Pests of Crops in Warmer Climates and Their Control

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Preface

The original project was to produce a textbook for teaching agricultural entomology in the tropics (initially in Uganda) as at the time no suitable text was available. The accumulation of information for that compilation was generally regarded as successful; the first two editions published by C.U.P. are out of print and it was thought that a new version would be timely.

In the UK Europe and North America there are various textbooks available in English, but none gives an overall (international) view of the subject and none has quite the same approach as this, where large amounts of information have been incorporated into a summarized form for easy assimilation.

Initially only insect and mite pests were included, but it was felt useful to mention some of the other important pest animals.

The sources of information are many, and are listed in the bibliography; some are referred to in the text. In a number of cases the original publication was not seen; the information was taken from a review article or from an abstract.

Specimens for drawing were either personally collected or loaned from various institutions or collections, especially from the British Museum (Natural History) through the Keepers of Entomology (Dr P. Freeman, and Dr L. Mound), and the Trustees are thanked. Drawings were made by Hilary Broad, Karen Phillipps, and Alan Forster; a few were from other sources. Photographs were mostly taken by the author, but a few were from other sources and have appropriate acknowledgement under the plate.

Identifications of insect specimens were made by staff of the Commonwealth Institute of Entomology and the Department of Entomology, British Museum (Natural History), who were also sources of general information and advice.

Initial support for the project was made by the Rockefeller Foundation through a grant to the Faculty of Agriculture, Makerere University, Uganda.

General facilities were made available by the Department of Zoology, University of Hong Kong, Alemaya University of Agriculture, Ethiopia, and University of Malaysia Sarawak.

The successful completion of this project would not have been possible without the help of many colleagues, especially those from ADAS, and the Harpenden Laboratory of MAFF; also from Rothamsted Experimental Station, from FAO (Rome) and from many chemical companies.

I would like to take this opportunity to thank specifically the following for their help in many different ways: Dr D.V. Alford, Mr R. Bardner, Dr V.F. Eastop, Susan D. Hainsworth, Mr C. Furk, Mr T.J. Crowe, Dr D.J. Greathead, Mr A. Lane, Dr Lee, Hay Yue, Mr R.J.A.W. Lever, Dr Li, Li-ying, Dr W. Linke, Professor B. Lofts, Professor J.L. Nickel, Professor J.G. Phillips, Mr G. Rose, Dr K.A. Spencer, Dr D.L. Struble, Dr J.D. Sudd and Mr R. Wong.

Dennis S. Hill
April, 2007

This book is dedicated to Dr John L. Nickel and Terry Crowe without whose support the original project could never have started.

Contents

1 *Introduction*

This book is intended for use as a student text for courses in 'Applied entomology', 'Crop pests' and 'Crop protection'. at both undergraduate and post-graduate level. It presupposes a basic knowledge of entomology to the level of that in Imms, A.D. (1960) *A general textbook of entomology*, or alternatively Borror, D.J. & D.M. Delong (1971) *An introduction to the study of insects*. In other words, the reader should be acquainted with the major groups of insects and their characteristics, which may mean order, suborder or superfamily in some cases, but in the more economically important orders this would mean familiarity with superfamilies or families, for example in the Hemiptera, Lepidoptera, Coleoptera, and Diptera.

There is more information in the 10th Edition of 'Imms' (Richards & Davies, 1977), but this is now so expensive that most students are probably still using the previous edition.

It is hoped that some sections of the book will also serve for reference purposes, as these sections represent the distillation of much information acquired by extensive experience and detailed literature searching.

Certain tropical crops, such as rice and citrus fruit, can be cultivated in countries outside the tropics. A recent trend in many countries is to make the effort to diversify local agricultural crops: in the tropics many temperate crops are now being grown in cooler locations, and in temperate countries some tropical crops are being successfully grown both in greenhouses and in the open. The breeding of new varieties of crops has made the more widespread cultivation more feasible.

Because of the escalating costs of publication the overall size of the book is limited and so the number of pests and crops studied in detail is less than desired. In an attempt to compensate for this the pest section is aimed at generic level rather than individual species, where possible; some pests are pantropical at the genus level, occurring as several distinct allopatric species. Where an important group of pests is only sparsely represented then a brief review of the group is presented in a couple of pages of text.

To make it as clear as possible which insect species are being referred to in the text both the scientific name (genus and species) and a suitable common name are used in conjunction. Unfortunately there is a lack of international agreement over the use of names, despite the efforts of the *International Code of Zoological Nomenclature*. Similarly with the different taxa used: what is often regarded as a distinct family in one country may be relegated to subfamily status in another. In this respect the present text shows a bias towards the classification used in the UK, and particularly that employed in 'Imms' *General textbook of entomology*, 10th edition, by Richards & Davies (1977).

In a text such as this, where the aim is an international coverage, inevitably some names given here will differ from those used in other parts of the world, but hopefully the identity of the pest will not be in doubt. The scientific names given in the book are those used by the Commonwealth Institute of Entomology (CIE) on their distribution maps, and those listed in Seymour (1979) and Kloet & Hincks (2nd edition – revised, 1964–78) for the UK, Werner (1982) for the USA, and the checklists for China, Japan, Australia, etc., listed in the bibliography. Clearly, some of these major publications are already out of date, and some major name changes have taken place very recently, within the last year or two.

The question as to whether very recent name changes for insect pests should be followed in a student text is very vexing. The taxonomic purists will, of course, insist that all name changes be strictly adhered to. But in many parts of the world the news of such name changes is slow to arrive, and so far as students are concerned the great majority of their reference sources, if not all, will be using the previous name for the pest, if not even earlier ones. As a practical entomologist I am loathe to see well established names being changed, unless really necessary, because of the confusion that will ensue. But of course, if there is good reason for the name change then it must be accepted. In chapter 9, where individual pest species are described, if there has been a recent name change the former name is included in parentheses as a synonym, or whatever. Older previous names are not included, for many of the widespread crop pests have lists of synonyms and misidentifications of interminable length.

The common names used are from the same sources generally as the scientific names. There are considerable divergences in usage of common names; for example in Europe it is traditional to refer to the adult insect (such as Onion Fly) whereas in the New World the damaging stage is referred to (that is Onion Maggot); but in these cases the identity is fairly obvious. In some cases though, for the purpose of this text, an arbitrary choice of common names has had to be made as to the more appropriate when used internationally.

It should be stressed that some records are taken from local or regional publications, and sometimes there are complications in that a particular pest may either have been misidentified or else have been identified correctly but referred to by an invalid name. Sometimes the use of an invalid scientific name is obvious and the record can be rectified, but with some less well-known species it may not be evident, and so some incorrect names will inevitably be included.

Finally it should be remembered that the writing of many book manuscripts takes several years, and then actual publication generally takes 1–2 years to complete, so it is inevitable that the published book will be out of date scientifically, both with regard to names used and also pesticides and their recommendations, even on the day of release. But hopefully by the combined use of scientific and common names for each pest it will be clear as to the identity of the organism concerned.

The distributions given are summarized from the maps produced by the CIE, and in the cases where a map has not been produced for a particular species the appropriate distribution data have been made available from the CIE card index system (now computerized). Reference to the CIE map, where one is available, is made at the end of each summary of distribution.

In the section on control, emphasis has been placed on methods of cultural control whenever these are available, and so far as pesticides are concerned no details as to rates, etc., are included. Pesticide recommendations vary extensively from country to country, and also from season to season, so only the barest details of pesticide recommendations are included. For full details of these for local crops in each country, the appropriate Ministry or Department of Agriculture or Regional Entomologist should be consulted. It would be quite impossible to provide adequate pesticide detail suitable for practical use in all the different parts of the tropical world.

When considering some aspects of the basic principles underlying the study of crop pests and their control, some of the examples given are from non-tropical situations. They are used because they are particularly suitable as examples, and are usually very well-known pests.

The section on pesticides was compiled from data published in *The Pesticide Manual* (A World Compendium) (10th Edn) (Tomlin, 1994), and from various original data sheets provided by the firms concerned, and that part dealing with application equipment largely from Matthews (1979). It is not feasible to generalize extensively about persistence, efficiency, pre-harvest intervals, toxicity, and tolerance levels, for not only do these characteristics vary considerably according to local climatic conditions, but each country has its own requirements with regard to residues and toxicity. Some countries are more concerned with operator safety, whereas others regard consumer hazards the more important. Thus the same chemical may have a pre-harvest interval of seven days in one country and as many as 28 in another: or alternatively an approved pesticide in one country may be banned in another.

In chapter 9 on pest descriptions, biology and control measures, the original scheme was to illustrate all the important stages of the major insect pests and to show the damage done to the host. But it was not possible to provide all stages and damage for more than 300 major pests, and so in some cases only the adult insect is drawn. Unfortunately, some of the earlier drawings were designed more to give an impression of the pest and the crop plant rather than accurate detail of the insect. In the more recent drawings by Hilary Broad Alan Forster, and Karen Phillipps we have endeavoured to reproduce morphological details which are taxonomically specific.

The species here designated as major pests have, in a few instances, been chosen for academic reasons or to demonstrate a point of particular biological interest rather than always being primarily economic pests. I have attempted to include a well-balanced range of pests, most of which are important on major crops, and widely distributed throughout the warmer parts of the world. The denotation of the term 'major pest' to a species is necessarily somewhat arbitrary when dealing with 100 crops grown throughout the warmer parts of the world. However, this term has usually only been applied to species which are economically important over a wide part of the range in which the crop is cultivated.

