Geo-Eco-Trop, 1978, 2 (4) 443-454

ZUNACETHA ANNULATA (LEPIDOPTERA ; DIOPTIDAE), AN OUTBREAK INSECT IN A NEOTROPICAL FOREST

H. WOLDA* & R. FOSTER**

RESUME

Zunacetha annulata (Lépidoptères, Dioptides) a présenté des pullulations en 1971 et 1973 dans une forêt tropicale de l'île Barro Colorado, produisant une défoliation sévère de sa plante-hôte Hybanthus prunifolius (Violaceae). Ces pullulations furent très efficacement arrêtées par un champignon et (ou) une maladie. On compte, au cours d'une année de pullulation, jusque sept générations, la première ou les premières possédant la densité la plus élevée. L'espèce est absente de la forêt au cours de la saison sèche. Il est suggéré que l'on a affaire à une espèce migratrice saisonnière en provenance d'une région inconnue, vraisemblablement de la face atlantique de l'isthme de Panama. Les conditions qui prévalent dans cette région fixent le nombre de papillons susceptibles de migrer au cours de la saison des pluies précoces et le vent contrôle le nombre d'individus atteignant l'île de Barro Colorado. L'exemple ici décrit ainsi que quelques autres démontrent que les pullulations d'insectes en forêts tropicales ne sont pas rares et peuvent même atteindre des fréquences analogues à celles de la zone tempérée.

ABSTRACT

Zunacetha annulata (Lepidoptera : Dioptidae) was observed to reach outbreak densities in a tropical forest on Barro Colorado Island (BCI), in both 1971 and 1973, severely defoliating the food plant Hybanthus prunifolius (Violaceae). The outbreaks were very effectively ended by a fungus and/or a disease. There are up to seven generations per year, the first or first few of which have the largest densities in an outbreak year. In the dry season the species is absent from the forest. It is suggested that it is a seasonal immigrant from some unknown area, possibly on the Atlantic side of the Isthmus. The events in that area determine how many moths

* Smithsonian Tropical Research Institue, P.O. Box 2072, Balboa, Panama.

** Department of Biology, University of Chicago, Chicago, Illinois 60637, U.S.A.

will be migrating in the early rainy season and the wind may determine how many of those reach BCI.

This and some other examples discussed show that outbreaks of insects in a tropical forest are not rare and may be as frequent as they are in the temperate zone.

INTRODUCTION

The idea that ecosystems rich in species in a stable, benign climate should be less variable, more stable, than other systems has gained wide acceptance. It has been shown, however, that insects in a tropical forest fluctuate in abundance as much as (no more and no less) those in temperate areas (WOLDA, 1976). It was suggested that the reason why temperate insects are considered very variable might partly be due to the fact that many of those that have been chosen for study were selected because they fluctuate widely and thus constitute a highly biased sample. They are often pest insects in forestry or agriculture. In the tropics, in spite of the "benign" and "stable" climate, many insects are known as pests in agriculture or horticulture (LESTON, 1970; CRANHAM, 1966; LONG & HENSLEY, 1972; PATHAK, 1968; YASAMATSU & TORII, 1968) or in forest plantations (GRAY, 1972). It has been suggested that in complex tropical forests outbreaks of insects do not occur (VOUTE, 1946; ELTON, 1958; FITTKAU & KLINGE, 1973). However, GRAY (1972) lists several species as pests in natural tropical forests. He is of the opinion that "insect communities in mixed tropical rain-forests are not as stable as is commonly believed." We agree. These tropical forest insects are not conspicuous in the literature. In fact, none of them has been given an attention that even remotely resembles the intensive studies devoted to temperate forest pests. As far as we are aware, for none of them has the pattern of fluctuation in abundance even been documented. In the present paper we will present some such documentation for *Zunacetha annulata* (Lepidoptera : Dioptidae). Some other insects that at times reach outbreak levels will also be mentioned.

