CHAPTER VIII
POPULATION DYNAMICS OF H. PUERA -
A SYNTHESIS OF AVAILABLE INFORMATION

8.1. INTRODUCTION

The study of population dynamics is an old discipline that antedates the modern science of ecology (Cappuccino, 1995). Insects have been a much-researched group owing to their short-life span and role as pests. Of the various pests, those that dwell in forests have attracted much interest since they occupy relatively natural environment as compared to those in many agricultural systems (Berryman, 1986). H. puera outbreaks that occur in teak stands with a normal rotation period of 60 years present a unique case to study population dynamics. Moreover, teak defoliator outbreaks occur more than once every year compared to the 8-11 years frequency seen in the case of many temperate species of forest defoliators (Myers, 1998).

According to a classification scheme based on the spread of outbreaks (Berryman, 1987), teak defoliator outbreaks have been recognized as belonging to the eruptive type (Nair, et al., 1994). The main characteristics of insects that display eruptive outbreaks is that their populations remain at relatively stable levels for long periods but then suddenly erupt to very high densities. These eruptions usually begin in particular localities (epicentres), and then spread over large areas. This theory implied that controlling the initial epicentres could lead to suppression of large-scale outbreaks.

The epicentre hypothesis has practical value, if it is proved that progenies of epicentre populations cause the large-scale outbreaks. This needs simultaneous observation in large areas and precise information on the time of start of each outbreak. Then, based on the generation time needed for each population, we can determine whether the large-scale outbreaks could originate from initial epicentres. Such an attempt was made in the present study. Flight characteristics of moth were also studied to explain the population dynamics exhibited by the insect. Since the spatial scale of the
This chapter attempts to synthesize the earlier available information and those generated in the present study in the light of recent advancement in theory on insect population dynamics. Important aspects influencing the population dynamics of the insect, namely aggregation, flight, origin of outbreaks, and the pattern of spread of outbreaks are discussed and an attempt is made to develop a theoretical framework appropriate for describing teak defoliator outbreaks.

8.2. AGGREGATION AND FLIGHT OF MOTHS

It has been recognized that the tendency to aggregate is a characteristic of outbreak species of insects (Cappuccino, 1995). In the case of *H. puera*, the sudden appearance of heavy infestation with thousands of larvae per tree, following a period of near absence of infestation had indicated that aggregation of moths occur prior to egg-laying at the site. Moth aggregations have been observed earlier within teak plantation and nearby natural forests (Nair, 1988). In the present study aggregations of moths were observed in teak plantations immediately before the plantation was infested (Chapter 6). These aggregations consisted of uneven aged moths of both the sexes. This indicates that an aggregation is composed of moths that emerged from different sites or moths that emerged from the same site on different days. The fact that aggregations were predominantly found on hillocks suggests that moths use topography as a guiding cue to form aggregation.

Circumstantial evidence for short-range (Nair and Sudheendrakumar, 1986) and long-range (Vaishampayan et al., 1987) movement of moths was obtained earlier based on independent studies at Kerala and Madhya Pradesh. In the present study, direct observations revealed two types of flight behaviour in *H. puera*.
1. Dispersal flight: observed during dawn and dusk in all directions within teak plantations at the canopy level,
2. Directional flight: not restricted to dawn and dusk, moths moving in the same direction in a swarm.

8.3. ORIGIN OF OUTBREAKS

This study showed that in 1993, within the nearly 9,000 ha teak plantations at Nilambur, the first outbreaks occurred during the month of February in a few small scattered patches. These patches varied in size from 1.8 to 12 ha. These initial patches could originate in two possible ways:
1. A change in behavior of endemic population of the insects within the area leading to aggregation and mass egg-laying.
2. An influx of moths from a distant area

Correlation between the time of occurrence of first outbreaks and pre-monsoon showers has been observed earlier. Since there is no report on diapause in *H. puera*, rain cannot be a factor that triggers the emergence of moths. Even though new flushes come up profusely after the pre-monsoon showers, it is observed that tender foliage sufficient to support epidemic populations of the insect are present even before the pre-monsoon showers. It could be thought that the first rains could have an impact on the behaviour of moths, inducing them to aggregate. Alternatively, the wind system associated with the pre-monsoon showers can assist in long distance immigration of moths. The present data are not sufficient to prove any one of the above.