According to figures provided by Dr R.G. Fennah for Wilson (1971) it can be said that there are some 30 000 insect pest species, but Fletcher (1974) referred to there being only about 1000. Later in the book he mentioned that the total number of insect and mite pests species recorded from several major crops ranges from 1400 on cocoa and cotton to 838 on coffee. It seems reasonable to assume that on a worldwide basis there is something in the region of 1000 species of 'serious' crop pest species, including pests of forests and ornamentals, and may be up to 30 000 minor pest species. In chapter 10, under the headings of the 100 crops considered, are listed the more important major pests, many of which were included in chapter 9, and in addition a selection of the minor pests recorded from each crop. In some of the more restricted crops the number of recorded pest species is very small, whereas the widespread crops may have more than 1000 recorded minor pests. In these cases the list of minor pests has been restricted to the more important, more interesting, or more widespread of the minor pest species.

2 *Pest ecology*

The information provided in this chapter has been separated off in an attempt to emphasize the need for a greater understanding of the complex ecological relationships between the insects and plants in the agricultural context. Here are also included various aspects of basic biology that have broad ecological relevance. There is clearly overlap between this and the next chapter, as various factors in the consideration of basic principles relating to pest control are aspects of the pest/crop ecology.

Ecology and pest control

The earliest recorded attempts at pest control were often basically concerned with the biology of the pests and their ecology, and attempts were made to make the environment less favourable for the pests by various physical and cultural means. With the recent disillusionment with pesticides and with the increased awareness of the importance of ecological aspects of the pest/crop situation, as now defined by most integrated pest management (IPM) programmes, there has been a reversal of approach to basic ecological aspects.

Ecology

The complex and interacting system comprising all the living organisms of an area, and their physical environment (soil, water, climate, shelter etc.) is termed the *ecosystem*, and the study of ecosystems is called *ecology*. Definitions of ecology vary according to the speciality of the definer: botanists often have a different viewpoint from zoologists, and agriculturalists may have a third view. In its simplest form ecology can be defined as 'the total relationships of the plants and animals of an area (habitat) to each other, and to their environment'.

Environment has been defined by Andrewartha & Birch (1961) as being composed of four main factors: weather, food, other animals and plants, and shelter (a place in which to live).

For convenience it is customary to lump together environmental factors into two broad categories, biotic (i.e. organic) and physical (i.e. abiotic or inorganic). Weather and shelter (usually) are clearly physical factors, although shelter for a parasite could be regarded as biotic. Other animals and plants clearly constitute a biotic factor. Food is a biotic factor for animals which are holozoic (heterotrophic) in their feeding habits, but could possibly be more suitably described as physical for plants, which are holophytic (autotrophic) in their nutrition.

The *environmental factors* can be further defined as follows.

Weather

(a) Temperature – ranges defined as tropical, temperate, arctic or boreal
(b) Humidity – ranges from moist, moderate, to dry conditions
(c) Water – includes groundwater, rainfall, etc.
(d) Light – intensity important for many organisms
(e) Wind – important for dispersal, and drying effects

Food

(a) For animals
 (i) Organic remains – detritivores
 (ii) Plant material – herbivores (phytophagous)
 (iii) Other animals – carnivores and parasites
(b) For plants
 (i) Organic remains – saprophytes (mostly fungi and bacteria)
 (ii) Other plants – parasites and pathogens
 (iii) Animals – insectivores (carnivores)
 (iv) Sunlight, water, carbon dioxide, minerals, chlorophyll (autotrophs)

Other animals and plants (i.e. the community)

(a) Competition – intraspecific (within the species)
 – interspecific (between different species)
(b) Predation
(c) Parasitism
(d) Pathogens causing diseases

Shelter (a place in which to live; habitat)

(a) For animals (insects) and pathogens – frequently a plant, and often a specific location on the plant, e.g. in the cases of a leaf-miner, stem borer, bollworm and leaf-roller. Some insects are soil-dwellers (e.g. termites, crickets, beetle larvae), and adult, winged insects may not be very habitat-specific (i.e. eurytopic).
(b) For plants – usually a physical location (habitat), including the soil (e.g. hilltop, valley, field) together with the other plants that constitute the community.

Two basic ecological terms should perhaps be included here for reference.

Habitat. The place where the plants and animals live; usually with a distinctive boundary, e.g. a field, pond, stream, sand-dune or rocky crevice. Often initially broadly subdivided into terrestrial, marine, and freshwater habitats

Community. The collection of different species and types of plants and animals, in their respective niches, within the common habitat, e.g. lake community, mangrove community or ravine community. The basic plan for all communities is the same, i.e. they are composed of saprophytes, autotrophic plants, detritivores, herbivores, carnivores, parasites, etc.

With the general disillusionment that followed the widespread continual use of synthetic chemical pesticides, especially the early organochlorine compounds, the situation has changed so that now attention is focussed on biological and ecological understanding, linked with careful application of selected pesticides. This approach was initially called *integrated control* but was more recently redefined as *pest management* (PM), and is now finally referred to as *integrated pest management* (IPM).

As indicated above, the number of different factors operating in an insect pest host plant relationship is large and hence the different possibilities available for ecological manipulation are considerable. But, of course, a vital prerequisite is a detailed knowledge of the insect's life-history and biology, and especially its relationship with the host plant.

As mentioned later (p.5), an insect species is only a pest (that is an economic pest) at or above a certain population density, and in any pest ecosystem any one (or more) aspect of the environment may be of over-riding importance. In the study of pest populations the key to control will inevitably lie in the understanding of the complex of environmental factors and their relative importance. However, our knowledge at present of most pest situations falls short of this ideal, and much basic ecological study is still required. Too frequently pest control still consists of hastily and ill-considered applications of chemical pesticides, which sometimes wreak ecological havoc, especially in the tropics, often without controlling the pest at which they were aimed. Progress is gradually being made though, as evidenced by the ever-growing number of IPM programmes for different crops in different parts of the world.

Agroecosystems

An agroecosystem is basically the ecosystem of an area as modified by the practice of agriculture, horticulture or animal rearing. Agriculture consists of methods of soil management and plant cultivation so as to maintain a continuous maximum yield of crop produce, in the shortest time possible. This is achieved by manipulation of the environment so as to make growing conditions for the crop plants as near ideal as possible, and also to minimize damage to the crop by pest and disease attacks. Obvious manipulations are listed below, under the appropriate environmental headings.

Weather

(a) Temperature control by shading (lowering) or use of greenhouse (raising)
(b) Humidity control by spraying or altering plant density
(c) Irrigation (below or above-ground) and drainage
(d) Light increased by use of ultra-violet lamps, or reduced by shade trees, shelter, etc.
(e) Wind protection by growing shelter-belts, windbreaks, tall trees and hedgerows

Food

(a) Animal feedstuff, grazing leys, dietary supplements
(b) Plants are 'fed' by addition of fertilizers, minerals, and trace elements; sometimes increased radiation by use of extra illumination

Competition – intraspecific, reduced by careful crop spacing
– interspecific, reduced by weeding and use of herbicides

Predation, parasitism and disease reduced by crop protection procedures

Shelter

(a) Animal houses
(b) Windbreaks, shelter-belts, greenhouses, polythene shelters, protected seedbeds, etc. Also soil improvement by drainage, irrigation, liming, fertilizers, deep ploughing, hardpan breaking, manuring etc.

Thus it is clear that every aspect of the environment can be (and usually is) manipulated in the course of modern sophisticated agriculture. Generally though, only practices that show a definite economic profit are indulged.

The major ecological modifications that are made during the process of agriculture (*sensu lato*) that affect pest populations are as follows.

Monoculture – the extensive growth of a single plant species, with a simplification of the flora, partly by weed destruction.

Increased edibility of crop plants – the crop plants are more succulent, larger and generally more attractive to pests than the wild progenitors.

Multiplication of suitable habitats – the habitat and the microclimate becomes uniform over a large area.

Loss of competing species – may lead to the formation of new pests.

Change of host/parasite relationships – will lead to the development of secondary pests.

Spread of pests by man – as crops are grown in more parts of the world, the pests are also eventually spread around by accident.

These and other topics will be looked at in more detail in later sections of this chapter.

It should be stressed at this point that the vast majority of crop pests are in fact human-created through the ancient practice of agriculture. Completely 'natural' serious crop pests are very few and are limited to locusts, possibly a few tropical armyworms, and some defoliating caterpillars and sawfly larvae that occur in the extensive natural semi-monocultures of the northern taiga in N. Europe, N. Asia, and N. America and the northern deciduous forests.

Pest populations

The important point to remember about any pest is that it is only an economic pest at or above a certain population density, and that usually the control measures employed against it are designed only to lower the population below the density at which the insect is considered to be an economic pest; only very rarely is complete eradication of the pest aimed at. The schematic representation of the growth of a population in fig. 1 (adapted from Allee *et al*, 1955) has had four separate population levels indicated; these are represented by the numbers 1 to 4. These population levels indicate purely hypothetical densities at which any particular insect species may be designated an, economic pest. Population level 1 might well represent an economic pest level for such an insect as Rosy Apple Aphid (*Dysaphis plantaginea*), for in this case control measures are recommended when the population density reaches one aphid per tree (at bud-burst), and similarly for a pest such as Colorado Beetle.

