delays (Figs. 2.1, 2.2, 2.3 and 2.4). Monthly rainfall intensities regressed against monthly mealybug densities show a negative response as a general trend. As rainfall increases in intensity low mealybug densities are recorded at all locations. All slopes of regressions are negative but most of the t values of slopes are not significant. Rain intensities differ significantly only between Begoro in the rainforest zone and Kasoa/Accra in the coastal savannah (Appendix A2) (see Figs. 2.9, 2.10, 2.11 and 2.12).

2.3.5 Relationship between ant natural enemies and mealybug average densities

Fig. 2.13 suggests that mealybug densities are higher in the coastal savannah but ant densities show higher densities in the rainforest ($t =$

Fig. 2.9 Cassava mealybug densities as a function of monthly rainfall (in mm) at Koforidua in the rainforest zone (relationship described by simple linear (A) and polynomial of 2nd order (B) regressions for $N = 24$)

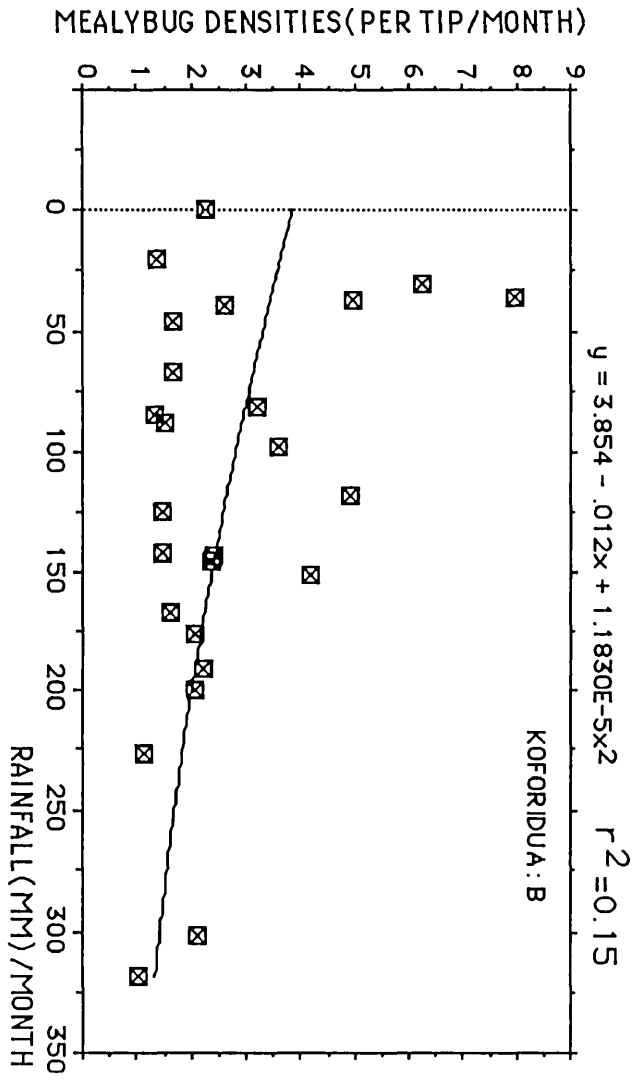
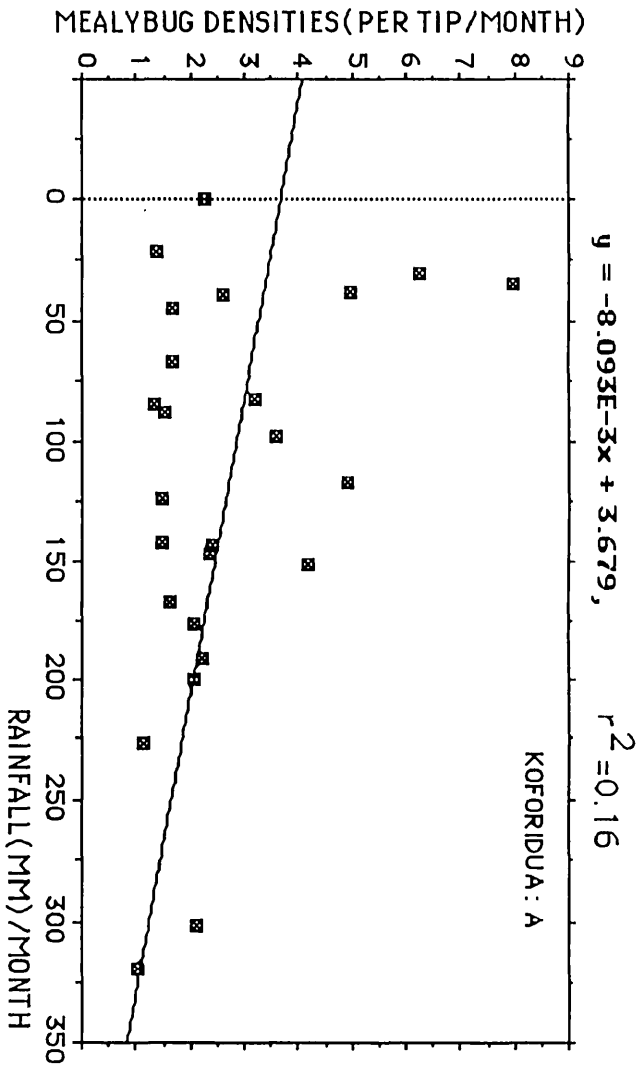


Fig. 2.10 Cassava mealybug densities as a function of monthly rainfall (in mm) at Begoro in the rainforest zone (relationship described by simple linear (A) and polynomial of 2nd order (B) regressions for $N = 24$)

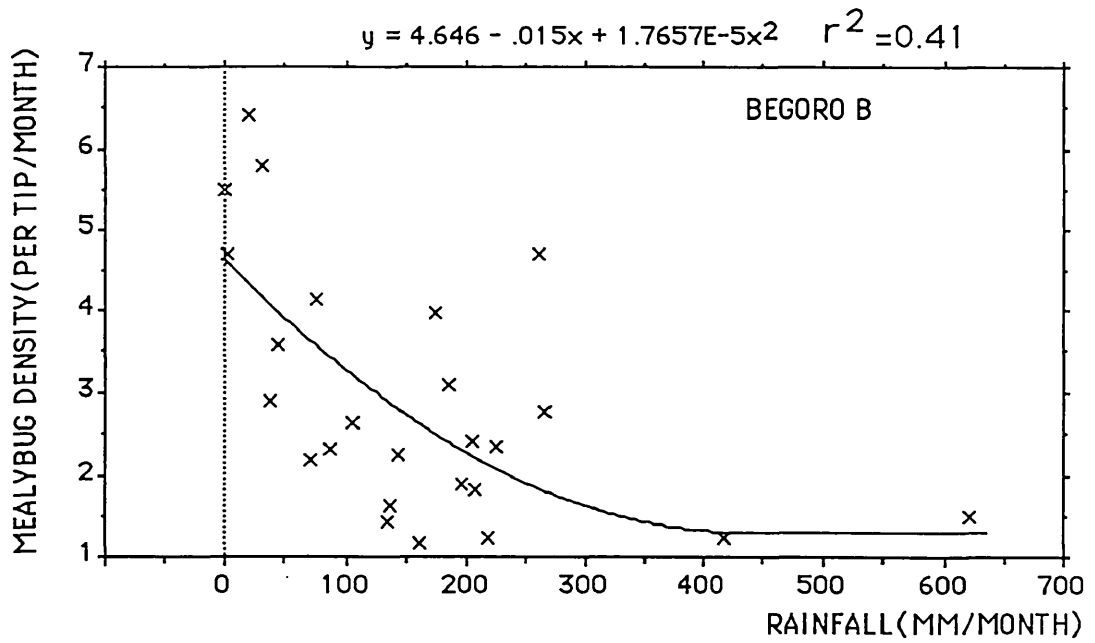
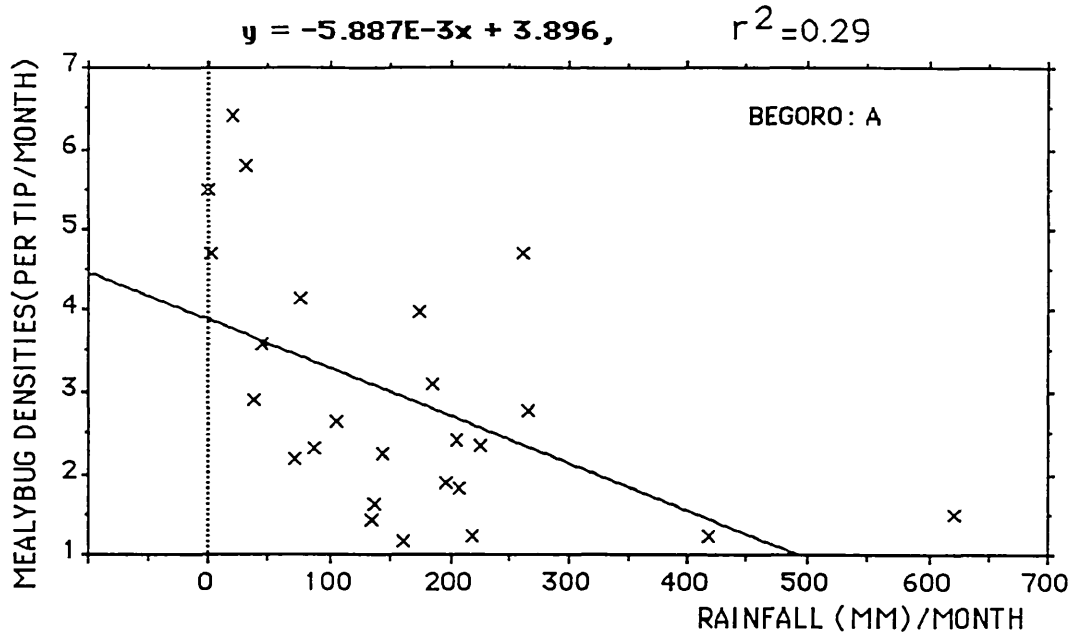


Fig. 2.11 Cassava mealybug densities as a function of monthly rainfall (in mm) at New Tafo in the rainforest zone (relationship described by simple linear (A) and polynomial of 2nd order (B) regressions for N =24)

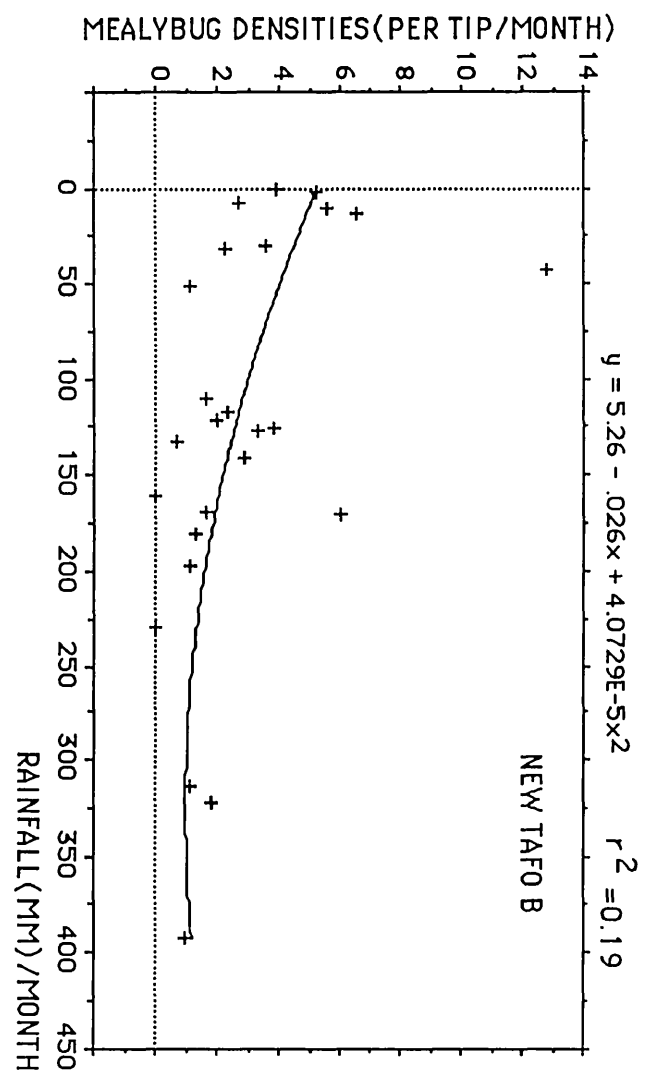
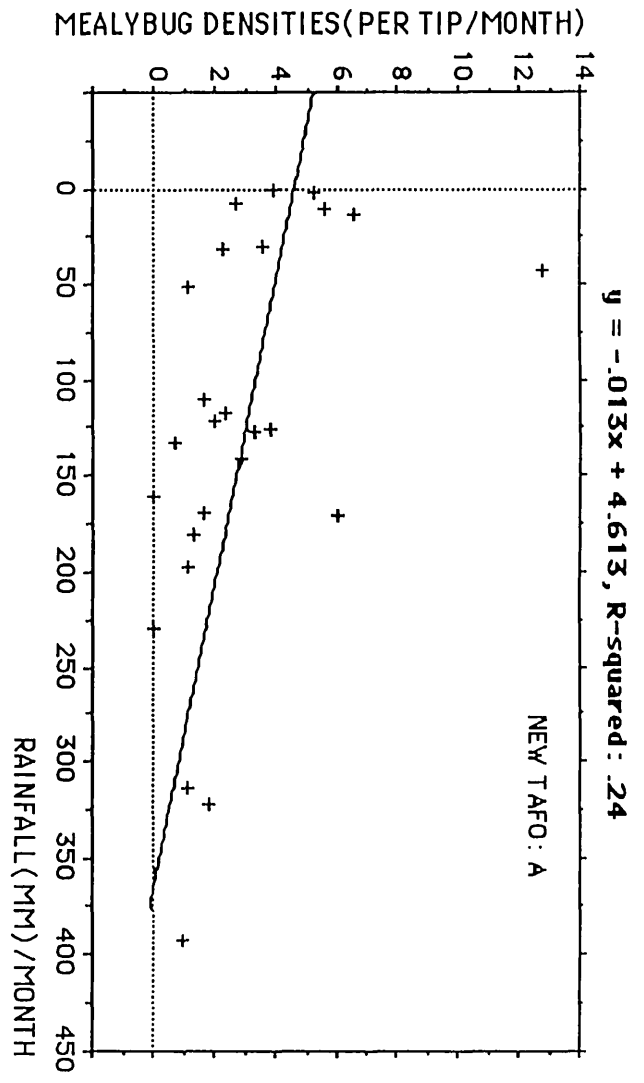


Fig. 2.12 Cassava mealybug densities as a function of monthly rainfall (in mm) at Kasoa/Accra in the coastal savannah zone (relationship described by simple linear (A) and polynomial of 2nd order (B) regressions for N =24)

Fig. 2.13 Cassava mealybug and ant phenologies in the rainforest versus savannah

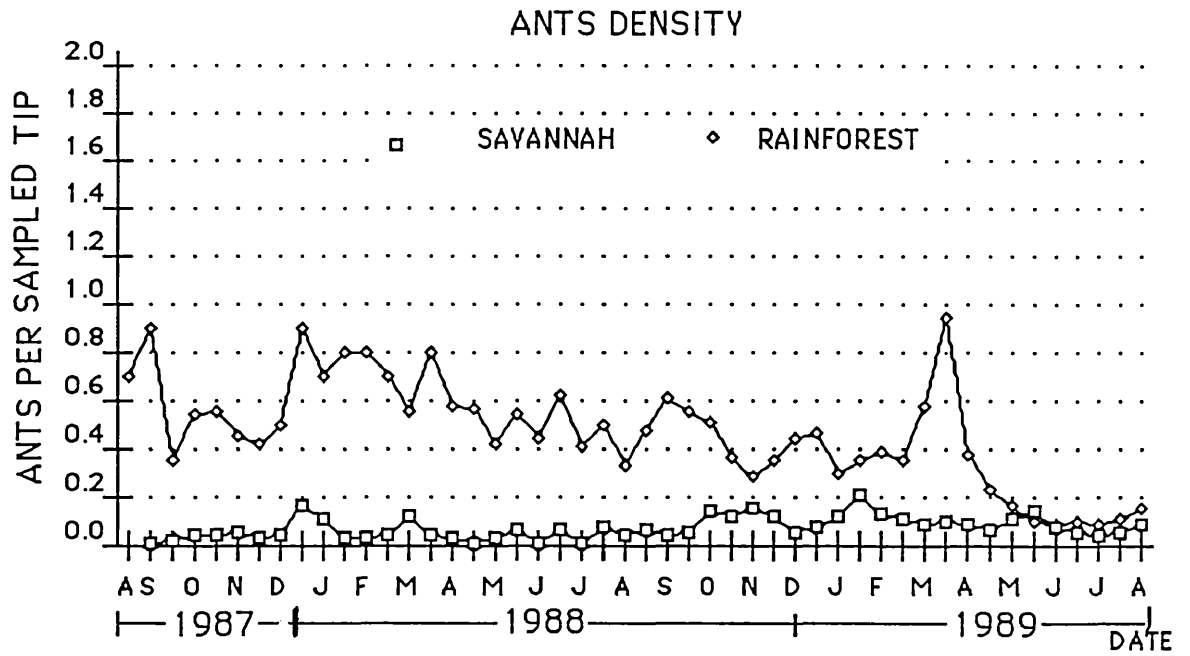
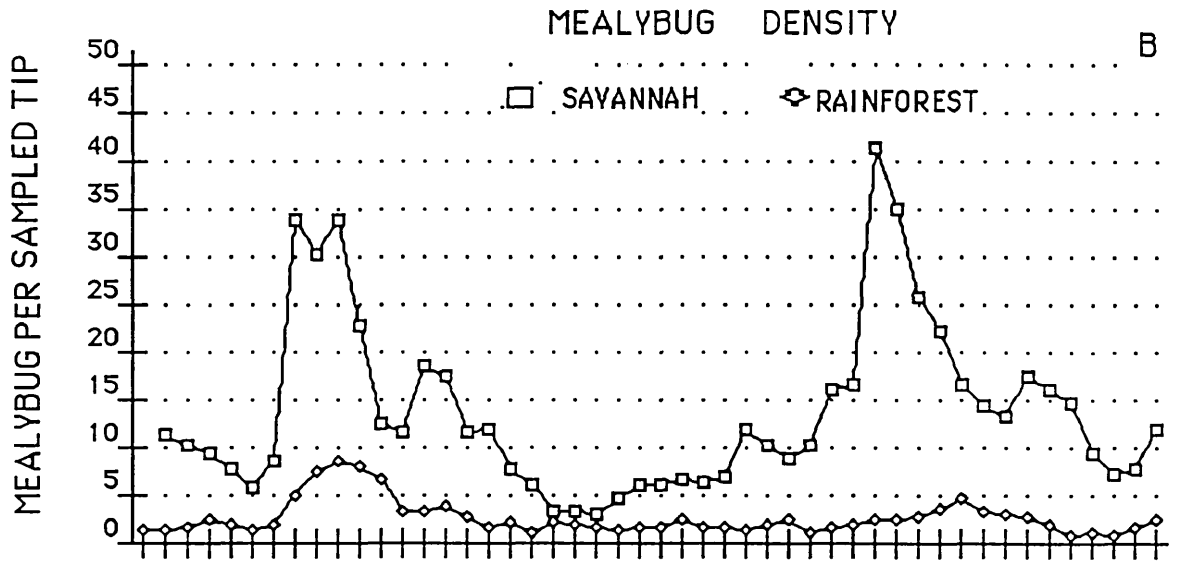


Fig. 2.14 Ant densities as a function of mealybug densities, (relationship described by a simple linear (A) and polynomial (2nd order) (B) regressions for $N = 48$ means) in the Savannah zone of Ghana

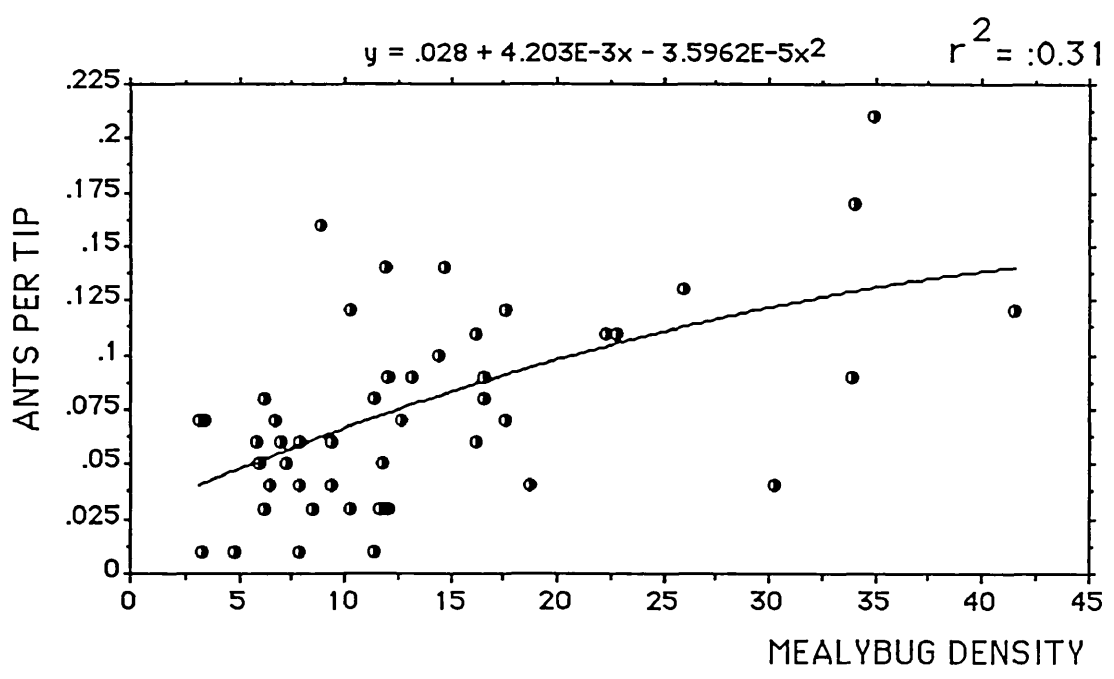
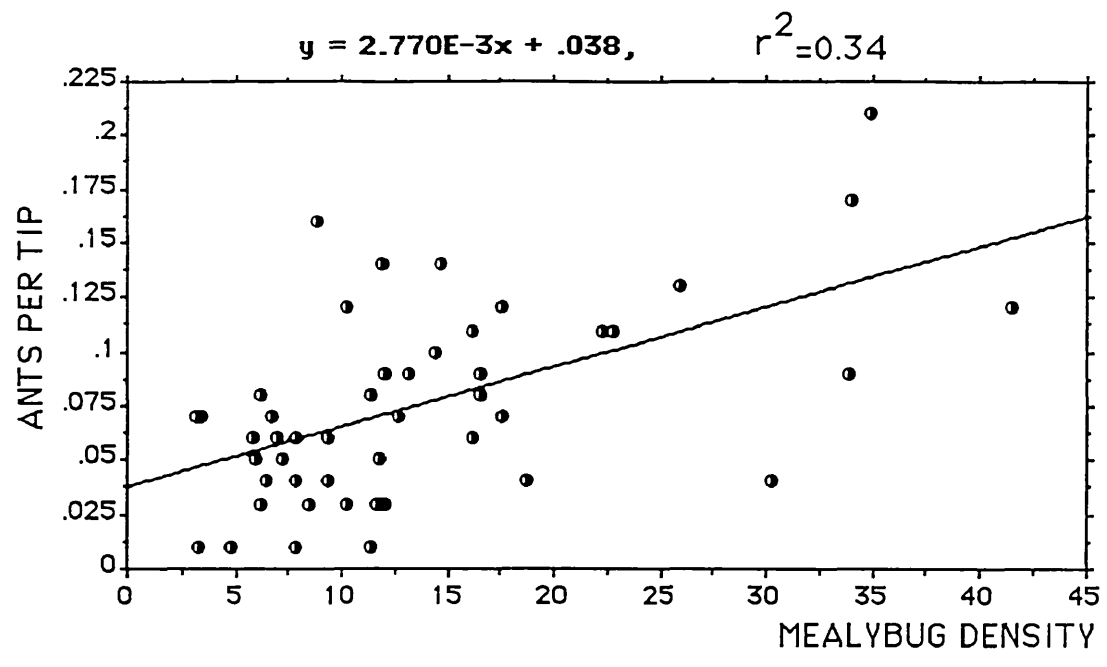


Fig. 2.15 Ant densities as a function of mealybug densities,
(relationship described by a simple linear (A) and polynomial
(2nd order) (B) regressions for $N = 48$ means) in the *rainforest*
zone of Ghana

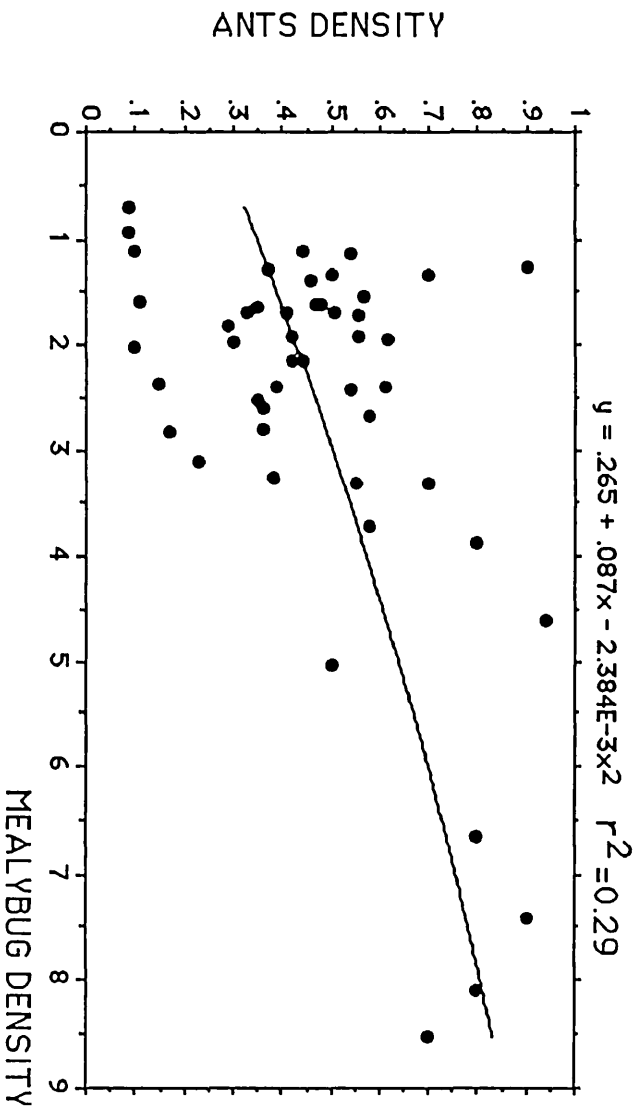
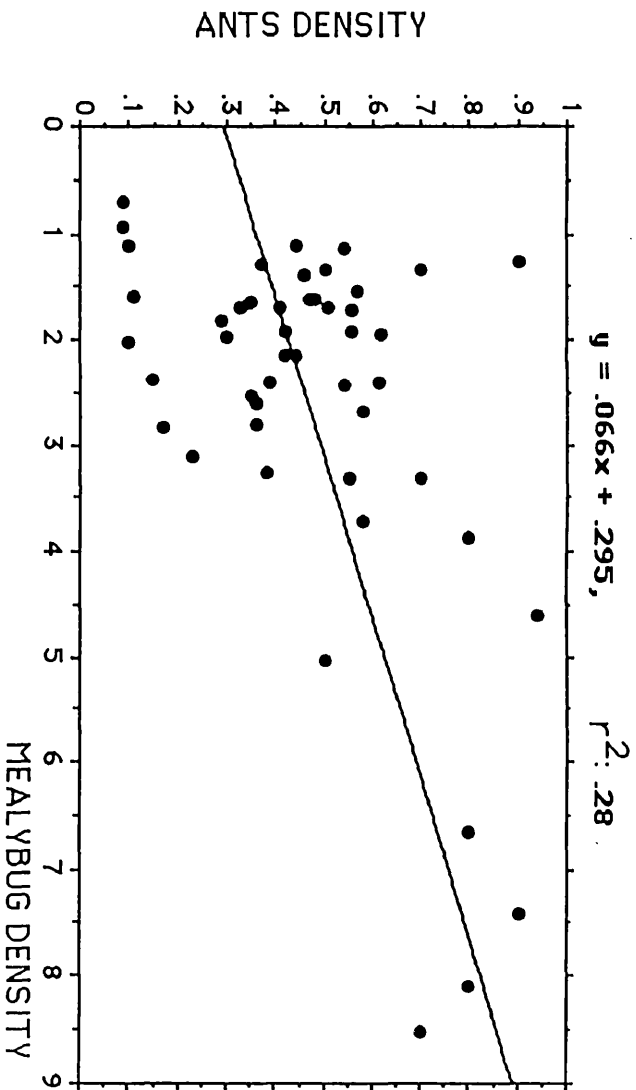
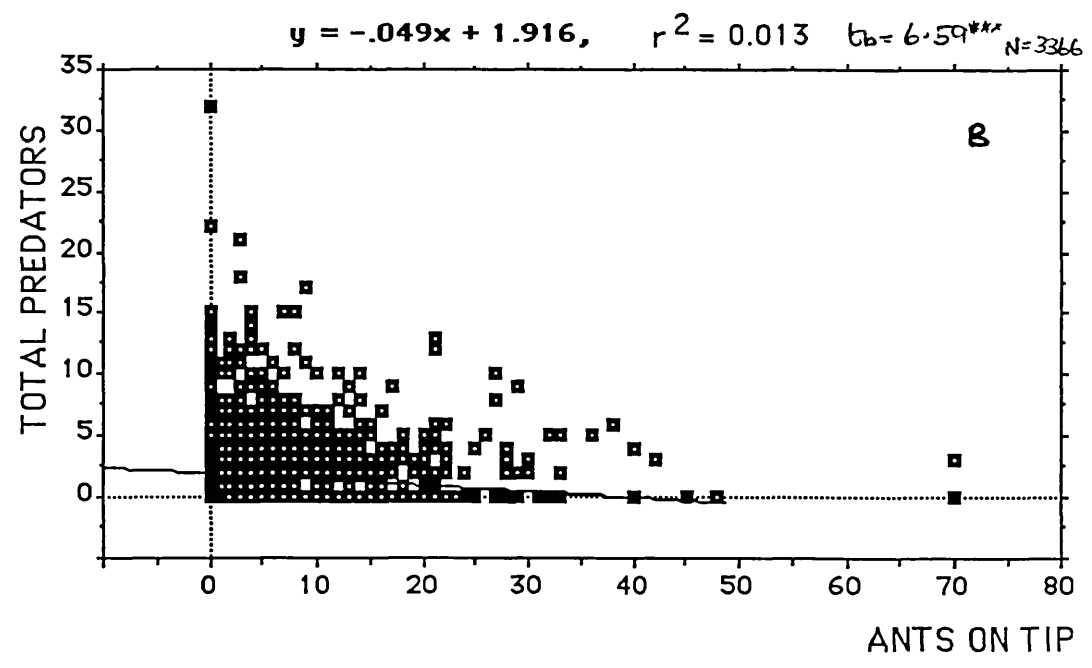
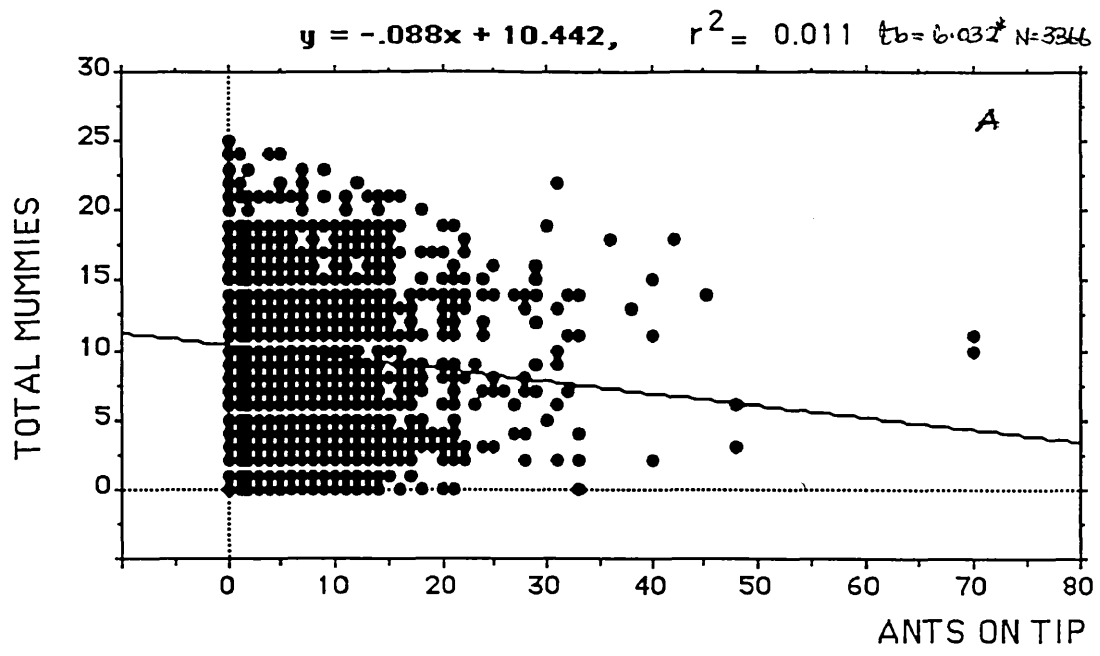


Fig. 2.16 Total natural enemies as a function of total ants on tips described by simple linear regressions for parasitoid mummies (A) and predators (B) for $N = 3668$ tips



9.2* df = 45 for mealybug densities and $t = 12.084^{**}$ df = 45 for ants between the two zones).

This raises the question as to what role ants play in the observed differences in mealybug densities? Higher ant densities in low mealybug infested rainforest and the opposite in the savannah zone suggest a reduction effect of ants on mealybug densities counter to our expectation. However, varied environmental (abiotic) factors in the two zones may also explain the observation. In both ecological zones increasing mealybug densities attracted more ants as shown by regressions in Figs. 2.14 and 2.15. However more ants on tips showed an inverse relation with parasitoid mummy and predator numbers (Fig. 2.16).

2.4 DISCUSSION AND CONCLUSIONS

The phenology curves for all locations provided valuable information on population levels of cassava mealybugs and their natural enemies in two contrasting ecological zones.

The low cassava mealybug populations, especially in the rainforest zone, provide optimism for sustained biological control of a pest which threatened to wipe out the most reliable staple food crop in Africa.

Natural enemies' phenology curves showed that the major role in control achieved so far was played by parasitoids, especially the introduced exotic parasitoid E. lopezi, judging from its predominance in samples expressed as per sampled tip densities.