PROCEDURES

The study area is Barro Colorado Island in the Panama Canal Zone. It is covered with a lowland tropical monsoon forest. There is a rather severe dry season from January to April with a monthly rainfall of some 6 cm. During the rainy season, rainfall averages some 30 cm per month.

Zunacetha annulata (Guér.) occurs from Texas to Paraguay (Gates Clarke, pers. comm.). The larvae, in Panama, feed on leaves of *Hybanthus prunifolius* (Schult.) Schultze (Violaceae), a common shrub in the under-story of the forest.

For the first few weeks after the outbreak was first observed on 27 April 1971, no counts were made of the number of caterpillars present. However, on 21 June, two sets of fifty shrubs were tagged and the number of eggs, caterpillars, and pupae on them were regularly counted until the end of the season in 1974. *Hybanthus* has its leaves in horizontal planes much like a beech tree and the first two instars of the caterpillars skeletonize the leaves, producing clearly visible glassy windows. We are confident that we did find the vast majority of the caterpillars present, if not all.

These counts produced indices of abundance rather than good estimates of population size. Due to the highly patchy distribution of the caterpillars, such an estimate would have required a much larger number of shrubs. For rough estimates of abundance, the data are good enough. If we saw only a few on our tagged shrubs, we saw only a few elsewhere; if there were many, we saw many elsewhere.

Some caterpillars were reared in the laboratory in order to obtain information on their life history.

RESULTS

Life History of *Zunacetha*.

The highest concentrations of eggs and larvae were found under gaps in the forest canopy. Adult *Zunacetha* were caught almost exclusively at night in the canopy level (27 m) of a series of ultraviolet light-traps in the forest (courtesy of N. SMYTHE). This suggests that adult moths fly above the canopy and come mostly down in gaps in that canopy to lay their eggs. Eggs were only found on *Hybanthus*, not on any other species of shrub. The eggs are laid in clusters on the underside of leaves. The number of eggs per cluster varies between 20 and 120 with an average of 70.

Except during outbreaks, survival of eggs was usually very high, some 90-95 percent. There was some, but very little, egg parasitism by