At the other extreme population level 4 could well apply to insects such as various cutworms which are only economic pests in Europe at irregular intervals at times of population irruption. Most of the more common pests would come into the categories which reach pest density at population levels 2 and 3. The growth of a population can be expressed very simply in the equation:

$$P_2 \leftrightharpoons P_1 + N - M \pm D,$$

Where P_2 = final population, P_1 = initial population, N = natality, M = mortality, D = dispersal.

To simplify this equation, natality can be regarded as synonymous with birthrate, mortality with deathrate, and dispersal is either regarded as movement out of the population (emigration), or movement into the population from outside (immigration). The object of pest control is to lower P_2, which quite clearly can be done by either lowering the birthrate of the pest, increasing the deathrate, or inducing the pest to emigrate away from the area concerned.

Four hypothetical pest populations are illustrated graphically in Stern, Smith, van den Bosch & Hagen, (1959), in relation to their equilibrium position, economic threshold, and economic injury levels; these graphs are illustrated in fig. 2.

Life-table

The examination of a pest population and its separation into the different age-group components, i.e. eggs, larvae, pupae and adults, enables a life-table for that pest population to be compiled. The construction of a life-table for a pest species is an important component in the understanding of its popu-

Fig. 1. The growth of populations (after Allee *et al*., 1955).
Stage I Period of positive, sigmoid growth; population increasing
A Establishment of population
B Period of rapid growth (exponential growth)
C Population levelling off
II Equilibrium position (asymptote); numerical stability
III Oscillations and fluctuations
A Oscillations – symmetrical departures from equilibrium
B Fluctuations – asymmetrical departures
IV Period of population decline (negative growth)
V Extinction

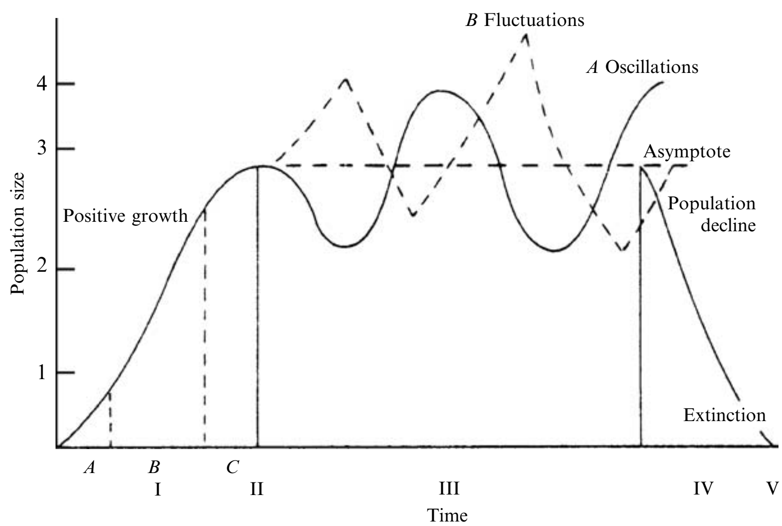
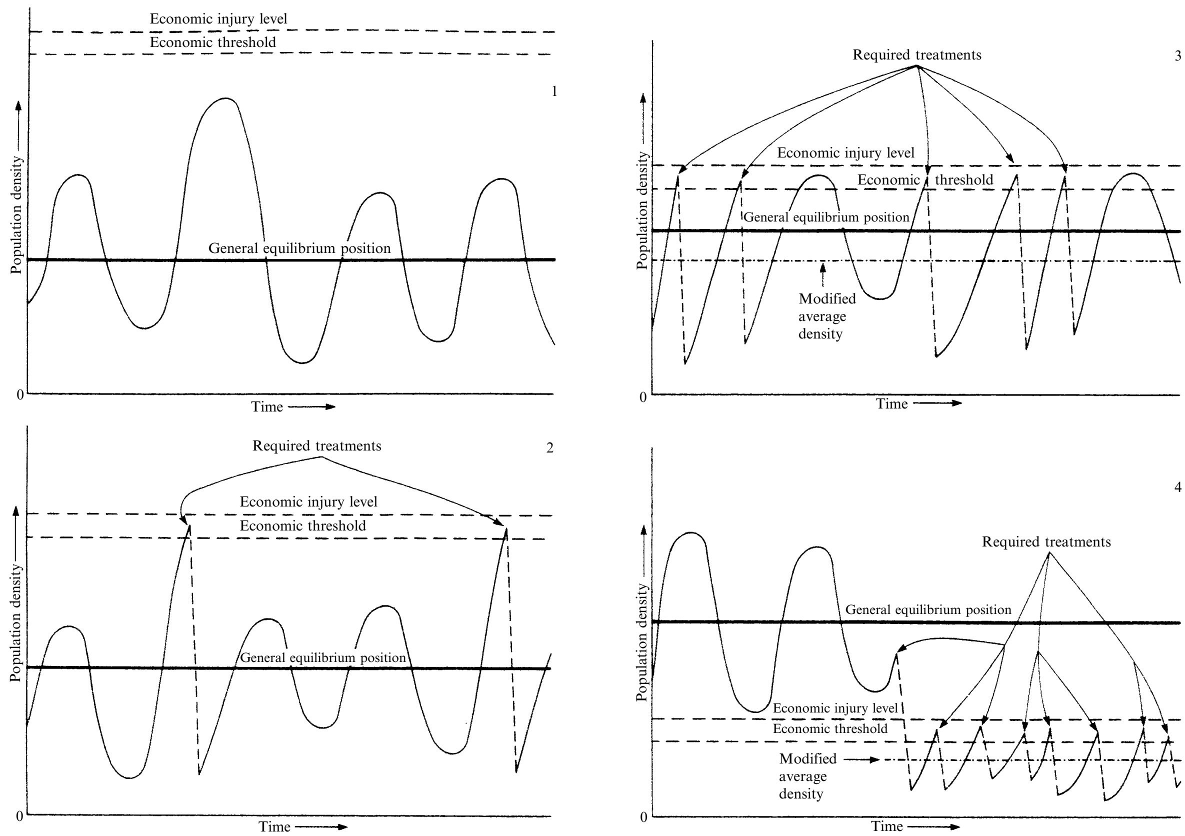


Fig. 2. Schematic graphs of the fluctuations of four theoretical arthropod populations in relation to their general equilibrium position, economic threshold and economic injury levels (from Stern *et al*., 1959).

1. Non-economic species whose general equilibrium position and highest populations are below the economic threshold, e.g. *Aphis medicaginis* on alfalfa in California, USA.
2. Occasional pest whose general equilibrium position is below the economic threshold, but whose highest population fluctuations exceed the economic threshold, e.g. *Cydia molesta* on peaches in California, USA.
3. Perennial pest whose general equilibrium position is below the economic threshold, but whose population fluctuations frequently exceed the economic threshold, e.g. *Lygus* spp. on seed alfalfa in western USA.
4. Serious pest whose general equilibrium position is above the economic threshold, usually requiring insecticide application to prevent economic damage, e.g. *Musca domestica* in milking sheds of dairy farms.



lation dynamics, particularly in relation to natural predation and mortality, and is, in point of fact, a vital part of any IPM programme. The growth of an insect population, especially the recruitment and the survival of the different stages, varies considerably according to the type of insect concerned. One result of this variation is that there are half-a-dozen different methods for the construction of a *budget* (for further details see chapters 10 and 11 in Southwood (1978)). As pointed out by Harcourt (1969), it is necessary to be careful in the choice of the appropriate method for compiling a life-table budget when planning the sampling methods to be used.

Resurgence

The term resurgence is used to express a sudden increase in population numbers. One type occurs when the target species, which was initially suppressed by the insecticidal treatment, undergoes rapid recovery after the decline of the treatment effect.

It may also occur as a result of the development of a new biotype of the pest, or if the insecticide treatment kills a disproportionate number of the natural enemies of the pest species.

Population fluctuations

Insect populations are frequently subjected to dramatic fluctuations and this is especially true for pest species that have an unlimited food supply. Often the cause lies with the natural parasites and predators, such as with some pests of cocoa and oil palm in S.E. Asia, but sometimes it is inexplicable. In Sarawak in 2002 a croton bush was heavily infested with mealybugs (Fig. 3.1) – it had been like this for eight months, and then suddenly within a period of 14 days the infestation completely disappeared (Fig. 3.2).