Though the results were the first in-depth studies from the rainforest zone, they compare very well, apart from their exclusively low density levels, with those obtained with the same wasp in Nigeria (Herren and Lema, 1982; Odebiyi and Bokonon-Ganta, 1986; Hammond et al., 1987; Neuenschwander et al., 1988 and 1989), in Zaire (Hennessey and Muaka, 1987), and in Southern Ghana (Korang-Amoakoh et al., 1987).

The low percentage parasitism (rarely exceeding 30%), though low for a parasitoid proclaimed efficient, could mislead one to make erroneous conclusions, doubting its efficiency. However, previous experimental evaluations revealed that the parasitoid E. lopezi, also killed mealybugs by mutilation and host feeding (Neuenschwander and Madojemu, 1986). Host feeding, for example, in which mealybugs are utilised for adult nutrition

rather than reproduction, has been shown to contribute about 11-50% of all parasitoid-induced host mortality for a variety of hosts (Cate et al., 1973; Van Driesche and Taub, 1983) and may also occur in areas unsuitable for parasitism (Legner, 1977). Parasitoid-induced mortality may also include hosts that are paralysed but on which no oviposition occurs, or hosts that die from trauma after parasitoid oviposition (Legner, 1969). Hosts could also have their normal behaviour disrupted by adult parasitoids in such a way that they suffer higher mortality from predators or environmental conditions (Tamaki et al., 1970; Ruth et al., 1975).

The magnitude of any wasp-inflicted mortality, apart from active parasitism, was not assessable in the field and, judging from the low mealybug levels observed in the field study, it could only be speculated that it was considerable under field conditions. The high searching efficiency, coupled with high mobility of E. lopezi could be exploited to the maximum, hence low host densities (Hammond et al., 1987).

An overwhelming density-dependent relationship between natural enemies and cassava mealybugs, considered crucial in biological control (Hassell, 1978, 1980; Hogarth and Diamond, 1984), could not be detected with the erratic phenological curves. The non-detection, if it existed, could be due to the inclusion of large numbers of tips without mealybugs and natural enemies in samples during the calculation of field means which were used for plotting the phenological curves. However, non-detection of a positive density-dependent relationship should not be a criterion for refuting a successful control (Hassell, 1985; Murdoch et al., 1985; Dempster and Pollard, 1986).

In very isolated cases, relatively higher mealybug densities were observed on very poor sandy soils in West Africa (Neuenschwander et al., 1989; Kyei-Antwi, Afram plains in Ghana; personal communication) and for man-induced factors such as high dosage chemical control of variegated grasshoppers (Zonocerus variegatus L) on cassava, which resulted in killing most natural enemies. Also bad and unacceptable farming practices such as growing cassava continuously on the same piece of land for ten or more years resulted in outbreaks of mealybugs. These examples cited were exceptions but not the rule and in most cases the parasitoid recolonised severely attacked fields once the chemical sprayings were stopped. Chemical exclusion experiments presented in Chapter 5 of this thesis further show the impact of chemicals on natural enemies.

Ant attendance of cassava mealybugs was relatively important in the rainforest zone, though mealybug densities were low. Natural rainfall exerted a mechanical impact on mealybug densities as shown by negative slopes of regressions for all locations with increasing rainfall intensities.

CHAPTER 3

NUMERICAL RELATIONSHIP BETWEEN THE EXOTIC PARASITOID EPIDINOCARSIS LOPEZI DE SANTIS, HYPERPARASITIDS, LOCAL PREDATORS AND CASSAVA MEALYBUGS, PHENOCOCCUS MANIHOTI MAT-FERR.

3.0 ABSTRACT

Numerical relationships between cassava mealybugs, the exotic parasitoid, indigenous hyperparasitoids and local predators were studied on individual infested tips instead of field means which usually included large ^{numbers of} uninfested tips. Analysis of data from four fields involving 3368 tips for detection of density-dependence was done with the statview program of an Apple Macintosh computer.

The existence of positive density-dependence between mealybugs and the exotic parasitoid E. lopezi at host densities of 1-39.8 per tip was detected. Inverse density-dependent relationships at higher mealybug densities, i.e. above 39.8 per tip was also observed in relation to the exotic parasitoid. Presence:absence data of the parasitoid on tips also showed a positive density-dependent relationship. Predators also showed a slow response to numerical increases in mealybugs but a positive relationship. Positive density-dependence was also observed between mummies of parasitoids and emerged hyperparasitoids.

The mealybug-exotic parasitoid numerical relationship was placed in between two extremes of population regulation theories or models but fitted well in a domed response which accounted for 4% of 51 cases reviewed by Lessells (1985).

3.1 INTRODUCTION

The effectiveness of natural enemies in biological pest control is explained through several attributes. Some of these attributes are their adaptability to a new environment, searching efficiency, reproductive capacity, synchronisation of their phenologies to those of their hosts or prey and eventually the permanent reduction of pest densities below economic damaging levels following their release (Stern et al., 1959; Legner, 1969).

Several methods or techniques have been used or recommended for

assessing efficiencies of natural enemies. Some of the techniques are exclusion experiments (Hodek et al., 1972; Franz, 1973; Kiritani and Dempster, 1973; van Lenteren, 1980) and population dynamic studies, as well as, theoretically, simulation models for predictions.

Some of these methods have been used to assess the efficiency of the exotic parasitoid, Epidinocarsis lopezi de Santis and local predators in the biological control of cassava mealybug Phenacoccus manihoti Mat.-Ferr. in Africa. Neuenschwander et al. (1986) showed the ability of the exotic parasitoid to reduce population levels of mealybugs by about 7-100 fold. Hammond et al. (1987) showed the efficiency of the wasp in Nigeria through population dynamic studies. Data on the mealybug, predators, parasitoids and cassava plant interactions were incorporated into simulation models which also showed the efficiency of E. lopezi (Nwanze et al., 1979; Nsiama She et al., 1984; Boussienguet, 1986; Le Ru and Papierok, 1986; Schulthess et al., 1987; Guitierrez et al., 1987).

Attempts have been made to explain the mechanism of natural enemy efficiencies in reducing pest population levels through theories and hypotheses.

Positive density-dependent relationships between natural enemies and their hosts are considered crucial in population regulation (Hassell and May, 1973; Hassell, 1980; Hogarth and Diamond, 1984). On the other hand it is suggested that regulation of pest population could be achieved without the detection of positive density dependence (Hassell, 1985). Also, inverse density-dependent processes, such as aggregation of parasitoids independent of host density (Reeve and Murdoch, 1985) and local extinction of sub-populations of the host caused by parasitism (Murdoch et al., 1985) may lead to successful control.

A synthesis of nearly all the above theories was also considered (May and Hassell, 1988).

The aim of the analysis presented here is to relate population data from the rainforest zone to the different theories and suggestions of population regulation mechanisms briefly discussed above.

3.2 MATERIALS AND METHODS

The difficulty in detecting density-dependence by alternating mean

percentage parasitism with host densities in Chapter 2 coupled with the strong aggregation index of mealybugs judged by Taylor's (1961) power law in Chapter 8 suggest the need to evaluate numerical relationships on an individual infested tip basis, thus excluding many uninfested tips which may not be visited by an efficient host-searching parasitoid such as E. lopezi.

Individual mealybug infested tips data from four fields totalling 3,368 were entered and analysed on the "Statview" program of an Apple Macintosh computer.

Total mealybugs plus mummies per tip were log transformed. Percentage parasitism was calculated for each tip by the conventional method and then arcsin \sqrt{p} transformed. Log transformed densities per tip were regressed against arcsin \sqrt{p} transformed rates of parasitism.

For the evaluation of numerical relationships between mealybugs, predators, mummies of parasitoids and hyperparasitoids, each of them was log transformed and regressed against log mealybug densities plus mummies. Data based on presence-absence of E. lopezi on tips was also related to mealybug densities. Tips in each category and cumulative data of tips in each category of host densities were related to averages in density ranges of mealybugs.

For statistical analysis, slopes of regression lines, t values of slopes and r^2 values were tested for significance.

3.3 RESULTS

Density-dependent relationships were detected between mealybugs and natural enemies. Figs. 3.1A, B, & C show density-dependence with both percentage parasitism and presence-absence data^(Fig. 3.1D) for the exotic parasitoid plus its local hyperparasitoids. Fig. 3.1A is a relationship of arcsin \sqrt{p} transformed parasitism and mealybug plus mummy densities with the best fitted polynomial curve. Each point on the graph represents percentage parasitism on one tip. Dark regions are repeated observations. Rates of parasitism increased to a maximum then steeply dropped to the minimum at higher mealybug densities though simple linear regression gave an overall negative slope ($N = 3366$, $b = -8.67$, $t_b = 14.02^{**}$, $r^2 = 0.06$, $P \leq 0.05$) (Fig. 3.2), but polynomial regression showed a dome response (Fig. 3.1C).

Fig. 3.1 Density-dependent relationship between the parasitoid E. lopezi and its cassava mealybug host. Percentage tips in category (frequency and cumulative), as a function of average mealybug densities (A), percentage tips with parasitoids as a function of average mealybug densities including mummies (B) and arcsin \sqrt{p} transformed (percent parasitism) as a function of mealybug (II-IV+mummy densities) on individual tips described by 2nd order polynomial regression^(c) for N = 3668 tips

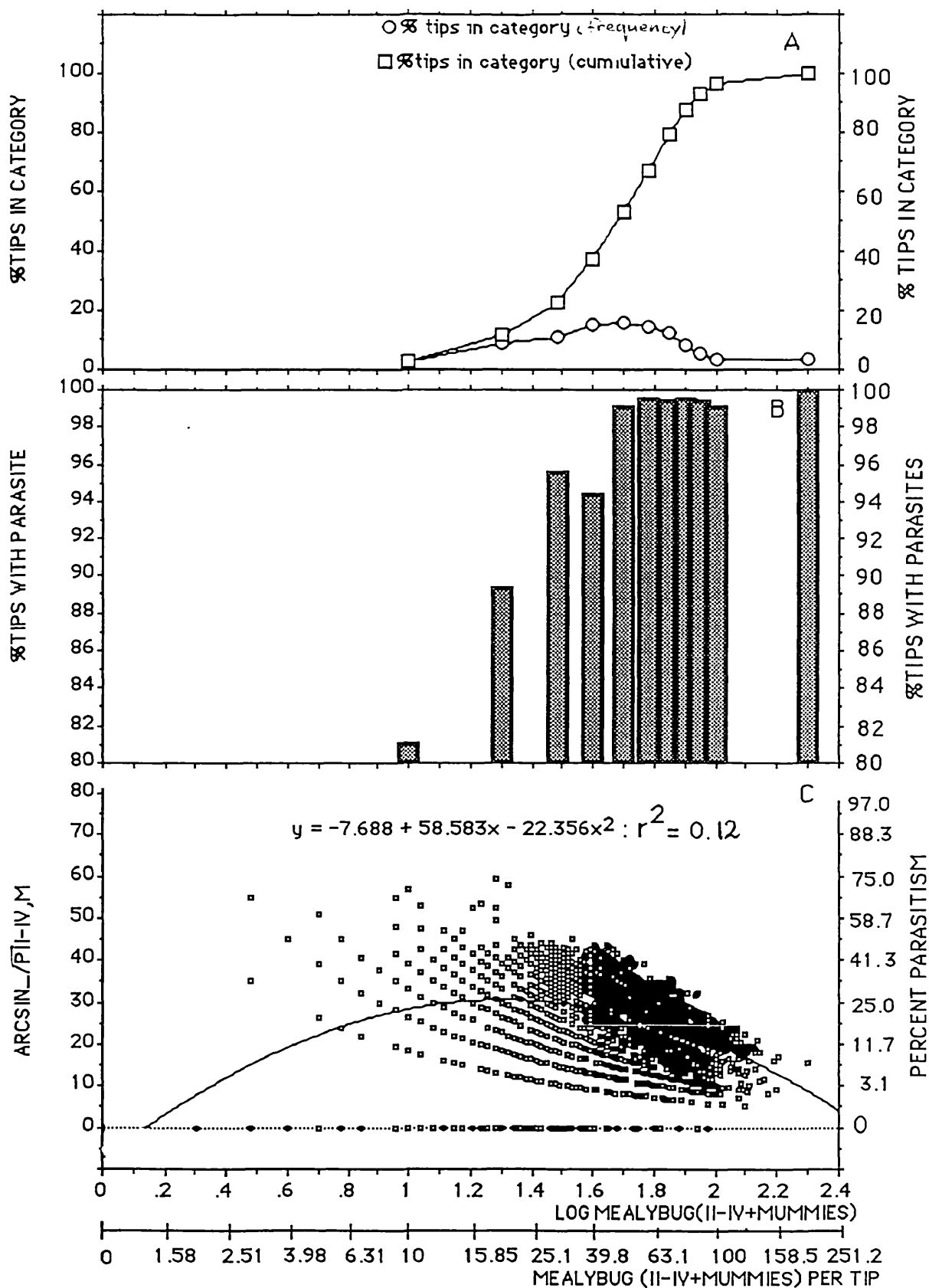


Fig. 3.2 Density-dependent relationship analysis between the parasitoid E. lopezi and cassava mealybug host. Percentage parasitism ($\arcsin \sqrt{p}$ transformed) calculated from all hosts and parasitoids of a particular infestation class (half shaded circles for positive density-dependent relationship and unshaded circles represent inverse-density relationship) (A) individual tip densities showing positive relationship up to approximately 40 mealybugs per tip (B) and inverse relationship with individual tip data in (C) in simple linear regressions

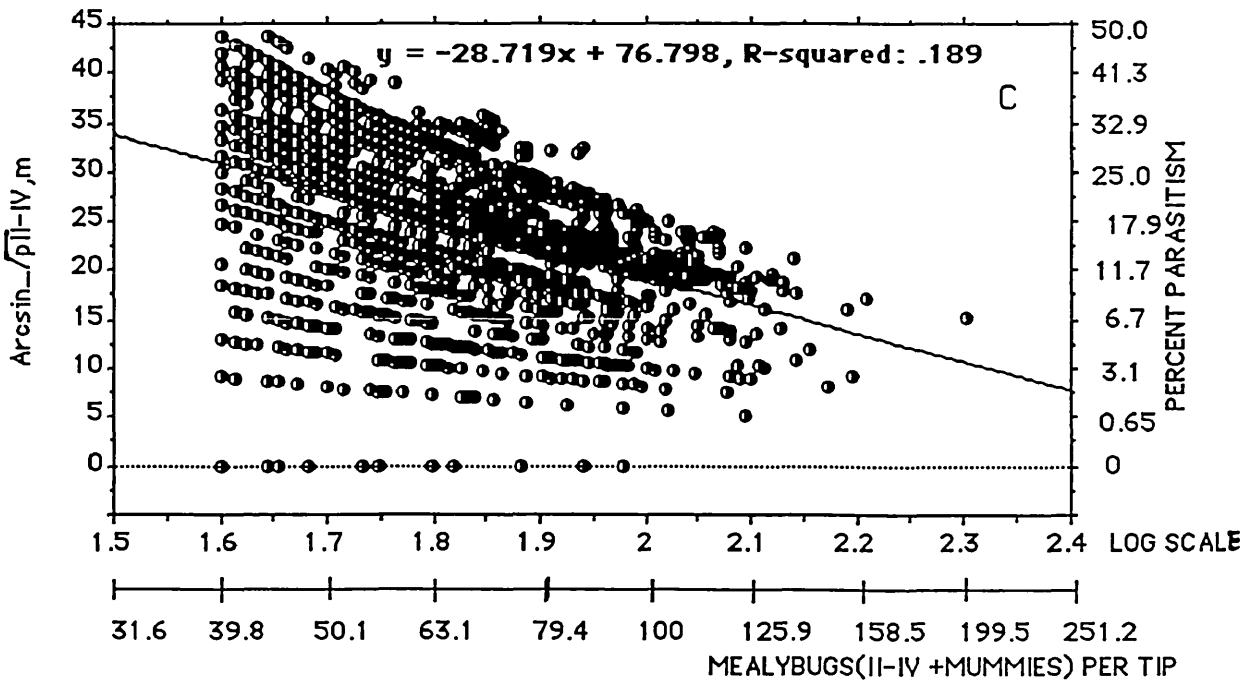
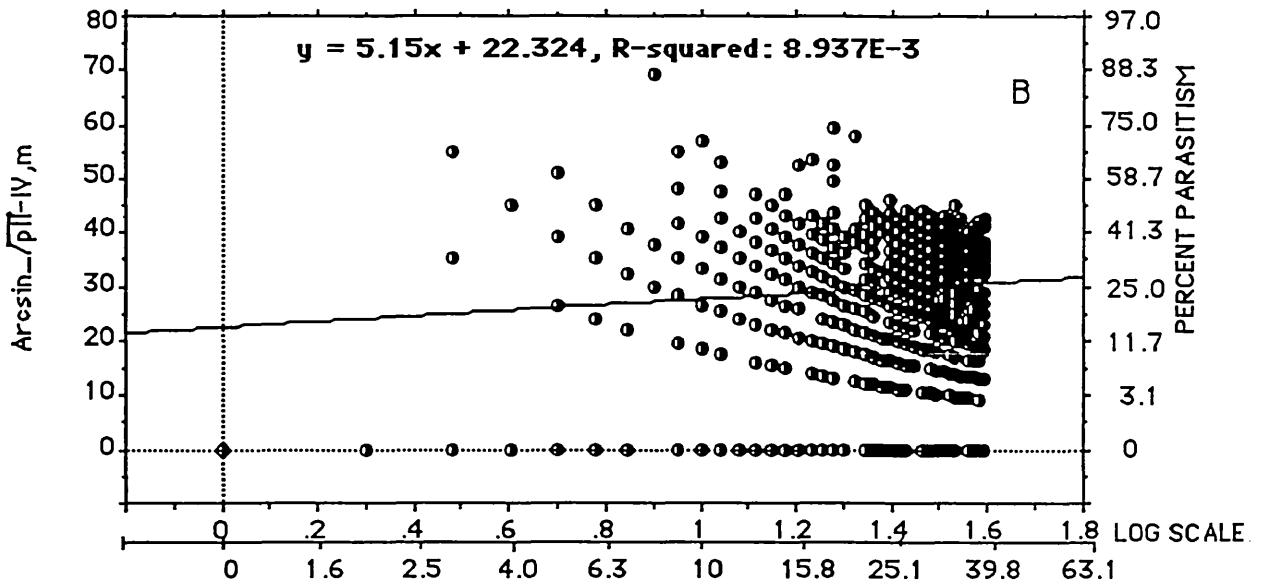
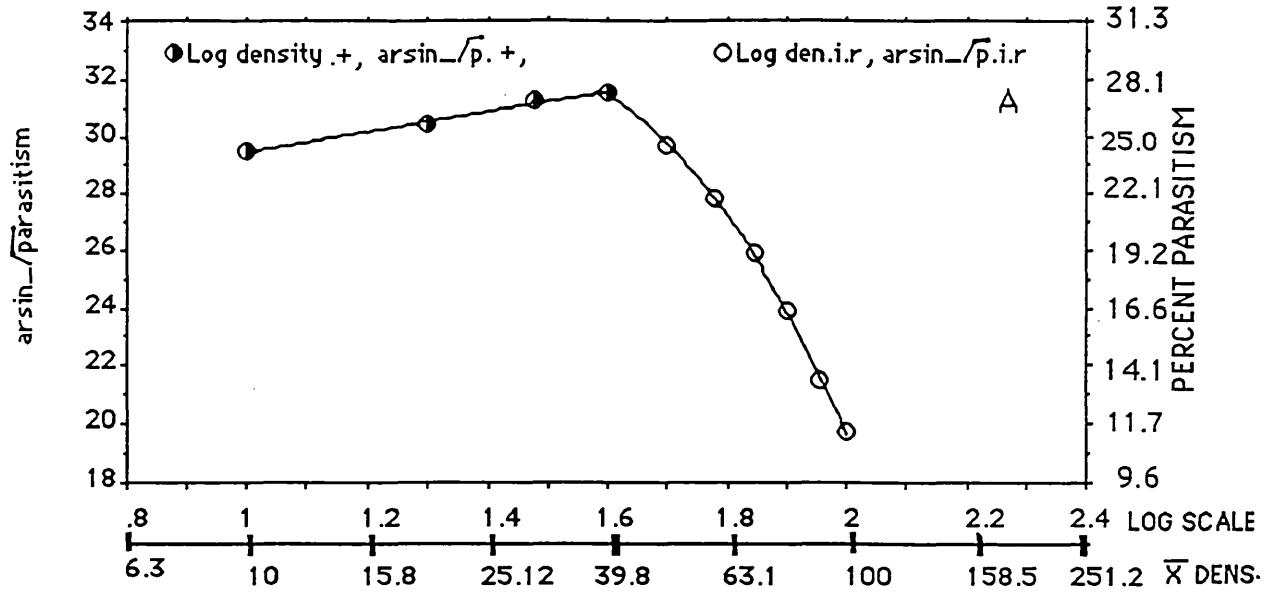


Fig. 3.3 Numerical relationships between natural enemies and cassava mealybugs. Total mummies as a function of mealybug densities in a 2nd order polynomial (A) and densities of predators as a function of mealybug densities in a 2nd order polynomial regression (B). 2nd order polynomial gave better fits by showing superior R^2 values as against linear regression for the relationship

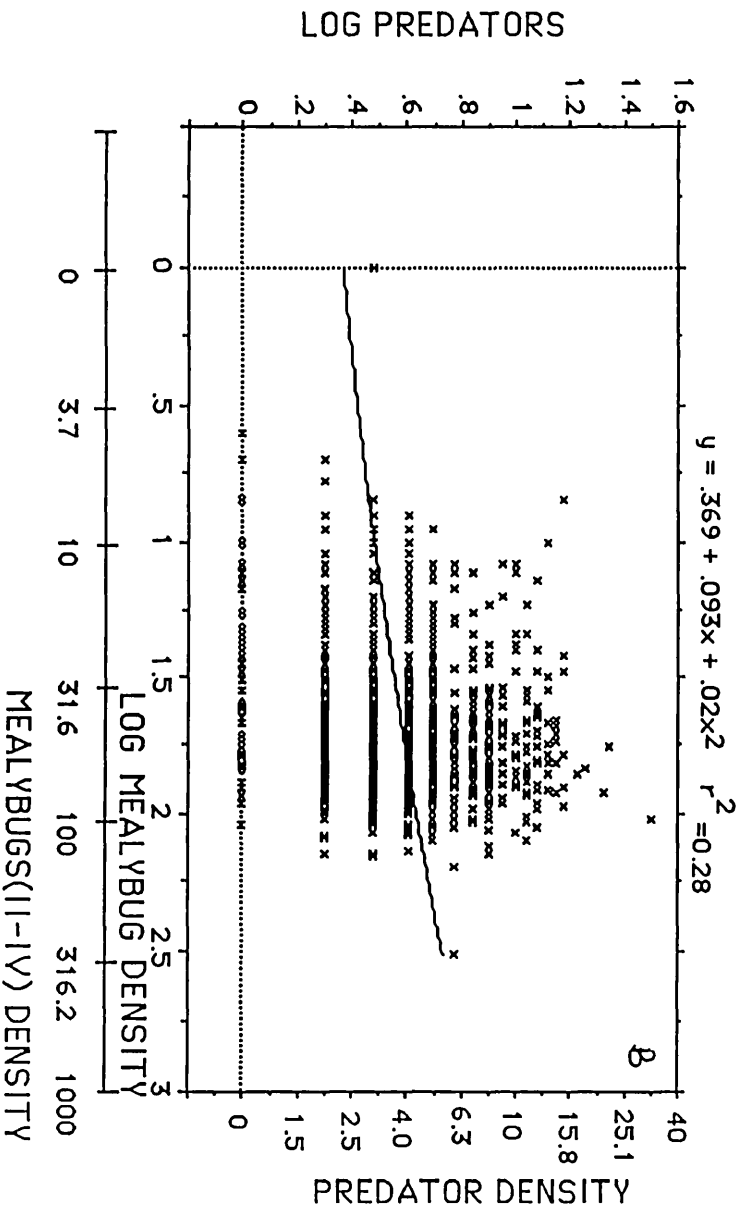
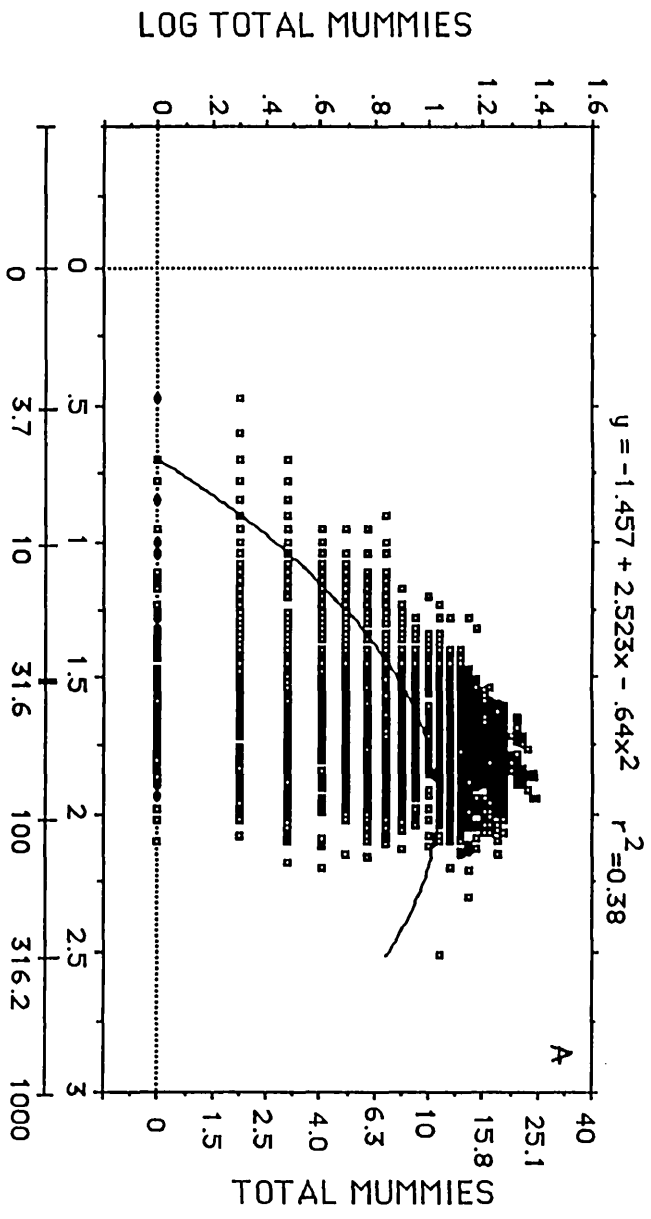
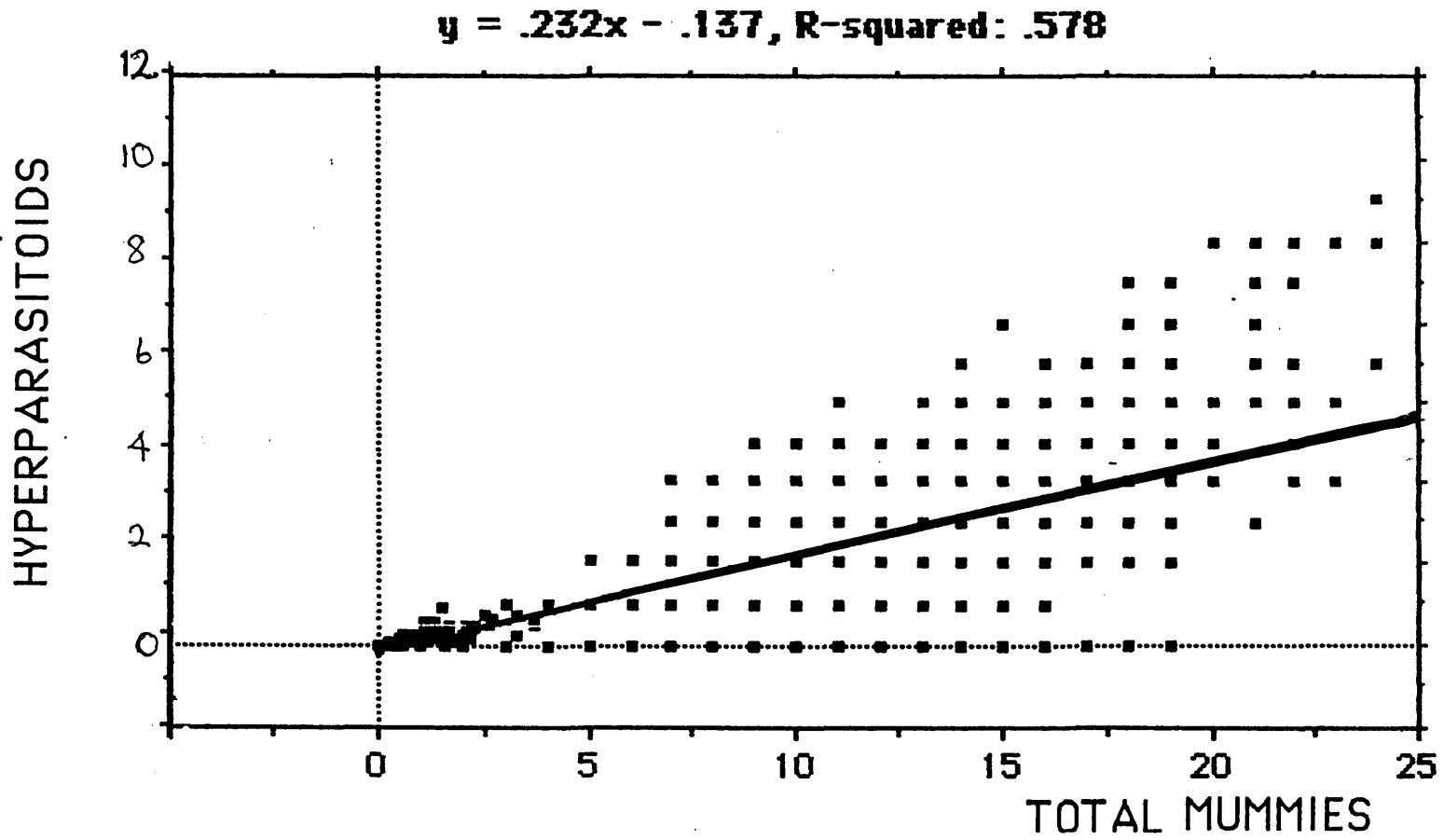


Fig. 3.4 Numerical relationship between mummies of parasitoids and their hyperparasitoids in a simple linear regression



When mealybug plus mummy densities were restricted to ranges of 10 interval classes or from 0-log 1.6 and 1.6-2.4 and regressed against $\arcsin \sqrt{p}$ rates of parasitism, two distinct portions of a fitted curve were obtained, one showing a positive slope, and the other an inverse relationship (Fig. 3.2A, B, C). There was an increase in rates of parasitism from average mealybug densities of $\bar{X} = 1$, corresponding to $22.32 \arcsin \sqrt{p} = (14.4\% \text{ parasitism})$ to $32.5 \arcsin \sqrt{p} (\approx 29\% \text{ parasitism})$ at log 1.6 mealybug densities ($\bar{X} = 39.8$ per tip) ($N = 1197$, $b = 5.15$, $t_b = 3.3$, $P \leq 0.001$). At higher densities above log 1.6 ($\bar{X} = 39.8$ per tip) there was a sharp fall in rates of parasitism indicating an inverse relationship ($N = 2167$, $b = -28.72$, $t_b = 22.44^{**}$, $r^2 = 0.19^*$) Fig. 3.2 A, B, C).

The presence-absence data for the same infestation classes as in Fig. 3.1B showed increases in the percentage of tips with parasitoids with increasing mealybug plus mummy densities. The inverse relationship observed at higher host densities with the rates of parasitism data was not detected with the presence-absence data (Fig. 3.1B).

The percentage of tips in each category of infestation showed an increase up to 20% with increases of mealybug plus mummy densities, after which it dropped steadily towards higher densities, whereas cumulative percentage tips in the category increased at higher host densities (Fig. 3.1A).

Log mummies and log mealybug densities also showed a positive response with a slope of $b = 2.52$, $t_b = 10.71^{**}$ (significant at $P \leq 0.01$, for $N = 3368$) (Fig. 3.3A).

The slope and t value of the regression of log predators against log mealybug plus mummy densities were also significant at $P < 0.05$ ($b = 0.093$, $t_b = 5.98^*$, $N = 3368$). Hyperparasitoids showed numerical response in relation to mummy densities ($b = 0.232$, $t_b = 67.91^{***}$, $r^2 = 0.57$, significant at $P \leq 0.001$, $N = 3368$) (Fig. 3.4).

For the whole study period cassava mealybugs (II - IV stages) on per tip basis never exceeded 323, mummies of parasitoids were never above 25 per tip, predators were 22 as maximum number per tip and fungi, 25 per tip maximum. A maximum of 70 ants per tip was also recorded (Table 3.1).

Table 3.1 Pooled data for all locations on CM-associated fauna numerical relationships

Insects & fungi	Sum of insects or fungi	Mean per tip	Standard error	Minimum count	Maximum count
Cassava mealybug (stages 2-4)	171,641	50.98	0.44	1	323
Mummies of parasitoids	33,621	9.90	0.10	0	25
Predators	5,597	1.70	0.05	0	22
Ants	17,552	5.21	0.11	0	70
Fungi	2,823	0.84	0.03	0	25

3.4 DISCUSSION

It is suggested that the difficulty in detecting a density-dependent relationship between natural enemies, especially E. lopezi and the cassava mealybug, with field means is overcome by individual tip data (Hammond and Neuenschwander, 1989).

The parasitoid does not need the numerous uninfested tips from which field means are calculated. It probably needs only infested tips to judge host densities for an appropriate response. With very high aggregation indices according to Taylor's (1961) power law for mealybugs (Schulthess et al., 1989, in this thesis Chapter 8) and for the parasitoid (Hammond et al., 1988), field means of host densities blur the detection of density-dependence.

E. lopezi showed both positive and inverse density-dependent relationships with cassava mealybugs. Host densities up to about 40 per tip attracted a positive numerical response from the wasp, whereas higher densities showed an inverse relationship (a domed response). Predators and hyperparasitoids also showed a continuous positive density-dependent relationship to mealybugs.

However, the fact that E. lopezi showed both positive and inverse density-dependent relationship to mealybug densities, does not fit directly into any of the extreme population regulation theories, hypothesis or suggestions.

It rather falls between two systems: positive density-dependence, fitting the Hassell and May (1973), Waage (1983) and Hogarth and Diamond (1984) models; and inverse density dependence, which fits the Murdoch et al. (1985) or Hassell's (1984) model, where inverse density-dependence is stabilising or the absence of positive density-dependence results in population control.