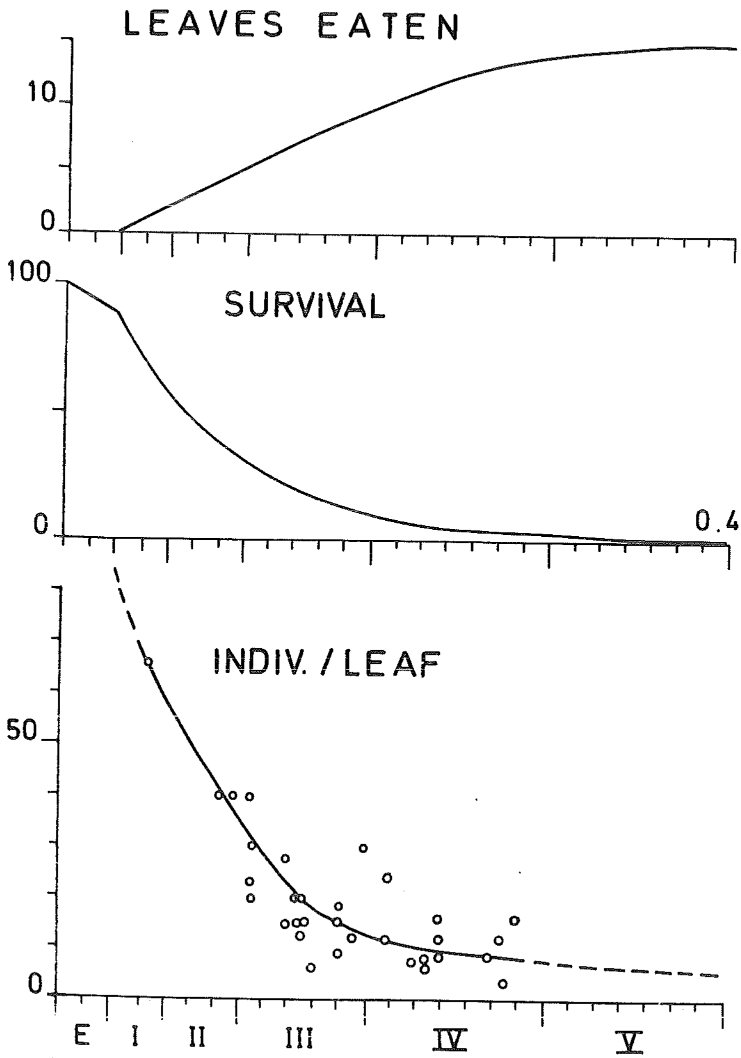

Fig. 1 : Distribution of the size of head capsules of caterpillars of *Cunacetha annulata*.

an unidentified hymenopteran.

There are five larval instars (Fig. 1), the fourth of which is rather variable in size. The first two instars, which can be recognized by a black head capsule, skeletonize the leaves; the other instars eat them.

The time from egg to adult is estimated as thirty-three days : two days for the eggs, two for instar I, three for II, five for III, seven each for IV, V, and the pupa. Pupation occurs between two leaves that are glued together. We suspect that it may also occur elsewhere, but have no observations to prove this.

Survival of larvae in the forest, of course, varies a great deal, but was usually of the order of 80 % per day for all instars, except during outbreaks, when it was lower.

We have no evidence for parasitic wasps or flies attacking the larvae. They are probably there, but, if so, are not important. Most of the mortality, normally, seems to be through predation. We have observed hemipteran nymphs, ants and spiders eating the caterpillars, but have no quantitative data. During outbreaks an entomophagous fungus is a major cause of mortality of eggs, larvae and pupae.

Some estimate was obtained in the laboratory for the amount of food eaten per day. For instar IV, the estimates probably are too low. Several of them died soon after the experiment and may, during the experiment, have been in a bad condition. No data are available for instar V. Using the data as they are and expressing them as the number of individuals of a given age needed to eat one entire leaf per day, one obtains the bottom graph of figure 2. The center graph of that figure shows the survival curve, the number of individuals surviving to a certain age assuming that the survival per day of larvae is 80 % and that survival of eggs is 90 % . A combination of the two graphs results in a total number of fifteen leaves eaten by the caterpillars coming from one hundred eggs (top graph in figure 2). We suspect that the actual number eaten in the forest might be closer to twenty leaves. An average shrub has some two hundred leaves, so that some one thousand three hundreds eggs would produce complete defoliation of a shrub. During an outbreak, however, when the fungus is active, many more would be needed.