Population dynamics theory

(After Southwood, 1977.) Applied biologists have for a long time been concerned with two basic aspects of

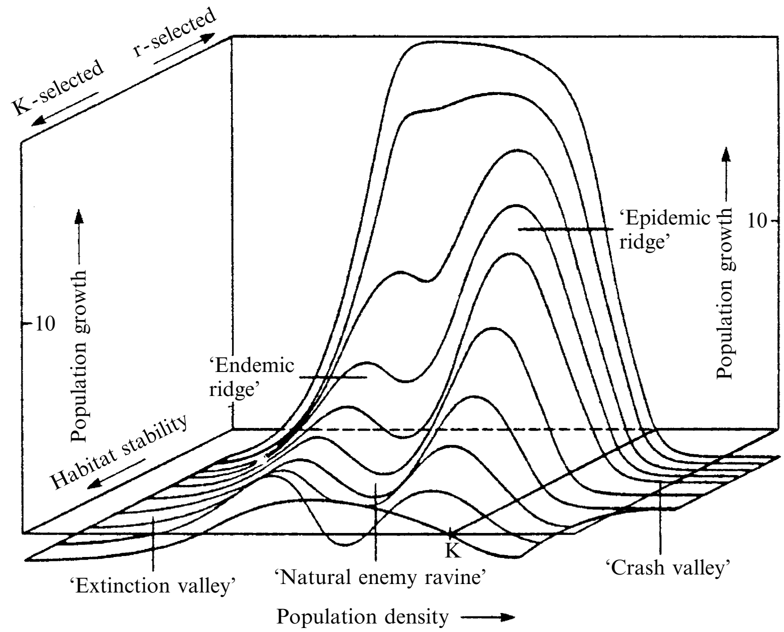
Fig. 3.1. Mealybug infestation of Croton foliage, BDC estate. September, 2002. All stems were heavily infested.

Fig. 3.2. Mealybug infestation completely disappeared after 10 days. October, 2002. B.D.C.

animal numbers: firstly that population numbers may change greatly, as pointed out by Andrewartha & Birch (1954), and secondly that most animal populations are relatively stable in comparison with their prodigious powers of increase. It now seems that certain species of animals belong to the one category and others to the second. Southwood pointed out that the change of the population fluctuation to a state of stability is associated with an increasing duration of stability in the habitat, and may be conveniently equated with the *r–K continuum. r-strategists* are opportunists, living in temporary (ephemeral) habitats and adapted to obtain maximum food intake in a short time; they are generally small, mobile and migratory, and have a short generation time. *K-strategists* live in stable habitats, often in crowded conditions, with their population size near the carrying capacity of their habitat; they are usually larger in size, less migratory and have a long generation time.

Fig. 3 is a synoptic population model. Three regions can be recognized. First the r-strategists, whose habitats are ephemeral and whose numbers are characteristically 'boom and bust': this strategy is dominated by large-scale migration, massive population losses, and new populations continually developing from a handful of colonizers. Secondly, the K-strategists represent the other extreme, maintaining a steady population at or near the carrying capacity of the habitat, basically in equilibrium with their resources; recruitment, mortality, and migration are low, so there is less opportunity to adapt to changed environments. These animals are specialized to their particular environment, and if their numbers are reduced to a low level they are liable to become extinct.

Fig. 3. The synoptic population model (after Southwood & Comins, 1976). K = carrying capacity (as in K-selected)
Note: equilibrium points only occur where an 'east-facing slope' cuts a zero population growth contour, as only here does negative feedback occur.



Finally, the middle region recognized is the 'natural enemy ravine'. Both kinds of strategists have a stable equilibrium point, the upper one at the population density of the carrying capacity of the habitat. Where the 'natural enemy ravine' dips below the zero population growth contour there is a second equilibrium point, and where it rises through the contour on the other side of the ravine is the release, or escape, point from natural enemies. Above this point, in the absence of density-independent catastrophes, the population rises to the upper equilibrium point where intraspecific competition mechanisms (disease, etc.) operate. These two levels have been referred to as the endemic (lower) level and the epidemic (upper) level.

r-pests include species such as locusts, armyworms, leafhoppers, aphids, planthoppers, many flies, and, in plants, the ruderals (weeds) belong to this category. *K-pests* include elephants in Africa, tapeworms, Codling Moth, ants, tsetse flies, and many beetles. Obviously the r- and K-pests represent the extremes of a continuum, and there is correspondingly a large group of *intermediate pests*. It is with this large group that natural enemies have most population impact.

Applied biologists generally appreciate that habitat characters are important indicators for IPM strategies, and Conway (in May, 1976) has shown that as the r–K continuum is related to habitat characteristics it is relevant to decisions on the choice of a particular control strategy.

Insect pest diversity (competitive exclusion)

Many zoology students have been taught the idea that no two animal species can occupy the same ecological niche without one species (the 'stronger') replacing the other (the 'weaker') over a period of time. Supporting evidence was usually an experiment carried out by Gause in 1934: he kept *Paramecium aurelia* and *P. caudatum* together in nutritive fluid in a small container; after about three weeks the latter species was exterminated. This idea is generally referred to as 'Gause's hypothesis', or 'the principle of competitive exclusion'. By definition this refers to the exclusion of one species by another when they compete for a common resource (often food) that is in limited supply; the principle being that two species with identical ecological requirements cannot coexist indefinitely.

It would seem that the basic principle of competitive exclusion is clearly valid, and it may be a factor of importance in evolution. But the *Paramecium* experiment was clearly a very simple case where both species ate the same simple food within an enclosed habitat, and as such represented a very artificial situation. For most phytophagous insects either the food sources are not limited, or else the ecological requirements of the different insect species are not identical, even though they may be quite similar.

When a student finds a particular crop pest species *in situ* on a host plant, frequently the assumption is made that 'that niche is clearly occupied so there will not be another species in that microhabitat'! In practice the converse situation prevails, as is generally recognized by most experienced field biologists: if one particular insect species is found on a plant at a particular location on the plant body, then the student should expect to find other species at the same location. It should never be assumed that an infestation is a single-species population; it is actually preferable to assume that each infestation may be a mixed population of several closely related (or otherwise) species, until proven otherwise. Many ecological studies have failed because of the inability of the observer/recorder to recognize a mixed-species population.

Thus it should be expected that many natural animal populations are likely to be composed of several (often closely-related) species, sometimes very similar in appearance and occasionally indistinguishable morphologically. Common examples in agricultural entomology include the following: the stalkborer complex on maize, rice, sorghum and sugarcane (Lep., Pyralidae, Noctuidae); scale insects on *Citrus*; mealybugs on sugarcane; aphids on lettuce; aphids on potato; leafminers on apple; chafer grubs eating the roots of sugarcane; weevil larvae eating roots of strawberry.

On many agricultural crops, food for an insect pest can be regarded as virtually unlimited; also most closely related insects have slight differences in their basic ecology or diet, so in most insect/crop plant situations the concept of competitive exclusion does not apply.

Insect pheromones in relation to pest control

Pheromones, originally referred to as ectohormones, are complex chemical compounds, basically long-chain hydrocarbons such as alcohols, esters, ketones, aldehydes and sometimes ethers. Many have now been successfully identified, and some synthesized; a number are now available commercially from some chemical companies, for pest monitoring or control purposes.

They are secretions from several different types of glands, on different parts of the insect body, which open directly to the exterior, the secretory product is usually airborne for its distribution. Their basic function is for communication of a specific type between individuals of the same species, and the chemical elicits a specific reaction in the receiving individual. Within the large, complex, social colonies of ants, bees, wasps and termites, apparently quite sophisticated systems of communication have evolved, mostly based upon the use of pheromones.

The term 'pheromone' is usually regarded in a behavioural context in that it is a chemical or chemical complex that elicits a specific behavioural response in the receiving insect. Apparently some glands secrete a single chemical, whereas others secrete several which appear to act in concert. Generally there has been no overall agreement for a scheme of classification, but most workers favour the basis to be the type of behaviour released in the receiving insect. One approach is to consider them to be of two basic types, those which give a releaser effect (this entailing a more or less immediate and reversible effect on the behaviour of the recipient), the others having a primer effect (this starting a chain of physiological events in the receiving insect). The latter group are usually gustatory in operation and typically control the social behaviour in Hymenoptera and Isoptera. Behaviour-releasing pheromones are typically odorous and their action is direct upon the central nervous system of the recipient, usually through the chemoreceptors in the antennae.

Recent work has demonstrated that most insect pheromones are in fact a complex of chemicals, and the individual chemicals are referred to as *components*. For example, the Smaller Tea Tortrix Moth sex pheromone has four components, two are major components and two are minor. Current opinion is that further research will reveal that almost all pheromones are actually chemical complexes of several compounds, and that the original idea of there being only one chemical present is completely incorrect, and originated because at the time the methods of chemical analysis were insufficiently sensitive to detect the minor components.

It is now apparent that much of the early work on insect pheromones is largely worthless (or, at best, of limited value) in that the researchers did not appreciate that almost invariably each pheromone was in fact a complex of major and minor components acting in concert on the receiving insect. Experimentation using only some of the chemical components of a particular pheromone inevitably led to anomalous results.

The types of behaviour (pheromones) used by Shorey (1976) were aggregation (including aerial and ground trail-following), dispersion, sexual, oviposition, alarm and specialized colonial behaviour. Some pheromones appear to have more than one function so these categories are of somewhat limited application.

Aggregation

The reasons for aggregation are numerous and varied, and include collection around or to a food source, a shelter site, a site for oviposition or colonization, recruitment of a sexual partner, and aggregation for swarming or dispersal purposes.

One of the most obvious cases can be seen by watching ants on their foraging trails, where the scouts are clearly laying scent trails. Trail-following by ants has been well studied. The scouts, after having located a food source, deposit droplets of pheromone on the ground and this stimulates trail-following behaviour amongst other workers. While the food source persists the ant workers continually reinforce the scent trail, but after depletion trail reinforcement ceases and the trail eventually disappears. Some trails are ephemeral but others persist for weeks or months. The Imported Fire Ant (*Solenopsis saevissima*) in the USA uses short-lived trails near the nest, but some species of Leaf-cutting Ant (*Atta* spp.) lay persistent trails to leaf sources up to 100 m distant which may last for months. Similar trails are laid by termites when foraging.