In the May and Hassell (1988) concept of population regulation, a synthesis of theories suggests that on ^{the} one hand combined functional and numerical responses of parasitoids would be of major importance, and on the other hand local extinction of hosts and parasitoids within patches would be the most important feature for pest control. Localised host aggregations may be detected by parasitoids with higher probability than less dense patches and suppressed before significant numerical increases occur. Low density patches may have a low probability of detection by

the parasitoids and therefore act as refugia for the host. Refugia can stabilize the interactions between parasitoid and host populations (Hassell, 1978). On the other hand, if parasitoids are able to find and exploit low density patches, local extinction of the host may result.

A direct functional relationship between parasitoid aggregation and host density, resulting in a direct density-dependent regulation was found by Summy et al., (1985). In another study, a weak aggregative response without any evidence of density-dependence for parasitism was measured although successful biological control was achieved (Smith and Maezler, 1986). Most inferences about foraging in the field are drawn from observed patterns of parasitism in relation to host density (Morrison and Strong, 1980; Hassell, 1980; Head and Lawton, 1983).

It is most appropriate to place the case study of the E. lopezi mealybug system in between the two extremes of May and Hassell (1988) synthesis. On the other hand, the mealybug-parasitoid interaction directly fits into the 4% domed response out of the 51 reviewed cases by Lessell (1985).

It is, however, suggested that the three trophic levels of cassava, mealybug and natural enemies interact in complex ways and need to be understood as a unit rather than pairwise comparison of only host and natural enemies (Price et al., 1980; Price and Clancy, 1986a). According to Thompson (1982, 1986a,b), the three trophic level interactions represent evolutionary units. Therefore, the answer to the question as to why parasitoids or predators should respond to host populations in a certain manner could be provided by a functional ecological study of the units and the evolutionary forces that shape them.

3.5 CONCLUSION

The individual cassava mealybug infested tips (totalling 3,368) showed a positive density-dependent and inverse density-dependent relationship between parasitoids and cassava mealybugs.

At host densities not exceeding 40 per tip the exotic parasitoid showed a positive density-dependent relationship. But at higher densities (above 40 per tip) an inverse density dependent relationship was shown by the same parasitoid. Predators and hyperparasitoids showed a direct positive density-dependent relationship with their hosts. Local

hyperparasitoids were therefore less likely to offset the control programme.

In a nutshell, the prevailing cassava mealybug densities suggest a sustained biological control with parasitoids, especially E. lopezi and local natural enemies.

CHAPTER 4

FOOD WEB, RELATIVE IMPORTANCE AND SEASONAL ABUNDANCE OF THE MOST
IMPORTANT FAUNA ASSOCIATED WITH CASSAVA MEALYBUG IN THE RAINFOREST
ZONE OF GHANA

4.0 ABSTRACT

Numerical abundance, species composition, and seasonal changes and importance of fauna associated with the cassava mealybug were studied at three locations in the rainforest for two years. A food web based on the food habits of the most important groups was constructed.

The predominance of the exotic parasitoid, Epidinocarsis lopezi De Santis and its local hyperparasitoids was overwhelming (accounting for nearly 80% of all fauna encountered in samples). In comparison, local predators constituted a low level of abundance (up to 20% of all fauna encountered). Coccinellid predators, e.g. Exochomus spp were the most important predators. Species ^{of insects} were numerically abundant during late dry and early rainy seasons when mealybug populations reached their peaks.

4.1 INTRODUCTION

Before the accidental introduction of the destructive exotic pests, the Cassava Mealybug (Phenacoccus manihoti Mat.-Ferr and Green Spider Mite, Mononychellus tanajoa Bondar sensu lato, into Africa, cassava Manihot esculenta Crantz (Euphorbiaceae), had relatively few insect pests or fauna associated with it.

The most important insect pests on cassava were the indigenous and cosmopolitan variegated grasshoppers Zonocerus variegatus L (Orthoptera: Acrididae) and two indigenous mealybugs, Ferrisia virgata Cockerell and Phenacoccus madeirensis Green. A few ants were occasional visitors to cassava, probably to collect ^{from} interfloral nectaries or hunt for prey.

With the exception of grasshoppers, no visible damage (e.g. bunch top) was inflicted on cassava by the indigenous mealybug.

The exotic mealybug, since the 1970s, has spread and inflicted severe damage (root and leaf losses) on cassava (Fabres and Boussienguet, 1981; Nwanze, 1982; Herren and Lema, 1982; and Herren et al., 1983).

90

The new pest introduction saw a rapid increase in abundance and complexity of arthropod fauna on cassava and more so after the introduction of the exotic parasitoid Epidinocarsis lopezi De Santis for biological control. The astonishing rate of multiplication and spread of the parasitoid meant more places were colonised resulting in dynamic changes of fauna associated with the wasp and the host, cassava mealybug.

The aim of this study is to trace the food web, species involved, their relative importance and changes in abundance according to the seasons in the low cassava mealybug populated rainforest zone of Ghana, where in-depth studies have not been carried out previously.

4.2 MATERIALS AND METHODS

To assess the composition of fauna associated with the cassava mealybug in the rainforest, three large fields of cassava each at Koforidua, New Tafo and Begoro, were sampled once monthly for two years. Sampling of chosen fields involved the collection of 10 severely infested tips at regular intervals along one of the transect lines across the field in arbitrarily chosen directions referenced to trees on the horizon. When ten bunch tops or severely infested tips could not be found by this method, the rest of the field was searched for severely infested tips which were collected when and as encountered. Tips were collected by carefully breaking them over an open sampling paper bag so that adult insects could not escape. Each set of ten tips in sealed sampling paper bags were taken to the laboratory where active adults of identifiable insects were removed and counted. The samples were then rebagged after getting rid of spiders, sealed and stored at 20°C–30°C (room temperature) for 3–4 weeks to allow total development and emergence of maturing insect larvae and pupae. The emerged adults were also identified and counted.

Additionally or concurrently ten representative samples were taken from the same field by the same method to estimate mealybug densities by accurate counts under a binocular microscope.

4.2.1 Analysis

The relative abundance of any species or group of insects was expressed as a proportion of species or groups reared from tips to the

total of all species or groups from those tips over the same period.

The total number of insects reared from ten tips (adjusted if less than ten tips were heavily infested in the field) was a measure of abundance of this insect on the tips. Zero values were excluded and the estimate presented here was only for those fields where the insect was recorded.

Mummies and predators on tips could not be removed and reared individually in gelatin capsules, except in small experiments to determine average number of emergence per host in order to adjust numbers for gregarious hyperparasitoids, i.e. two for Chartocerus and five Metastenus sp from one Coccinellid predator parasitised.

Mealybug densities calculated from ten infested tips sampled concurrently were used as a baseline information on general population levels in fields since this could not be extracted from tips without dissection. This was not possible with tips for faunal studies because dissection could destroy a lot of the fauna in their immature stages.

The diagrammatic food web of fauna was constructed on the basis of their food habits.

For a general picture of relative abundance of species, numbers of encountered insects were pooled for the whole rainforest zone and study period.

4.3 RESULTS

4.3.1 Food web of species of fauna on cassava

The food web in Fig. 4.1, shows insect species and predators depending on one another for their source of food or for reproduction.

Mealybugs and other homopterans which feed directly on cassava (the producers) are in turn fed on or used for reproduction by predators and parasitoids. Predators have their parasitoids whereas primary parasitoids have their hyperparasitoids. Ants and saprophages, on the sideline, either derive their food source by attending mealybugs and homopterans or prey on living and dead mealybugs. Parasitoids of predators and hyperparasitoids of primary parasitoids are in turn parasitised by other insects. Each of the groups is put in its own trophic level. The most important species in each group are cited, where

Fig. 4.1 Food web of fauna associated with the cassava mealybug in the rainforest zone in Ghana. Fauna arranged in trophic levels according to food habits

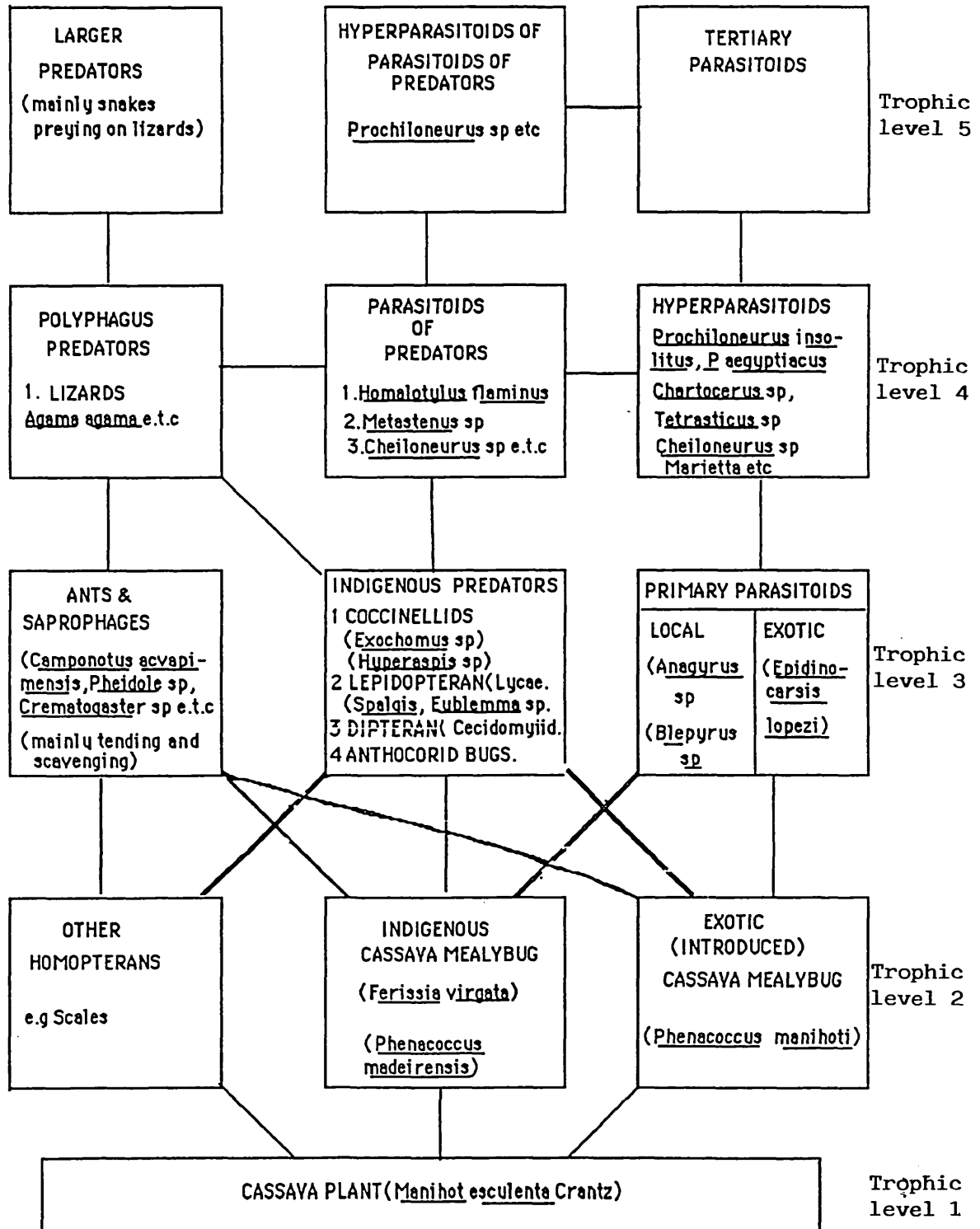


Table 4.1 Relative importance (%) of fauna associated with cassava mealybugs

Fauna	Koforidua	Locality New Tafo	Begoro
Total bunch tops reared	220	220	220
*No of predators & parasites	2598	2626	2513
Fauna per bunch top	11.8±1.7	11.9±1.9	11.4±1.5
**Estimated CM density (average±se)	35.3±2.6	38.7±2.1	32.7±1.8
Primary parasitoids (%)	54.8	51.6	50.3
Hyperparasitoids (%)	15.7	19.3	16.7
Predators (all) (%)	17.4	23.5	18.1
Parasites of predators (%)	3.1	2.7	4.2
All others (%)	9.0	2.9	10.7
TOTAL (%)	100.0	100.0	100.0

* Counts after rearing tips

** Counts on dissection of concurrently sampled tips

Fig. 4.2 Total numbers of species of insects associated with the cassava mealybugs in the rainforest of Ghana ($N=760$ tips)

SPECIES

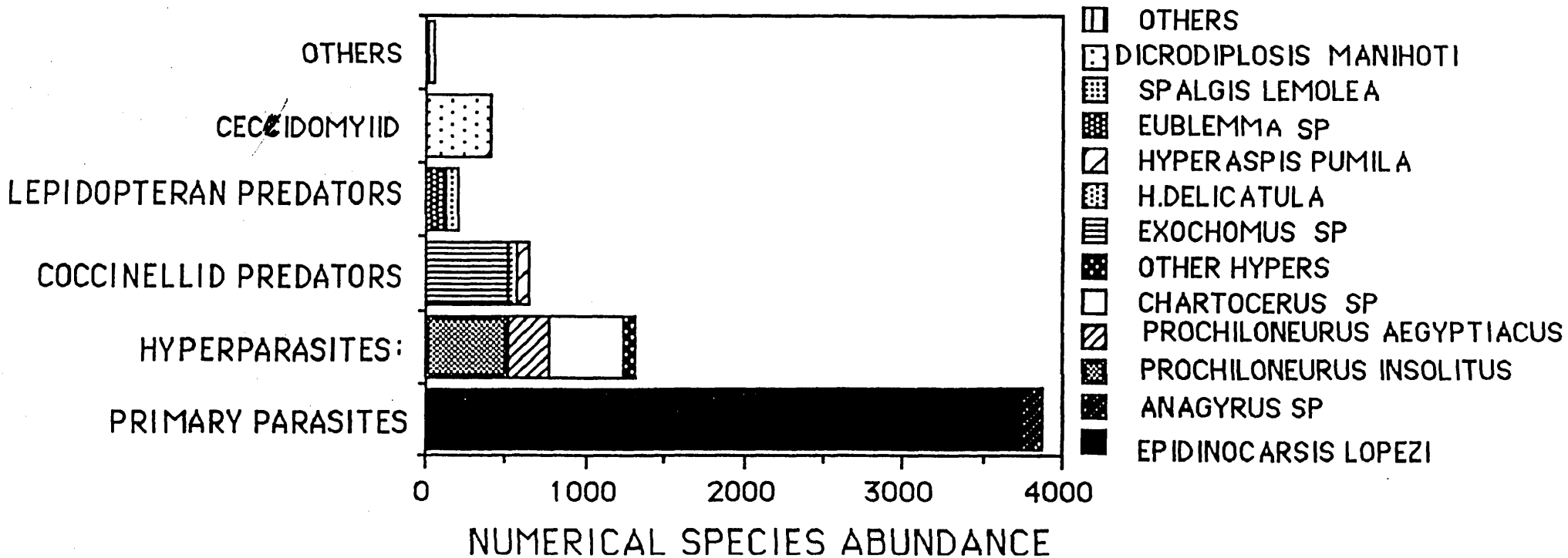
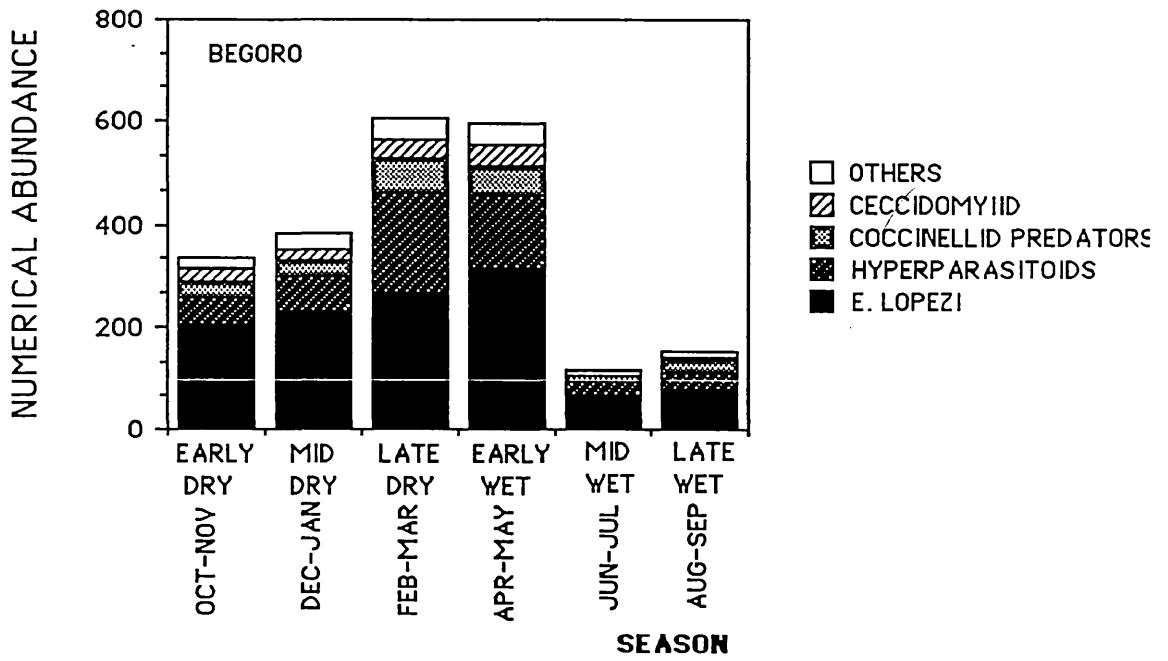
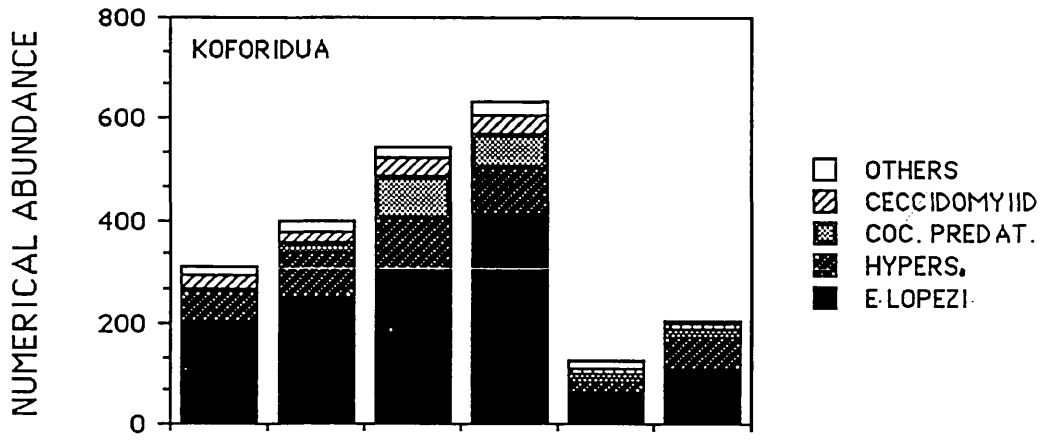
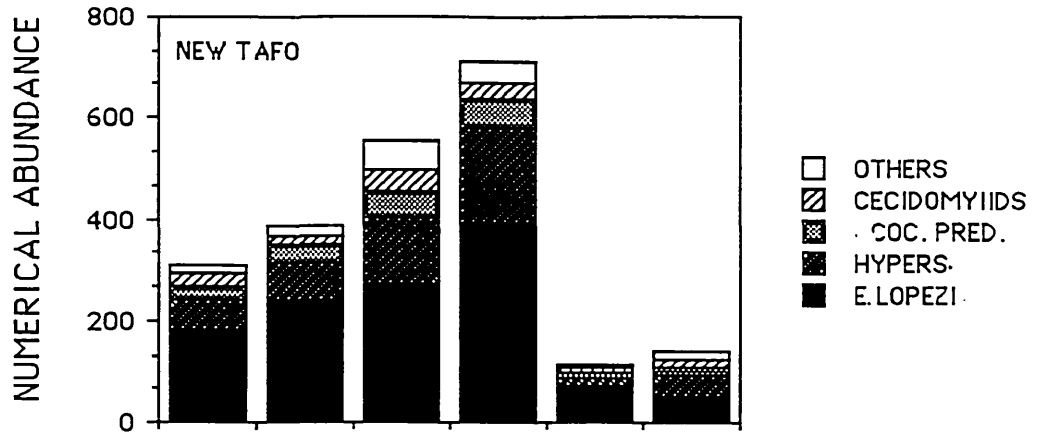


Fig. 4.3 Seasonal abundance of groups of insects associated with cassava mealybugs in the rainforest zone in Ghana



possible. Many more insect species may be involved in the food web but the study was confined to those usually encountered.

4.3.2 Relative importance of groups of fauna on cassava associated with mealybugs

Primary parasitoids were the most important group, accounting for over 50% of all reared fauna on cassava tips with mealybugs in all three locations. The local hyperparasitoids of primary parasitoids (E. lopezi and Anagyrus spp) accounted for up to 19.3% of total fauna. The two groups together accounted for nearly 80% of all insects on cassava. Predators and their parasitoids were only up to 20% (26.2% as upper limit). Saprophages and other less important groups (excluding ants) accounted for a small percentage (not exceeding 5%) of all fauna encountered on tips.

A cursory examination of the data suggested no important differences between locations and therefore did not warrant a comparison on the basis of location. Average mealybug densities also did not differ very much between locations (Table 4.1).

4.3.3 Individual species abundance and relative importance of natural enemies of mealybugs from pooled data for all locations in the rainforest

a. Primary parasitoids. The exotic parasitoid, Epidinocarsis lopezi De Santis accounted for about 94% of the two primary parasitoids encountered (3575 out of 3819, reared from 760 heavily infested tips). Anagyrus spp. accounted for only 6% of all primary parasitoids (Fig. 4.2).

Blepyrus insularis Cameron was occasionally found in samples but this came exclusively from other mealybugs which were also on those tips collected for rearing, e.g. from Ferrisia virgata Cockerell and Phenacoccus madeirensis Green.

b. Hyperparasitoids. From samples Prochiloneurus insolitus Alam. was the most common among the nearly ten indigenous hyperparasitoid which transferred to E. lopezi (> 50%). The gregarious signiphorid Chartocerus spp. was the next most abundant hyperparasitoid accounting for nearly 42% of all encounters. The rather poor third position of

relative importance was shared between Prochiloneurus aegyptiacus (Mercet) and Tetrasticus spp (<5%). All other hyperparasitoids accounted for less than 1% of the group.

c. Coccinellid predators. This was the biggest group among predators. Exochomus flavipes Thunberg was the commonest among coccinellids. Two other coccinellids were encountered in small numbers in the samples. These were Hyperaspis delicatula Mulsant and H. pumila Mulsant. Many tiny coccinellids, Nephus sp were encountered patchily, probably from indigenous mealybugs on the same tips as the cassava mealybug.

d. Dipteran predators. The only important dipteran predator worthy of consideration was the cecidomyiid, Dicrodiplosis manihoti Harris. It was the next most important predator to Exochomus sp.

e. Lepidopteran predators. A considerably richer group of species were encountered in samples for this group. Numerically, they were only inferior to the already mentioned groups. However, the obligatory lycaenid ^{predator} (monkey face pupa), Spalgis lemolea Druce and Eublemma sp. are worthy of mentioning because on individual tips of some samples their numbers were substantial though they had an erratic distribution.

f. All other insects. Other predators, mainly Hemiptera (Anthocorid Bugs) and Neuroptera (Chrysopidae) were very uncommon.

Parasitoids of coccinellids, Homalotylus flaminus Dalman and gregarious Metastenus sp were found in low numbers in samples.

4.3.4 Seasonal abundance of fauna from pooled data for all locations in the rainforest zone

Fig. 4.3 shows the total of fauna associated with cassava mealybug at New Tafo, Koforidua and Begoro during wet and dry seasons divided into early, mid and late seasons. Peaks of abundance of insects occurred between the late dry and early wet seasons (i.e. between February and the end of May). Lowest fauna levels were recorded between mid and late wet seasons, which probably coincides with lowest mealybug densities. Early dry and mid dry seasons (i.e. October-January) showed insect numbers falling between the two extremes of highest and lowest numbers.

4.4 DISCUSSION

The inherent problem of getting enough specimens for quantitative analysis by the two weekly regular sampling method in low mealybug density rainforest zone was overcome by the adoption of a monthly regular sampling approach. When this failed to give adequate tips, an active (bias) search for bunched or heavily infested tips was used.

The food web showed a very diverse fauna association with cassava mealybug and its exotic parasitoid and supports or adds to earlier reports (Matile-Ferrero, 1977; Fabres and Matile-Ferrero, 1980; Bousienguet, 1986; Neuenschwander et al., 1987a). The introduction of E. lopezi diversified further the faunal association with mealybugs by the addition of extra guilds resulting from the presence of hyperparasitoids and tertiary parasitoids in contrast to the exclusive dominance of predators prior to the introduction of the wasp. It should be stressed that all the hyperparasitoids encountered were indigenous, presumably on indigenous parasitoids like Anagyrus sp but shifted to the new exotic parasitoid.

The overwhelming predominance of the exotic parasitoid in samples is a further testimony to its important role in the reduction of cassava mealybug populations. This is also a measure of its efficiency as a biological control agent. The low proportion of hyperparasitoids in samples also testifies to the assumption that they are not likely to upset the control program.

Bousienguet (1986) found 47% hyperparasitism on two African Anagyrus spp which attack the new cassava mealybug in Gabon, but do not effectively control it. Zinna (1960) measured increasing hyperparasitism rates of up to 25% on Leptomastix dactylopii Howard, a parasitoid which effectively controls Planococcus citri Risso. Hyperparasitism on overwintering pupae of Clausenia purpurea Ishii by two generations of hyperparasitoids reached 90% and precluded efficient biological control of Pseudococcus comstocki Kuwana. Berlinger (1977) reported 29% hyperparasitism in a study of Planococcus vitis Niedielki. Bennett (1981) reviewed hyperparasitism in other systems where successful biological control was recorded. The density dependent behaviour reported in Chapter 3 of this thesis is likely to enhance the achievement of an equilibrium at low levels of mealybugs and E. lopezi with hyperparasitoids.

The shift in the composition of fauna from the previously dominant position of local predators especially the polyphagous indigenous coccinellids in favour of the exotic parasitoid and its hyperparasitoids is due to the drop in the abundance of mealybugs. Coccinellids have higher food requirements and will need higher host densities than do small hymenopterous parasitoids (Hagen and van den Bosch, 1968; Hagen, 1976).

The lower encounters with Hyperaspis spp could also be explained by the fact that even at higher host densities, they frequently resort to other sources of food. They have been observed feeding on nectaries of weeds (Lema, 1984), thus diminishing relative importance of local predators. This supports the simulation model in which it is suggested that in the presence of the parasitoids, the regulatory role of mealybugs by coccinellid predators is largely dispensable (Gutierrez et al., 1987).

The impact of parasitoids on coccinellid predators is estimated to be lower than has been reported elsewhere. The report that Metastenus sp reduced a population of Hyperaspis marmottani Muls (= H. pumila) in Eastern Nigeria was not observed with the low coccinellid and their parasitoid numbers. Homalotylus flaminus Dalman was also reported to parasitise Exochomus sp at 7-10% rate (Fabres and Matile-Ferrero). In Gabon, Boussienguet (1986) reported a 15-20% parasitism of Nephus sp on mealybugs by H. quaylei Timberlake.

The regulatory role played by other insects in the association with mealybugs under the conditions studied do not seem to be very competitive, probably due to the very low numbers encountered in samples.

4.5 CONCLUSION

The exotic parasitoid E. lopezi and its indigenous hyperparasitoids are the predominant insects associated with the cassava mealybug in the rainforest. Local predators feature in the food web but remain relatively low in numbers as compared with parasitoids. Insects associated with mealybugs are abundant during late dry and early rainy seasons.

CHAPTER 5

EXPERIMENTAL DETERMINATION OF THE EFFICIENCY OF NATURAL ENEMIES WITH
SPECIAL REFERENCE TO THE EXOTIC PARASITOID EPIDINOCARSIS LOPEZI DE SANTIS
THROUGH PHYSICAL AND CHEMICAL EXCLUSION

5.0 ABSTRACT

The efficiency of natural enemies, especially the exotic parasitoid, E. lopezi in the reduction of mealybug populations on cassava was studied through exclusion experiments.

Physical and chemical exclusion experiments proved beyond doubt the efficiency of E. lopezi and the coccinellid predator, Exochomus flavipes larvae. In the physical exclusion experiments, where sleeve cages were used, an increase of more than twenty-fold in mealybug numbers on tips with total exclusion of all natural enemies was observed when compared with open tips where access to mealybugs was allowed. In the chemical exclusion experiment, in which an insecticide was used to exclude all natural enemies, an increase in mealybug numbers was observed to occur every week continuously up to the 9th week when spraying was terminated. Significant differences between mean densities were observed with control where water was used.

However an attempt at evaluating the impact of individual natural enemies through their inclusion in some sleeve cages could not show very appreciable reductions in mealybug numbers under such artificial conditions.

5.1 INTRODUCTION

The reduction in pest numbers after the introduction of a natural enemy is a judgement of its effectiveness in a biological control program. One way of assessing a reduction or otherwise of pest numbers involves long-term population dynamic studies which could be slow and time-consuming.

There are also relatively quick methods of evaluation (Hodek et al., 1972; Kiritani and Dempster, 1973; van Lenteren, 1980). Some of the quick methods of evaluation are achieved through physical exclusion of parasitoids by use of sleeve cages (Smith and Debach, 1942) and an

insecticidal check method (Debach, 1946).

The exotic parasitoid, Epidinocarsis lopezi De Santis (Hymenoptera: Encyrtidae) was released in Ghana in 1984 and 1985 to control cassava mealybugs (Phenacoccus manihoti Mat. Ferr. (Homoptera: Pseudococcidae)). A year later it was confirmed established in large expanses of cassava fields and later on all over Ghana's cassava belt (Korang-Amoakoh et al., 1987; Neuenschwander et al., 1989).

Successful establishment of the wasp and a tremendous impact on mealybug populations have been observed in many African countries (Herren and Lema, 1983; Hammond et al., 1987; Neuenschwander and Hammond, 1988; Hennessey and Muaka, 1987). Establishment and positive impact by the wasp have also been observed but not quantified in many more countries with varied ecological zones in Africa.

The observed reduction in mealybug populations is generally attributed to the exotic parasitoid, although a few scientists also attribute the reduction to good rainfall patterns in the last few years (Fabres, 1981; Schulthess, 1987; Gutierrez et al., 1987; Biassangama et al., 1988; LeRu et al., 1989). Rain-induced mortality cannot be ruled out but the good rains did not stop the spread to new areas.

High mealybug densities in a few countries with exceptionally good rains but no wasp or late establishment of the wasp is another testimony to the impact of the wasp.

The effectiveness of the parasitoid has been evaluated in Nigeria through population dynamic studies (Hammond et al., 1987), exclusion experiments (Neuenschwander et al., 1987b) and a tritrophic computer simulation model (Gutierrez et al., 1988b).

Considering the fact that insect parasitoids could be efficient only in some ecological niches and inefficient in others (Debach et al., 1971), it was considered useful to evaluate the efficiency of the exotic parasitoid in the rainforest zone where very little is known about the interactions of the wasp with the host. A quick method of evaluation, exclusion method, was used to get the results presented in this chapter.

5.2 MATERIALS AND METHODS

Two types of exclusion experiments were conducted exclusively at

Koforidua in the heart of the rainforest. Physical exclusion (Smith and Debach, 1942) and chemical exclusion (Debach, 1946) were used to evaluate the efficiency of natural enemies, especially the exotic parasitoid, E. lopezi and the most important local predator, Exochomus flavipes larvae. Experiments were all conducted at the peak of the dry season of 1987/1988 as described below:

5.2.1 Physical exclusion and inclusion experiments

Sleeve cages measuring 40 cm x 20 cm and made of 0.8 mm plastic-mesh were used in a six-treatment experiment, each with twenty replicates (each tip representing a replicate).

Clean, non-infested cassava plants were selected at the beginning of the studies. The selected and tagged plants were then either not infested at all depending on the treatment as described below or artificially infested with mealybug ovisacs with eggs. The latter contained approximately 50 eggs showing dark "eyes" of crawlers which were expected to hatch the following morning. This guaranteed some degree of homogeneity in age in order to avoid probable variance arising from age difference.

1. Control Tips were tagged but not infested with mealybugs. Natural infestation by both mealybug and its natural enemies was allowed to occur under field conditions (no or minimum interference occurred).
2. No sleeve cages but tips artificially infested Tips were left open to natural enemies after infestation. Sleeve cages were not used at all.
3. Open sleeve cages but tips artificially infested Tips were enveloped in sleeve cages and artificially infested with mealybugs, but lower ends of sleeve cages were left open to allow entry of natural enemies with some restriction. Wires attached to the lower ends of cages and connected to nearby branches held them in an open position and gave secured anchorage against strong winds.
4. Total exclusion with sleeve cages Artificially mealybug infested tips were completely sealed off to natural enemies by tightening the lower ends of the cages with insulation tape. A sandwich of rubber foam between cassava branch and tape prevented the probable

phytotoxic effect of the tape on the plant.

5. Closed sleeve cage, artificially infested with mealybugs and inclusion of 2 female E. lopezi As in above treatment with the exception of the inclusion of 2 E. lopezi females 2.5 weeks approximately after artificial mealybug infestation of tips. The 2.5 weeks lapse was to enable mealybugs to reach higher stages (2-4) so that they were likely to be the suitable host of E. lopezi.
6. Closed sleeve cage, artificially infested with mealybugs and inclusion of local predator (Exochomus flavipes) larvae Same as above except with the inclusion of 2 larvae of the most important local predator after 2.5 weeks.

After 52 days all tips for each treatment were broken and dissected for mealybug counts. Means for the twenty replicates were calculated with standard deviations (s.d.). Bar charts were plotted and each treatment was compared with the control.

5.2.2 Chemical exclusion experiments

Almost concurrently with the physical exclusion experiments, 10 pockets per treatment of cassava plants were demarcated in a field a mile away for chemical exclusion of natural enemies.

Each pocket contained ten plants with only one tip each. Ten pockets were used for chemical exclusion and another ten used as a control.

1. Control The control involved the weekly spray of ordinary water on cassava of the ten pockets chosen. The water spray was meant to avoid variation which could have occurred due to artificial changes in microclimate and water stress on the control arising from the water used for the chemical treatment.
2. Chemical treatment The ten pockets for chemical treatment received a weekly spray of a chemical, "Decis" which contains the active ingredient deltamethrine at 1.2 g/litre and is recommended to be used at a dosage of 2.5 cm³/litre of water.

All spraying was done with a CP-15 knapsac spraying machine and was confined to the canopy of cassava plants. Prior to each spraying exercise mealybug stages 2-4 were counted in situ on all ten tips in a

pocket. Mean densities were calculated for each treatment. Due to large variations between densities in control and chemical treatment by the end of the 9th week of spraying, densities were $\text{Log}(\bar{x}+1)$ transformed and presented in bar charts. The means for mealybug densities were compared statistically (SNK-test) for untransformed data.