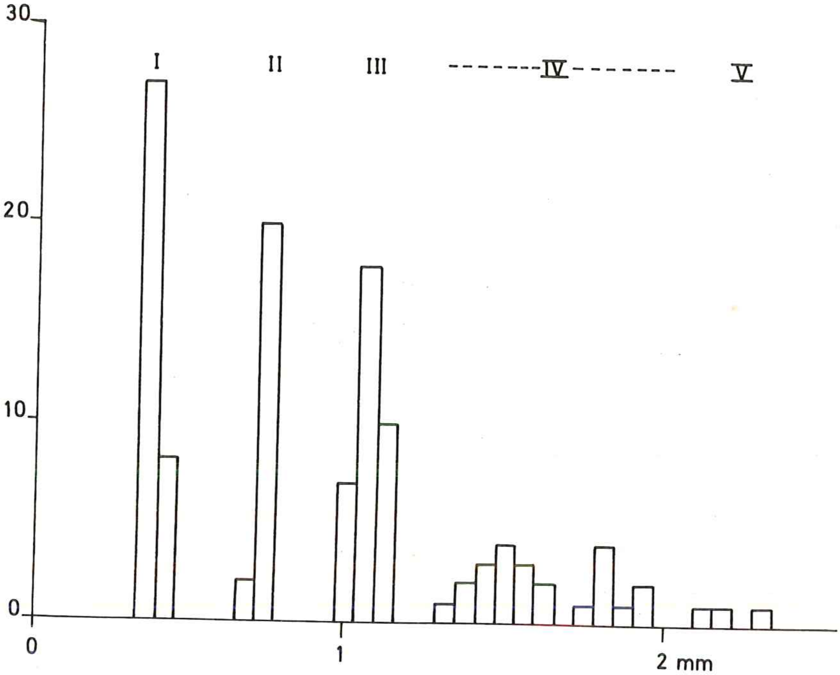

Fig. 2 : The estimated number of caterpillars of *Zunacetha* needed to eat, or skeletonize, an entire leaf of *Hybanthus*, depending on their age in days. The survival curve assuming that survival of eggs is 90 % and of caterpillars 80 % per day. The estimated number of leaves eaten by the caterpillars surviving from one hundred eggs.

The Fluctuation Pattern.

Large numbers of caterpillars were first observed on 26 April 1971 in a treefall area on the central plateau of Barro Colorado Island. We do not have estimates of the numbers present, but they had already eaten 50 to 70 % of the leaf area of the plants. By 11 May the larvae were observed over the entire top plateau of the island, but rather patchily distributed. There were least frequently observed on *Hybanthus* in deep shaded ravines and had their highest density where *Hybanthus* was most common. The plants were putting out new leaves, apparently as a result of the heavy rains in early May, the start of the rainy season. In places where *Hybanthus* was especially dense, such as near the junction of Zetek and Armour trails, denudation was estimated to be 95 to 100 % . In these denuded areas caterpillars were dropping on threads to the ground in great abundance, making it unpleasant to walk through without holding a hand in front of one's face. Many of these caterpillars, seemingly for lack of *Hybanthus* leaves, could be found attacking and denuding understory plants of *Oenocarpus* (Palmae), *Acalypha* (Euphorbiaceae), *Calathea* (Marantaceae) and many others, but without an obvious secondary preference, not even for *Rinoria sylvatica*, which is also in the Violaceae and fairly abundant.

By 20 May most of the caterpillars had pupated. At the end of May adults were found on UV lamps in the laboratory clearing on the island. By 9 June, small caterpillars were found again on *Hybanthus* which had new leaves now fully expanded. This second generation was found all over the island. The invasion of the new areas was apparently more spread out in time and for the most part later than the recolonization of the original outbreak area, since there was a greater range of size classes in the invasion areas with most of the populations lagging a week or more in development behind those on the plateau.

From 21 June onwards, counts were made of the number of eggs, caterpillars, and pupae present on fifty shrubs on the plateau and fifty shrubs in the invasion area. The data for the caterpillars are presented in figure 3.