8.4 SPATIAL SPREAD OF OUTBREAKS

The spread of outbreaks during a year within nearly 9,000 ha teak plantations at Nilambur can be summarized as follows:

It was observed earlier that initial outbreaks occurred in small patches covering 0.5 – 1.5 ha in area which are widely separated. The present study showed that the initial epicentres could be much larger extending to a
maximum of 13 ha (see Section 5.2, Chapter 5). It was noticed that these epicentres originate during the month of February. As discussed above, origin of epicentres remains an unresolved problem. During the months March and April, infestations occur in patches of a wide range of sizes (0.1 to 934 ha), which are still widely separated in space. Most of these outbreaks occur simultaneous with the emergence of moths from the populations during the first phase (the epicenter phase), but some populations occur when there are no locally emerged moths. Widespread outbreaks occur in a large number of patches during May and June. Progenies of populations, which occurred during the build-up phase, could cause all the outbreaks during this phase. While the life stage of the insect is uniform within an outbreak patch, there is considerable difference between patches. This could be because of the fact that moths emerged from different outbreaks that occurred during build-up phase cause these wide spread outbreaks. During July there is a reduction in both the number of patches infested and the size of outbreak patches. All outbreaks that occur during July could be explained as caused by progenies from earlier populations. Outbreaks during this period do not cause further outbreaks in the area even if tender foliage is present. This may be because of collapse of population due to natural mortality factors or the emigration of moths from the area. A few outbreaks covering around 1-40 ha occur during the period August - September. With respect to origin of these outbreaks, this phase resembles the period of epicentres. These outbreaks seldom cause subsequent outbreaks in the area.

8.5. THE BACKGROUND TO WORKING TOWARDS THEORY

The following specific details hitherto generated are relevant to explaining the observed dynamics of teak defoliator outbreaks:

1. At the global scale (encompassing all places were *H. puera* is present i.e., India, Myanmar, Sri Lanka, Indonesia, Papua-New Guinea, the Solomon islands, *etc*) the insect occurs in outbreak density at different places at different times.
2. At a still lower regional scale (for example the Indian Subcontinent) there is a directional progression of outbreaks, which seems to be linked with the movement of monsoon wind system.

3. At the local level (like the teak plantations of Nilambur), outbreaks occur only during some part of the year. During the outbreak period, infestations originate in a few small epicentres. Later, outbreaks spread to larger and larger areas. While most of the outbreaks could be caused by previous outbreaks, a few are not so. During the final phase of the outbreak period, a few outbreaks occur that can only be explained either as caused by long-range migration of moths or by aggregation of moths from the endemic population. After this, the population density remains low until the next year when the sequence of outbreaks is repeated. Thus, the teak defoliator displays population cycles at a frequency of one year.

Various explanatory hypotheses have been proposed for the dynamics of forest lepidoptera that exhibit population cycles (Myers, 1988). These include:

a) Variation in insect quality: Chitty (1967) proposed that density-related selection on genetically controlled variation in behaviour and physiology of animals could provide the basis for self regulation of populations. Experimental proof is still non-existent for this hypothesis (Myers, 1988).

b) Climatic release hypothesis: Uvarov (1931) and Andreartha and Birch (1954) proposed that weather and climate are major controlling factors of insect abundance. Climate can cause direct and indirect impact on population size, but the hypothesis remains untestable due to the difficulty in differentiating the impact due to climate from that caused by other factors (Myers, 1998).
c) Variation in plant quality / availability: Two hypotheses have been proposed based on the quality of food available for the insect. The first is that the quality of foliage may deteriorate following herbivore damage and thus act in a delayed density-dependent manner to reduce the population size. The other is that the nutritional quality of foliage improves following environmental stress from drought, waterlogging etc. so that the population size increases. The availability of food can also cause population cycles. In a deciduous tree like teak, it is probable that the absence of tender foliage during some part of the year can cause population decline of the herbivore.

d) Disease susceptibility: This hypothesis proposes that as the population of an insect increases, individuals interact more frequently, thus allowing the transmission of disease. Stress associated with food limitation or poor weather could further accentuate the susceptibility to disease, which results in an epizootic. High mortality from disease selects for resistant individuals and the epizootic ends as the host density declines. Sub-lethal effects of disease may reduce vigor and fecundity for several subsequent generations.

e) Metapopulation theory: Metapopulation is a set of local populations inhabiting spatially distinct habitat patches. A conceptually important assumption is that local populations have a significant risk of extinction (Moilanen and Hanski, 1998). The metapopulation is assumed to persist in a stochastic equilibrium between local extinctions and colonizations. Thus migration is a major driving force in metapopulation dynamics.