5.3 RESULTS

5.3.1 Physical exclusion and inclusion of natural enemies

The least of mealybug densities was recorded for the control in which no artificial infestation and no sleeve cages were used ($\text{Log}(\bar{x}+1) = 0.23$ corresponding to 1.7 per tip). The highest density was recorded in completely closed cages ($\text{Log}(\bar{x}+1) = 2.3$, corresponding to about 200 per tip. This density is about 130 times when compared with control. However when artificially infested tips were not enclosed in sleeve cages densities of mealybugs differed only slightly but not significantly from control (only 1.3 times; $\text{Log}(\bar{x}+1) = 0.34$ as against $\text{Log}(\bar{x}+1) = 0.23$, corresponding to 2.2 and 1.7 per tip respectively). Differences were statistically significant at $P \leq 0.05$ between control and variants 4, 5 and 6 (see Appendix F).

In the treatment, where sleeve cages were open, thus allowing entry of the most efficient host-searching natural enemy, mealybug densities were 27 times lower than closed sleeve where exclusion was complete, but 5 times higher than control. Differences were highly significant at $P \leq 0.05$ level (Fig. 5.1) (see one factor ANOVA and SNK-test in Appendix F).

The above differences in densities of mealybugs show convincingly that natural enemies have a positive regulatory impact on mealybug populations.

However, the inclusion of individual species of natural enemies did not produce larger differences in mealybug densities, when compared with closed sleeve density. There were only decreases of 3 times and 1.7 times for inclusion of E. lopezi and coccinellid larvae in sleeve cages respectively.

5.3.2 Chemical exclusion of natural enemies

After nine weekly sprayings mealybug densities were becoming alarmingly high within the pockets chemically treated. Further treatment

Fig. 5.1 Physical exclusion and inclusion of natural enemies of cassava mealybugs through the use of sleeve cages. (Mealybug densities $\log(\bar{x}+1)$ transformed and are averages of 20 tips for each treatment)

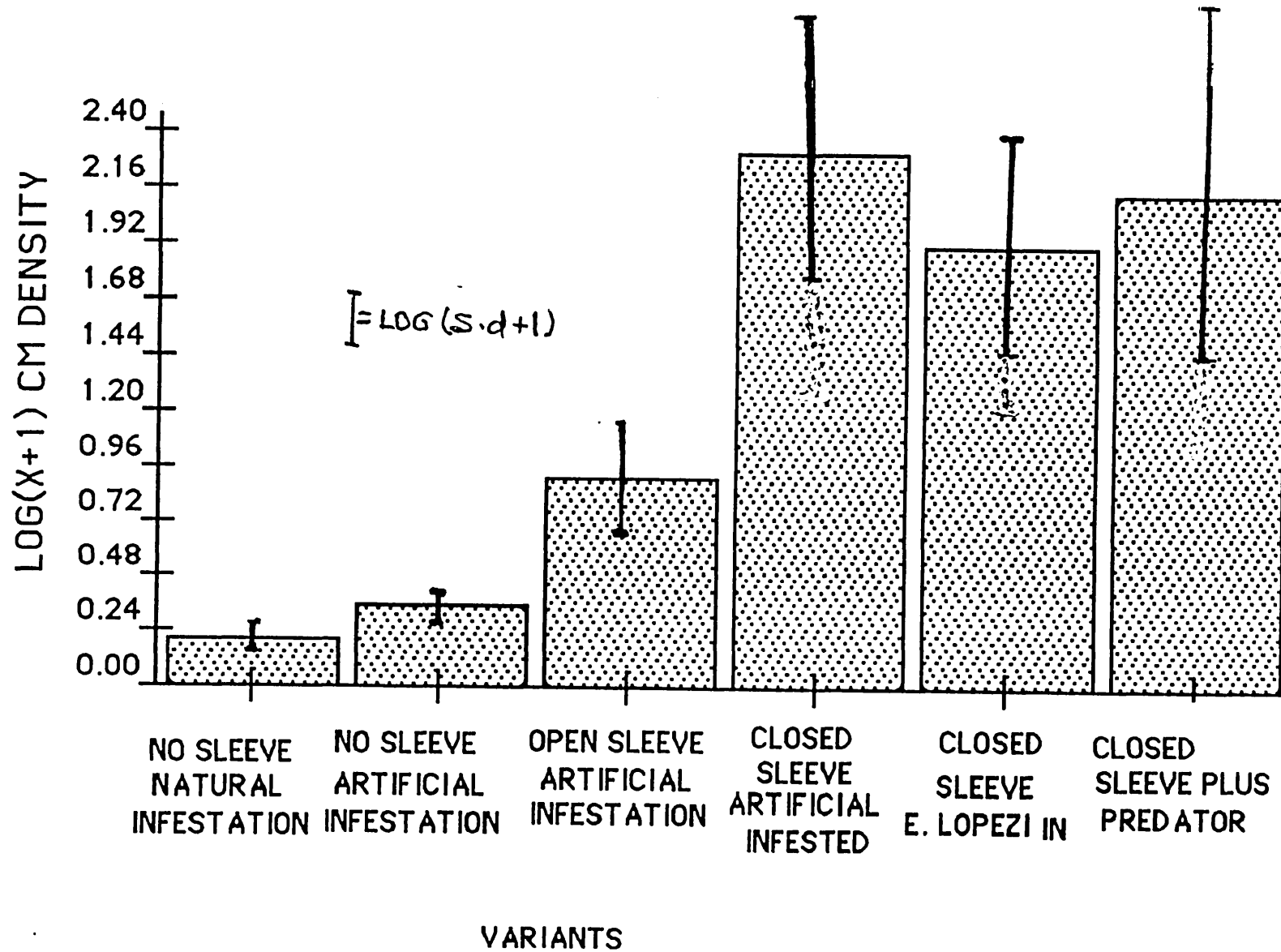
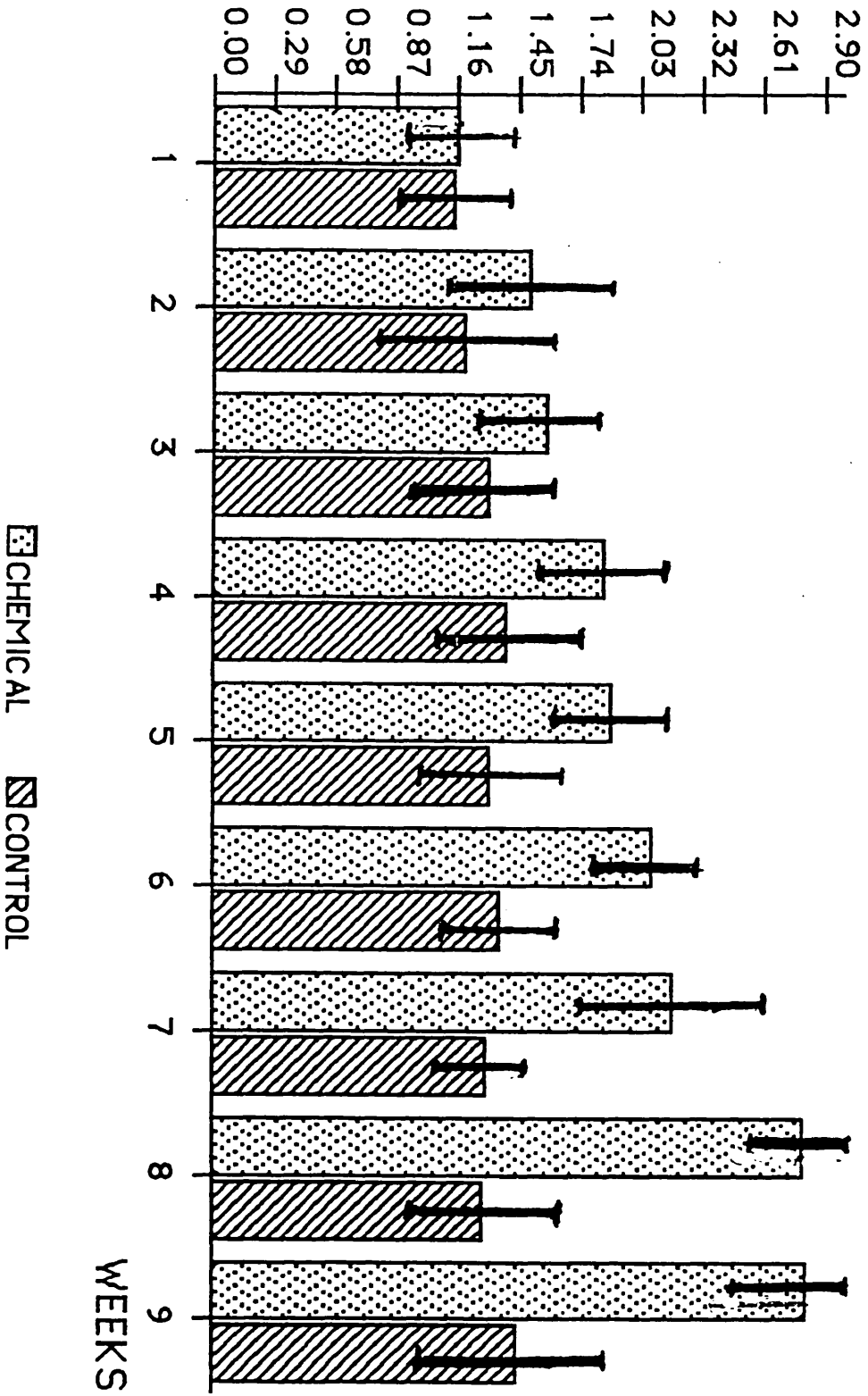


Fig. 5.2 Chemical exclusion of natural enemies of cassava mealybugs through the use of synthetic pyrethroid *Decis* as against a control experiment of spraying equal volume of clean water confined to cassava canopy. Mealybug densities were $\log(\bar{x}+1)$ transformed for average densities in 10 pockets per treatment. A pocket consisted of 10 tips. $I = \text{s.d.}(\log \bar{x}+1)$ transformed

LOG (X+1) MEALYBUG DENSITY/POCKET



☐ CHEMICAL

▨ CONTROL

WEEKS

was discontinued due to fear of disapproval by the farmer who owned the cassava field. However, a substantial increase in mealybug density between treated pockets and control was already glaring after the third spraying. Statistically significant difference between densities of control and chemical treatments were observed after the sixth week of treatment (Appendix E, Fisher PLSD test and Scheffe's F-test).

In the control experiment mealybug densities fluctuated between 10 and 32 which compared very well with peak densities in population dynamic studies in Chapter 2. The chemical exclusion experiment had mealybug densities rising each week from 10 to over 600 per tip. A peak increase of about 19-fold demanded $\log(x+1)$ transformation of data to stabilise the error variance with control and make presentation in a bar chart possible.

5.4 DISCUSSIONS

The results of the two exclusion experiments support the positive impact of natural enemies on the reduction of cassava mealybug populations. The exclusion experiments also were a faster way of evaluating the role of natural enemies in pest population regulation.

However the impact of individual beneficials was difficult to evaluate and did not give an expected bigger reduction of mealybug numbers in cages in which they were included. It is suspected that included beneficials in cages died earlier or could not act normally under artificially imposed conditions. In addition, enough time probably did not lapse for off-spring of the two beneficials included in cages to have any impact on mealybugs considering the initial delay in their introduction. Their free-living counterparts had the option of invading when they chose to and in the numbers their population allowed per tip and not two.

But on the basis of predominance of E. lopezi in field population of natural enemies it could be assumed that the exclusion experiments are a testimony to the efficiency of E. lopezi (nearly 80% of natural enemies in fields). Efficiency of natural enemies was solely judged from mealybug densities rather than parasitisation rates of parasitoids, since exclusion of natural enemies from some treatments made comparison of parasitism not worthwhile.

In Nigeria, Neuenschwander et al. (1985) showed 70-100-fold decrease

in mealybug densities in similar exclusion experiments. It was also observed that the natural enemies responsible for reduction of mealybug numbers late in the dry season were E. lopezi, local coccinellids and cecidomyiids.

Natural collapse in mealybug densities were observed in several studies conducted at the end of the dry season (Leuschner, 1978; Fabres, 1981; Herren and Lema, 1982; Umeh, 1984; Lema and Herren, 1985; Neuenschwander et al., 1986). The peak of the dry season was therefore good for exclusion experiments to avoid natural collapse of mealybug densities.

5.5 CONCLUSIONS

Both physical and chemical exclusion of natural enemies overwhelmingly support the efficiency of natural enemies in reducing mealybug densities. The quick evaluation methods reflect the situation under field conditions and present an optimism of achieving control on the cassava mealybug.

CHAPTER 6

ANTS IN ASSOCIATION WITH THE CASSAVA MEALYBUG IN GHANA: I. EXTENT OF MEALYBUG ATTENDANCE, IMPORTANT SPECIES INVOLVED, RELATIVE IMPORTANCE OF ATTENDANCE EACH MONTH, WEEDINESS OF FIELDS, INFLUENCE OF MEALYBUG DENSITIES AND EDGE EFFECTS ON THE DISTRIBUTION OF THE MOST IMPORTANT SPECIES OF ANTS

6.0 ABSTRACT

Field surveys to establish the extent of mealybug attendance by coccidophilic ants in the coastal savannah and rainforest were conducted. The most important ant species, judged by numerical abundance and number of tips on which they were encountered in both ecological zones, were identified. The effect of edge of field on ants' distribution was studied for three dominant ant species. The inter-relationships between mealybug densities, weediness of fields and ant densities were assessed. Through observations in the field, the duration of ant attendance of mealybugs was estimated and categorised into diurnal permanent and nocturnal to identify species most likely to affect other fauna.

Survey data suggested that three main ant genera were dominant in both ecological zones. The dominance was shown in descending order of relative importance as follows: Camponotus spp, Crematogaster spp and Pheidole spp. There were significant differences between species data on number of tips they attended and their total populations on infested tips. Crematogaster sp showed preference for edge of fields whereas the other dominants preferred inner fields. Crematogaster spp and Pheidole spp spent a longer time or were permanent on tips in carton tents and were therefore the most likely to influence efficiency of natural enemies.

6.1 INTRODUCTION

The fauna associated with the cassava mealybug was reported from many countries in Africa: in Congo (Matile-Ferrero, 1977; Fabres and Matile-Ferrero, 1980), in Zaire (PRONAM, 1978), in Nigeria (Akinlosotu and Leuschner, 1981; Iheagwam, 1981; Akinlosotu, 1982; Umeh, 1984; Neuenschwander and Hammond, 1988), in Gabon (Boussienguet, 1986), and on a continental basis (Neuenschwander et al., 1987).

Almost all reported associated insects were parasitoids and predators with only a brief mentioning of ants which were presumably encountered in substantial numbers on infested cassava tips.

Interactions between ants and mealybugs or other Homopterans on cocoa, especially the mealybug, swollen shoot virus vectors, Planococcoides njalensis Laing, in Ghana were studied and reported for about 75 species of ants on 14 known vector species (Strickland, 1951; Cornwell, 1958). The observation of ants on cassava mealybug colonies in the rainforest raises suspicion that ants could influence the biological control of the mealybug in the same ecological zone where most studies were made on ants. The failure of a successful biological control of cocoa mealybugs could partly be attributed to ant attendance.

This chapter explores the most important ant species and the extent of their attending cassava mealybugs from survey data. It also looks at the influence on cassava mealybug densities of ant attendance, the distribution of relatively important ant species in relation to edge of field to forest or cocoa farm. The chapter forms an introduction to a second one that is to follow on the influence of ants on the ongoing biological control of cassava mealybugs in Ghana.

6.2 MATERIALS AND METHODS

6.2.1 Extent of ants attendance of cassava mealybugs and important species involved in the rainforest and savannah zones from survey data

The relative abundance of ants on cassava mealybug infested tips, the species involved and extent of tips attended were evaluated through field surveys in the rainforest and savannah zones. Data based on field means in Chapter 2 of this thesis could not give great detail on the ants' interaction with cassava mealybugs and was general for all ants.

Surveys covering over 40 fields (approximately 30 ha) were carried out in November-May 1988 and 1989 for each ecological zone.

A present-absent of ants sampling procedure for mealybug infested tips on one hand and non-infested tips on the other as a control was used. At ten tips per field a total of 400 infested and non-infested tips each were analysed for each zone. The control was to give an idea of the extent of ants' presence on uninfested tips in order not to overestimate ant-attendance of mealybugs when nectar-gathering visits were considered.

6.2.2 Ants' attendance in relation to mealybug densities, weediness of fields and edge effects of fields to forest or cocoa farms based on monthly field studies

The numerical relationships between ants and mealybug densities were assessed on mealybug infested tips. Twenty-five tips were evaluated each month for 9 months. Monthly means of ants and mealybugs were compared for tips with and without ants.

To evaluate the influence of weediness of fields on extent of ant attendance of mealybugs, a "clean" i.e. weed-free and "weedy" i.e. weeds overgrown fields were chosen. The chosen fields represented the two extreme categories of fields usually encountered in the predominantly peasant cassava farms in Ghana (see Plate 6). Fifty mealybug infested tips in each of the two types of fields were analysed in situ each month for 9 months. Monthly ant densities were compared between the two types of fields.

The distribution of three most important ant species on mealybug infested tips was assessed in relation to edge effect of fields to forest or cocoa farms. Preliminary observations revealed the presence of the same species of ants in the forest or on cocoa attending other mealybugs or homopterans. Ants were also seen attending aphids on weeds especially Chromolaena odorata = (Eupatorium odoratum). It was therefore suspected that the proximity of such forest and cocoa farms could influence ants distribution. During the study on edge effects, cassava fields were cursorily divided into three parts: close to the edge, the middle and the inner centre. In each of the arbitrary divided sections, 5 mealybug infested tips were actively searched for (adjusted where 5 tips could not be found). The tips were then examined in situ for ants. Ants on tips within mealybug colonies were counted according to species. Number of each species occurring in one of the sections was expressed as its proportion of distribution in that section relative to the pooled numbers for all the three sections.

6.2.3 Estimated duration of ant attendance of mealybugs based on observations at six hour intervals

Five tips for each of the three important ant species were tagged for observation at six hour intervals for 28 times. Presence or absence of ants on tagged tips at a particular time of observation were recorded.

Ants which were always present during the day only were said to have diurnal tending behaviour; those present during night only were nocturnal and those present at all times and had carton nests over mealybug colonies were said to be permanent attendants. The observations could not establish the continuous attendance of a particular individual or group of ants. However the same species of ant could be determined in the observations.

6.3 RESULTS

Survey data showed that the scale of ant attendance of cassava mealybugs was indisputably higher in the rainforest zone than in the coastal savannah, 78.6% of tips had ants in the rain forest against 21.4% in the coastal savannah, (χ^2 ldf = 246.6***) when tips with and without ants in the two zones are compared (Table 6.1). There were notable differences in abundance of ants encountered (total 415, only 6% of grand total in favour of the coastal savannah and 6405 making 94% of grand total in favour of the rainforest zone (Table 6.1).

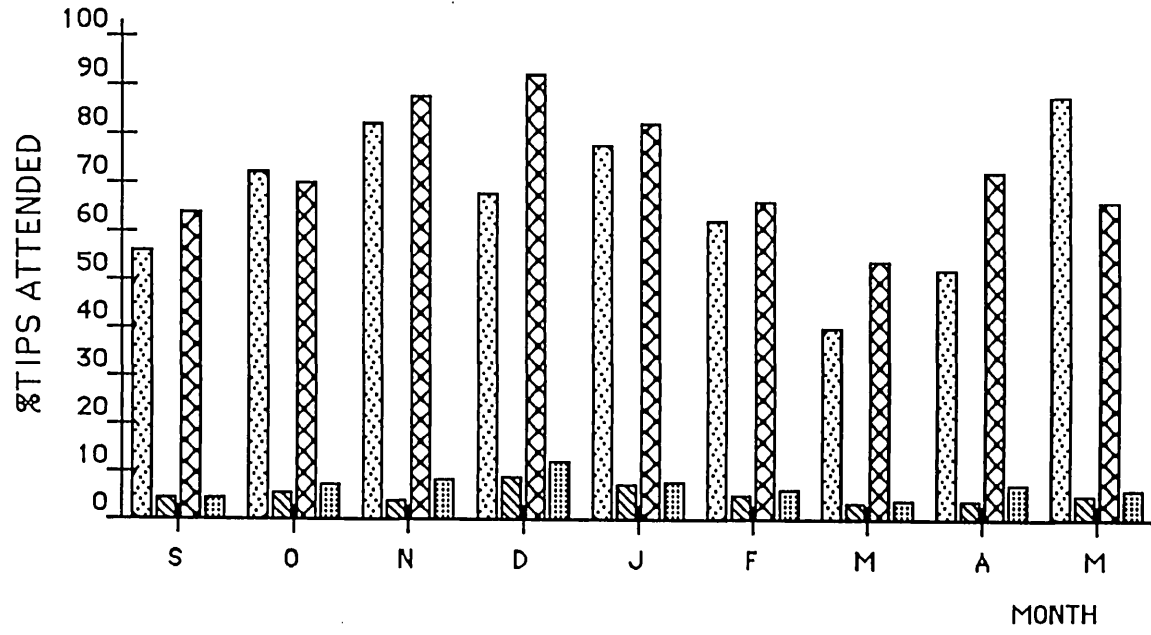
Ants were more likely to be encountered on tips with mealybugs than on tips without mealybug colonies (χ^2 ldf = 25.22) (Table 6.3) in the coastal savannah and (χ^2 ldf = 307.66) in the rainforest zone (Table 6.2).

Three major ant genera, Camponotus, Pheidole and Crematogaster dominated in both the coastal savannah and rainforest zones (Tables 6.4 and 6.5). If the three dominant species were the only ants encountered in the savannah, up to about 8 species were encountered on tips in the rainforest zone, although the other 5 species were relatively minor in importance. The scale of ant attendance on tips with and without mealybugs in weedy and clean fields confirmed the results of earlier surveys. ~~Important~~ differences in percentage of tips with ants were observed between weedy and clean fields in December, March, April and May (Fig. 6.1).

Ant densities showed erratic differences from month to month between clean and weedy fields. Four out of 9 months of the study showed no ~~important~~ differences in ant densities between clean and weedy fields (Fig. 6.2).

Mealybug densities on ant-attended tips were generally higher than ant densities on the same tips. However curves of mealybug densities

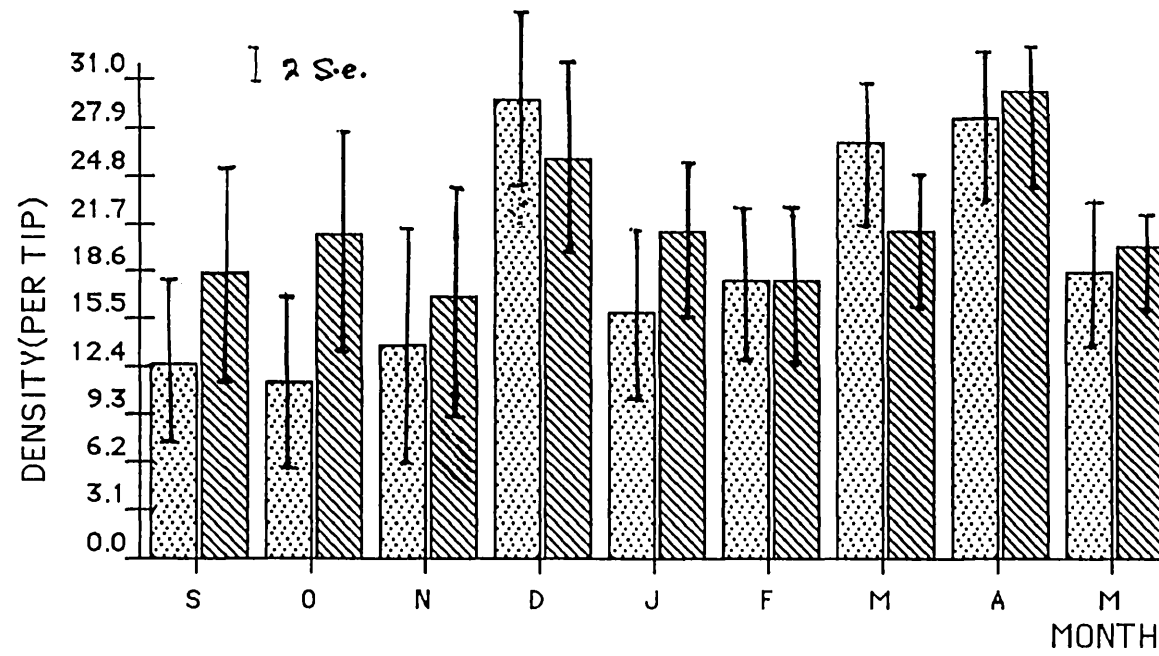
Fig. 6.1 Extent of cassava mealybug attendance by all species of ants according to month of the year in weedy and clean fields. N = 25 tips per month per field per treatment. Control treatment had no mealybugs (CM) on tips



CLEAN FIELD, TIPS WITH CM
 CLEAN FIELD, NO CM ON TIPS

WEEDY FIELD, TIPS WITH CM
 WEEDY FIELD, NO CM ON TIPS

Fig. 6.2 Ant densities on cassava tips with mealybugs in weedy and clean fields according to months of the year. N = 25 tips per field per month

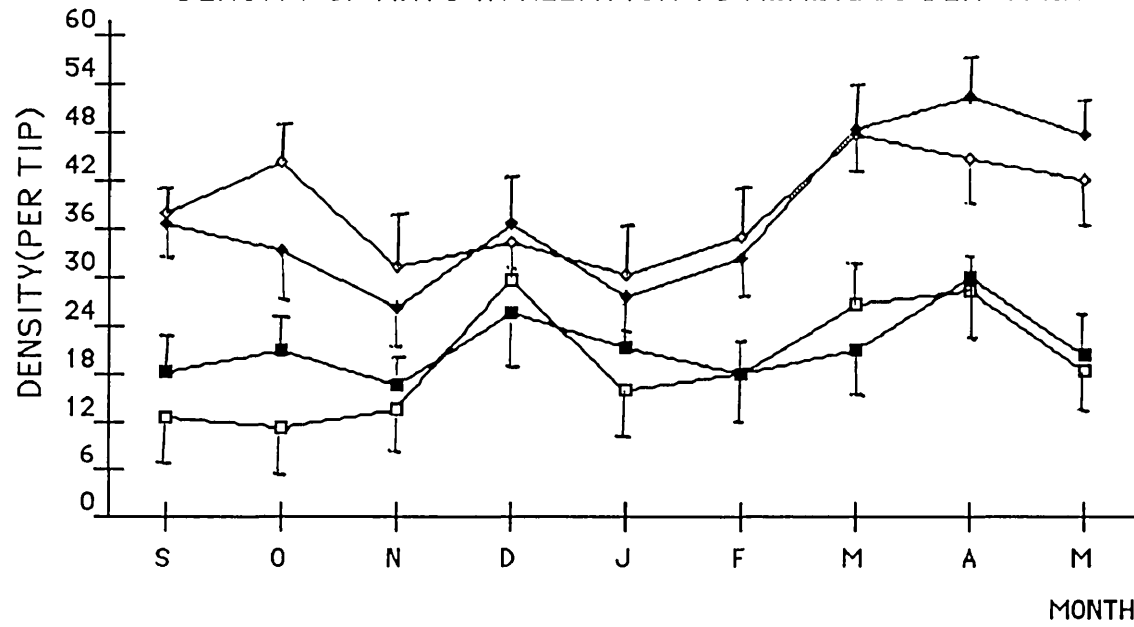


☐ ANTS DENSITY IN CLEAN FIELD

▨ ANTS DENSITY IN WEEDY FIELD

Fig. 6.3 Densities of ants and mealybugs on tips on which they occur together in weedy and clean fields. N = 25 tips per field per month. Bars = 1 s.e.

DENSITY OF ANTS IN RELATION TO MEALYBUG DENSITIES



◇ MEALYBUG DENSITIES IN CLEAN FIELDS □ ANTS DENSITIES IN CLEAN FIELDS

◆ MEALYBUG DENSITIES IN WEEDY FIELDS ■ ANTS DENSITIES IN WEEDY FIELDS

Table 6.1 Relative abundance of ants attending cassava mealybugs in savannah and rainforest zones

Ecological zone	Tips with ants (percent of total)	Tips without ants (percent of total)	Total number of ants on tips (percent of total)
Coastal savannah	83 (21.4%)	317 (70.94%)	415 (6%)
Rainforest	305 (78.6%)	95 (23.06%)	6405 (94%)
Total	388 (100%)	412 (100%)	6820 (100%)
χ^2_{1df}	246.6***		

Table 6.2 Extent of ant attendance of cassava mealybugs in fields in the rainforest zone

Variant	Tips with ants (percent of total)	Tips without ants (percent of total)	Total number of ants on tips (percent of total)
Tips with cassava mealybug	305 (84%)	95 (21.74%)	6405 (96.5%)
Tips without cassava mealybugs	58 (16%)	342 (78.26%)	232 (3.5%)
Total	363 (100%)	437 (100%)	6637 (100%)
χ^2_{1df}	307.66***		

Table 6.3 Extent of ant attendance of cassava mealybugs in fields in the coastal savannah

Variant	Tips with ants (percent of total)	Tips without ants (percent of total)	Total number of ants on tips (percent of total)
Tips with cassava mealybug	83 (71.55%)	317 (46.35%)	415 (92.2%)
Tips without cassava mealybugs	33 (28.45%)	367 (53.65%)	35 (7.8%)
Total	116 (100%)	684 (100%)	450 (100%)
χ^2_{1df}	25.22***		

Table 6.4 Relative importance of ant species attending cassava mealybugs in the coastal savannah

Ant species encountered on cassava tips	Total ants on 400 tips	Percent of total
1. Camponotus spp	205	49.4%
2. Pheidole spp	112	26.99%
3. Crematogaster spp	63	15.2%
4. All other spp	35	8.4%
Total (all spp)	415	100%

Table 6.5 Relative importance of ant species attending cassava mealybugs in the rainforest zone

Ant species encountered on cassava tips	Total ants on 400 tips	Percent of total
1. Camponotus spp	3239	50.6%
2. Pheidole spp	820	12.8%
3. Crematogaster spp	2104	32.8%
4. All other spp	242	3.8%
Total	6405	100%

showed a general trend of decreases and increases corresponding to the same pattern as ants in both clean and weedy fields (Fig. 6.3). Regressions of ant and mealybug densities suggested linear or curvilinear relationship for both ecological zones in Chapter 2 (Figs. 2.14 and 2.15).

In relation to edge of field the distribution of ants followed the following pattern: Crematogaster sp were encountered in decreasing numbers from edge of fields (51% at edge, 35% in midfield and 14% in inner field. Pheidole spp showed a direct opposite trend of preference (23% at edge, 28% in midfield and 49% in inner field, though the general trend was in favour of edge attendance for all ant species together (Table 6.6 showing 38% at edge, 31% in the middle and 31% in innermost sector).

Camponotus sp were evenly distributed in the field (30% at the edge, 32% in mid-field and 38% in inner field). All minor ants together showed a strong preference for the edge of field (75% at the edge, 20% in mid-field and 5% in inner field) (Table 6.7, figures in brackets). Relative importance of distribution of any of the species in one of the sectors also suggest the predominance of Crematogaster at the edge (43%) Pheidole in the innermost sector (42% of all ants) and Camponotus showing almost even distribution in all sectors.

Observations on estimated duration of ant attendance of cassava mealybugs based on the three most important ant species suggested that Crematogaster and Pheidole spp obtained longer attendance capabilities through the exclusive habit of constructing carton tents over mealybug colonies. The carton tents were also likely to protect mealybugs from parasitoids and predators. It was also suspected that strong carton tents usually constructed by Crematogaster spp could serve as refugia for mealybugs against the mechanical effects of rains and winds. Therefore the two ant species were most likely to influence the protection of mealybugs from abiotic and biotic factors than Camponotus and other minor ants, effects of which were almost dispensable (see Table 6.8).

It should, however, be noted that apart from the numerical superiority of Camponotus sp on tips, this particular ant specie also built loose soil nests over colonies of aphids on Chromolaena = (Eupatorium) odorata, a weed commonly found in cassava fields in Ghana. Probably due to the height of mealybug colonies on cassava tips, this

Table 6.6 Field edge effects on relative importance of ants attendance of cassava mealybugs

Sector of field	All ants attending mealybugs in sector on 150 tips	Percent of total
Edge (closest to forest or cocoa farm)	1207	37.9%
Middle sector	990	31.1%
Innermost sector	987	31.0%
Total	3184	100%

Table 6.7 Field edge effects on preference of attendance of mealybugs by important ant species

Relative abundance of ants species on mealybugs					
Sector of field	Crematogaster sp	Camponotus sp	Pheidoline sp	All others	Total
Edge (closest to forest or cocoa farm)	520 (51%) *43%	328 (30%) *27%	197 (23%) *16%	162 (75%) *14%	1207 *100%
Middle sector	357 (35%) *36%	350 (32%) *35%	240 (28%) *24%	43 (20%) *5%	990 *100%
Innermost sector	142 (14%) *14.6%	415 (38%) *42%	419 (49%) *42%	11 (5%) *1.4%	987 *100%
Total	1020 (100%)	1093 (100%)	856 (100%)	216 (100%)	

() Percent of total number of ants for the same specie (vertical column)

* Percent of total number of ants of all species (horizontal column)

Table 6.8 Period of ant attendance of cassava mealybugs as estimated by tips attended in 6 h. intervals

Ant species	*Total (cumulative) tips with or without ants				Carton tent Attendance	Remarks
	Day (6am-6pm)		Night (6pm-6am)			
	With	Without	With	Without		
Crematogaster sp	140	0	112	28	140	Longer or more permanent attendance behaviour of species
Pheidole sp	140	0	84	56	112	Longer and slightly permanent attendance behaviour of species
Camponotus sp	140	0	56	84	0	Long but more diurnal attendance behaviour of specie. Do not construct carton tents
Total tips attended	420	0	252	168	252	

* 5 attended tips per specie per period (6 h interval) for 28 observational periods = 140 tips cumulatives

nest building behaviour was not possible over mealybug colonies, hence less protection was provided by Camponotus sp.

6.4 DISCUSSIONS AND CONCLUSIONS

Coccidophilic ants are very important fauna associated with mealybugs and other homopterans which produce honeydew.

The ant-mealybug association influences the regulatory role of introduced or indigenous natural enemies of the mealybugs. It is quite natural that in a symbiotic relationship between mealybugs and ants, the latter gives protection to mealybugs by warding off potential natural enemies or hiding mealybugs under carton tents as a reward for the honeydew received from them. There could also be a dispersal role played by ants during the establishment of new colonies of homopterans, especially mealybugs, most of which are vectors of diseases. The major pests and diseases of cocoa are influenced by the distribution of the principal dominant ants (Leston, 1971, 1973; Majer, 1972).