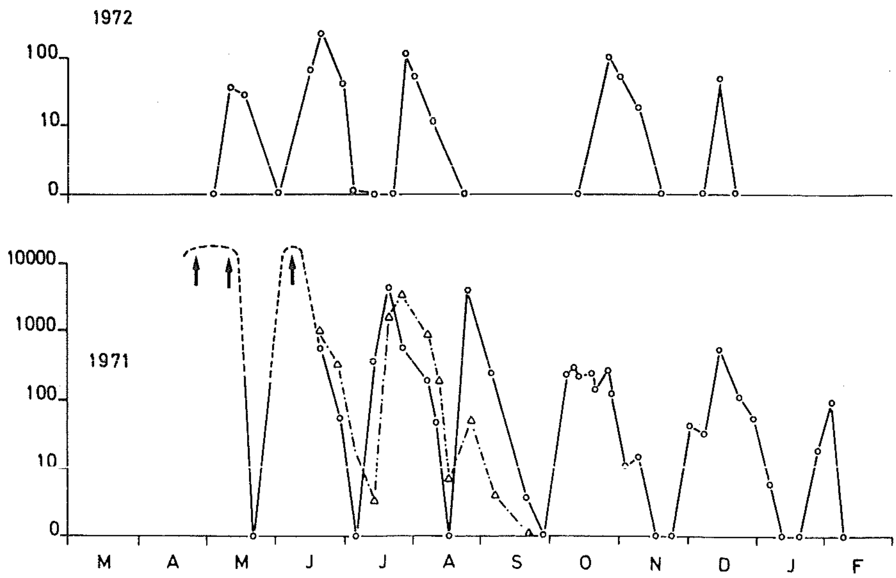

Fig. 3 : The number of *Zunacetha* caterpillars on fifty shrubs of *Hybanthus* in 1971 and 1972. Circles indicate the plateau area; crosses, the invasion area (see text).

On the plateau, towards the end of the second generation, the caterpillars were attacked by an unidentified fungus which formed a major cause of mortality of the larvae. Of the pupae found on 5 July, some 90 % had been killed by this fungus. A week later the fungus began sporulating from yellow stalks emerging from the dead bodies of caterpillars and pupae still attached to the plants. Eggs and small caterpillars of the third generation were then abundant and within two weeks virtually all of these had been killed. We did not find any that reached the pupal stage. Nevertheless, there were four more generations of *Zunacetha* this year, the last one in January. In October, the fungus had disappeared and the caterpillars were back at a low level of abundance.

In the invasion area there were only three generations in 1971. After September they were absent here. The fungus was rare, if present at all. Many caterpillars, however, succumbed to what appeared to be a bacterial or viral disease.

In 1972 no caterpillars were found in the invasion area and after this year the survey of fifty shrubs there was discontinued. On the plateau they were absent in the dry season, but reappeared in May and produced six generations. The fourth of these did not appear on the tagged shrubs, but was found on other shrubs nearby. Numbers were low throughout.

In 1973, the caterpillars again were absent in the dry season and did not appear until June (Fig. 4). We do not have counts for the first generation because both of us were absent during most of the time. However, we received various reports about the caterpillars being very abundant. The damage we observed towards the end of the generation confirmed this. This outbreak was different from that in 1971 in that it appeared simultaneously all over the island and that it lasted only one generation. Many caterpillars were found killed by this fungus which also had reappeared. The two other generations observed this year had moderate to low numbers. The fungus did not attack the last generation.

In 1974 there were only three generations of very low numbers. Two of these were observed, the last one inferred from observed damage.

During periods of low densities most of the caterpillars are concentrated on a few shrubs that stand below a gap in the forest canopy.

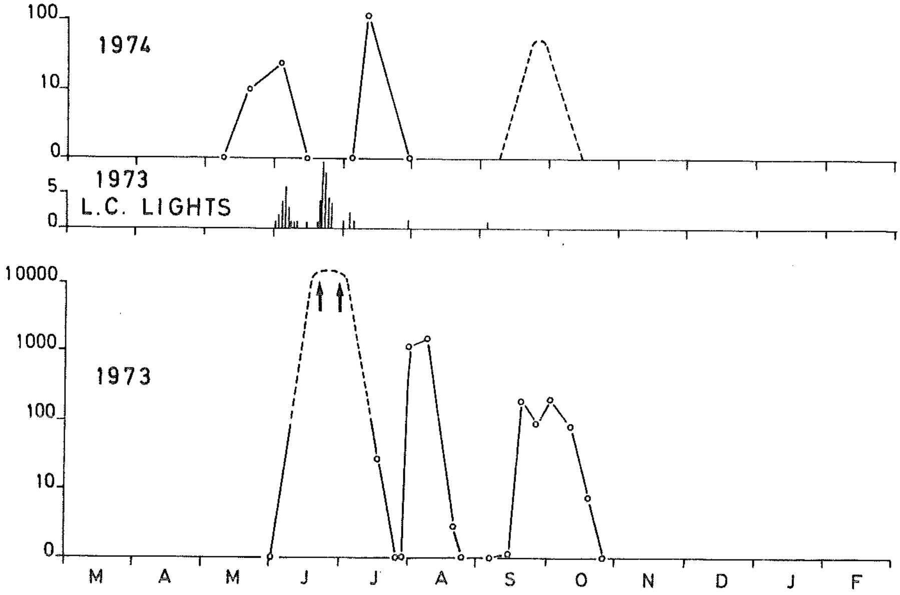

Fig. 4 : The number of *Zunacetha* caterpillars on fifty shrubs of *Hybanthus* in 1973 and 1974. Also given the number of moths caught on the lights in Las Cumbres.