Bees and wasps (*Vespa vulgaris*) leave a scent trail from their feet which is important in delimiting the entrance to their nests.

Bark beetles (Scolytidae) use aggregation pheromones to designate host trees suitable for colonization, as these beetles only flourish when present in quite dense populations. The pheromones are released from the hindgut of the beetle mixed with the various terpenoid compounds of the host tree which initially attracted the first invaders to the tree. These aggregation pheromones can be released by either sex and serve to attract individuals of both sexes. Colonization is usually succeeded by mating which involves the use of sexual pheromones. This type of aggregation can also be seen in the Japanese Beetle (*Popillia japonica*) and the Cotton Boll Weevil (*Anthonomus grandis*).

Certain mosquitoes release pheromones into the water at oviposition which attract other females. Sheep Blowfly (*Lucilia cuprina*) females apparently use an aggregation pheromone to form dense populations at sheep carcases for oviposition.

Aggregation at a suitable resting site has been demonstrated for the Bed Bug (*Cimex lectularis*) and some other cryptozoic species.

The mechanism for aggregation at a chemical source is usually chemotaxis where the insect can detect the gradient of odour molecules, and it often involves orientation by anemotaxis, that is positive orientation to air currents, particularly in the case of flying insects.

Dispersal

Dispersal is clearly the opposite of aggregation, but it is not encountered very often. However, some bark beetle males produce pheromones after mating which repel other males, and some female beetles release a repelling pheromone when they are unwilling to mate. *Tribolium confusum* females release a pheromone in the foodstuff they infest which repels other females and ensures a uniform population distribution throughout the available space. It is thought that the female Apple Fruit Fly leaves a pheromone trace on the apple surface after oviposition, for she can be seen to drag her ovipositor over the surface and generally other females do not lay their eggs in the same fruit.

It seems that some dispersal secretions are the same as the defence secretions; for instance, nymphs of *Dysdercus* produce stinking coxal gland secretions when disturbed (thought to be a defence against predators) which causes the gregarious bug nymphs to scatter. Certain species of ants have alarm pheromones which in some circumstances (in the nest) induce aggregation but under other conditions (away from the nest) result in dispersal.

Sexual behaviour

Sex pheromones may be produced in either sex and stimulate a series of behavioural sequences that usually results in mating. Typically, there appears to be a hierarchy of behavioural responses with increasing stimulation by sex pheromones. Once the two sexes are in proximity there is usually a close-range series of behavioural reactions, referred to as courtship behaviour.

The most usual situation is that a receptive virgin female insect will announce her availability through release of aerial sex pheromones, known as 'calling', and these cause a flight response and approach by receiving males. The night-flying moths (especially Saturniidae, Geometridae, and Noctuidae) are best known for their nocturnal emission of sex pheromones, which reputedly can attract males from as far as 5 km downwind. Males may produce a pheromone (sometimes called an 'aphrodisiac') when in the immediate vicinity of the female, which operates by inhibiting the female's tendency to fly away.

Sex pheromones are commonly referred to as 'sex attractants' or 'sex lures', which is misleading in that it implies that the odorous chemicals simply cause attraction, which is a great oversimplification. As will be discussed later, the male response to a female pheromone is complicated and sequential, involving half-a-dozen or more separate stages.

Most of the sex pheromones that have been isolated, identified and synthesized are from the Lepidoptera, and include Red Bollworm, Spiny Bollworm, Pink Bollworm, *Heliothis* spp., *Spodoptera littoralis*, *Chilo* spp., *Prays citri*, *Prays oleae*, Gypsy Moth, *Bombyx mori*, Cabbage Looper, Codling Moth, and Honey Bee queen. Pheromones of some of the most important fruit flies (Tephritidae) such as *Dacus* and *Ceratitis* spp. have also been synthesized, as have some for Scarab Beetles and Scolytidae. Many of the sex pheromones are either difficult to synthesize or else expensive to produce, and this has led to the development of chemical pheromone mimics for large-scale management programmes. These chemicals are discussed in the section on 'attractants' which follows later.

Oviposition

As already mentioned, Sheep Blowfly females release an aggregation pheromone when they oviposit on a suitable sheep carcase in Australia, and the result is the formation of a dense population. Bark beetles (Scolytidae) aggregate on suitable trees as a result of use of aggregation pheromones, but the ultimate purpose of the aggregation is for oviposition and breeding. Thus, functionally many of the aggregation pheromones are also used to stimulate oviposition upon the correct host plant. This point is mentioned later under the heading of 'plant odours', as there appears to be probable interaction between plant volatiles and pheromones connected with the oviposition of many phytophagous insects.

Alarm behaviour

This is characteristic of social Hymenoptera and Isoptera, and may be seen most dramatically when field workers disturb a nest of Paper Wasps (*Polistes* spp.) or arboreal ants in plantation trees. The wasps (and bees) produce alarm pheromones both when they sting and when gripping with their mandibles. The pheromone is released from glands in the stinging apparatus and from the mandibular glands, but apparently the worker can open the sting chamber and emit the pheromone without the necessity of stinging.

It has recently been demonstrated that aphids secrete alarm pheromones from their siphunculi when distressed. Recent work at Rothamsted has shown that a wild potato (*Solanum berthaultii*) produces a chemical mimic of this pheromone from special secretory hairs on the foliage which appears to repel aphids from its leaves.

Attractants

Initial experimental studies on female sex pheromones were conducted using live virgin females that had been laboratory-reared, or else a chemical extract was made from the abdomen tips of many young females and this was used instead of the live insects. It was soon apparent that these sex pheromones have considerable potential application in pest management programmes and so many organic chemists in government and industrial establishments started work in this field.

One approach was to carefully analyze the tiny quantities of natural pheromone produced by virgin females, and, when the chemical components were isolated and identified, to attempt to synthesize the same chemical compounds in the laboratory.

The second approach was to try and synthesize closely related chemical compounds which might possess the behavioural qualities of the natural pheromone, but were easier and cheaper to manufacture. In this way pheromone homologues and analogues have been produced commercially. A *pheromone homologue* is a very closely related compound, which differs only from the natural pheromone by chain lengthening or shortening following, for example, addition or removal of a methylene group. A *pheromone analogue* is a less-closely related compound that has major basic differences in structure, such as the change of a functional group or its position, for example an alcohol, ester or ketone.

The third approach was to use a vast range of organic chemicals, which it was thought might possibly function in a manner similar to sex pheromones, and to use them in laboratory and field trials in a purely empirical manner to see if they did possess such qualities. The organic chemicals that have been found to be successful in attracting certain male insects are collectively referred to as *sex attractants*. Obviously for monitoring purposes it does not matter how the chemical attracts the insects so long as it does attract them sufficiently well, and a great deal of research effort is being expended in this field at present. Sometimes these chemicals are termed *pheromone mimics*, for the obvious reason that they produce a similar reaction in the receiving male insect. 'Hexalure' is a chemical attractant produced commercially in the USA for use with Pink Bollworm on cotton, in a disruptive technique to prevent mating.

Recent work has demonstrated that many pheromone complexes are subjected to *synergism* in one way or another. In some cases it appears that some of the minor components have a synergistic effect on the major components or else on the pheromone complex as a whole. Sometimes the synergist may be a chemical released by the host plant; this may be of more importance in aggregation or oviposition behaviour, for example in scolytid infestations of forest trees various terpenoids are released by the injured tree which interact with the aggregation pheromones released by the beetles. Empirical chemical testing has discovered a number of synergists for use with sex pheromones that appreciably enhance their performance.

The sex pheromones of insects must, by their very nature, be quite specific to each species but some of the attractants have a very useful and much broader response, for example 'Cu-lure', developed initially for Melon Fly (*Dacus cucurbitae*), and methyl eugenol both attract all species of *Dacus* and some other fruit flies in addition, which makes these chemicals very useful for survey studies.

Sex attraction in Lepidoptera

Most of the work on sex pheromones and attraction has been done on the Lepidoptera, and the greatest potential for pheromones in pest management is in this group.

The 'calling' female moth emits her sex pheromones from the genital opening on the abdomen tip and the chemical complex is carried downwind as a plume. The odour plume is basically cone-shaped, but is flattened ventrally if the moth is close to the ground; the plume widens and the chemicals disperse as they are carried from the source. The shape of the plume is clearly controlled by wind speed and direction, the contours, and the presence of tall vegetation such as trees. Most virgin female moths 'call' at dusk or at night when there may be strong temperature gradients, or even inversions, over the ground, and these will obviously have effects on the spread of the pheromone.

The male moth responds to the pheromone by anemotaxis, in that it flies upwind in a zig-zag pattern. At first (assuming the male to be some distance from the female) the flight pattern of the male moth diverges from the plume of pheromone quite often, but as it approaches the female the pheromone concentration increases and the flight of the male moth becomes more direct.

The patterned response by a resting male moth to female sex pheromone can generally be described in half-a-dozen sequential stages, as follows:

(a) reception – antennal elevation or twitching,
(b) activation – wing fanning or fluttering,
(c) active flight,
(d) orientation to the source of pheromone – i.e. anemotaxis,
(e) alighting – landing in the immediate vicinity of the female moth,
(f) courtship – including gland extrusion and release of male pheromone,
(g) mating.