Several workers have attempted to elucidate the factors governing ant distribution in tropical localities (Way, 1951, 1954, 1963; Brown, 1959; Vanderplank, 1960; Greenslade, 1971; Leston, 1971). The tropical studies have concentrated on observing changes in ant distribution and then attempting to explain the change. Due to the complexity of the tropical ecosystem many findings are very uncertain (Majer, 1976). The higher incidence of ants' attendance of mealybugs in the rainforest is an indication of the presence of more coccidophilic ants in that ecological zone. Majer (1976) observed that the composition of cocoa fauna was influenced by weather, cocoa canopy density and to some extent the proximity of cocoa to secondary forest and the dominant ants. He concluded that a characteristic community was associated with each of the three common dominant ants, the composition of which depended on their predatory and tending habits as well as their type of feeding specialisation.

In the cassava ecosystem, three dominant ants, Camponotus sp, Crematogaster sp and Pheidole were encountered in both savannah and rainforest zones. In addition to the dominant ants,^a a few minor ants were encountered in the forest, though two of the minor species did not show any clear mealybug attendance role. This dominance by a few ant species shows similarity with the cocoa ecosystem, though cocoa forms a denser

canopy whereas cassava has a very sparse canopy. This explains the overall dominance of Camponotus acvapimensis, a savannah species of ant, in both zones. The distribution of ants in fields in relation to edge effects, supports the idea that shade-loving ants e.g. Crematogaster spp showed preference for field edges nearer to forest or cocoa farms whereas open-canopy lovers, e.g. Camponotus sp and Pheidole sp showed preferences for inner fields or were uniformly distributed. Observations on mealybug attendance by ants suggest that the ants, Pheidole and Crematogaster spp are the most likely to influence biological control of mealybugs as judged by their longer attendance and carton tent protection of mealybugs. Crematogaster striatula excluded all other co-dominants and non-dominant species probably due to the exceptionally aggressive habits and high density of the species on tips on which they were encountered (observational citation only).

On the basis of the above observations it is concluded that the incidence of ant attendance of mealybugs is a very important phenomenon in the rainforest of Ghana.

The exclusive behaviour of two ant species, Pheidole and Crematogaster sp in the construction of carton nests over mealybug densities is likely to make them the most important ant species influencing the efficiency of natural enemies of mealybugs. Detailed studies on the possible influence of ants on parasitism is presented in Chapter 7.

CHAPTER 7

ANTS IN ASSOCIATION WITH THE CASSAVA MEALYBUG IN GHANA: II. THEIR
INFLUENCE ON BIOLOGICAL CONTROL OF CASSAVA MEALYBUGS

7.0 ABSTRACT

The influence of coccidophilic ants on biological control of cassava mealybugs was quantified in the rainforest zone. Field assessment of reduction in parasitism and predator densities was carried out on cassava infested tips with ants' attendance versus tips without ants. Further studies on three dominant ant species substantiated the antagonistic relationship between ants and natural enemies of mealybugs. To further substantiate the observed field results, ants were chemically excluded from tips and parasitisation rates were compared with tips with ants.

Important differences were observed in parasitism between tips with and without ants for both field and experimentally evaluated studies involving chemical exclusion of the ants.

Densities of predators (mainly coccinellids) were significantly different between tips with and without ants. Losses of the larvae of the predator, Exochomus sp which were placed on tips with and without ants were also significantly different.

7.1 INTRODUCTION

The use of predaceous ants to control crop pests was probably the earliest attempt at the biological control of insects (Clausen, 1940). Friedericks (1920, cited by Way, 1954) describes how the 12th century southern Chinese protected fruiting citrus plants by placing nests of the ant Oecophylla smaragdina F on the trees. On the basis of the regulatory role of pests, some ant species have been introduced or encouraged on numerous occasions to protect both temperate (Adlung, 1966) and tropical crops (Leston, 1973). However attempts to introduce beneficial ants have often failed because of hostility from ants already present on the crop (Phillips, 1940; Brown, 1959). Way (1955) suggested that in terms of food supply any ant species, in order to maintain continuous large colonies, had to change foraging grounds periodically, as doryline ants do, or to tend Homoptera which provide honeydew to carry the ants over periods when animal prey is scarce. It has also been suggested that ants

have a major influence on the composition of fauna in tropical ecosystems (Way, 1952, Wilson, 1959).

Leston (1971, 1973) and Room (1971, 1972) working in Ghana concluded that with each of the 14 or so dominant ants found in cocoa farms there is distinctive associated fauna. Cocoa fauna was thus highly influenced by dominant ants and proximity of cocoa to secondary forest which could be rich in ant species.

The influence of ants on biological control of pests is probably acknowledged but not quantified in many control programs. Cornwell (1958) observed that the presence of mealybug-attending ants was almost essential for infestations of Planococcoides njalensis to develop in cocoa. The ant Crematogaster striatula Emery carried mealybug adults in its mandibles from one place to another probably to establish new colonies. The distribution of ants was also suspected to contribute substantially to the amoeboid pattern characteristic of swollen shoot disease outbreaks, vectors of which were ant-associated mealybugs e.g. P. njalensis.

This study aims at quantifying the influence of ants on parasitism of mealybugs and on predator densities on tips with ants through field assessments and ant exclusion experiments.

7.2 MATERIALS AND METHODS

7.2.1 Evaluation of rates of parasitism on cassava tips with and without ants

Twenty-five tips of cassava each with and without ants tagged and monitored for a week, were each month broken and dissected in the laboratory for counts of mealybugs (II-IV), mummies of parasitoids and ants. After rearing of mealybugs and mummies rates of parasitism and hyperparasitism were calculated by the conventional method. Significant differences between tips with and without ants were taken as the influence of ants on the efficiency of parasitoids and hyperparasitoids. The individual influence of three most important ant species, namely Crematogaster, Camponotus and Pheidole spp was also evaluated with tips on which each species was encountered alone.

7.2.2 Evaluation of densities of predators of mealybugs on cassava tips with and without ants

In the same way as on tips in 7.2.1 densities of predators (mainly larvae and adults of coccinellids) were calculated each month for the two types of cassava tips.

7.2.3 Chemical exclusion of ants and effect on rates of parasitism and predator densities

In order to substantiate the results of field observations, ants were chemically excluded on twenty-five tips in the field whereas another twenty-five with mealybugs were chosen with ant attendance for comparison. Chemical exclusion of ants was achieved by the use of concentrated Diazinon solution (a broad spectrum insecticide with strong formicidal action). Cotton wool soaked in Diazinon solution was used to encircle bases of tagged single cassava stems with approximately the same sizes of mealybug colonies. Ants encountered on tips with the chemical exclusion were initially aspirated and killed. Rates of parasitism on tips with ants and those with ants excluded were compared for significant differences.

7.2.4 Evaluation of the antagonistic relationship between ants and predators

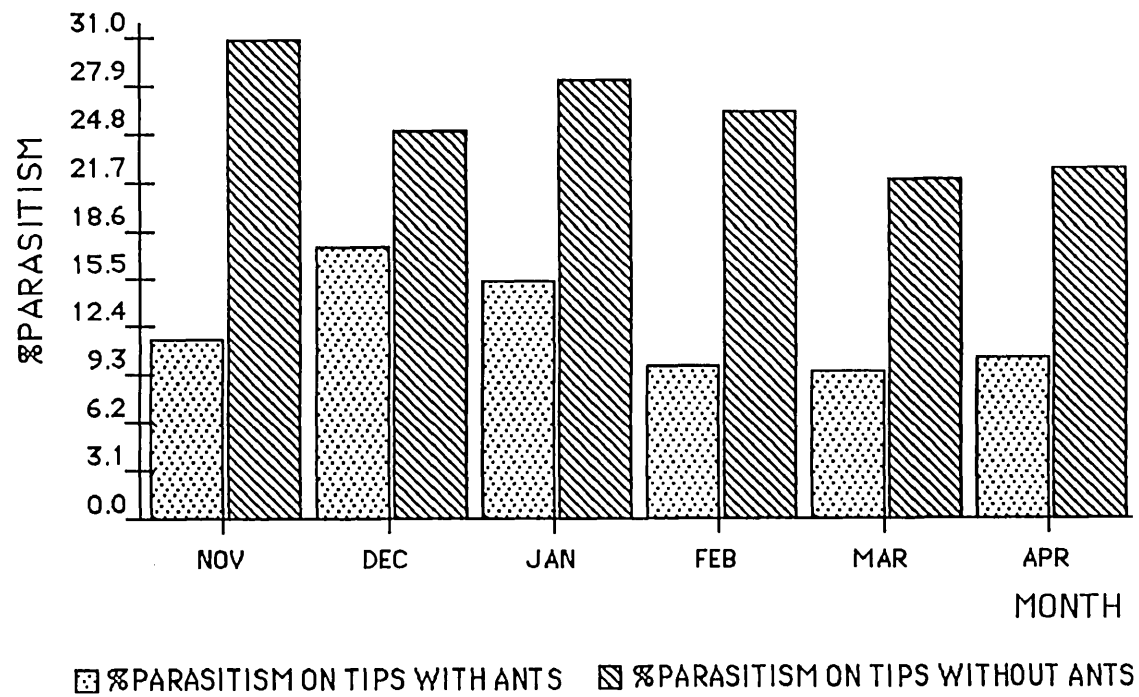
To substantiate the results of field observations 2 larvae each of the most common coccinellid predator, Exochomus sp were placed in mealybug colonies with and without ants on tips in the field. The active removal of larvae by ants or the disappearance of the larvae after 4, 8 and 24 hrs was translated as an antagonistic interrelationship between the ants and predators.

7.3 RESULTS

Rates of parasitism differed significantly between tips with ant attendance and those without ants. On the average a difference of about 15% lower rates of parasitism was recorded for tips with ants (Fig. 7.1). Individual species of ants also showed slightly different influence on rates of parasitism (Fig. 7.2).

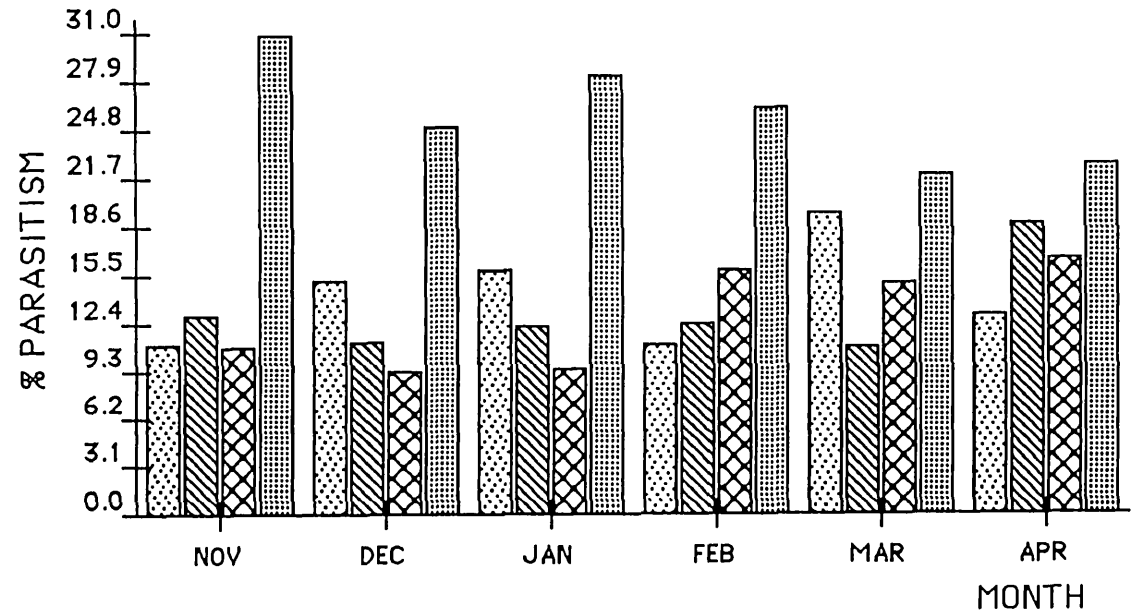
Important differences were also recorded for rates of hyperparasitism between tips with ants and those without though two months out of six showed no differences in rates of hyperparasitism (Fig. 7.3). Predator (mainly coccinellids) densities were significantly higher on tips without ants (Fig. 7.4).

Fig. 7.1 The influence of ants' attendance of cassava mealybugs on rates of parasitism. Rates of parasitism are calculated from N = 25 tips each month as pooled data and not average



1 128

Fig. 7.2 The influence of individual major ant species on rates of parasitism. Rates of parasitism on tips attended by Crematogaster sp, Pheidole sp and Camponotus sp are calculated from N= 10 tips per species per month. Control tips had mealybugs but no ant attendance (Parasitism calculated from 10 pooled tips and not averages)



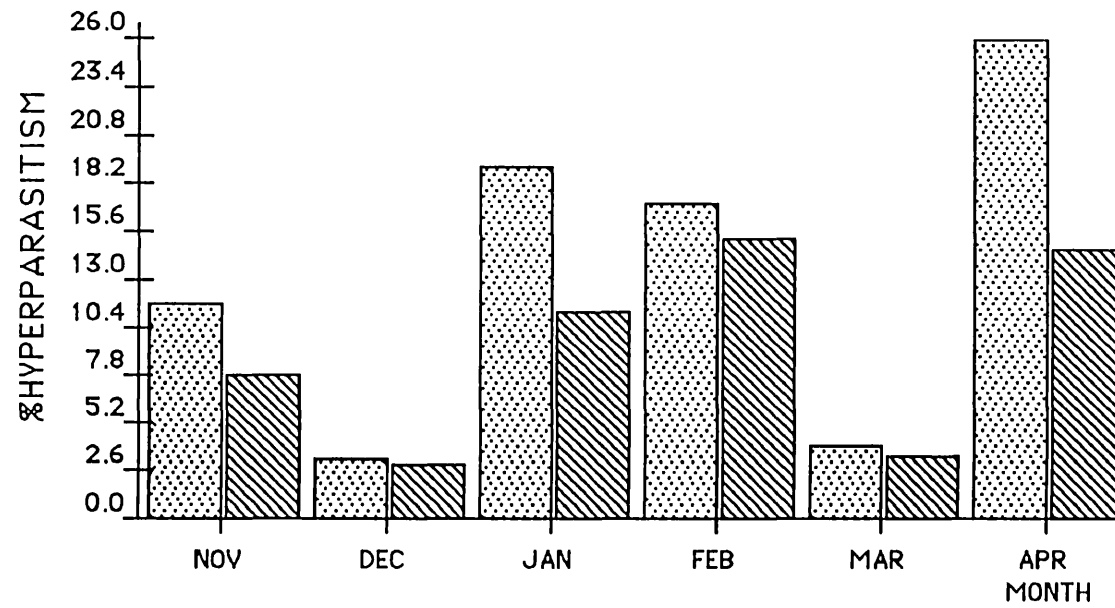
☐ % PARASITISM ON TIPS WITH CREMATOGASTER SP.

☒ % PARASITISM ON TIPS WITH PHEIDOLINE SP

☎ % PARASITISM ON TIPS WITH CAMPONOTUS SP

☐ % PARASITISM ON TIPS WITHOUT ANTS (CONTROL)

Fig. 7.3 The influence of ants on rates of hyperparasitism. Rates of hyperparasitism are calculated from $N = 10$ tips per month per treatment. Control tips had mealybugs but no ant attendance



▨ % HYPERPARASITISM ON TIPS WITHOUT ANTS

▩ % HYPERPARASITISM ON TIPS WITH ANTS

ANTS INFLUENCE ON HYPERPARASITISM

Fig. 7.4 The relationship between mealybug densities in colonies attended by ants and rates of parasitism. N = 25 tips for each variant (with and without ants) collected by bias sampling.

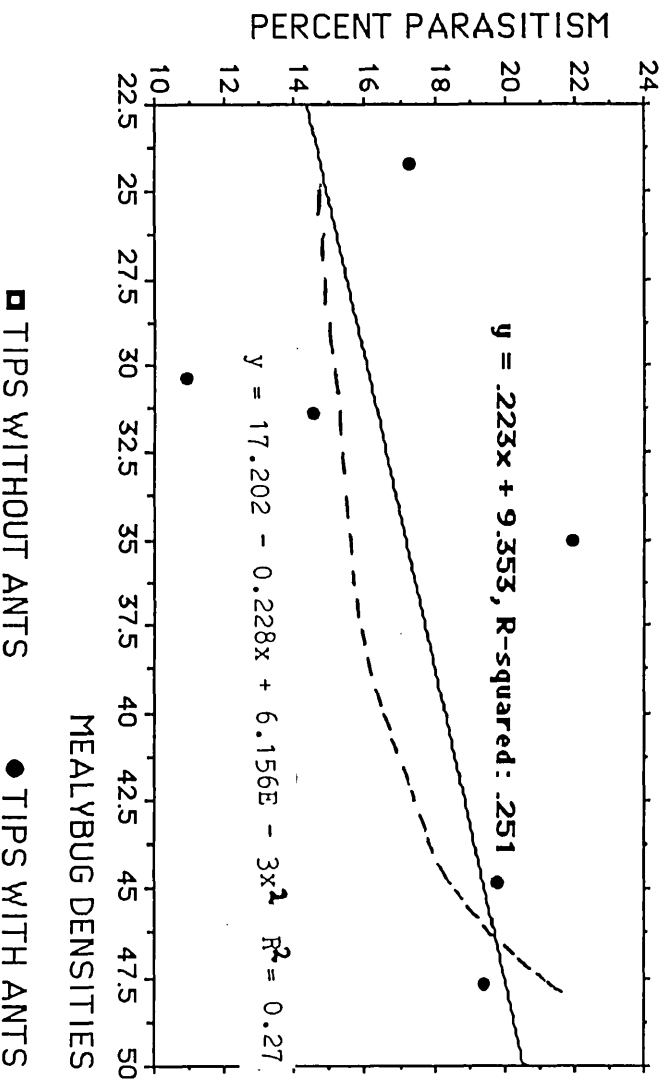
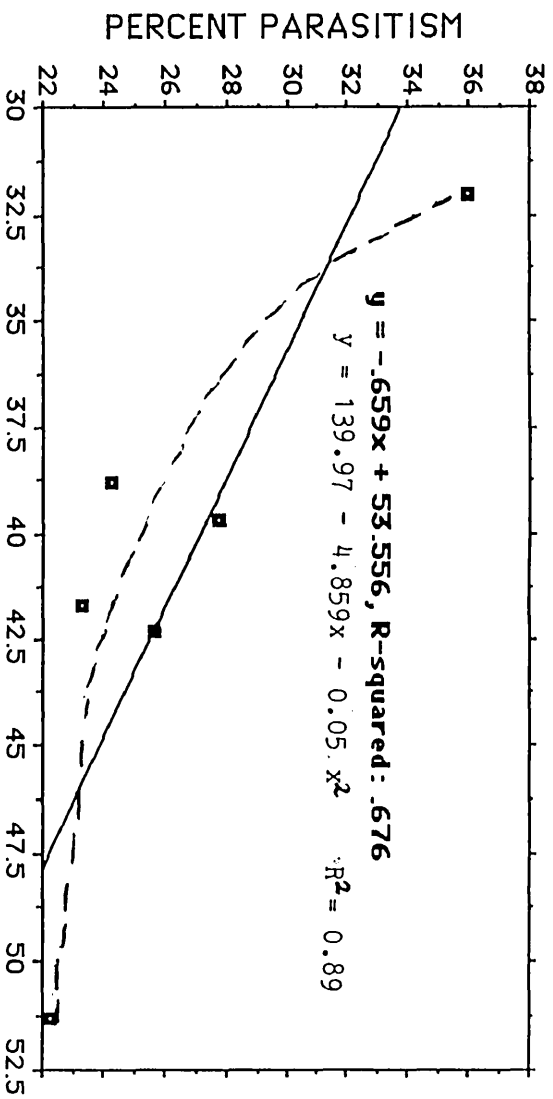
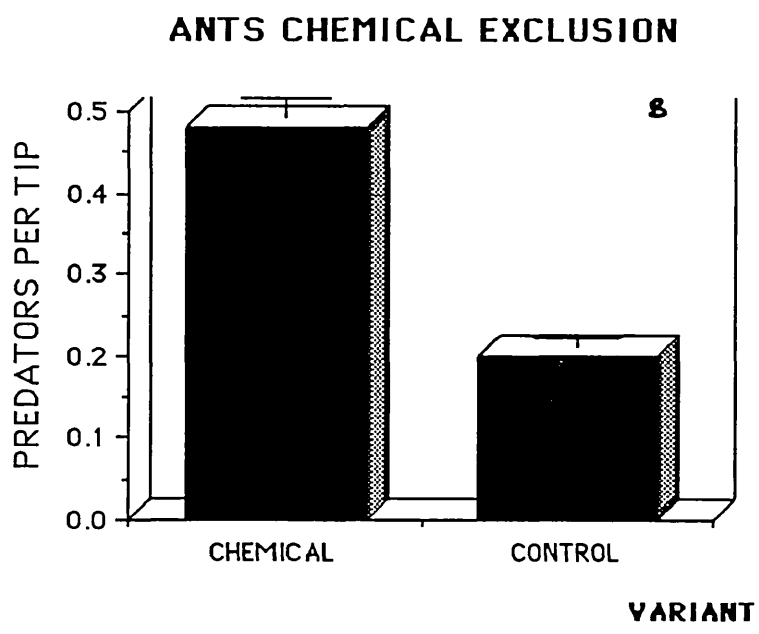
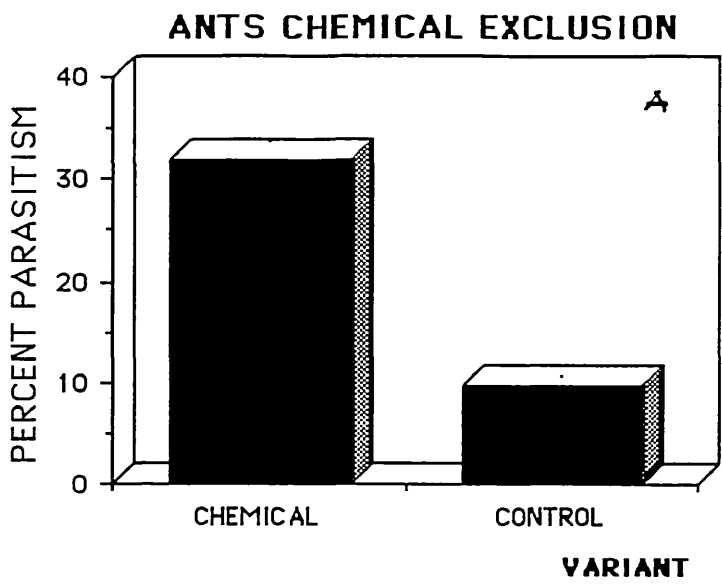
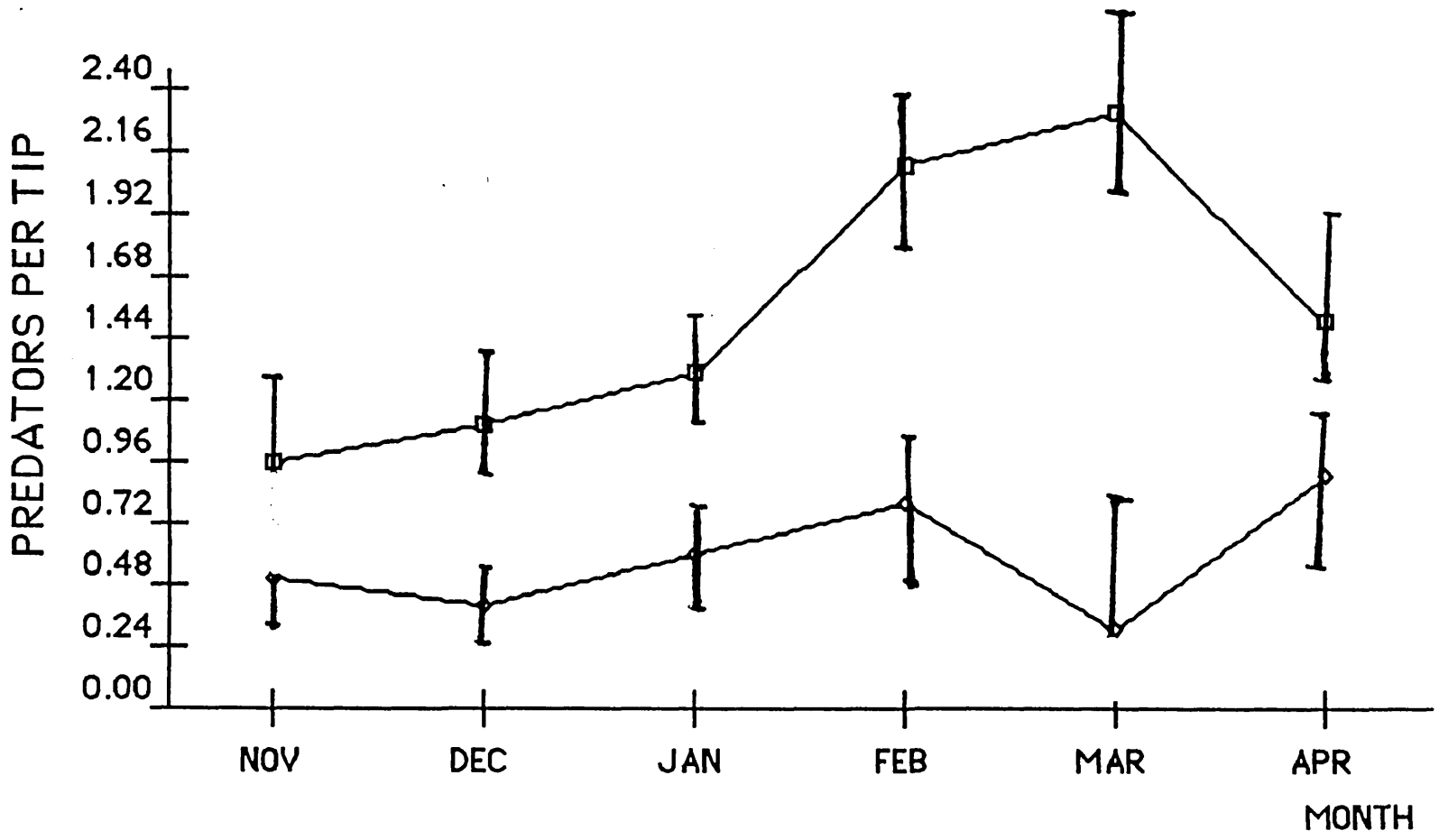


Fig. 7.5 The influence of ants exclusion by chemicals on the rates of parasitism and predator densities on tips. Rates of parasitism (A) and predator densities (B) are calculated from a total of 25 tips per treatment. bar = s.e.



N=25 TIPS

Fig. 7.6 The influence of ants on densities of coccinellid predators on tips with cassava mealybugs. N = 25 tips for each variant (with and without ants). Bar represents 2 s.e.

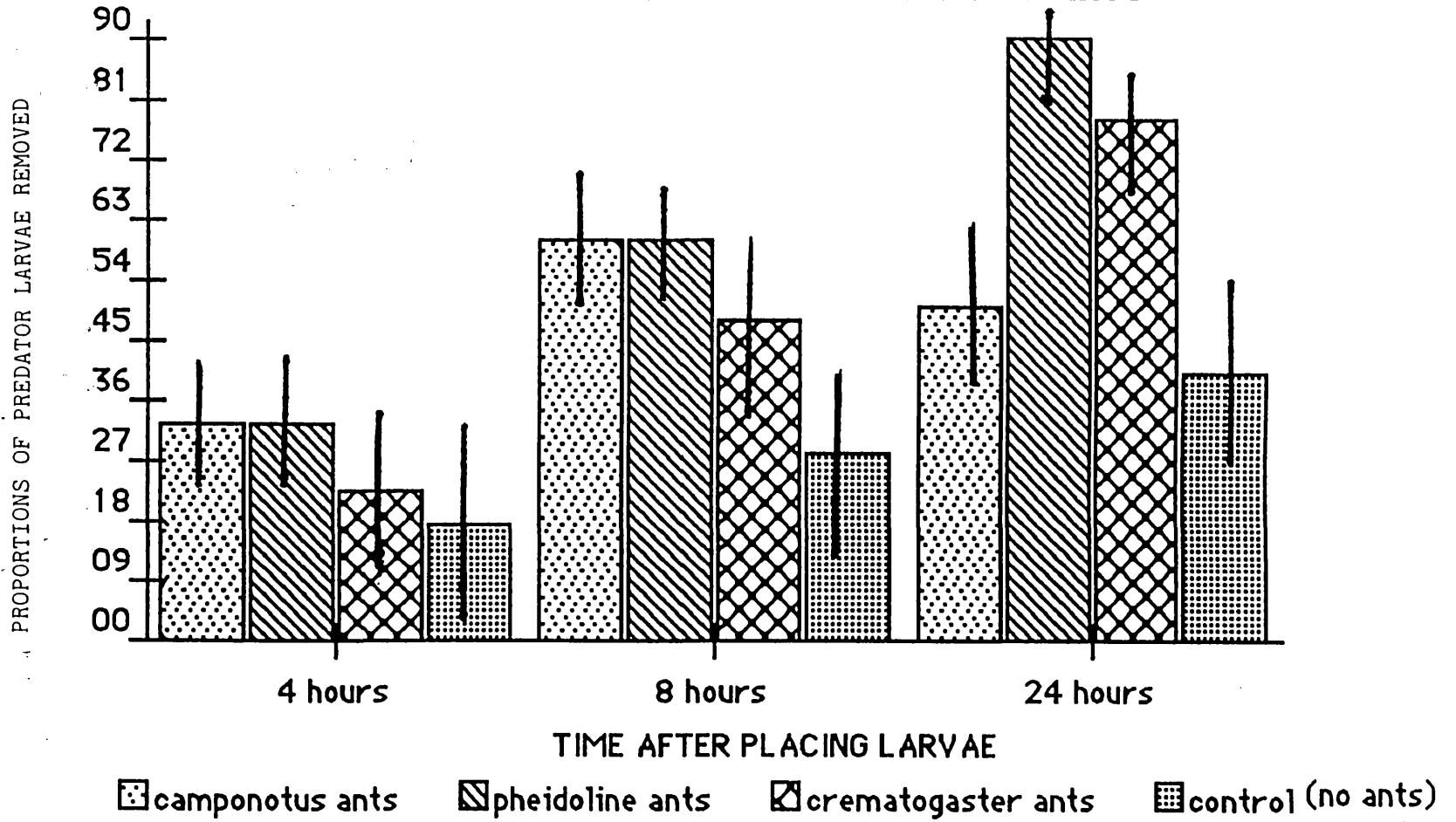


□ PREDATORS DENSITY ON TIPS WITHOUT ANTS

◇ PREDATORS DENSITY ON TIPS WITH ANTS

Fig. 7.7 Experimental evaluation of the degree of antagonism between ants and larvae of the coccinellid (Exochomus flavipes) predator. Larvae's disappearance on 40 tips per ant specie per treatment (with and without ants). Bar represents 2 s.e.

REMOVAL OF PREDATOR LARVAE BY ANTS



In relation to mealybug densities regressions show higher rates of parasitism on tips without ants (between 23-37%) and lower rates of parasitism (between 11.5-22.5%) on tips with ants. If rates of parasitism decreased with increasing mealybug densities on tips without ants, it was the opposite on tips with ants. Some mealybugs within big colonies attended by ants were not adequately protected by the ants, hence the relatively higher rates of parasitism at higher densities (Fig. 7.4).

Individual species of ants, namely Crematogaster species, Pheidole sp and Camponotus sp reduced rates of parasitism significantly from control where mealybugs were not attended by ants. However differences of rates of parasitism as influenced by each ant species were erratic from month to month and therefore made it difficult to find the overall most aggressive individual ant species (Fig. 7.2).

The chemical exclusion experiment on ants further substantiated the influence of ants (all species) on the rates of parasitism and reduction of densities of predators. Rates of parasitism were significantly different on tips with and without ants. Predator densities were also significantly different on the same tips (Fig. 7.5). Predators i.e. Exochomus larvae were lost or left tips with ants more frequently than they did on tips without ants (Fig 7.7).

7.4 DISCUSSION

Though ants do not entirely prevent parasitisation of mealybugs, they significantly reduce rates of parasitism on tips on which they are encountered. An average reduction of about 15% parasitism is substantial if the generally low rates of parasitism by E. lopezi in fields is considered. The reduction translates to 50% or more in some cases of the potential parasitism of the wasp (30% maximum parasitism). It could therefore be speculated that the low mealybug populations observed in the rainforest zone could even be much lower or even non-existent if ant attendance was not prevalent in the zone.

On the other hand ants reduced rates of hyper-parasitism which was the only positive role played in favour of the control effort.

In relation to predators ants also showed antagonism. Coccinellid predators, the most common of all mealybug predators, showed reduced densities on tips where ants were attending mealybugs.

When mealybug average densities on tips were considered ants were able to protect smaller colonies from parasitoids but with increasing mealybug colony densities on tips, some mealybugs escaped the ant protection and therefore were comparatively highly parasitised.

The observed negative influence of ants on natural enemies of cassava mealybugs seems to be the first reported case quantified in contrast to the general expectation but not often quantified.

Apart from the physical protection offered by ants to mealybugs resulting in reduced parasitism and predator densities it is also suspected that the removal of honeydew from mealybug colonies helps to prevent disease infection from entomophthora species of fungi, ^{or sooty moulds} which normally thrive on the honeydew. However the honeydew removal by ants could also result in the prevention of the growth of sooty mould on leaves which usually reduces photosynthesis thus consequently resulting in yield losses.

The merits of ant attendance of mealybugs are fewer than the penalties and therefore ants should be regarded as negative biotic factors in the control of cassava mealybugs.

Mealybug wilt of pineapples is always associated with mealybugs and ants. Without ants few mealybugs become established in fields (Carter, 1960) and wilt disease does not spread (Beardsley et al., 1982). Also when ants are present mealybug populations increase rapidly after spraying because of mealybug survival and immigration and ant attendance and protection. Pheidole megacephala, the big headed ant, is the most troublesome because it is the dominant species in areas in which pineapple is grown (Phillips, 1934).

In recent years, control of ants that tend mealybugs has been achieved with Mirex, Heptachlor and hydramethylnon (Amdro). Mirex and Heptachlor are phased out of pineapple production and Amdro is used only as a border treatment. Efficacy of hydramethylnon (Amdro) has been studied with a number of pest ants including Solenopsis invicta Bureu (Williams et al., 1983; Banks et al., 1981, 1988; Harlan et al., 1981; William and Lofgren, 1983; Lofgren and Williams, 1985), Pogonomyrmex maricopa Wheeler (Borth, 1986), Iridomyrmex humilis (Phillips et al., 1987) and Pheidole megacephala (Su et al., 1980; Reimer and Beardsley, 1989). In Ghana, Diazinon is effective on ants and therefore was a good

substitute for Amdro or Logic chemicals in the exclusion of ants.

In a similar effort to exclude the ant Pheidole punctulata Meyr Melville (1958) reported the use of dieldrin spray banding up to twelve inches high of coffee tree trunks in Kenya. This led to the reduction of the mealybug Planococcus kenyae Le Pelley to the status of minor pest because it proved possible to attain a degree of ant control never approached before. The method enhanced the power of the natural enemy complex.