Effects on *Hybanthus*.

During an outbreak most of the plants were almost completely denuded by the caterpillars. They put out new leaves immediately only to be denuded again by the next generation of caterpillars. During the four years of observations, four of the tagged shrubs died. They were not the ones which received most of the damage. The ones that were attacked most are still very much alive. *Hybanthus* has a concentrated period of flowering some two weeks after the first heavy rains after a dry period. There was no correlation between the damage in the previous season and the number of flowers and fruits. This suggests very strongly that neither mortality nor reproduction is affected by severe caterpillar damage. Successive generations of leaves were increasingly smaller as was found by CARLISLE *et al.* (1966) for *Quercus petraea*. The effort of having to produce new leaves after defoliation probably resulted in a slower growth, but this does not necessarily reduce the fitness of a long-lived understory shrub.

DISCUSSION

During the seven years of observation (1967-1974) *Zunacetha* reached outbreak levels only twice. In both cases the caterpillars, eggs, and pupae were killed in large numbers by a fungus or a disease which very effectively ended the outbreak. This is a good example of a density-dependent factor which brings the numbers down whenever they exceed a certain level. It is, however, not involved in regulation of population size at "normal" densities. It may also be irrelevant for the numbers present in the next rainy season. The beginning of an outbreak was abrupt, occurring immediately after the dry season when the species was invariably absent.

Where is *Zunacetha* in the dry season ? We don't think they are aestivating on the island, for three reasons. First, we have not found them. Second, there is no correlation between the start of the rainy season on BCI and the appearance of the first generation of caterpillars. In 1971 they were found before the rains started and in 1973 well after the first rains. Third, it is difficult to imagine how the large number of moths that started the outbreak in 1973 and 1971 could have come from the low numbers of caterpillars in the previous year. We like to think of *Zunacetha* as a seasonal migrant which is absent from BCI during the rainy season. It reinvades the forest after the rains started in their dry season habitat, wherever that is. There is one piece of information which supports this view. In 1973 daily collections were made of various insects from the wall lights of a house in Las Cumbres, a town some 34 km to the east of BCI. As far as we are aware, *Hybanthus* (the food plant of *Zunacetha*) does not occur within a radius of some 15 km of Las Cumbres. The moths, however, were found in fair numbers in 1973, just at the time when the species appeared on BCI (Fig. 4). In fact, one moth was also found at the time of the beginning of each of the later generations on BCI. We have not yet been able to find the area where *Zunacetha* occurs during the dry season.

The causes of the differences between years in abundance of *Zunacetha* on BCI are not located on BCI. The number of moths migrating in May will depend on the situation in the dry season in the area where the species does occur. How many of those invade BCI will depend on direction at night was north to northwest, suggesting that the moths came from somewhere on the Atlantic side of the Isthmus. That is, if they are affected by a wind which averages in velocity about one mile per hour (SMYTHE, 1974). It is tempting to draw parallels with the spectacular migrations of the day-flying moth *Urania fulgens* (SMITH, 1972). Large migrations of a small nocturnal moth such as *Zunacetha*, however, could easily go unnoticed. *Zunacetha* has a large geographic distribution. It has been found from Texas to Paraguay (GATES CLARKE, pers. comm.), and it is just possible that, like *Urania*, it also shows migrations on a large scale.