Thus it is clear that the behavioural response by a male moth to a 'calling' female is a complex sequential series of events and is not just a simple attraction.

The initial responses are made to a low concentration of pheromone, but the later events require an ever-increasing concentration of pheromone. It is now thought that the different components of the sex pheromone are responsible for different parts of the behaviour sequence. Thus, if in an experiment one minor component is missing, this will result in the behaviour sequence being broken, and the experimental results confusing.

With *Adoxophyes orana* it has been demonstrated that the female sex pheromone has two components and that there are three different types of chemoreceptors on the male antennae (Den Otter, 1980). One type of sensillum reacts to the first component in electroantennagram studies, the second type reacts to the second component in the female pheromone, and it is suspected that the third type of sensillum may react to the male pheromone at close range, but this has not yet been demonstrated.

Insect feeding on plants

Insect feeding

The feeding process in animals involves different aspects, all of which have some importance in relation to control of pests. The main aspects include:

(a) Recognition of food
  (i) distant
  (ii) proximal
  (iii) contact
(b) Manipulation of food
(c) Ingestion

(a) Recognition of food

(i) *Distant*. This is usually (for most animals) a sight reaction to shape and colour; at what distance host/food recognition is achieved is probably very variable. With some birds of prey it can be up to a kilometre, but at the other extreme for mammals such as moles it is probably only a few centimetres. For many haematophagous Diptera, host/prey movement is very important for distant recognition, followed by heat radiation when closer; but these factors are scarcely applicable to plant hosts. With herbivorous insects long-range recognition is probably a combination of sight and smell. A recent review on this topic is by Prokopy & Owens (1983). Presumably with a large crop, odour recognition from a distance may be achieved; this must give some crop pests a distinct advantage over insects feeding on wild hosts in natural (mixed) vegetation.

Yellow coloration is certainly an attraction to many insects, and it is thought that this is basically because the young and very old leaves have more available foodstuffs in the tissues than the mature leaves: there would certainly be soluble sugars in such leaves as opposed to insoluble starch deposits, and apparently a higher than usual nitrogen content usually confers (in young leaves) a yellowish coloration. Blue is attractive to some Tsetse, but aphids are repelled by blue colours.

(ii) *Proximal*. At closer quarters sight may still be important, as some plants do have what appear to be quite definite recognition signals for searching insects (although most of these are connected with the need to attract pollinators). Scent recognition is presumably of prime importance, utilizing both natural volatile elements and also metabolic by-products.

(iii) *Contact* (host-plant testing). If the host plant looks and smells correct then the insect alights and contact is effected. The aura of the plant will then be reinforced or superseded by the taste; these stimuli being received through chemoreceptors on the foretarsi and the palpi of the mouthparts.

(b) Manipulation of food. This involves the cutting up of pieces of plant material by the mandibles, tasting them, and their manipulation by the various mouthpart structures into a position for ingestion. For sap-sucking insects this involves the insertion of the proboscis into the correct site for food ingestion, sometimes into the xylem vessels (Cercopidae, etc.), usually into phloem tubes (Aphididae, etc.), and sometimes just into mesophyll tissues or a ripening fruit.

(c) Ingestion. For insects with biting and chewing mouthparts the addition of saliva to the chewed fragments is important for lubrication to avoid damage to the oesophagus. The Hemiptera apparently all inject saliva and/or regurgitate stomach enzymes when feeding. Precisely why this is done with plants is not clear, but obviously with blood-sucking and predacious bugs their saliva contains an anti-coagulant which permits them to feed without the blood clotting in the proboscis. The predacious forms also practise external digestion of part of their prey in order to be able to render their food liquid enough to be imbibed through their proboscis. The injection of saliva and/or enzymes into the host plant when feeding is of importance agriculturally as the plant reacts to the presence of these alien substances by growth distortion, or necrosis of tissues.

Plant odours

Most plants release volatile odorous chemicals into the atmosphere (although the majority are undetectable by human sense) and phytophagous insects react to these chemical stimuli when locating host plants. Monophagous and oligophagous phytophagous insects usually react to specific volatile odorous chemicals in, and emitted from, the host plant. It is thought that polyphagous insects either have no olfactory chemical response, or else react to general plant chemicals. The olfactory chemoreceptors are mostly situated in the antennae, but in some Diptera they are located on the tarsi (feet).

It has very recently been demonstrated that very strong plant odours can inhibit sex pheromone reception; the interaction of plant odours and sex pheromones is thought to be complementary under natural conditions, so that mating is more likely to be successful on appropriate host plants, whereas the chances of mating taking place on inappropriate host plants are reduced. As this is a very recent discovery, as yet little work has been carried out, but future studies might well give rise to a greater understanding of the general phenomenon of host-specificity in phytophagous insects.

The chemical attractants in plants, when identified, are usually a mixture of many different compounds, for example, cruciferin in the brassicas is a complex mixture of glucosides, amines, and other chemicals. Biochemical research has shown that most of the more important volatile chemicals in plants are secondary metabolites.

Work at Wellesbourne (NVRS) has demonstrated that Cabbage Root Fly are clearly attracted to some of the volatile chemical components released by plants of the Cruciferae, and some stimulate increased egg-laying. It was shown that gravid females could move at least 24 m upwind to a brassica crop in response to the odour stream. Volatile hydrolysis products are constantly released, at low concentrations, from Cruciferae during normal growth and development, resulting from damage or death of cells, and by the endogenous enzyme system. More than 23 different compounds were obtained from cultivated crucifers at NVRS (Cole, 1980); the actual component constitution varied with the species, the age and stage of development of the plants. Only a few of the 23 compounds actually elicited a response from the flies when used in isolation. The overall situation with regard to plant production of volatile chemicals is clearly complicated, but a great deal of research effort is being expended on this subject worldwide, and gradual elucidation is to be expected. Other relevant publications include Wallbank & Wheatley (1979), Ellis, Cole, Crisp & Hardman (1980), and Crowson (1981). An especially useful book is *Insect Herbivory* by Hodkinson & Hughes (1982).

Ferns as a group are little attacked by insects, and this is thought to be because they contain considerable quantities of repellent/toxic chemicals such as ecdysones, glycosides, phenols, sesquiterpenes, tannins, thiaminase, etc.; the group is ancient and has presumably been grazed extensively, particularly in the days before the evolution of the flowering plants. One striking feature in ferns is that the chemical production is at a peak very early in the growing season so that the youngest fronds are usually the most toxic as well as containing the most available protein.

Studies at Rothamsted have shown that a type of wild potato (*Solanum berthaultii*) from Peru, has two types of 'hairs' (trichomes) on its foliage: one type is short with a sticky head, and the secretion can trap insects on the leaves and stems by adhesion; the other hairs are longer and secrete fluid containing (E)-B farnesene, which is the main ingredient of the alarm pheromone in most species of Aphididae. Experiments showed that *Myzus persicae* aphids were reluctant to invade the foliage of this plant.

In addition to the attractive odours, plants also produce volatile chemicals that function as repellents (from a distance) or feeding inhibitors (at close range), and these form part of the plant defence mechanism against insect attack.

Plant resistance to insect feeding

A very recent and exciting development in insect/plant relationships is the concept of rapidly induced anti-insect defences in plants; this is mentioned at the end of this section. It has even been postulated that there can be communication between adjacent trees through airborne chemicals, so that neighbouring trees increase their defences before being attacked by the insects. However, it should be stressed that this line of research is very much in its infancy and the available data may have alternative interpretation (see Fowler & Lawton, 1984).

The basic resistance exhibited by plants to insect attack is partly physical and partly chemical. The physical properties include:

(a) Thickened cuticle
(b) 'Hairy' epidermis (trichomes may be hooked, secretory, or just physically close together)
(c) Hardening of tissues by general sclerenchymatization
(d) Increasing the extent of natural silica deposits in the tissues
(e) Spiny leaf margins (e.g. holly) may deter some leaf-margin eaters (the thorns and spines developed presumably to deter vertebrate grazers and browsers are not effective against insects; in fact some insects mine spines!)

The chemical defences include:

(a) Absence of specific attractants or feeding stimulants that would otherwise normally be present
(b) Presence of repellent odours to deter insects from alighting on the plant
(c) Presence of distasteful or poisonous chemicals in the tissues to deter feeding
(d) Absence of certain chemicals (often amino acids) required for normal development of the immature insects
(e) Presence of chemicals that mimic insect alarm pheromones, for example the wild potato already mentioned and the aphid alarm pheromone mimic

The major chemical repellents in plants seem to be terpenes, tannins and various alkaloids. Tannins are mostly found in horsetails, ferns, gymnosperms, and some angiosperms, and they are quite antibiotic to many pathogens. Alkaloids are mostly found in angiosperms and are thought to be of more recent origin. It is thought that tannins were developed initially in the process of evolution as a deterrent to grazing reptiles, and the alkaloids similarly evolved as a protective mechanism in angiosperms to repel grazing mammals. It seems unlikely that the Insecta were at all involved in the evolution of feeding repellents in plants, although these may now be of considerable importance with respect to phytophagous insect feeding behaviour. The insect biotypes that come to feed on 'repellent' varieties of crop plants (and other plants) usually develop biochemical detoxification mechanisms, so that the poisonous compounds are broken down into non-toxic degradation products.