CHAPTER 8

BETWEEN-PLANT DISTRIBUTION PATTERNS OF CASSAVA MEALYBUGS AND SAMPLING METHODS SUGGESTED BY DISPERSION ANALYSIS FOR CASSAVA FIELDS IN GHANA

8.0 ABSTRACT

Distribution patterns of cassava mealybug, Phenacoccus manihoti Mat-Ferr (Homoptera: Pseudococcidae) were evaluated in four locations in Ghana. Taylor's (1961) coefficients, a and b and Iwao's (1968) mean crowding statistics, α and β were used to describe distribution patterns. Both methods suggested very high aggregation of mealybugs in all four locations; i.e. dispersion coefficients b and β were significantly higher than 1. However, due to the fact that the relationship of mean crowding to mean is generally not linear over a wide range of densities (Taylor, 1984), the mean crowding statistics were not used to develop or suggest a sampling plan.

Taylor's coefficients were used to develop binomial and enumerative sampling plans.

8.1 INTRODUCTION

The cassava mealybug, accidentally introduced in the 1970s into Africa, became the target for continent-wide biological control since 1982 until the present day. For a good monitoring programme, there is the need for an elaborate sampling plan or method, the development of which requires dispersion coefficients.

Though there are existing sampling plans or methods for cassava mealybugs, they were developed at a time when densities of mealybugs were excessively high. Sampling of tips has involved the destruction of tips or in situ tip analysis usually used for extensive surveys. However at lower mealybug densities which are now prevalent, the dispersion coefficients could change, thus requiring new sampling plans or substantiating the validity of the existing methods.

The within-plant distribution pattern for mealybugs does not seem to change with time and density since all observations in fields showed the 10 centimetre tip as the part of the cassava plant in which most mealybugs are found and therefore is the most appropriate sample unit (Hammond et al., 1987; Schulthess et al., 1989).

The aim of the analysis presented here was to evaluate between-plant dispersions of mealybugs in fields and use dispersion coefficients to suggest sampling methods for the existing low population densities of mealybugs.

8.2 MATERIALS AND METHODS

8.2.1 Sampling procedure

For the evaluation of between-plant distribution patterns, three fields in the rainforest and one at the coastal savannah were sampled, every two weeks for two years. The sampling procedure involved the combination of non-destructive, i.e. in situ analysis, and destructive methods. Cassava tips were initially analysed in situ (non-destructive), breaking only tips showing mealybug infestation (destructive). The details of the procedure is described in Chapter 1, Section II of this thesis and elsewhere (Hammond et al., 1987; Neuenschwander et al., 1987; Schulthess et al., 1989). Counts of mealybugs were made on each tip. Densities (m) per sampled tip were calculated. Variances (S^2) were calculated according to Cochran (1956) as follows:

$$S^2 = \frac{\sum_{i=1}^n (Y_i - \bar{Y})^2}{n - 1}$$

where n = number of tips sampled = 100
 Y_i = number of mealybugs on each tip
 \bar{Y} = average mealybug numbers or density per tip
 S^2 = variance

8.2.2 Dispersion analysis

The variances (S^2) and mean densities (m) were related by two widely used models for describing the relationships: Taylor's Power Law (Taylor, 1961) and the mean crowding statistics (Lloyds, 1967; Iwao, 1968).

Taylor (1961) showed that the variance is related to the mean according to a power law as follows:

$$S^2 = a.m^b \quad (2)$$

where a and b = Taylor's coefficients
 m = mean density
 S^2 = variance

The simplest method of evaluating Taylor's coefficients is a linear regression of $\text{Log } S^2$ against $\text{Log } m$ (Southwood, 1978).

Iwao (1968) and Lloyds (1967) showed that mean crowding (\bar{m}^*) measured by the mean number per individual of other individuals on the same tip, is also linearly related to the mean density in most theoretical and biological distributions.

$$\bar{m}^* = m + \left(\frac{S^2}{m} - 1 \right) \quad (3i)$$

where \bar{m}^* = mean crowding

m = mean density

S^2 = within-field variance (= between-plant variance)

$$\text{or } \bar{m}^* = \alpha + \beta m \quad (3ii)$$

where α = index of basic contagion

β = density contagiousness coefficient

The coefficients b for Taylor (coefficient of dispersion of the sample mean) and β for Iwao describe the dispersion of mealybugs:

when b or $\beta = 1$, distribution is random

b or $\beta > 1$, distribution is contagious

b or $\beta < 1$ but > 0 , distribution is regular.

8.2.3 Development of sampling plans with dispersion coefficients

Taylor's coefficients a and b were used to develop two sampling plans. The relationship between proportions of mealybug-infested tips and mean densities was analysed after Wilson and Room (1983).

$$P_{(1)} = 1 - e^{-m \log_e (am^{b-1})(am^{b-1})^{-1}} \quad (4)$$

where a and b = Taylor's coefficients

m = mean density

$P_{(i)}$ = Proportion of infested tips.

Wilson and Room (1983) proposed sampling plans using Karandinos' (1976) equation for binomial sampling:

$$N = \frac{t^2}{D^2} \cdot q/p \quad (5)$$

where N = number of samples to be taken
 D = reliability level (0.2-0.4)
 t = standard normal deviation with
 $Z_{\lambda/2} = 1.68$ for $\lambda/2 = 0.1$

 P = proportion of infested tips
 q = 1 - P

For the development of an enumerative sampling plan the number of samples (N) needed to achieve a predetermined level of reliability was calculated as a function of the mean density per sampling unit by using Taylor's coefficients (Wilson and Room, 1983).

$$N = \left\{ \frac{t}{D_0} \right\}^2 a \cdot m^{b-2} \quad (6)$$

where t = standard normal deviate $Z_{\lambda/2}$ which equals to 1.68 for $\lambda = 30$
 D₀ = predetermined level of precision expressed as a ratio of

 the standard error to the mean (s.e./m) = (0.2-0.4)

8.3 RESULTS AND DISCUSSIONS

8.3.1 Dispersion coefficients

The regressions of log variance ($\log S^2$) to log mean ($\log m$) showed linearity for all locations (Figs. 8.1 and 8.2). The relationship between mean crowding (\bar{m}^*) to mean density (m) also showed rather superior curvilinearity than linearity (Fig 8.3 & 8.4)

Slopes of regression lines did not differ remarkably from each other in both variance to mean and mean crowding to mean regressions for all locations. Data was therefore pooled to calculate a common slope and intercept for Taylor's coefficients and Iwao's mean crowding statistics (Figs. 8.1, 8.2, 8.3 and 8.4).

The dispersion coefficients b according to Taylor (1961) and β

according to Iwao (1968) gave very significant values, greater than 1 ($P \leq 0.01$, 85df for each location).

The t values of slopes and r^2 values supported very significant slopes indicating a contagious distribution (Table 8.1).

The values of the coefficients a and b reported here were similar in some instances and far greater than those reported for cassava mealybugs in Nigeria a few years back (Schulthess et al., 1989). However the a and b coefficients are not constant and could be affected if the distribution changes (Wilson, 1982).

8.3.2 Sampling plans

A scattergram of percentage infested tips plotted against mean densities of field data showed a general trend of increasing proportions of infested tips with increasing mealybug densities for all locations. Pooled data from all locations showed the same trend. At the low mealybug densities observed, 100% infestations of tips were never recorded in contrast to reported cases (Schulthess et al., 1989).

The relationship of percentage infested tips to mean densities analysed by equation 4, according to Wilson and Room (1983), showed a similar trend as the field data (Fig. 8.5).

The higher aggregation indices in the dispersion analysis were confirmed by the small proportions of infested tips ($P(i)$), for any given mean.

Wilson (1982) showed that the more clumped the species, the smaller the $P(i)$ - m relationship. The $P(i)$ - m relationships could be used to quickly determine the required number of samples at given mealybug densities and infestation levels and consequently the choice of a sampling plan to achieve a reliable level of precision.

A general slope and intercept for pooled data analysed according to Taylor (1961) were used to develop binomial and enumerative sampling plans according to equations 5 and 6 respectively.

Mealybug densities based on accurate counts were used to estimate model parameters to test the quick count or presence-absence binomial sampling plan.

The proportions of infested tip mean relationships derived from

Fig. 8.1 Log variance to mean mealybug densities for the calculation of dispersion coefficients according to Taylor (1961). Data represent 48 sampling periods at New Tafo, Begoro and Korofidua all in the rainforest zone of Ghana

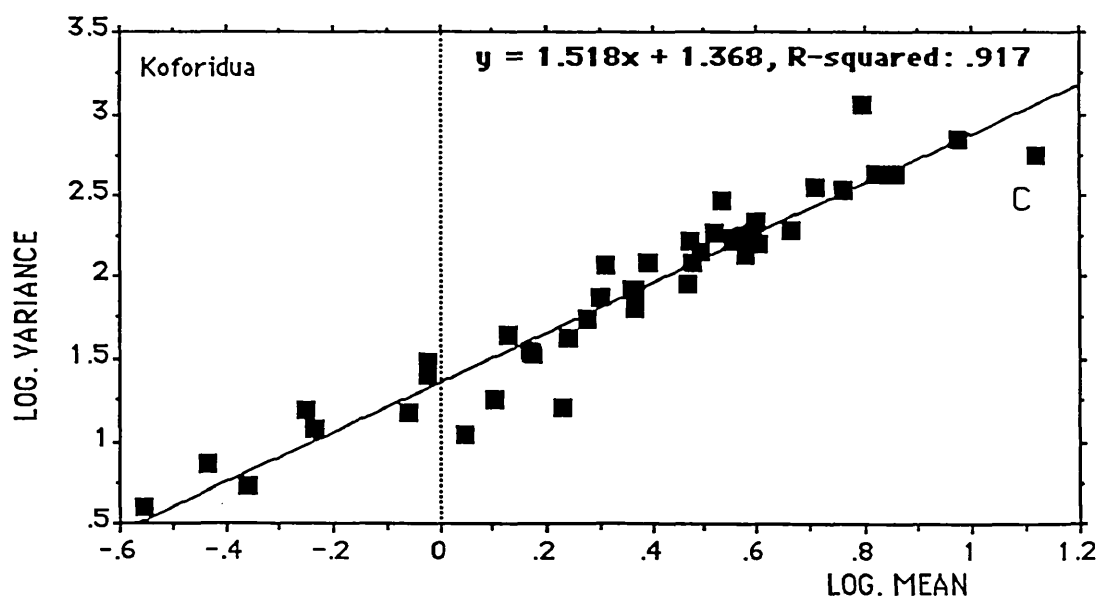
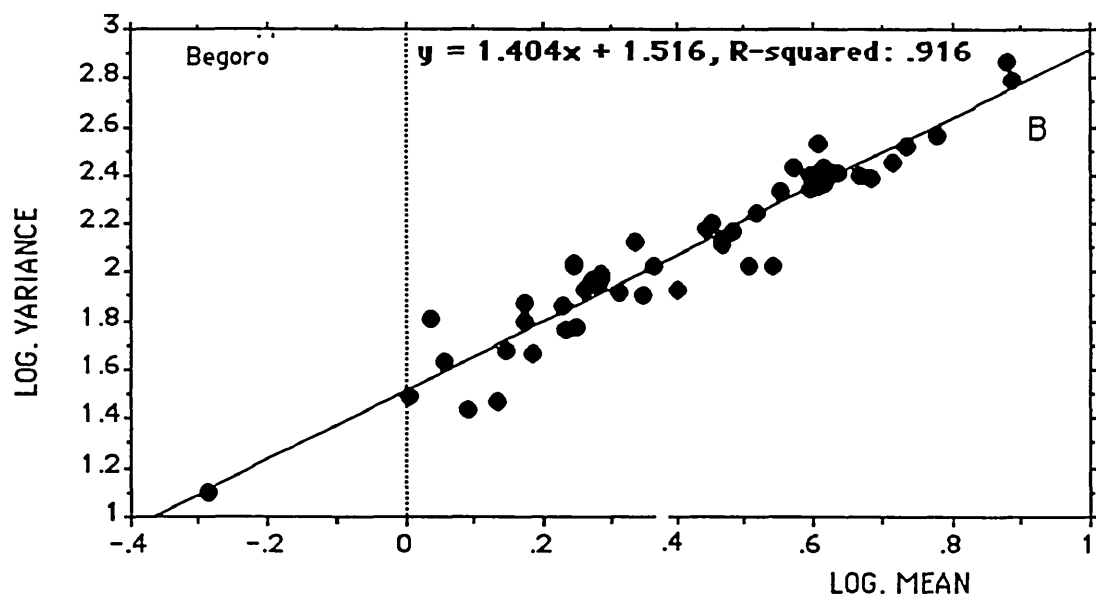
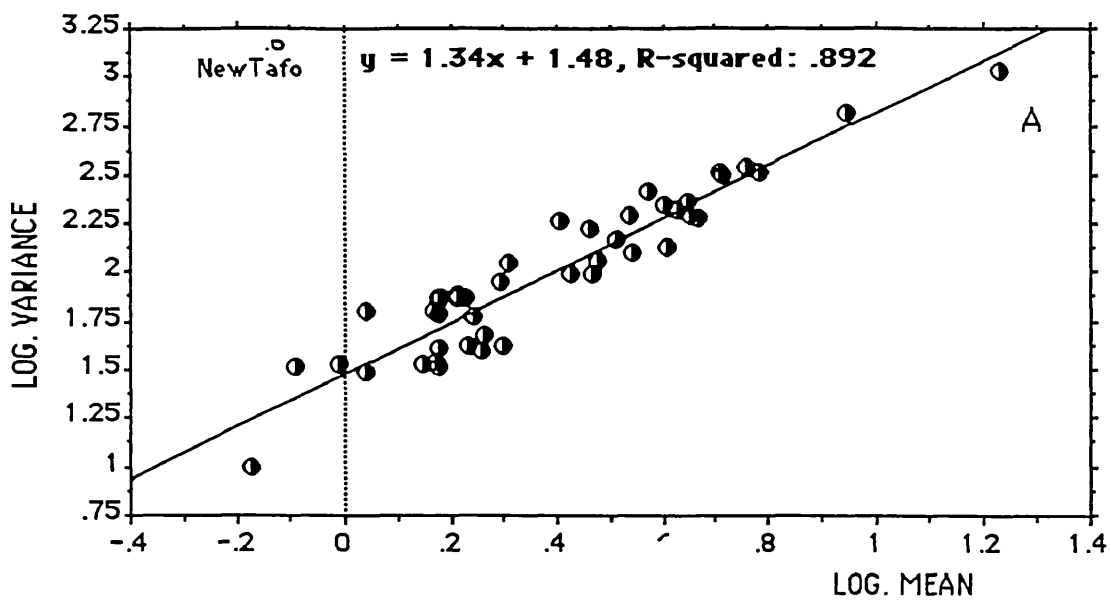


Fig. 8.2 Variance to mean relationship for the calculation of dispersion coefficients according to Taylor (1961). Data represent 48 sampling periods at Kasoa/Accra in the coastal savannah (D) and slopes of regression lines for the forest zone were compared graphically in (E). Data was pooled for all 4 locations for a general slope in (F)

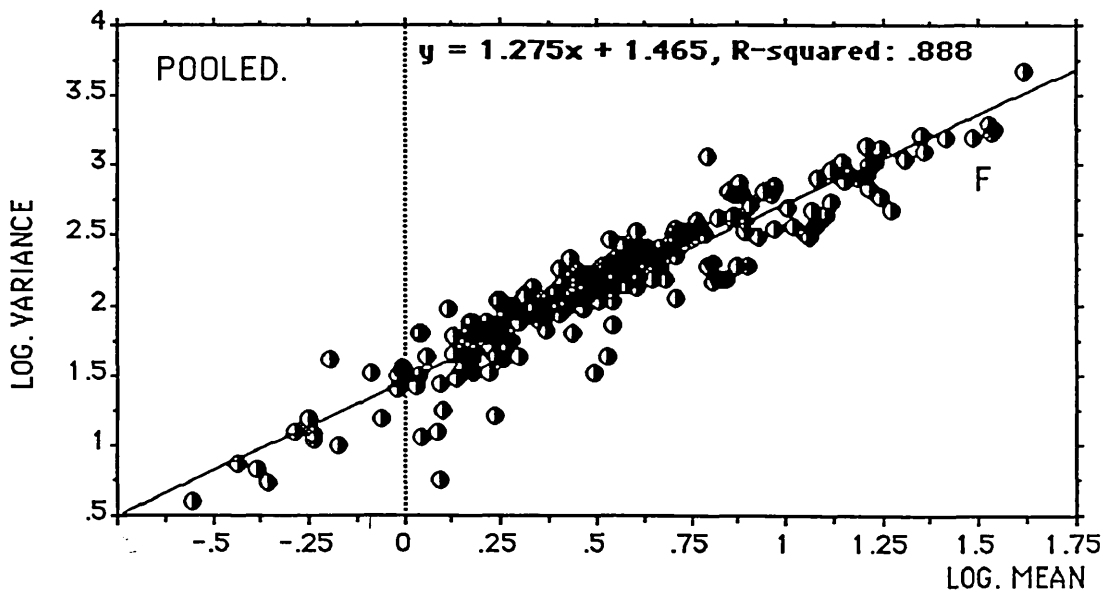
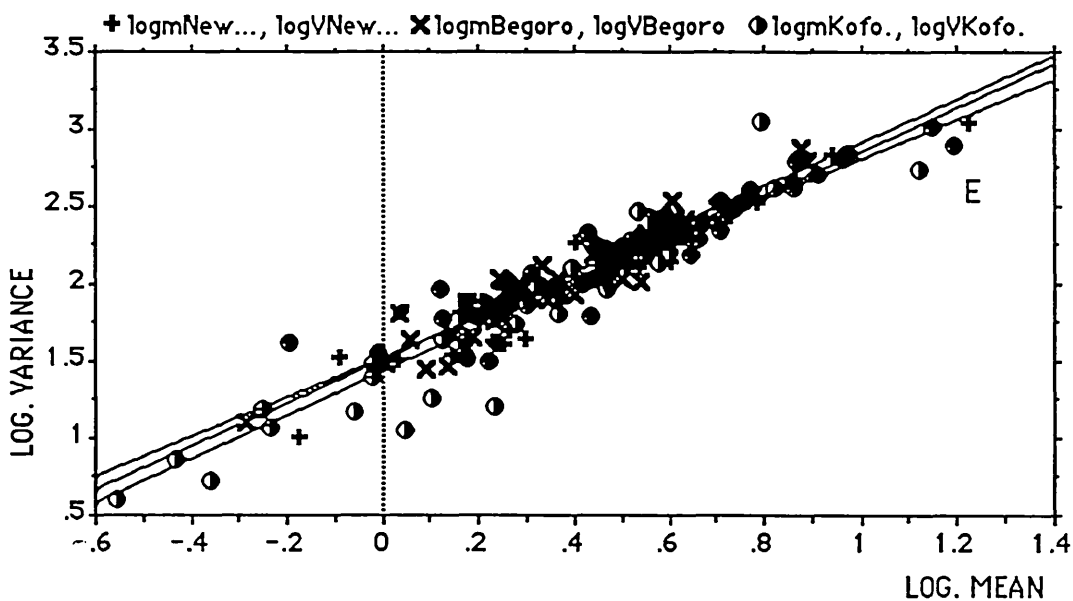
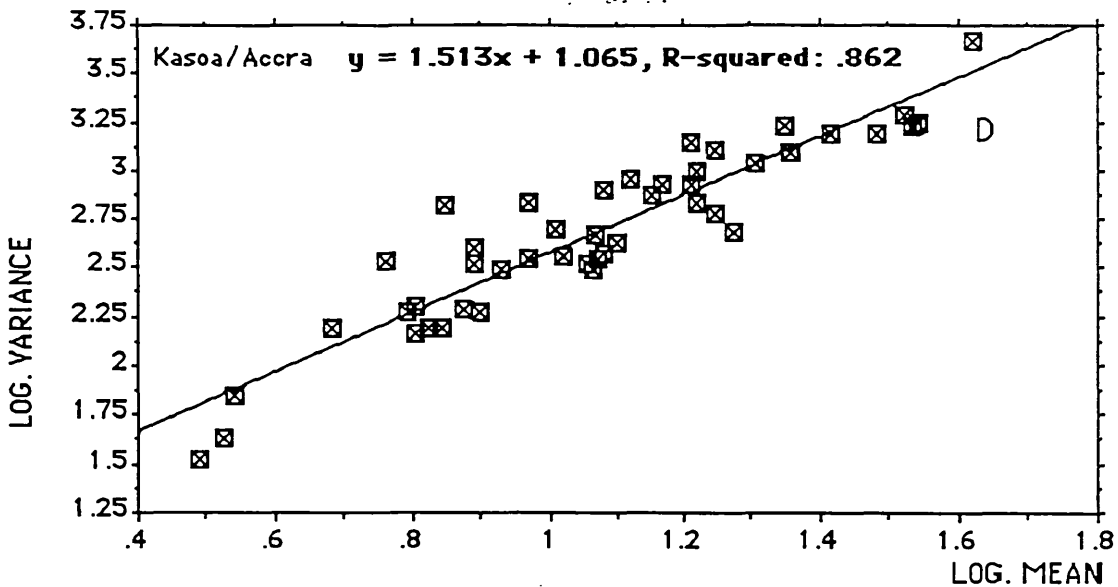


Fig. 8.3 Mean crowding ($M+S^2/M-1$) to mean density relationship for the calculation of dispersion coefficients for cassava mealybugs according to Iwao (1968). Data represent 48 sampling periods at New Tafo, Begoro and Kororidua in the rainforest zone of Ghana

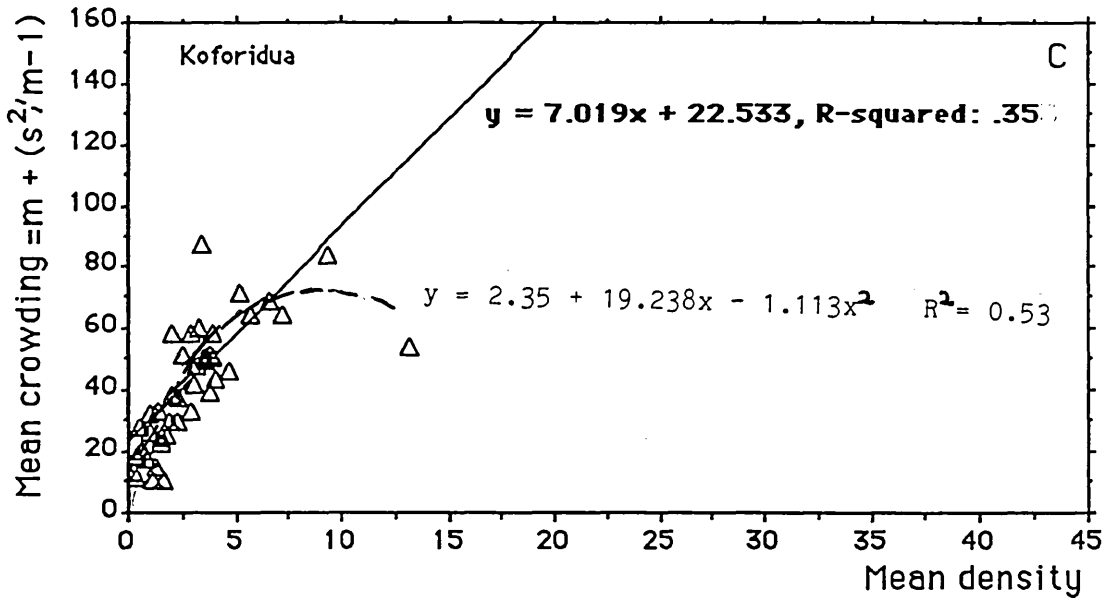
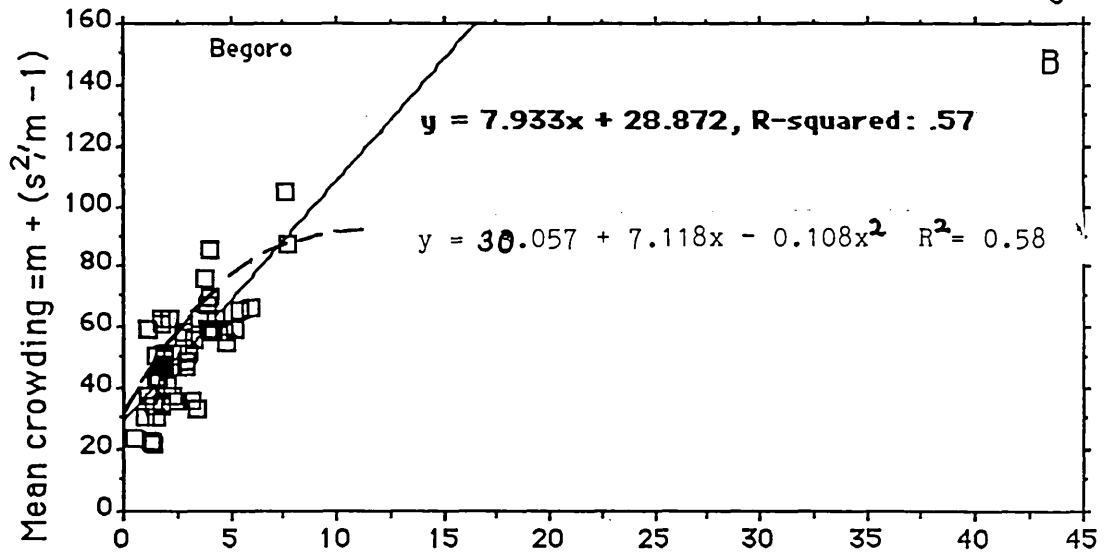
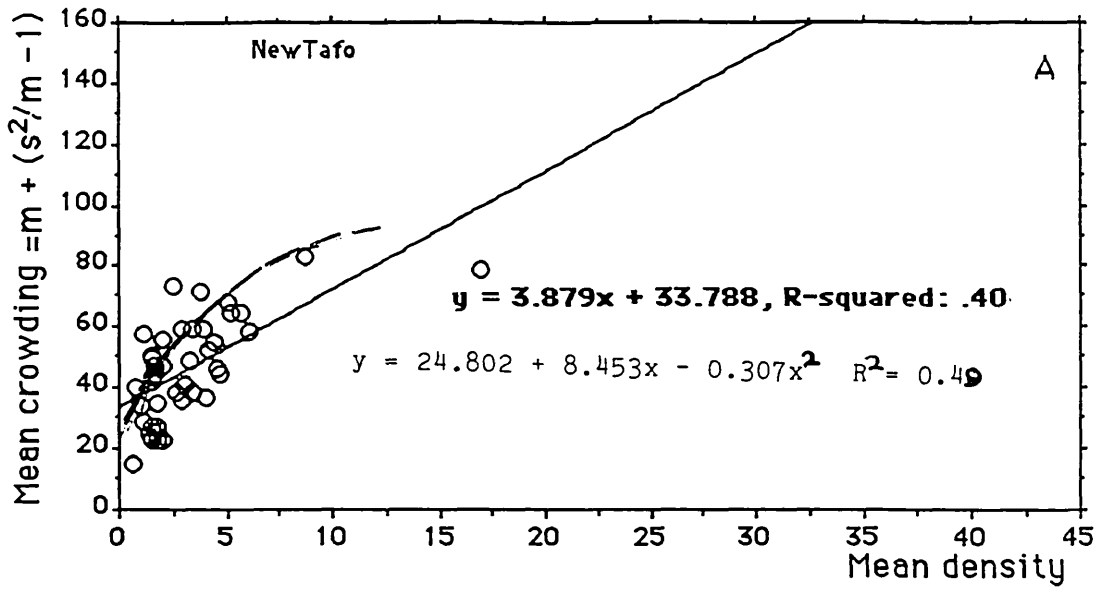


Fig. 8.4 Mean crowding ($M + \frac{S^2}{m} - 1$) to mean density of mealybugs for the evaluation of dispersion coefficient according to Iwao (1968). At D = Kasoa in the coastal savannah E = Pooled data for rainforest F = For both savannah and rainforest

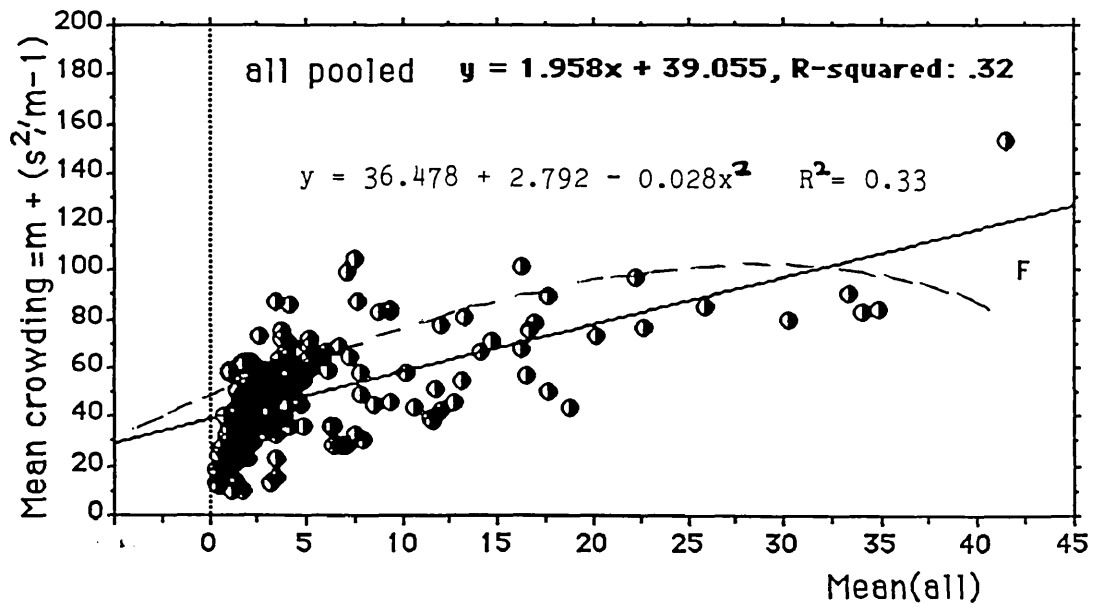
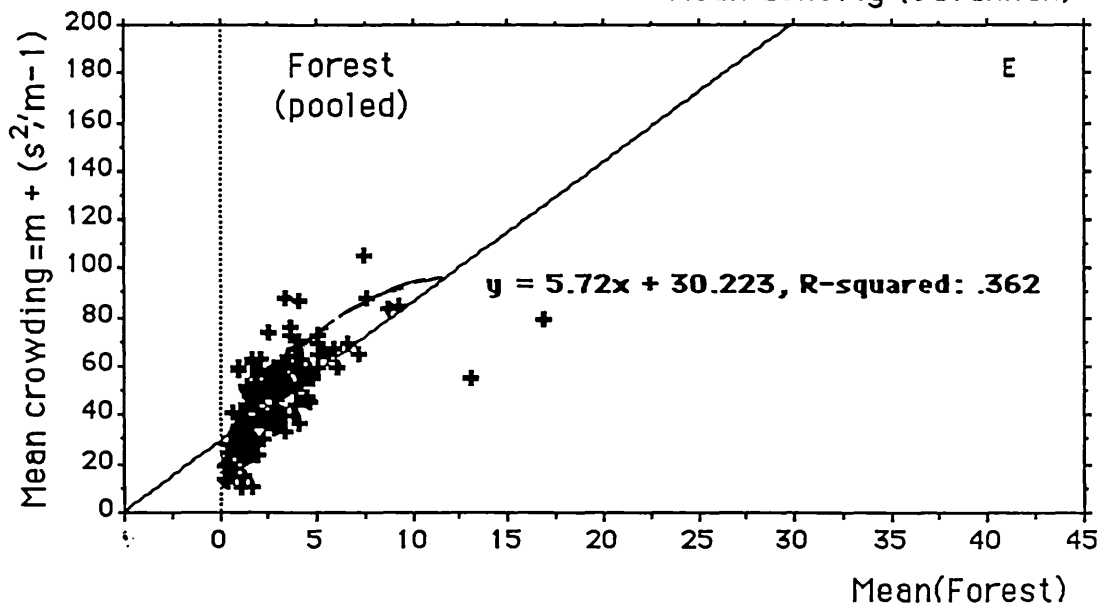
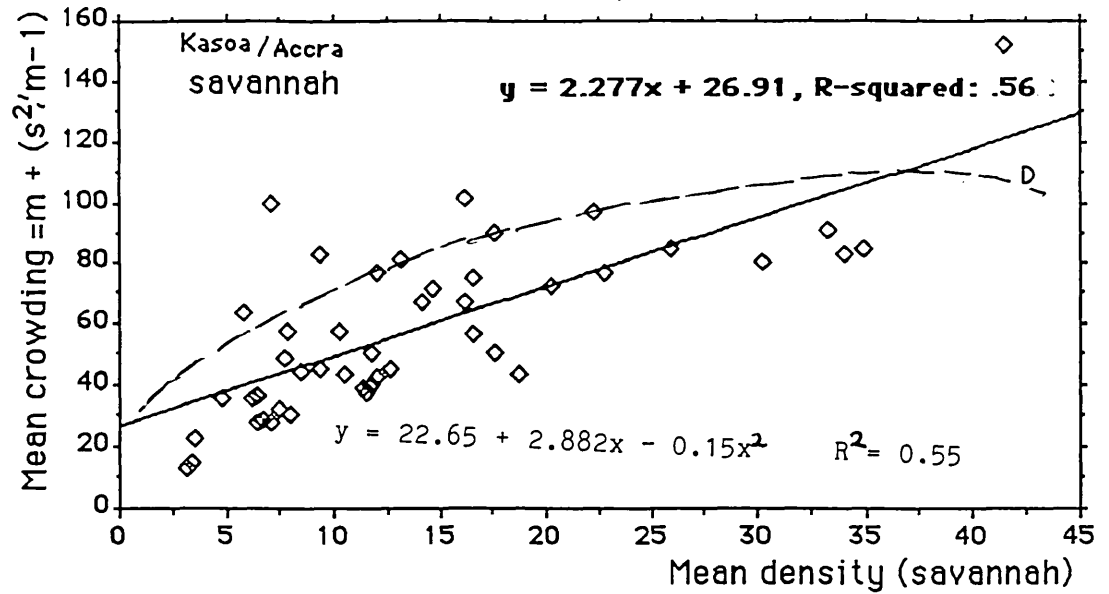


Table 8.1 Comparison of mean crowding statistics and Taylor's coefficients for dispersion analysis of cassava mealybugs in Ghana

	Mean crowding statistics				Taylor's power law coefficients				CM
	α	β	r ²	t slope	a	b	r ²	t slope	density range
Koforudua	22.53	7.019	0.355**	4.75**	26.42	1.44	0.903***	21.25***	1-16
Begoro	28.87	7.93	0.577***	8.01**	25.35	1.52	0.916***	22.57***	1-10
New Tafo	33.78	3.88	0.404***	5.34**	19.19	1.52	0.895***	18.61***	1-20
Kasoa/ Accra	26.91	2.28	0.562***	7.52**	32.58	1.07	0.862***	16.59***	3-40
Pooled data (all localities)	39.06	1.96	0.320**	9.24**	18.83	1.47	0.888***	18.54***	1-40