Zunacetha is not an exception to a general rule of stability in a tropical forest. It has been shown (WOLDA, 1976) that insects in a tropical forest fluctuate as much in abundance as they do in the temperate zone. Data presented by GRAY (1972) support this view. *Zunacetha* outbreaks are spectacular because the food plant is common. So are others. The arctiid *Ammalo* sp. attacks trees of the genus *Ficus*. The caterpillars feed at night and descend at dawn to form large conspicuous black clusters on the tree trunks. Such large clumps were observed on BCI in June 1972 and from August to November 1973. In November 1972, when they were absent on BCI, they were attacking *Ficus* in large numbers in Madden Forest, some 24 km to the east of BCI. At the same time there were many in the town of Ancon, 38 km to the southeast of BCI. The only ones we saw in 1974 were in Ancon, in May, and there were only a few of them. They were absent from BCI, in spite of weekly inspections of some one hundred selected trees (ESTRIBI, pers. comm.). In November 1973, towards the end of the outbreak, MORRISON (pers. comm.) made estimates of the number of caterpillars present. Of sixty individuals of *Ficus yoponensis*, 43% had caterpillars on them, some seven hundred and thirty per tree. Of thirty *Ficus insipida*, 16% were infected with some five hundred and thirty caterpillars per tree. At the height of the outbreak, the numbers probably were much larger. This also seems to be a migratory species.

By just looking at the canopy of *Ficus* trees, it is very difficult to tell whether more open areas in the foliage were caused by caterpillars or by the trees just dropping their leaves. If the caterpillars did not have this peculiar roosting behavior, they might very well have gone unnoticed. There could be several other species partly defoliating their food plants without being noticed for this reason. Another reason is that many species of trees in a tropical forest are rather sparsely distributed and even severe defoliations of those species would not be very conspicuous. Only outbreaks of insects in the understory will be easily detected. *Erythrina costaricensis* on BCI is sparsely distributed and was defoliated by one or the other of two species of caterpillars in every year we have looked at them, sometimes more than once per year. So we could go on. The point is it seems that outbreaks of insects in a good tropical forest are by no means rarer than they are in a temperate forest.

REFERENCES

CARLISLE, A., BROWN, A.H.F. and WHITHE, E.J., 1966. Litterfall, leaf production and the effects of defoliation by *Tortrix viridana* in a sessile oak (*Quercus petraea*) woodland. *J. Ecol.*, 54 : 65-85.

CRANHAM, J.E., 1966. Tea pests and their control. *Ann. Rev. Entom.*, 11 : 491-514.

ELTON, C.S., 1958. *The Ecology of Invasions by Animals and Plants.* Methuen, London.

FITTKAU, E.J. and KLINGE, H., 1973. On biomass and trophic structure of the Central Amazonian forest ecosystem. *Biotropica*, 5 : 2-14.

GRAY, B., 1972. Economic tropical forest entomology. *Ann. Rev. Entom.*, 17 : 313-354.

LESTON, D., 1970. Entomology of the cocoa farm. *Ann. Rev. Entom.*, 15 : 273-294.

LONG, W.H. and HENSLEY, S.D., 1972. Insect pests of sugar cane. *Ann. Rev. Entom.*, 17 : 149-176.

PATHAK, M.D., 1968. Ecology of common insect pests of rice. *Ann. Rev. Entom.*, 13 : 257-294.

SMITH, N.G., 1972. Migrations of the day-flying moth *Urania* in Central and South America. *Carib. J. Sci.*, 12 : 45-58.

SMYTHE, N., 1974. In : *R.W. Rubinoff* (ed.), 1973 Environmental Monitoring and Baseline Data. Smithson. Inst. Environ. Sci. Program.

VOUTE, A.D., 1946. Regulation of the density of the insect populations in virgin forests and cultivated woods. *Arch. Neerl. Zool.*, 7 : 435-470.

WOLDA, H., 1976. Fluctuation in abundance of some *Homoptera* in a neotropical forest. *Geo-Eco-Trop*, 1 : 229-257.

YASUMATSU, K. and TORII, T., 1968. Impact of parasites, predators and diseases on rice pests. *Ann. Rev. Entom.*, 13 : 295-324.