It has been suggested that 'dominant' (termed 'apparent') species of plants have chemical defences that tend to cause digestive difficulties and retard development of insects feeding on their foliage, rather than actually causing death (see Crowson, 1981; chapter 18); and also that the pests of these plants tend to be polyphagous (and possibly the more ancient) species. Good examples of such dominant plants include the oaks (*Quercus* spp.) and beech (*Fagus* spp.); their main defences against insect herbivores appear to be a combination of sclerification of the leaf tissues and accumulation of tannins. After about a week or two from leaf-unfolding, the young leaves become quite inimical to the insects; larval development slows, mortality increases, fewer eggs are laid, etc. Many insects have adjusted their life cycles so that they are able to feed on the young leaves during the short period of time while they are palatable. The less-dominant plants (termed 'unapparent'), which are usually the more recently evolved, tend to be the ones to develop actual poisons (alkaloids, etc.) as their chemical defence.

It is now clearly established through recent research that some plants respond to insect feeding damage by active production of deterrent chemicals, so that their final concentration in the leaf tissues is considerably greater than before. In some cases the whole tree produces more chemicals, not just the damaged leaves. The entire subject of insect/plant relationships has recently been evoking a great deal of interest and much has been published of late.

As mentioned at the start of this section, it has been said that insect-injured plants emit volatile chemicals that stimulate neighbouring trees to produce defensive chemicals irrespective of whether they are attacked or not. But the data at present are not really conclusive, and are usually open to other interpretation. It might be expected that the levels of chemical secreted into the air would be too low a concentration to elicit such a response from a receiving tree.

Food sources for adult insects

When considering the subject of insect pest feeding, it is invariably assumed that it is the pest stage of the insect feeding on the cultivated plant. With groups such as Orthoptera, Hemiptera, and some Coleoptera (e.g. Chrysomelinae) both adult and immature insects are found side-by-side on the crop and both cause damage (often identical, sometimes different). However, within the Diptera and Lepidoptera it is the larval stages that are agricultural pests; the adults are free-living and with a very few exceptions (such as fruit-piercing moths) not crop pests, although some females may cause damage to the plants when ovipositing. Most of these adult insects (females anyway) require food prior to ovulation or egg development, and in temperate regions the spring/summer emergence of adults is often closely synchronized with the flowering of various local wild herbs and shrubs.

A striking example of this dependence upon local vegetation is seen with many flies (Muscidae, Anthomyiidae, Psilidae, etc.) in Europe where the newly emerged adults congregate and feed upon the flowers of wild Umbelliferae common on headlands and in hedgerows. The most abundant and widespread species of Umbelliferae concerned as nectar sources as follows:

Common name	*Scientific name*	*Flowering period*
Cow Parsley	*Anthriscus sylvestris*	April–June
Hemlock	*Conium maculatum*	June–July
Hogweed	*Heracleum sphondylium*	June–September
Upright Hedge Parsley	*Torilus japonica*	July–August
Wild Angelica	*Angelica sylvestris*	July–September
Fennel	*Foeniculum vulgare*	August–September

One reason for the importance of this group, apart from their widespread distribution, is the sequential flowering periods which result in a continuous flower availability in hedgerows from early April until the end of September, or even into October. Thus there is nectar available for each successive generation of adult flies as they emerge.

For many groups of insects there is no obvious link with a particular group of nectar-producing plants upon which they are dependent. Many moths are quite opportunistic in their feeding and will take nectar from many different sources. The early spring in Europe is characterized by a paucity of flowers: only a small number of plants have flowers at this time so natural sources of nectar for early-emerging flies (and moths) in April are quite limited. Later, by June and July, the countryside is a profusion of flowers, and nectar sources are numerous.

Adult insects that emerge and oviposit over the winter period, such as Winter Moth and other hibernal Geometridae, use their fat body for nutrients and they lay their eggs without feeding at all; but, of course, their pupal period was relatively brief.

Many of the muscoid flies, whose maggots attack vegetables in the soil, or cereal seedlings, feed predominantly on the flowers of the wild Umbelliferae listed above, and in most cases it appears that the nectar feed is necessary for egg development. These flies typically emerge from overwintering pupae in April, in the UK; they include Cabbage Root Fly, Onion Fly, Bean Seed Fly, and Carrot Fly amongst others.

Knowledge as to the feeding requirements/preferences of the adult insects can be ecological information of great use in survey studies and in population monitoring, and might on occasion be used for an adult insect control programme. This would be a line of research that might be profitably pursued for a number of important crop pests.

Abundance and richness of insect (arthropod) faunas on host plants

Another aspect of insect-plant relationships receiving attention recently is the analysis of the factors seemingly responsible for the abundance (numbers of individuals of each species) and richness (numbers of different species) of the insect fauna (including phytophagous mites) on trees. Most of the published studies refer to indigenous trees, but the basic ecological concepts involved should have application to the study of long-term orchard and plantation crops and their pests. Clearly these studies are, at present, confined to more or less permanent hosts such as trees, for the study of annual plants would present additional complications reflecting their ephemeral nature.

In a recent paper by Kennedy & Southwood (1984) (which includes a comprehensive bibliography) they investigated the following factors with reference to insects on British trees: host-tree abundance, time, taxonomic isolation, tree height, leaf size, and two more nebulous characters termed 'coniferousness' and 'deciduousness'. The most important factors were the first two. *Host-tree abundance* refers to the overall area of habitat available for colonization; a larger area is also likely to provide more different microhabitats and thus a wider range of niches for a larger group of associated species. *Time* refers to the evolutionary age of the tree species, and would seem to be positively correlatable to the species richness of the insect community, although there has been some controversy on this point. Of the other five factors considered by Kennedy & Southwood all, with the exception of 'coniferousness', apparently made significant contributions to the present recorded diversity.

Banerjee (1981) made an analysis of tea pest species and reported that time (measured as the age of the plantation) was the major factor in relation to pest recruitment; pest diversity reaching maximum at a plantation age of about 35 years. With other tropical plantation crops it seems that other factors may be more important in relation to pest diversity.

A number of useful papers on insect–plant relationships are presented in the Royal Entomological Society of London, Symposium Number Six, edited by H.F. van Emden (1972).

Insect (pest) distributions

The distribution of animals and plants throughout the world is controlled by many different factors. With cultivated plants clearly the most dominant factor has been the deliberate transport by man. For insects and other animals the evolutionary history of the area is of importance, but probably the overriding factor is the climate. Of the climatic factors temperature is the most important (and most easily measured). As insects are poikilothermic they have only a little influence over their body temperature over which the various bodily functions operate most efficiently, and they have a heat death point and a cold death point at which they die. From the point of view of distribution globally the cold death point is the most important, and the insects can be divided into three main groups on this basis, as follows:

(a) Tropical insects – cold death point circa 10–15°C
(b) Temperate insects – cold death point at 0°C (death because of ice crystal formation in the cells/tissues)
(c) Boreal (Arctic) insects – death point well below 0°C (−20–30°C often); body fluids supercool and freeze to glass

A few well-known species are clearly *eurythermal* and are able to have a worldwide distribution as they can function over a wide range of ambient temperatures. Some others are *stenothermal* and only thrive in a narrow range of temperatures, either low, high or intermediate.

Pest organisms are species renowned for their biologically aggressive and opportunist nature in relation to hosts, and on the whole their distribution tends to be ever-increasing to the limits of suitable environmental conditions; these limits are often climatic.

Knowing the *optimum* conditions of temperature and relative humidity for the development/activity of an insect species, and its preferred range of conditions, it is possible to plot a *climatograph* with different areas of suitability/abundance for the species. This is sometimes used in making prediction assessment of the climatic suitability of an area for an outbreak/invasion of a particular pest; knowing the zones of suitability in regard to climate for the pest, if the monthly means of temperature and humidity are plotted on to the graph a polygonal diagram results, and the placement of the diagram indicates the likelihood of climatic suitability. In fig. 4 is shown the climatograph for the Medfly (*Ceratitis capitata*) in relation to (A) Orlando, Florida, (B) Naples, Italy and (C) Ankara, Turkey (from Edwards & Heath, 1964). If temperature and rainfall are used as criteria the diagram is called a *hythergraph*.

After extensive laboratory studies and field observations it is possible to designate three fairly distinct zones of abundance for each insect (pest) species, as follows.

(A) (Endemic) zone of natural abundance. Here the pest species is always present, often in large numbers, and regularly breeding. Environmental conditions are generally optimal for this species, and in this zone the species is regularly a pest of some importance.