* Significant at $P \leq 0.05$

** Significant at $P \leq 0.01$

*** Significant at $P \leq 0.001$

Student t at 47 df

Fig. 8.5 Scattergram of the relationship of percentage infestation and mealybug densities from field data (A) and as described by binomial equation (B)

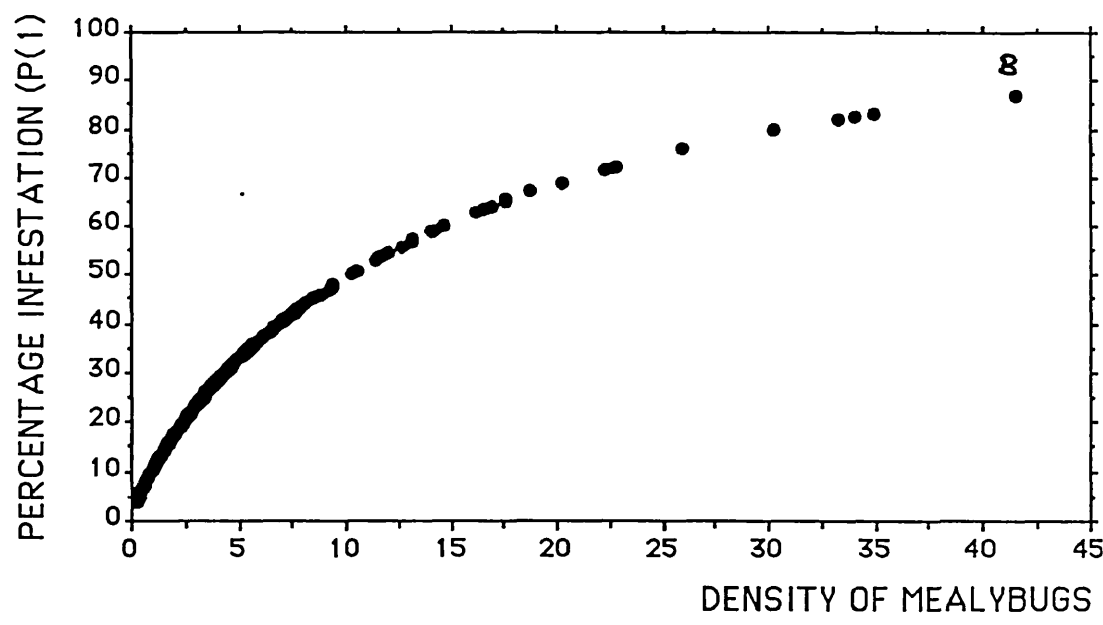
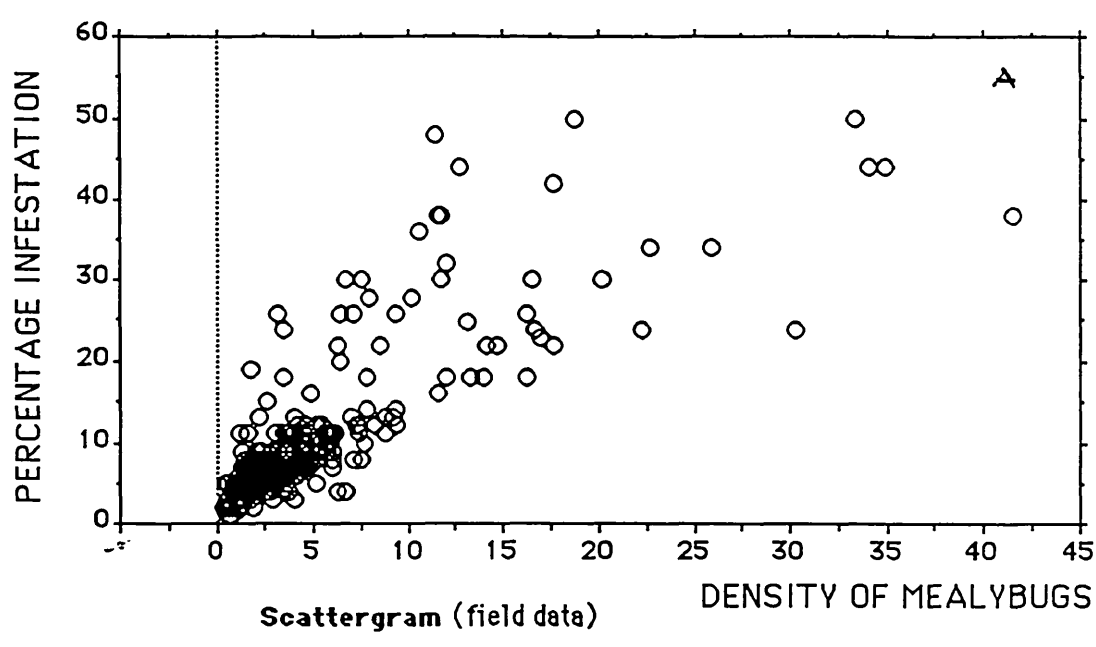
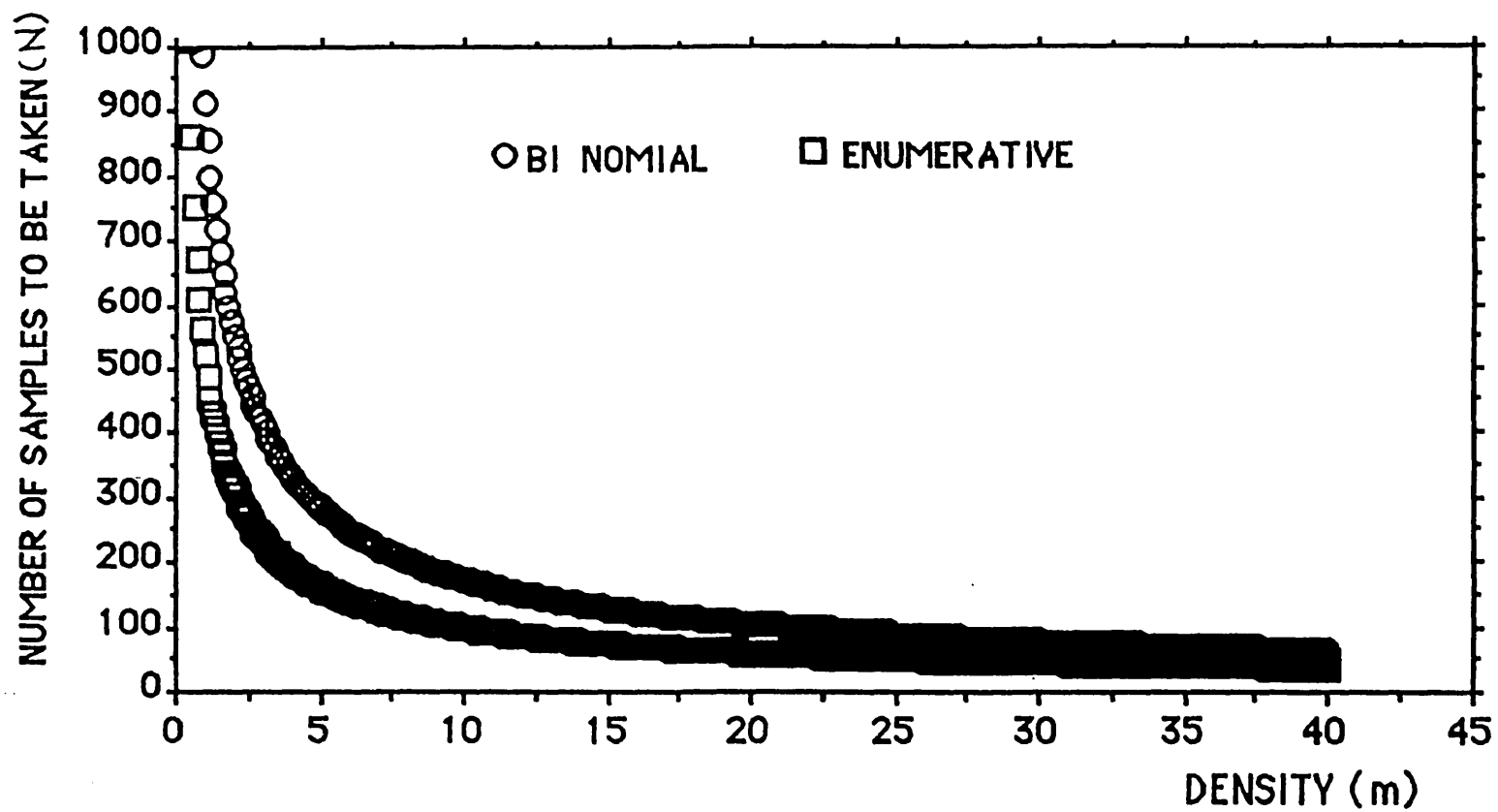


Fig. 8.6 Estimating the sample size (N) as a function of the mean-density (m) of cassava mealybugs using binomial (●●●) and enumerative (□□□) sampling programs at $N(D_0) = 0.3$ level of reliability



Scattergram for estimating sample size as a function of cassava mealybug density

quick counts could be a reasonable estimate of accurate counts at very low densities. However at very low mealybug densities (<2.5 per tip) both the enumerative and to a greater extent, the binomial sampling plan, propose a huge sample size which is impractical in smaller peasant farms.

All sample sizes decrease asymptotically with increasing mealybug densities up to about 20 mealybugs per tip and stay the same for the rest of the densities (Fig. 8.6).

8.3.3 Criteria for selecting a sampling plan

The binomial sampling plan, involving the presence-absence method, is less time-consuming (Wilson, 1982). When a field is to be sampled repeatedly, binomial sampling helps to avoid destruction to field and a possible change to microclimatic conditions. It is most appropriate for large-scale surveys involving large areas.

The enumerative sampling plan, involving accurate counts is a destructive one since each tip should be dissected for counts of mealybugs. However, for qualitative analysis of mealybug-parasitoid interactions, involving mummies, the method provides the only option for such evaluations.

At higher mealybug densities, above 20 mealybugs per tip, both methods require nearly the same sample size. This means at higher densities any of the methods could be used for the same degree of accuracy. Below 10 mealybugs per tip the sample size suggested by the binomial plan becomes twice or more times larger than the enumerative plan. At such low densities the choice of any of the two sampling plans is dictated by the aims of the study.

8.4 CONCLUSION

Dispersion coefficients derived from Taylor's and mean crowding statistics show very high aggregation of cassava mealybugs in all fields and locations.

At low mealybug densities (<10 per tip) the enumerative sampling plan offers the most practically reasonable sample size from an average size field.

At densities above 20 mealybugs per tip both binomial and enumerative sampling plans are complementary.

SECTION III

SEMI-FIELD AND LABORATORY EXPERIMENTS

CHAPTER 9

SEMI-FIELD AND LABORATORY EXPERIMENTS TO EVALUATE THE IMPACT OF RAIN AND WIND ON CASSAVA MEALYBUGS

9.0 ABSTRACT

An evaluation of the impact of rain and wind on cassava mealybugs on tips was done in the field under natural rainfall and winds. The impact of the two factors on mealybugs was also assessed in the laboratory by their simulation with a bath shower and electric fan.

A dose response curve for completely exposed mealybugs to natural rains showed a percentage washed-off, increasing from just below 20% in rains of less than 10 mm per day to almost 90% in rains above 70 mm per day. Winds accompanying the natural rains, the intensity of which could not be separated and measured, contributed only 5% blown-off mealybugs with the lowest rainfall intensity, increasing to 30% blown-off with rainfall above 70 mm per day.

Laboratory simulated rain and wind had a mechanical impact on crawlers and early second instar mealybugs but showed little or no effects on more advanced stages. Rain is therefore more likely to be the most important abiotic factor exerting impact on cassava mealybug populations during the rainy season, hence observed low densities of mealybugs and the opposite during the dry season.

9.1 INTRODUCTION

Outbreaks of cassava mealybug occur during the dry season in the absence of its natural enemies. The outbreak associated with dry seasons could be related to two factors i.e. the absence of rain as a natural control factor and favourable changes in the physiology of the cassava plant under drought stress that increases the nutritional value of the food (Fabres, 1981; Fabres and Le Ru, 1986).

Low mealybug densities usually observed in the rainy season could be due to the mechanical effect of the rain (Fabres, 1981) and the incidence of entomophagous fungi (Le Ru, 1986). Other environmental factors like temperature and air humidity have little influence on mealybug densities (Le Ru and Fabres, 1986). In general, daily average temperatures in Ghana's cassava growing areas are rarely outside 24-30°C. For this temperature range, differences in the life table statistics due to

drought stress are rather small and hence, are unlikely to explain mealybug outbreaks in the dry season (Schulthess et al., 1987) (see Appendix for range of monthly temperatures).

In this thesis, Section II, Chapter 2, mealybug densities were negatively correlated with increasing rainfall intensities. To quantify the impact of rainfall and winds, usually associated with it, a field experiment involving natural rains with winds and the simulation of the two factors in the laboratory were performed on mealybugs.

The aim of the studies presented here was to use approximate or improvised equipment to get an idea of the degree of wash-off or blow-off of mealybugs by rain and wind to justify the mechanical role usually assigned to the factors.

9.2 MATERIALS AND METHODS

9.2.1 Semi-field experimental assessment of natural rain and wind impact on cassava mealybugs

A wooden cage covered from all sides with an 0.8 mm diameter nylon-mesh and partitioned into two by completely covering the top of one half and the middle wall with a polythene sheet, whilst the other half was left open was used to assess rain and wind impact on cassava mealybug in the field (see Plate 7). Potted plants with a known number of mealybugs on them were placed ten each in the two compartments of the cage. The cage was placed in the middle of a cassava field in the evening prior to expected rains. After each daily rain (24 hrs), during which exposure of mealybugs to rains occurred, counts of mealybugs left on tips were done. The procedure was repeated 16 times for different rainfall intensities. Percentage of mealybugs lost from the initial numbers on tips exposed to factors was taken as wash-off when it was rainfall with wind and blown-off when it was wind alone. The amount or intensity of rain for the 24 hrs was obtained from a nearby meteorological station at the Cocoa Research Institute of Ghana.

However average wind speeds for the same period were unsuitable because they could differ from speeds during the hours of the rain. Rainfall data was cumulative for the period and therefore reflected the actual intensity which produced the observed losses.

Dose response curves were obtained for the two compartments of the



Plate 7 The double cage used to evaluate the impact of rains and wind on cassava mealybugs in semi-field experiments

cage: i.e. open cage, where mealybugs were exposed to the rains and partially closed part, where mealybugs were exposed to only winds from the sides of the cage.

For statistical analysis the slopes, t value of slope and r^2 values of regression lines of losses against intensity of rains or wind, were tested for significance. Percentage washed-off was compared with percentage blown-off of mealybugs by multiple comparison ANOVA (Scheffe's F-test).

9.2.2 Laboratory simulated rain and wind impact on cassava mealybug

In the laboratory, rainfall was simulated by improvising a bath shower for rain-generating equipment and wind was generated by table top electric fan.

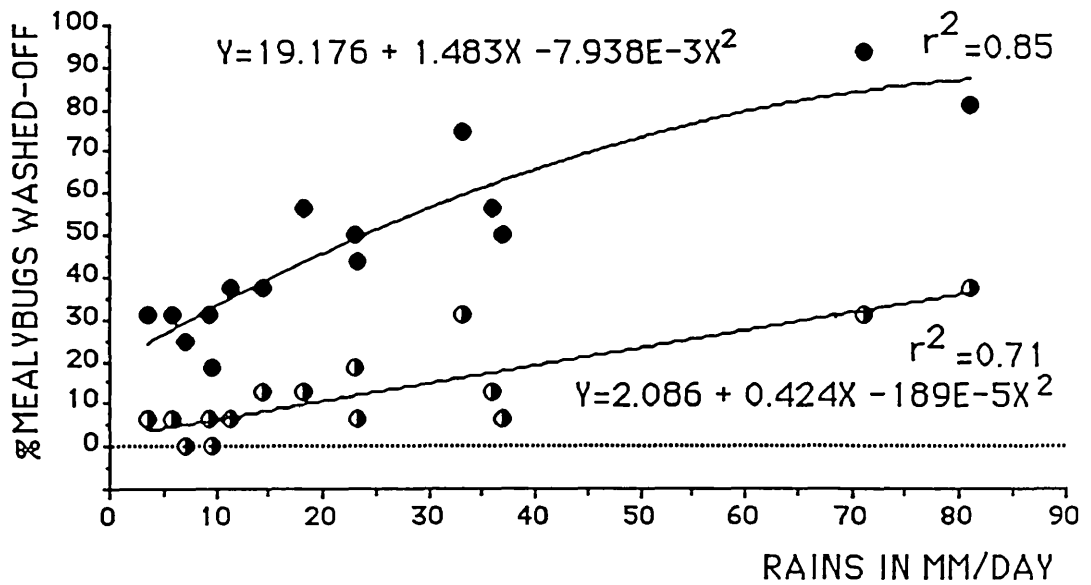
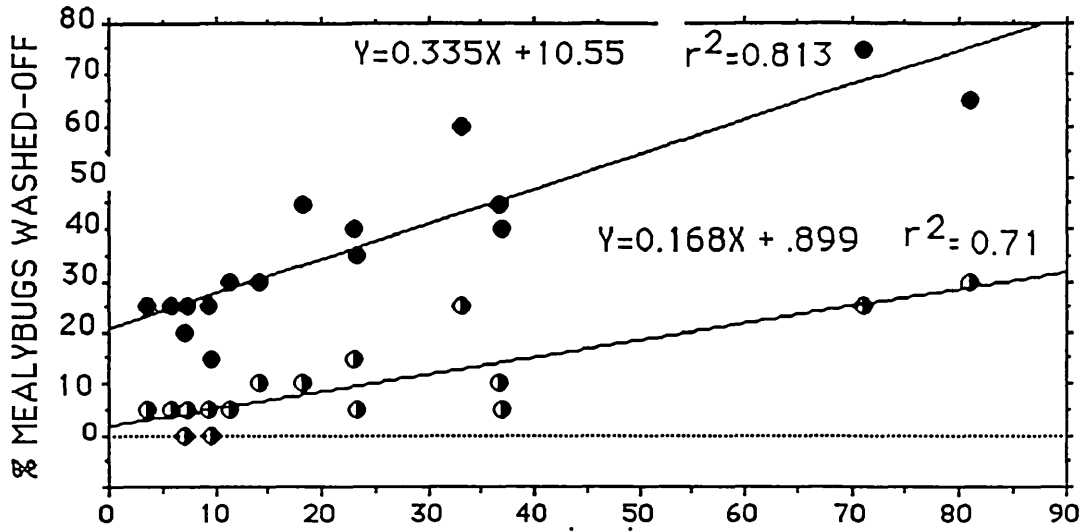
The impacts of each of the two factors were assessed separately and then collectively on mealybug stages. The bath shower output was calibrated by measuring the amount of water collected in rain gauge at 5 minutes and 10 minutes running. The optimal position of the shower head gave 25 mm after 5 minutes and 50 mm at 10 minutes of running. The 3-switch electric fan gave output on medium and high speed button positions of 2.8 metres per second and 4.2 metres per second respectively at 26.3°C on the Testovent 4000 anemometer and thermometer integrated instrument placed a metre from the fan at the position of the potted plant with mealybugs. On the Beaufort wind scale, speeds of 3.4 metres and 5.3 metres per second are capable of causing constant leaf and twig movement. Though the wind speeds generated by the fan were far less strong than those observed during stormy conditions prior to or during rainfalls in the tropics, they could adequately represent prevailing wind speeds under normal conditions at New Tafo.

In another study, cassava mealybugs on tips (a mixture of all stages pre-counted) were completely immersed in a bucket of water. Detachments and floating of each stage were monitored at 5, 10, 20, 40 and 80 minute intervals. Ten tips with 40 mealybugs each were separately tested. Mean percentage detachment of stages of mealybugs from tips were related to time after immersion in the bucket of water.

9.3 RESULTS

The dose response curve for mealybugs exposed to rains in the wooden

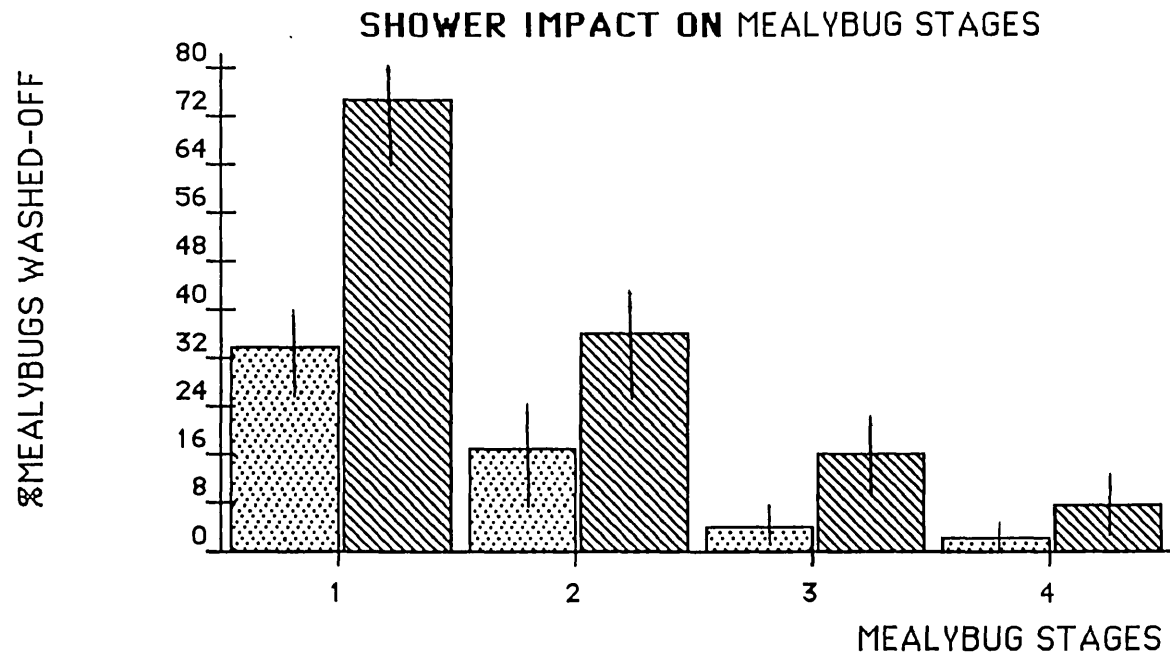
Fig. 9.1 Impact of natural rains on cassava mealybugs in a semi-field double-cage experimental evaluation. N = 10 tips each with 40 mealybugs per daily rain intensity. Dose response curves are derived from linear and polynomial (2nd order) regressions of proportions of mealybugs lost in each cage against daily rain intensities



- % MEALYBUGS LOST IN CAGE EXPOSED TO WINDS ONLY
- % MEALYBUGS LOST IN CAGE EXPOSED TO RAIN AND WIND

Fig. 9.2 Laboratory simulation of rain through the use of bath shower and its impact on cassava mealybug stages 1 to 4. N = 10 tips with 40 mealybugs of each stage. Losses due to shower rain expressed as % washed off are proportions lost from the lot exposed to shower. Bars = 2 s.e.

LABORATORY EXPERIMENTS.

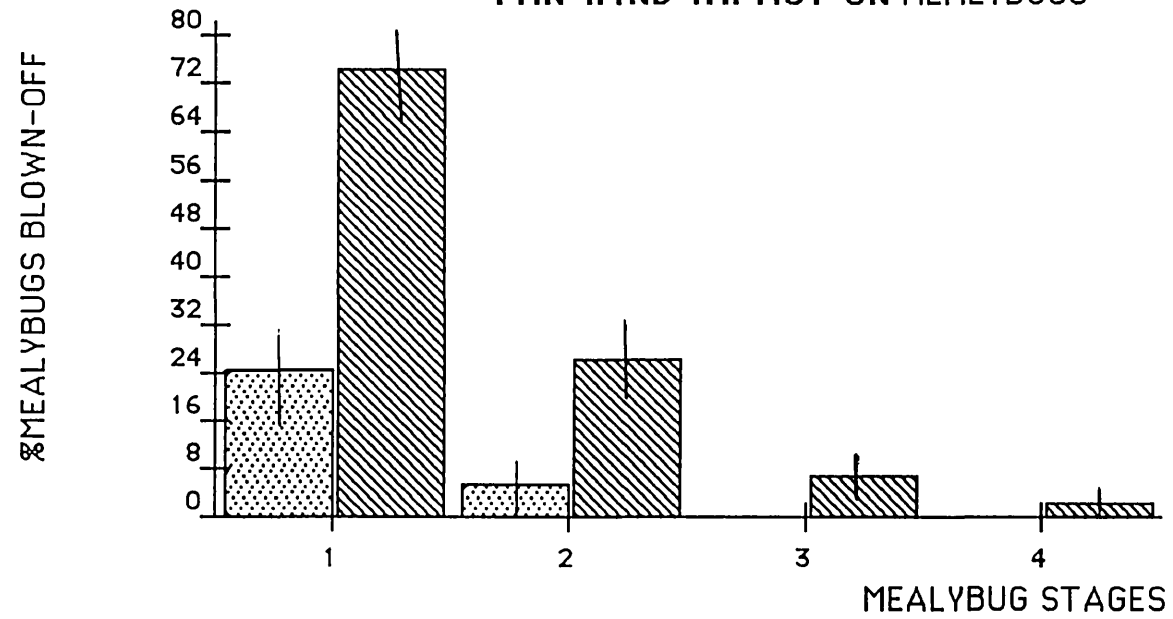


▣ % WASHED-OFF AT 25MM SHOWER INTENSITY

▤ % WASHED-OFF AT 50MM SHOWER INTENSITY

Fig. 9.3 Laboratory simulation of wind through the use of electric fan and its impact on cassava mealybugs stages 1 to 4. N = 10 tips with 40 mealybugs of each stage. Losses due to fan expressed as % blown off are proportions lost from the lot exposed to fan wind. Bars = 2 s.e

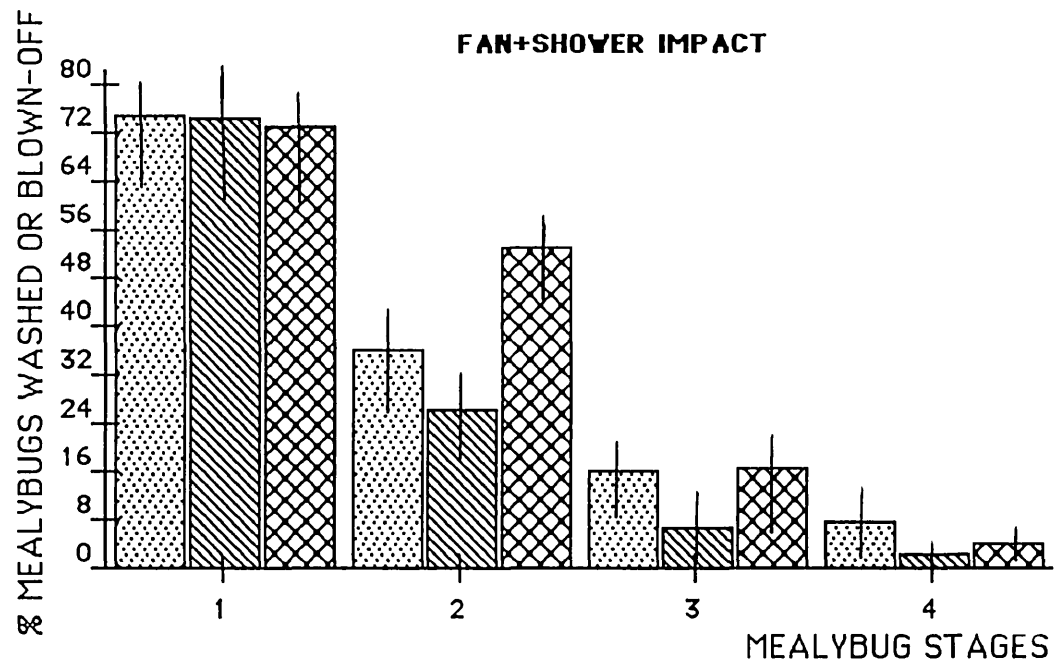
FAN WIND IMPACT ON MEALYBUGS



▨ % BLOWN-OFF AT 2.8M/SEC.

▨ % BLOWN-OFF AT 4.2M/SEC.

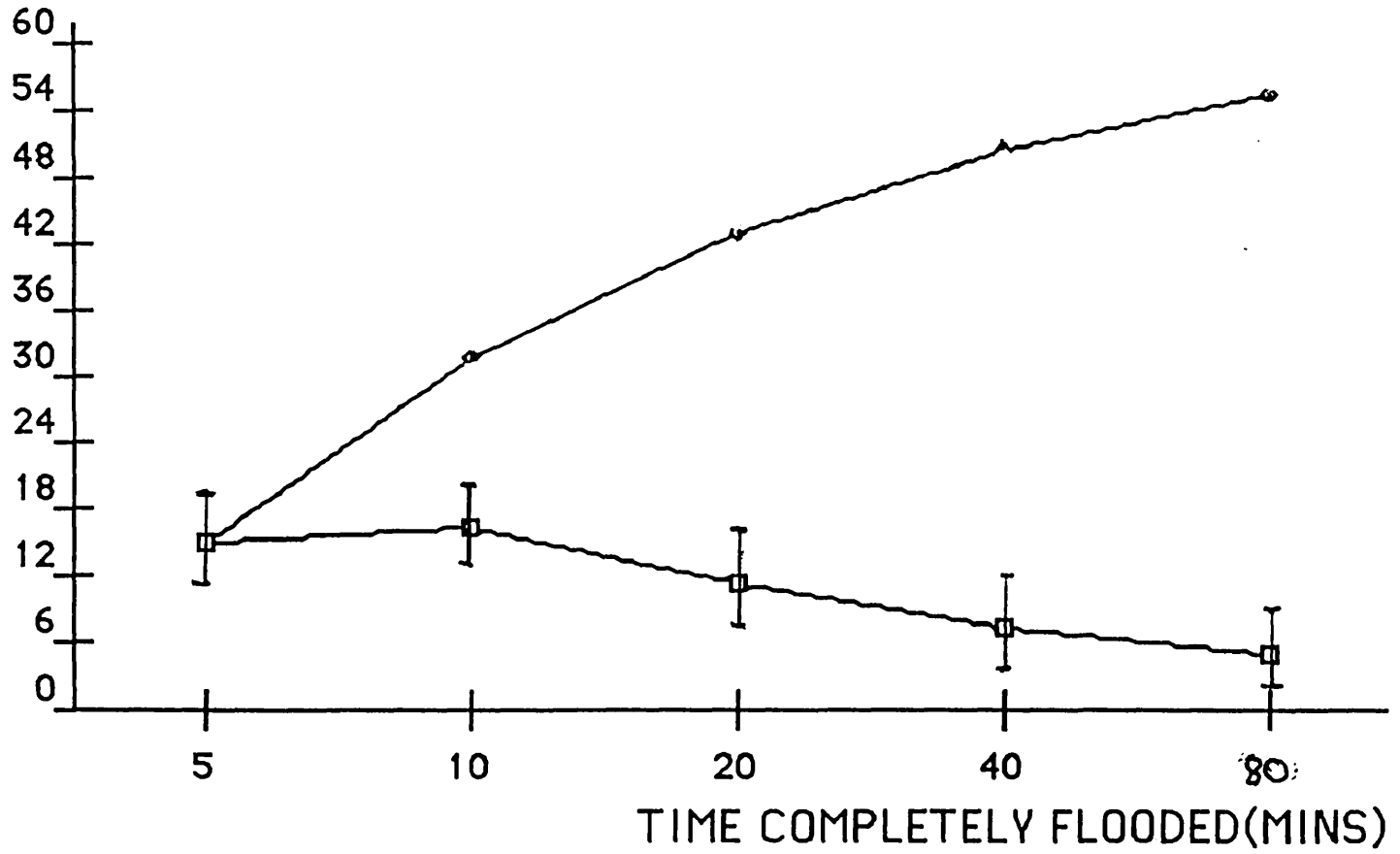
Fig. 9.4 Laboratory simulation of the combination of rain and wind through the use of bath shower and electric fan at dosages of 50 mm and 4.2 m/sec respectively as against the individual impact of each factor. N = 10 tips . with 40 mealybug of each stage. Bars = 2 s.e.



- ▣ % WASHED-OFF (SHOWER AT 50MM)
- ▤ % BLOWN OFF AT 4.2M/SEC
- ▥ % MORTALITY AT 50MM + 4.2M/SEC

Fig. 9.5 Laboratory simulation of flooding of cassava mealybugs through the immersion of tips with all stages of mealybugs in bucket of water. N = 10 tips with 40 mealybugs of all stages. Detachment and floating of mealybugs is expressed as proportions of mortality according to or after (cumulative) 5, 10, 20, 40 and 80 minutes from immersion. Bars = 2 s.e.

% MORTALITY (ALL MEALYBUG STAGES)



cage showed percentage washed-off increasing from just below 20% with rains less than 10 mm per day to almost 90% with rains above 70 mm per day.

On the other hand, winds accompanying rains contributed less than 5% losses of mealybugs at rain intensity of 10 mm per day, increasing to only 30% losses above 70 mm per day of rains though both factors acted significantly on mealybugs. The slopes of both regression lines; $b_r = 1.483$ and $b_w = 0.42$ and t values of slopes; $t_R = 3.618^*$ and $t_w = 1.403^*$; $df = 14$ ($r_R^2 = 0.842$ and $r_w^2 = 0.71$) were significant at $P \leq 0.05$. Very significant differences between mealybug losses due to rain and wind alone were observed in an ANOVA ($F = 61.062^{***}$) and wind only $F = 34.1^*$ (see Appendix C1).

In the laboratory simulated rain experiments, percentage washed-off of mealybug stages were 34% to 75% at shower intensities of 25 mm and 50 mm respectively for crawlers but steeply diminishing to 16% and 35% for the same respective rain intensities for second instars of mealybugs. Third and fourth instars showed a fairly high resistance to shower rain, rarely exceeding 16% washed-off even at the highest shower intensity (ANOVA, $F = 134.084^{***}$).

Since the most notable impact of the shower was on crawlers and second instars a multiple comparison based on ANOVA (Scheffe F-test) showed a very significant difference on impact between the two stages ($F = 37.173^{**}$ significant at $P \leq 0.001$) (see Appendix C2).

Winds simulated by electric fan exerted much lower impact on mealybugs causing losses of 24% and only 6% of crawlers and second instars at 2.8 metres per second. The 2.8 metre per second wind speed had no impact at all on third and fourth instars. At 4.2 metre per second wind speed crawler and second instar losses were 75% and 26% respectively. Less than 8% of third and fourth mealybug instars were lost at 4.2 metre per second wind speed ($F = 253.53^{***}$ see Appendix C.3).