When we attempt to explain the population dynamics of *H. puera*, it can be seen that no theory can explain it completely but all the theories provide insight into one or the other characteristics of teak defoliator dynamics at the population level. The first theory regarding variation in insect quality is important since morphologically distinct larvae are found in the field which tempted the early workers to classify them as two distinct varieties (see Chapter II). The second hypothesis on climatic release is interesting in the
Chapter II). The second hypothesis on climatic release is interesting in the scenario where the teak defoliator outbreaks start immediately after the premonsoon showers. The third hypothesis on variation in plant quality/availability is also important since teak is a deciduous tree which sheds its leaves during winter, thereby creating a time when no food is available for the insect larvae. The fourth theory on disease susceptibility is also of interest owing to the recent discovery of the baculovirus, which can cause wide-spread epizootics and can persist within the host insect. Even though none of the above theories can be explicitly ruled out, the metapopulation theory in which space is identified as a determinant in regulating population dynamics appears to hold good in the case of *H. puera* outbreaks. An attempt is made below to view the population dynamics of teak defoliator in the light of metapopulation theory.

8.6. AN EXPLANATORY MODEL FOR THE POPULATION DYNAMICS OF *H. PUERA*

A schematic diagram showing the population dynamics of *H. puera* is given in Fig. 8.1. The figure is divided into two parts. The upper part above the dotted line indicates the metapopulation, which is the assemblage of several local populations. This metapopulation can extend to the total distribution area and may exist in a high density (epidemic) level in one or the other areas while it remains at low density (endemic) level at the other places. Even when the size of the metapopulation remains stable, at the local level, population density can shift between endemic and epidemic levels. Below the dotted line, the local population dynamics at a place like Nilambur is represented.

At the local level, low density, endemic populations have been observed during the non-outbreak period. The insects are rare and distributed in a disperse manner throughout the plantation. Incidence of first outbreaks (epicentres) at a particular place (of several sq.km in area) can occur either by the aggregation of local endemic population or by immigration of moths from
a place under outbreak. Outbreaks occur in shifting large patches following the occurrence of epicentres. These wide-spread outbreaks seem to be caused by progenies of moths emerging from the epicentres. After the wide spread outbreaks, the population density declines to an endemic level. This decline may be due to the impact of density dependent mortality factors like diseases, and depletion of food source. Occurrence of several generations of the insect in the same locality can increase the viral load in the environment, which can lead to the collapse of a later population.

Fig. 8.1. Schematic diagram showing the population dynamics of *H. puera*

Subsequent small population peaks occur in September-October (Fig. 8.1) which cannot be caused by progenies of earlier populations. As in the case of initial epicentres, these outbreaks could be caused either by the aggregation of local endemic population or by the influx of moths from far
away places. These populations seldom cause further outbreaks in the area and the local population declines to endemic level. This may be due to the reduction in food source since most of the leaves would be mature and not acceptable to the early larval instars.

The graph in Fig 8.1. shows the temporal sequence of shifts in population density. At Nilambur the population density remains at endemic level during January and February (A). During late February or March, the initial epicentres occur causing an increase in population density (B). From April to July, the population remains at epidemic level, causing large outbreaks at different places (C). During August, the population reverts to endemic level (A2). During September - October further small-scale outbreaks occur (B2) followed by a period of endemic population (A3) which extends to February, next year.

At the local level a specific period can be identified during which control operations are feasible. Control of the epicentres and any new populations occurring during the build-up phase can theoretically prevent large-scale outbreaks. This would be an economical way of preventing outbreaks as compared to an attempt to control wide-spread outbreaks. The model also indicates that it will be impossible to prevent all outbreaks by this method of control since the outbreaks which occur during the final phase are independent from the sequence of outbreaks which occur during the early part of the year. But this study has shown that controlling the initial outbreaks can prevent outbreaks in nearly 78% of the total area under outbreaks. The model also indicates that since recolonization can occur from far away habitats, control operations have to be repeated every year.