When third and fourth instars were ignored because of virtually no impact on them by wind, the zero hypothesis was rejected for real differences between percentage losses for crawler and second instars ($F = 89.93^{***}$ significant at $P \leq 0.001$, in Appendix C.3 and also see Fig. 9.3).

In the combination of the two factors, i.e. shower "rain" and fan

"wind" there were only slight changes on impact of the two from the individual impact of the factors. For crawlers no significant difference was observed. However a general impact was exerted on mealybugs by the two factors together (ANOVA $F = 242.24$).

However slightly more second and third instars were lost; 52% and 16% respectively. Fourth instars showed virtually no response to the combination of factors even at the maximum doses (see Appendix C.4).

Complete immersion of tips with mealybugs in a bucket of water showed detachment and floating of 14% after 5 minutes, increasing cumulatively to over 50% by the end of 20 minutes (Fig. 9.5). Significant rates of mortality were observed between times of immersion (ANOVA $F = 7.96$) (Appendix C.5).

9.4 DISCUSSIONS AND CONCLUSIONS

The contrast of encountering higher mealybug densities during the dry season and the opposite during the rainy season suggests rainfall is a major abiotic factor in the regulation of mealybug populations.

The results of the laboratory simulated rain and wind impact on mealybug go further to testify the belief that rain and wind, among other factors, are also contribute to the observed seasonal fluctuations in mealybug densities in the field. In the rainforest zone, where daily rainfall at the peak of the rainy season could exceed 70 mm, up to 90% of mealybugs on tips could be washed-off. It therefore becomes difficult to locate cassava tips with large mealybug densities. Single mealybugs left on tips after the rainy season then give rise to the early colonies at the beginning of the dry season which explode later on as the dry months go by.

The mechanical impact exerted by the two usually combined abiotic factors, rain and wind, is more pronounced for younger instars of mealybugs. The most vulnerable stages to the two factors are the crawlers. Presumably this could be due to the small size and light weight of crawlers as compared to the more advanced stages. It could also be due to the fact that crawlers and early second instars do not have adequate waxy-coat body coverage, ovisacs and long stylets which could give extra protection and anchorage. Whereas 3rd and 4th instars are generally virtually sessile, crawlers and 2nd instars are very restless and mobile and are therefore more likely to be dislodged from

tips by the two factors.

If rainfall impact on mealybug is limited to the rainy season, wind could exert its impact throughout the year. Apart from the mechanical removal of young mealybug stages, which could result in their mortality, wind could also serve as a factor of dispersal of mealybugs. After removal and carriage of mealybugs by wind, the few which land on suitable host plant surfaces are more likely to survive and establish new colonies. This could explain the rapid and unstoppable spread of mealybugs in the huge cassava belt of Africa, which continues unabated.

The seasonality of mealybug outbreaks is a clear testimony to the fact that rainfall remains the most important abiotic factor regulating mealybug densities in the rainy season (Fabres, 1981; Schulthess, 1987; Gutierrez et al., 1987; Le Ru et al., 1989).

The revelation of cassava mealybugs (virtually all pre- and oviposition adults) withstanding up to ~~80 mins~~ complete flooding without detaching from cassava tips is astonishing. It could probably be due to the hydrophobic nature of the waxy-coat they have on their bodies which could prevent direct contact of water with the body. It is suspected that a thin film of air could be maintained between the body and the water thus providing the required oxygen for a fully grown mealybug to withstand longer periods of flooding.

In the field, therefore, matured cassava mealybugs on tips blown down and submerged in water for up to 80 minutes are likely to come out alive. This needs further investigations to find the threshold of survival under flooded conditions.

SECTION IV

GENERAL DISCUSSIONS AND SUMMARY OF CONCLUSIONS

CHAPTER 10

GENERAL DISCUSSIONS AND SUMMARY OF CONCLUSIONS

The cassava mealybug problem is no doubt one of the serious challenges to staple food production in Africa probably second or at par only to the threat of locust invasion. As in many other cases, a quick and straightforward solution to the mealybug problem eluded Africa until the launching of the Africa-wide Biological Control Programme (ABCP) by IITA. The problem also signalled a clear warning on the over-dependence on chemical control as a panacea to the increasing pest problems in Africa. Therefore the urgent need for strengthening biological control capabilities as the core in an Integrated Pest Control strategy cannot be over-emphasized.

The results of the biological control of cassava mealybug in Ghana in particular and elsewhere in Africa, as presented by many researchers, make the control attempt one of the success stories in the landmark of successful biological control. It is very similar to that of the cottony cushion scale, Icerya purchasi, in California, the mango mealybug, Rastrococcus invadens in West Africa (Williams, 1986), the gypsy moth, Lymantria dispar in the eastern United states of America or numerous other examples to be found in handbooks on classical biological control and invasions (e.g. Elton, 1958; DeBach, 1974; Mooney and Drake, 1986).

Low cassava mealybug populations in Ghana in general and in the rainforest zone in particular, as revealed by population dynamic studies following the introduction of the exotic parasitoid, E. lopezi, is a clear indication of positive impact on mealybugs by the wasp and local natural enemies. It is also one of the few examples where biological control works where conventional chemical control fails to have an impact on mealybugs in particular.

The phenomenal success is not limited to Ghana alone. By 1988 in 21 African countries in the cassava belt the introduced wasp had spread over an area of more than 1.5 million km² (Herren et al., 1987; Neuenschwander and Herren, 1988).

Regular monitoring similar to studies in this thesis in two areas near Ibadan and Abeokuta in Nigeria from 1981 to 1988 showed that mealybug populations declined dramatically after the releases of E. lopezi and remained low since then (Hammond and Neuenschwander, 1989).

All the surveys and monitoring had been done on regularly chosen fields without selecting for a particular mealybug population level thus increasing the level of precision of density levels. This is in contrast to persistent reports, albeit from small scale field trials or local observations of high mealybug populations in some countries, particularly in Congo (Nenon and Fabres, 1988; LeRu et al., 1989) which sometimes lead to conclusions that biological control by E. lopezi is not satisfactory under all conditions. If reported high mealybug populations in those countries are substantial it could be suspected that in those areas as in some cases, parasitoids of pests with a wide climatic range are efficient only in some ecological niches and inefficient in others (DeBach et al., 1971). It remains to be seen in which ways the environments of the ecological zones where high mealybug population still occurs in the presence of the wasp, differ from those in Ghana and other countries where the opposite is the case.

It is of great interest to discuss parasitoids or predator-host interaction in view of different theories and models of the mechanism of population regulation by biological control agents (Hassell, 1978, 1985; Murdoch et al., 1985; Dempster and Pollard, 1986; May and Hassell, 1988; etc.). The question that is answered by this discussion is: "Should population regulation be density-dependent or inverse-density dependent?"

With phenological curves and rates of parasitism based on field means, the relationship of host densities to parasitism or densities of mummies and predators are very erratic and difficult to show clear density-dependence or the inverse relationship. Similar data in Nigeria based on field means did not show density-dependence or otherwise for presumably the same reason (Hammond and Neuenschwander, 1987). However, data on parasitism and host densities based on individual tips suggest a domed response by the exotic parasitoid E. lopezi in relation to cassava mealybugs. This means that at lower host densities (less than 40 mealybug on a tip) the wasp shows a positive density-dependent relationship to mealybug densities on the tip. But as mealybug densities increase to above 40 on a tip the wasp reduces its rates of parasitism resulting in an inverse-density-dependent relationship. This behaviour of the parasitoid does not fit directly into the two extreme cases of population regulation theories. However it is one of the rare cases accounting for about 4% of domed responses in reviewed cases (Lessells, 1985). Re-analysis of data based on individual tips rather than field

means in Nigeria also gave a domed response (Hammond and Neuenschwander, 1989) but a positive density-dependent response was at a much lower host density (between 1 and 10 on a tip) than in this study. Predators and hyperparasitoids also show positive density-dependence in relation to their hosts.

The food web of insects on cassava mealybugs and the relative importance of the species involved suggest an overwhelming importance of the exotic wasp, E. lopezi and its hyperparasitoids in the association. With the wasp and its hyperparasitoids accounting for slightly over 80% of all fauna encountered on mealybug infested tips, it is strongly believed that much of the reduction in mealybug densities could be credited to the wasp. Since hyperparasitoids attack only already successfully parasitised mealybugs (mummies in most cases), the 70% relative abundance could be attributed to primary parasitoids mainly the exotic parasitoid, E. lopezi. This is similar to findings in Nigeria (Neuenschwander et al., 1987a).

In experimental evaluations of the efficiency of natural enemies in the reduction of mealybug densities, physical and chemical exclusion studies further support the proclamation of high efficiency of the natural enemies. Though the individual impact of E. lopezi and coccinellid predator larvae could not show far-reaching reductions in mealybug densities on open tips, this is not evidence to suggest inefficiency of the two insects.

Similar exclusion experiments in Nigeria also show an efficiency of about 100-fold reduction in mealybug densities by the exotic wasp. The wasp's efficiency in the rainforest zone is thus similar to some extent to the transition zone (Ibadan in Nigeria) (Neuenschwander et al., 1986) and elsewhere in Africa. The series of natural enemy's efficiency studies are confirmed by a tritrophic computer simulation model and field studies including yield and biometric parameters of the cassava plant (Guttierrez et al., 1988a, b; Neuenschwander et al., 1989).

The association of ants with mealybugs is not a new phenomenon. But for cassava mealybugs in the rainforest zone, the ant association is exceptionally significant. Again data based on field means usually give a distorted image of the role of ants in the observed mosaic of mealybug densities. Data based on mealybug infested tips and on tips with ants attending mealybugs show an influence of ants on parasitism and predator

densities. Generally parasitism by the wasp rarely exceeds 30%. Therefore a reduction to 15% on the average on tips with ants' attendance is quite substantial or significant. The observed low mealybug densities could have been lower or there could be virtually no mealybugs in the rainforest, if ant attendance was absent. A continued reduction in mealybug densities in spite of the presence of the ants is predicted because total prevention of parasitism and predation is never achieved by the ants. The presence of coccidophilic ants in nearby cocoa farms has been reported (Strickland, 1951; Cornwell, 1958; Campbell, 1983) especially at New Tafo. The influence of the proximity of fields to edges of the cocoa farms and forest is found to be dictated more by the individual characteristics of the ant species involved. ^Aboreal species tend to like mealybug infested tips nearer to edges whereas terrestrial nesting species are more likely to be encountered on tips in inner fields.

Distribution patterns of mealybugs is also presented and discussed with a view of suggesting sampling plans. Also, stability of host-parasitoid systems depend in part on the degree of clumping of the host and on the strength of the parasitoid's aggregative response (Hassell, 1978).

Aggregation indices denoted by b and β of Taylor's (1961) power law and Iwao (1968) mean crowding statistics, respectively, are very high and justify the individual tip analysis for density dependent reactions between mealybugs and their natural enemies. The aggregation indices based on Taylor's power law are used to suggest binomial and enumerative sampling plans. Surveys and quantitative analysis will require the quick and non-destructive "present-absence" binomial method whereas qualitative analysis will only be obtained by the "destructive" enumerative sampling plan.

The most important abiotic factor, rainfall, and its impact on mealybug densities receives an important consideration in the study.

Rainfall is the single most important abiotic factor which creates ecological zones (rainforest, savannah etc.) and is reported to have impacts on mealybug densities during seasons (rainy and dry) (Fabres, 1981; LeRu, 1986; Schulthess, 1987, 1989). Field data shows that increasing rainfall intensities resulted in low mealybug densities in all locations (forest and savannah). Experimental evaluation studies

confirmed the field data. Laboratory studies suggest the greatest impact of rainfall and wind on younger instars (crawlers especially).

The results of studies suggest an optimistic control success. A sustained biological control of mealybugs is achieved and this allows a sigh of relief to people concerned with agriculture and the prevention of famine in Ghana in particular, and Africa and the World as a whole. The studies are continuing and biological control is expanding to other pests like mango mealybug (Rastrococcus invadens Williams) etc.

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APPENDICES

Appendix A.1

Total monthly rainfall (mm)				
Month	Koforidua	New Tafo	Begoro	Kasoa/Accra
August 1987	85	314.1	417.0	79.3
September 1987	142	322.1	621.7	275.8
October 1987	190	117.5	207.4	83.2
November 1987	67	6.9	1.0	9.1
December 1987	30	10.8	20.0	41.9
January 1988	34.5	12.9	71.3	0.0
February 1988	37.2	42.4	105.6	9.2
March 1988	98.1	126.4	134.2	79.6
April 1988	301.8	169.3	226.6	50.8
May 1988	167.1	180.0	142.0	241.8
June 1988	199.2	120.7	204.8	254.9
July 1988	88.1	229.5	220.0	97.7
August 1988	44.8	5.16	37.9	12.0
September 1988	176.2	141.2	87.1	31.4
October 1988	124.5	197.7	197.5	9.1
November 1988	117.9	31.4	44.0	53.7
December 1988	20.4	29.5	74.3	27.5
January 1989	0.0	0.0	0.0	0.0
February 1989	39.3	1.9	30.3	4.1
March 1989	151.1	171.2	362.2	39.3
April 1989	82.3	126.0	173.8	132.9
May 1989	142.9	110.5	185.7	109.6
June 1989	319.3	392.4	266.1	148.7
July 1989	225.9	161.0	161.1	268.0
August 1989	146.1	132.0	135.0	115.0

Data recorded by Meteorological Services Department of Ghana

Appendix A.2

One factor analysis of variance (ANOVA) for rainfall intensities at Koforidua, Begoro, New Tafo and Kasoa

Source	DF	Sum of squares	Mean square	F-test	P-value
Between subjects	23	747294.409	32491.061	5.804*	0.0001
Within subjects	72	403031.76	5597.663		
Treatments (localities)	3	67928.885	22642.962	4.662*	0.005
Residual	69	335102.877	4856.563		
Total	95	1150326.172			

Group	Count	Mean	S.D.	s.e.
Rain (K)	24	120.192	85.52	17.458
Rain (B)	24	162.15	140.728	28.726
Rain (NT)	24	127.792	108.65	22.179
Rain (KA)	24	87.304	90.20	18.412

Comparison	Mean difference	F-test
Rain (K) vs Rain (B)	-41.958	1.45
Rain (K) vs Rain (NT)	- 7.6	0.048
Rain (K) vs Rain (KA)	32.887	0.891
Rain (B) vs Rain (NT)	34.358	0.972
Rain (B) vs Rain (KA)	74.846	4.614*
Rain (NT) vs Rain (KA)	40.487	1.35

K = Koforidua
B = Begoro

NT = New Tafo
KA = Kasoa/Accra

* Significant at $P \leq 0.05$

Appendix A.3

Average monthly min & max temperatures in °C									
Month	Koforidua		New Tafo		Begoro		Kasoa/Accra		
	Min	Max	Min	Max	Min	Max	Min	Max	
August 1987	21.2	29.5	23	29	21.1	32.0	23.7	29.1	
September 1987	21.9	29.9	23.2	30.7	21.0	31.0	23.5	29.1	
October 1987	21.3	31.0	21.8	32.0	21.2	31.1	23.8	30.6	
November 1987	21.7	31.2	21.5	33.0	21.1	29.5	23.9	31.8	
December 1987	19.6	31.4	16.5	30.5	19.8	29.5	23.9	31.8	
January 1988	20.3	34.0	21.0	34	21.3	30.8	23.9	32.8	
February 1988	22.0	34.8	22.0	33.8	20.6	29.4	24.7	33.5	
March 1988	21.4	33.6	21.5	33.5	21.5	29.6	24.8	32.7	
April 1988	22.7	33.3	23.0	32.0	20.5	28.3	24.9	33.0	
May 1988	23.7	32.5	22	32.5	21.3	30.0	24.4	31.8	
June 1988	22.4	30.4	22.5	31.0	20.6	31.0	23.4	29.6	
July 1988	21.8	28.7	21.5	27.0	20.2	27.0	23.9	30.3	
August 1988	21.7	28.8	21.5	29.0	20.6	28.9	22.0	28.4	
September 1988	22.4	29.8	22.3	29.7	19.8	28.6	22.7	29.6	
October 1988	21.2	30.9	22	30.8	21.4	30.8	22.4	29.9	
November 1988	21.5	31.8	20.7	30.5	19.4	26.0	23.7	31.4	
December 1988	19.4	31.7	19.8	31.8	20.1	28.0	23.1	31.4	
January 1989	18.7	33.1	20.0	32.8	20.6	29.6	22.5	31.7	
February 1989	20.5	35.3	23.0	36	20.5	34.2	24.4	32.7	
March 1989	21.7	33.8	21.5	33.4	20.3	31.5	24.9	32.4	
April 1989	21.3	33.9	21.2	33.4	20.3	29.9	24.4	32.7	
May 1989	20.7	32.7	21.2	32.0	20.6	32.1	24.2	31.1	
June 1989	20.4	31.8	20.8	30.1	20.3	31.1	23.4	29.6	
July 1989	20.1	31.2	20.2	32.3	20.6	29.8	23.3	28.2	
August 1989	20.3	31.5	20.5	30.7	20.1	31.2	23.1	29.1	

Data recorded by Meteorological Services Department of Ghana

Appendix A.4

Average monthly relative humidity (%)								
Month	Koforidua		New Tafo		Begoro		Kasoa/Accra	
	6am	3pm	6am	3pm	6am	3pm	6am	3pm
August 1987	92	75	92	67	95	73	96	77
September 1987	92	88	88	92	92	85	96	80
October 1987	96	76	95	61	95	83	97	75
November 1987	85	72	92	92	93	91	79	69
December 1987	88	75	88	56	91	78	93	61
January 1988	89	43	77	47	84	51	72	55
February 1988	94	53	92	67	93	69	77	61
March 1988	95	61	94	68	95	69	92	66
April 1988	85	65	82	66	89	72	78	66
May 1988	95	69	98	88	97	85	95	69
June 1988	96	77	92	87	98	76	84	76
July 1988	99	68	95	92	98	80	84	78
August 1988	96	75	96	81	96	78	95	73
September 1988	96	71	92	66	95	70	94	72
October 1988	96	71	92	72	94	73	95	71
November 1988	86	69	98	87	88	77	86	69
December 1988	86	60	85	71	85	51	80	63
January 1989	84	42	85	63	88	86	84	53
February 1989	82	35	82	74	85	70	80	53
March 1989	95	57	92	53	92	79	92	62
April 1989	96	61	94	67	96	87	95	68
May 1989	96	66	95	63	96	59	94	70
June 1989	97	79	96	74	95	69	92	77
July 1989	98	84	97	83	98	87	84	75
August 1989	93	78	92	71	94	80	89	73

Data recorded by Meteorological Services Department of Ghana

Appendix A.5

Climatic conditions of the rain forest (1976-1985)
(Koforidua as representative example)

Month	Average temperature		Average relative humidity		Average rainfall (mm)
	Min (°C)	Max	6am (%)	3pm	
January 1988	20.3	33.0	97	58	17
February 1988	21.7	34.2	97	59	55
March 1988	22.1	33.4	97	62	97
April 1988	22.6	32.9	97	67	137
May 1988	22.3	31.5	98	73	155
June 1988	22.2	29.9	98	79	184
July 1988	21.6	28.5	97	77	121
August 1988	21.6	28.8	96	74	85
September 1988	22.0	30.1	97	73	142
October 1988	22.0	31.1	97	72	190
November 1988	21.7	31.9	98	66	67
December 1988	23.0	31.7	97	59	30

Data recorded by Meteorological Services Department of Ghana

Appendix B.1

One factor analysis of variance for mealybug monthly densities at Koforidua, Begoro, New Tafo and Kasoa

Source	DF	Sum of squares	Mean square	F-test	P-value
Between locations	23	950.271	41.316	0.798	0.723
Within locations	72	3727.392	51.769		
Treatments (localities)	3	2290.597	763.532	36.668***	0.0001
Residual	69	1436.795	20.823		
Total	95	4677.663			

Group	Count	Mean	S.D.	s.e.
Density of mealybugs at				
Koforidua	24	2.711	1.762	0.36
Begoro	24	3.002	1.527	0.312
New Tafo	24	3.097	2.75	0.561
Kasoa	24	14.231	9.528	1.945

Comparison	Mean difference	F-test
CM(K) vs. CM(B)	-0.291	0.016
CM(K) vs. CM(NT)	-0.386	0.029
CM(K) vs. CM(KA)	-11.502	25.412*
CM(B) vs. CM(NT)	-0.095	1.718×10^{-3}
CM(B) vs. CM(KA)	-11.21	24.141*
CM(NT) vs. CM(KA)	-11.116	23.736*

K = Koforidua NT = New Tafo * Significant at $P \leq 0.05$
 B = Begoro KA = Kasoa/Accra

Appendix B.2

Analysis of variance (ANOVA) table for mealybug densities in the rainforest (FO) and coastal savannah (SA)

Source	DF	Sum of squares	Mean square	F-test	P-value
Between locations	47	2255.242	47.984	0.497	0.991
Within locations	48	4630.461	96.468		
Treatments (locality)	1	2944.40	2944.4	82.077***	0.0001
Residual	47	1686.062	35.874		
Total	95	6885.704			

Comparison	Mean difference	F-value
Mealybug densities (Forest vs Savannah)	-11.076	82.077*

* Significant at $P \leq 0.05$

	N	Mean	S.D.	s.e.
Mealybug in rainforest (Fo)	48	2.63	1.797	0.259
Mealybug in coastal savannah (SA)	48	13.706	8.979	1.296

Appendix B.3

Analysis of variance (ANOVA) table for ants densities in the rainforest (FO) and coastal savannah (SA)

Source	DF	Sum of squares	Mean square	F-test	P-value
Between locations	47	1.113	0.024	0.228	1.0
Within locations	48	4.991	0.104		
Treatments	1	3.709	3.709	136.044***	0.0001
Residual	47	1.281	0.27		
Total	95	6.104			

Comparison	Mean difference	F-test
Ants (Forest) vs ants (Savannah)	0.393	136.044**

* Significant at $P \leq 0.05$

	N	Mean density	S.D.	s.e.
Ants (Forest)	48	0.469	0.221	0.032
Ants (Savannah)	48	0.076	0.045	6.5×10^{-3}

Appendix C.1

Analysis of variance (ANOVA) for regressions of mealybug lost from natural rains and wind under field conditions

Rain and wind Source	DF	Sum of squares	Mean square	F-test	P-value
Regression	1	884.669	884.669	61.062*	$P \leq 0.0001$
Residual	14	202.831	14.488		
Total	15	1087.5			

Wind only	DF	Sum of squares	Mean square	F-test	P-value
Regression	1	221.544	221.544	34.1*	$P \leq 0.0001$
Residual	14	90.056	6.497		
Total	15	312.5			

Appendix C.2

Analysis of variance (ANOVA) for proportions of mealybug stages washed-off in laboratory shower (simulated rainfall)

Source	DF	Sum of squares	Mean square	F-test	P-value
Between subjects	9	540.606	60.067	0.063	0.999
Within subjects	30	28614.009	953.8		
Treatments (stages)	3	26814.181	8938.06	134.084***	0.0001
Residual	27	29154.614	66.66		
Total	39				

Group %	N	Mean (%)	S.D.	s.e.
CM 1	40	74.631	3.204	1.013
CM 2	40	46.072	12.031	3.805
CM 3	40	15.823	6.41	2.027
CM 4	40	7.604	7.997	2.529

Comparison	Mean difference (%)	F-test
CM 1 vs. CM 2	38.559	37.173*
CM 1 vs. CM 3	58.807	86.465*
CM 1 vs. CM 4	67.027	112.326***
CM 2 vs. CM 3	20.248	10.251*
CM 2 vs. CM 4	28.468	20.263*
CM 3 vs. CM 4	8.22	1.689NS

* Significant at $P \leq 0.05$

Appendix C.3

Analysis of variance (ANOVA) for proportions of mealybug stages blown off in laboratory simulated wind (from fan) at 4.2 m/sec

Source	DF	Sum of squares	Mean square	F-test	P-value
Between subjects	9	205.292	2.81	0.02	1.0
Within subjects	30	33866.539	1128.885		
Treatments (stages)	3	32705.515	10901.835	253.526***	0.0001
Residual	27	1161.024	43.001		
Total	39	34071.831			

Group	N	Mean (%)	S.D.	s.e.
% blown off				
CM 1	40	74.36	6.518	2.061
CM 2	40	26.191	7.906	2.5
CM 3	40	6.68	6.121	1.936
CM 4	40	2.21	3.059	0.967

Comparison	Mean difference (%)	F-test (SCHEFFE)
% blown off		
CM 1 vs. CM 2	48.169	89.93*
CM 1 vs. CM 3	67.68	177.538*
CM 1 vs. CM 4	72.15	201.764*
CM 2 vs. CM 3	19.511	14.755*
CM 2 vs. CM 4	23.981	22.29*
CM 3 vs. CM 4	4.47	0.774NS

Appendix C.4

Analysis of variance for proportions of mealybug stages lost in laboratory simulated combined rain and wind at 50 mm and 4.2 m/sec

Source	DF	Sum of squares	Mean square	F-test	P-value
Between stages	9	418.241	46.471	0.044	1.0
Within stages	30	31429.275	1047.643		
Treatments (stages)	3	30303.396	10101.132	242.238	0.0001
Residual	27	1125.879	41.699		
Total	39	31847.516			

Group %	N	Mean	S.D.	s.e.
CM 1	40	72.75	8.209	2.596
CM 2	40	52.83	8.63	2.729
CM 3	40	16.65	3.526	1.115
CM 4	40	4.01	4.155	1.314

Comparison	Mean difference	F-test
% lost		
CM 1 vs. CM 2	19.92	15.86*
CM 1 vs. CM 3	56.1	125.79*
CM 1 vs. CM 4	68.74	188.86*
CM 2 vs. CM 3	36.18	52.319*
CM 2 vs. CM 4	48.82	95.261*
CM 3 vs. CM 4	12.64	6.386*

* Significant at $P \leq 0.05$

Appendix C.5

Analysis of variance (ANOVA) for mealybug mortality under flooded conditions according to time of flooding

Source	DF	Sum of squares	Mean square	F-test	P-value
Between stages	9	413.349	45.928	0.913	0.5239
Within stages	40	2012.36	50.309		
Treatment (stages) <i>times</i>	4	944.199	236.05	7.956*	0.0001
Residual	36	1068.161	29.671		
Total	49	2425.709			

Group	N	Mean	S.D.	s.e.
% mortality after				
5 mins	40	15.14	8.211	2.596
10 mins	40	16.38	6.788	2.146
20 mins	40	11.34	5.313	1.68
40 mins	40	7.45	3.944	1.247
80 mins		5.03	2.71	0.854

Comparison	Mean difference (%)	F-test
5 mins vs 10 mins	1.24	0.065
5 mins vs 20 mins	3.8	0.608
5 mins vs 40 mins	7.69	2.491
5 mins vs 80 mins	10.11	4.306*
10 mins vs 20 mins	5.04	1.07
10 mins vs 40 mins	8.93	3.36*
10 mins vs 80 mins	11.35	5.42*
20 mins vs 40 mins	3.89	0.637
20 mins vs 80 mins	6.31	0.677
40 mins vs 80 mins	2.42	0.247

* Significant at $P \leq 0.05$

Appendix D

Forest and coastal savannah contingency table for ant attendance of mealybugs

	Observed frequencies		
	Forest	Savannah	Total
+ ants	305	83	388
- ants	95	317	412
	400	400	800

	Expected frequencies		
	Forest	Savannah	Total
+ ants	194	194	388
- ants	206	206	412
	400	400	800

$$\chi^2_{(r-1)(c-1)} = \frac{(305-194)^2}{194} + \frac{(83-194)^2}{194} + \frac{(95-206)^2}{206} + \frac{(317-206)^2}{206}$$

$$\chi^2_{(2-1)(2-1)} = 63.5 + 63.5 + 59.8 + 59.8$$

$$\chi^2_{df} = 246.6***$$

Coastal savannah

	Observed frequencies			Expected frequencies		
	+ cm	- cm	Total	+ cm	- cm	Total
+ ants	83	33	116	58	58	116
- ants	317	367	684	342	342	684
	400	400	800	400	400	800

$$\chi^2_{(r-1)(c-1)} = \frac{(83-58)^2}{58} + \frac{(33-58)^2}{58} + \frac{(317-342)^2}{342} + \frac{(367-342)^2}{342}$$

$$\chi^2_{(2-1)(2-1)} = 10.78 + 10.78 + 1.83 + 1.83$$

$$\chi^2_{df} = 25.22***$$

Rainforest

	Observed frequencies			Expected frequencies		
	+ cm	- cm	Total	+ cm	- cm	Total
+ ants	305	58	363	181.5	181.5	363
- ants	95	342	437	218.5	218.5	437
	400	400	800	400	400	800

$$\chi^2_{(r-1)(c-1)} = \frac{(305-181.5)^2}{181.5} + \frac{(58-181.5)^2}{181.5} + \frac{(95-218.5)^2}{218.5} + \frac{(342-218.5)^2}{218.5}$$

$$\chi^2_{(2-1)(2-1)} = 84.03 + 84.03 + 69.8 + 69.8$$

$$\chi^2_{df} = 307.66***$$

Appendix E

One factor ANOVA for chemical exclusion of natural enemies

Group	N	Mean \pm s.e.
Chemical 1	10	13.3+2.62
Control 1	10	13.6+2.38
Chemical 2	10	15.7+2.305
Control 2	10	15.8+3.151
Chemical 3	10	38.5+4.861
Control 3	10	19.2+3.777
Chemical 4	10	70.4+6.551
Control 4	10	21.2+5.125
Chemical 5	10	75.8+6.695
Control 5	10	19.5+4.153
Chemical 6	10	120.2+10.15
Control 6	10	21.8+3.486
Chemical 7	10	147.2+13.322
Control 7	10	18.2+1.914
Chemical 8	10	634.4+75.518
Control 8	10	19.0+1.909
Chemical 9	10	697.1+22.778
Control 9	10	18.9+3.355

Comparisons	Mean difference	Fisher PLSD	SCHEFFE F-test
Chemical 1 vs Control 1	0.3	54.762 NS	0.0004 NS
Chemical 2 vs Control 2	0.2	54.762 NS	0.0007 NS
Chemical 3 vs Control 3	19.3	54.762 NS	0.029 NS
Chemical 4 vs Control 4	49.2	54.762 NS	0.185 NS
Chemical 5 vs Control 5	56.3	54.762 NS	0.243 NS
Chemical 6 vs Control 6	98.4	54.762 *	0.741 NS
Chemical 7 vs Control 7	129.0	54.762 **	1.274 NS
Chemical 8 vs Control 8	615.4	54.762 **	28.99 **
Chemical 9 vs Control 9	678.2	54.762 ***	35.219 ***

ANOVA ($S\bar{x} = 11.06$, df 17; 153)

Appendix F
Physical exclusion of natural enemies

Variant	N	Mean	SD	SE
VC1	20	0.7	1.46	0.325
VA2	20	2.55	6.76	1.512
VA3	20	7.75	7.64	1.709
VA4	20	294.5	182.55	40.82
VA5	20	71.1	35.3	7.89
VA6	20	213.7	160.4	35.856

where VC1 = Control, no sleeves and no artificial infestation with mealybugs
 VA2 = No sleeves but artificially infested with mealybugs
 VA3 = Open sleeves and artificially infested with mealybugs
 VA4 = Closed sleeves, artificially infested with mealybugs
 VA5 = Closed sleeves, artificially infested and 2 female E. lopezi larvae included
 VA6 = Closed sleeves, artificially infested and 2 Exochomus larvae included

	VA6	VA4	VA5	VA3	VA2	VC1
Mean densities	294.5 a	213.76 b	71.1 c	7.75 d	2.55 d	0.7 d

Means with the same letter are not significantly different at $P = 0.05$
 (SNK-Test, EMS = 10037.623, $S_x = 22.402$ (95,20))

One factor ANOVA (comparison)

	Mean difference	Fisher PLSD	Scheffe F-test
VC vs VA2 =	1.85	62.903	6.82
VC vs VA3 =	7.05	62.903	0.1
VC vs VA4 =	293.8	62.903**	17.2**
VC vs VA5 =	70.4	62.903*	0.99
VC vs VA6 =	213	62.903**	9.04**

Appendix G

One factor ANOVA - repeated measures for the disappearance of Exochomus larvae placed on tips without and with ants attendance

	DF	SS	MS	F-test	P-value
Between subjects	39	9.648	0.247	0.992	0.49
Within subjects	440	109.75	0.249		
Treatments	11	20.373	1.852	8.89***	0.0001
Residual	429	89.377	0.208		
Total	479	119.398			

Treatment

	N	Mean number removed/40	S.D.	s.e.
Camponotus ants (4hrs)	40	0.325	0.474	0.075
Crematogaster ants (4hrs)	40	0.225	0.423	0.067
Pheidoline (4hrs)	40	0.325	0.474	0.075
Camponotus ants (8hrs)	40	0.60	0.496	0.078
Crematogaster (8hrs)	40	0.475	0.0506	0.080
Pheidoline (8hrs)	40	0.600	0.496	0.078
Camponotus (24hrs)	40	0.55	0.504	0.08
Crematogaster (24hrs)	40	0.85	0.362	0.057
Pheidoline (24hrs)	40	0.775	0.423	0.067
Control (no ants) 4hrs	40	0.175	0.385	0.061
Control (no ants) 8hrs	40	0.275	0.452	0.071
Control (no ants) 24hrs	40	0.40	0.496	0.078

Comparisons	Mean diff	(Fisher) PLSD	(Scheffe) F-test
Cont (4hrs) vs Crem (4hrs)	-0.05	0.201	0.022
Cont (4hrs) vs Crem (8hrs)	-0.2	0.201	0.349
Cont (24hrs) vs Crem (24hrs)	-0.45	0.201	1.767
Cont (4hrs) vs Pheid (4hrs)	-0.15	0.201	0.196
Cont (8hrs) vs Pheid (8hrs)	-0.325	0.201*	0.922
Cont (24hrs) vs Pheid (24hrs)	-0.375	0.201	1.23
Cont (4hrs) vs Camp (4hrs)	-0.15	0.201	0.196
Cont (8hrs) vs Camp (8hrs)	-0.325	0.201*	0.922
Cont (24hrs) vs Camp (24hrs)	-0.15	0.201	0.049
Crem (4hrs) vs Crem (24hrs)	-0.625	0.201*	3.41*
Camp (4hrs) vs Camp (24hrs)	-0.225	0.201*	0.44
Pheid (4hrs) vs Pheid (24hrs)	-0.275	0.201*	0.66
Camp (24hrs) vs Crem (24hrs)	0.3	0.201*	0.79
Camp (24hrs) vs Pheid (24hrs)	0.225	0.201*	1.227
Crem (24hrs) vs Pheid (24hrs)	0.075	0.201	0.05
Cont (8hrs) vs Cont (24hrs)	0.125	0.201	0.14