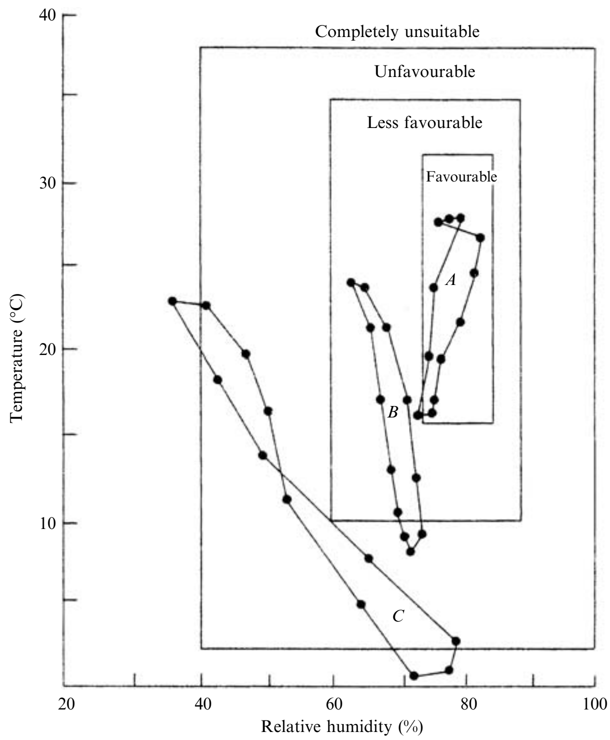
(B) Zone of occasional abundance. Here the environmental conditions are either less suitable (i.e. drier, cooler, etc.) or else with pronounced variation (often seasonal), having periods of suitable conditions alternating with unsuitable. The population is kept low by the overall climatic conditions; some breeding does occur, but only occasionally does the population rise to pest proportions. Sometimes climatic conditions are sufficiently severe to destroy the entire population, which then has to be re-established by dispersal from the endemic zone.

(C) Zone of possible abundance. This is essentially a zone into which adult insects spread (disperse) from zones (A) and (B). The immigrant population may survive for a time, and may actually be a pest for a while, until changing climate destroys the organisms. Breeding in this location is rare, but permitted occasionally by a period of mild weather. Occupation of this zone is strictly ephemeral (short-lived).

In fig. 4, the three boxes on the graph (A, B, C) could be regarded as corresponding to the three natural zones of abundance.

The basic nature of an insect population is to increase, and unless it is controlled by changing climate, heavy

Fig. 4. Climatograph for the Mediterranean Fruit Fly. A = Orlando, Florida; B = Naples: C = Ankara (from Edwards & Heath, 1964).



predation or parasitism, or artificial control measures (i.e. insecticide spraying) there is usually dispersal of part of the population to alleviate the competition pressure for food or other limited resources. Thus many pest species increase in numbers in zone (A), and when the population density is high some disperse into zones (B) and (C) from time to time. These three zones are not necessarily constant in their demarcation, depending in part upon the nature of the limiting factors controlling the distribution of the pest organism. Often the main limiting factor is available food, and if the host crop becomes more widely cultivated then many pests may follow the crop into the new regions.

The dispersal success of a pest organism depends upon several factors, including the effectiveness of the precise method of dispersal (e.g. insect flight, wind-carried fungal spores, transport on agricultural produce, etc.) and the adaptability of the pest. Many of the most successful pests have a eurythermal physiology and a polyphagous diet.

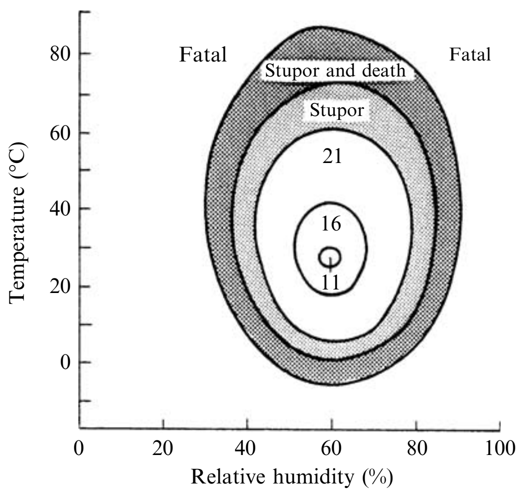
As an example of the interaction between temperature and relative humidity the diagram made by Uvarov (1931) for the Cotton Boll Weevil can be used (fig. 5). It may be generally regarded that conditions optimal for rate of development are also optimal for the whole organism and its general well-being. Strictly speaking this may not be true, for in some species the different physiological processes have slightly different optima.

Changing distributions

In the past many of the major changes in the distribution of a pest species were made through human agency, for example the Gypsy Moth or Colorado Beetle, either intentionally or accidentally. But occasionally an animal drastically increases its distributional range under its own powers of dispersal; the reason for the spread is generally not understood. These sudden changes are usually termed *invasions* so far as the new countries are concerned. There have been two quite recent and interesting invasions in the UK. Firstly, the Collared Dove (*Streptopelia decaocto*), an Asiatic species, normally resident (i.e. non-migratory), which invaded Europe through Turkey early this century and was first recorded in the UK in 1951 in East Anglia. This is now widespread and locally abundant, and has even bred in Iceland. It is somewhat urban in habits and regarded as a pest species by chicken rearers as it takes grain fed to the chickens in open runs. A recent insect pest to invade the UK is the American Lupin Aphid (*Macrosiphum albifrons*), first recorded in West London in 1981. It withstood the statutory eradication measures that were immediately implemented, and is now abundant and widespread in England and Wales as far north as Yorkshire. This pest is confined to lupins, so far as is known, and infested plants often die, unless control measures are applied. In both the UK and in many parts of Europe there is recent interest in lupins both as a break crop in cereals, and some annual species are grown for their seeds which have a protein content higher than soybean. Some perennial species are also being used very successfully as pioneer colonizers on open-cast mining reclamation sites. Thus the Lupin Aphid, which first seemed to be only serious to gardeners in destroying their flowers, now appears to have much more serious economic significance. At present it has not been recorded from Europe.

Pests that are *native*, or *endemic*, to a region are referred to as *autochthonous*, the implication being that they have evolved locally. Species now found locally, but which are thought to have originated elsewhere, are termed *allochthonous*; they are usually immigrants of one type or another.

Fig. 5. Time of development of the Cotton Boll Weevil (in days) in relation to two climatic factors (after Uvarov, 1931).



Pest distribution

When considering the different insect and mite pests in an area or on a crop it is sometimes necessary to regard them in a broader context of their overall distribution. To elucidate the terminology used in biogeography, fig. 6 shows a map of the World with the generally accepted major biogeographical subdivisions.

Zoogeographically a somewhat different terminology is used, as shown in fig. 7.

Dispersal

This is the natural spread of part of a population away from its source (origin) at a time of high population density. With birds and mammals, the dispersal is often partly to seek new territories, and sometimes it is a population survival mechanism to ensure that, on dispersal of the first brood, the parents find sufficient food in their territory to raise a second brood of offspring. With insects, dispersal sometimes appears to be obviously in response to dwindling food supplies, or a reduction in the availability of suitable food (such as progressive drying of leaves, etc.), and sometimes it appears more as a behavioural quirk which coincides with certain weather conditions. The overall effect is clearly beneficial from the point of view of survival of the species. Dispersal appears to be very important for the overall survival of the species as it enables diminished populations to be replenished, and the spread of genetic material through the entire population is advantageous. Also newly available habitats (such as new agricultural crops) can be colonized. In the same way that all animal and plant populations have

Fig. 6. General geographical/biological subdivisions of the World.

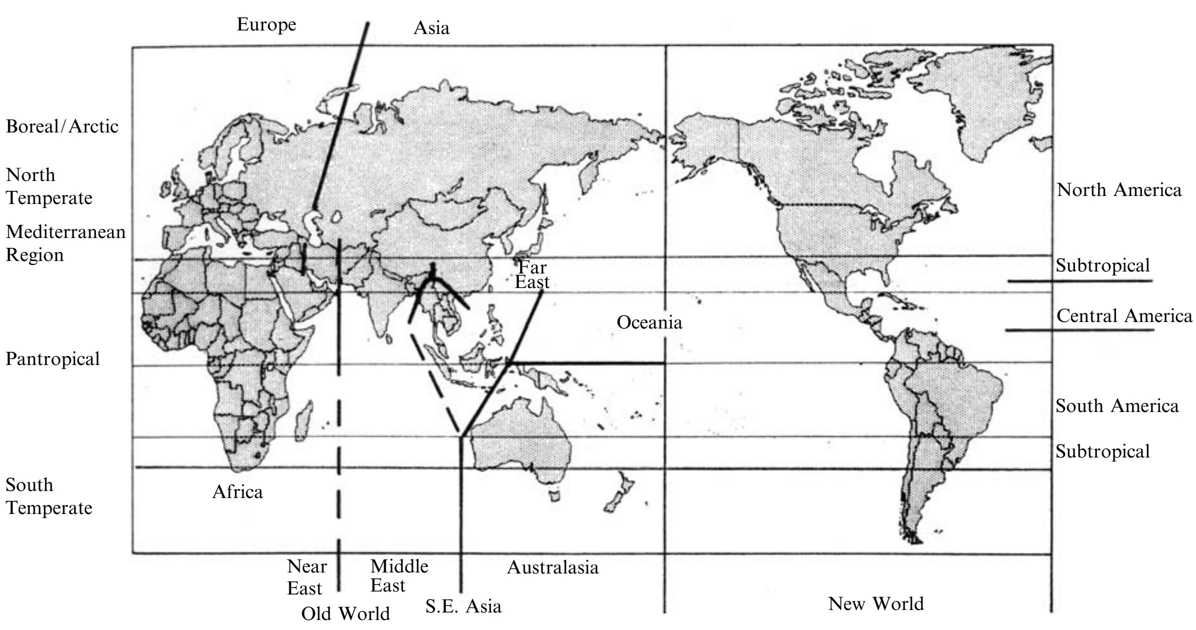
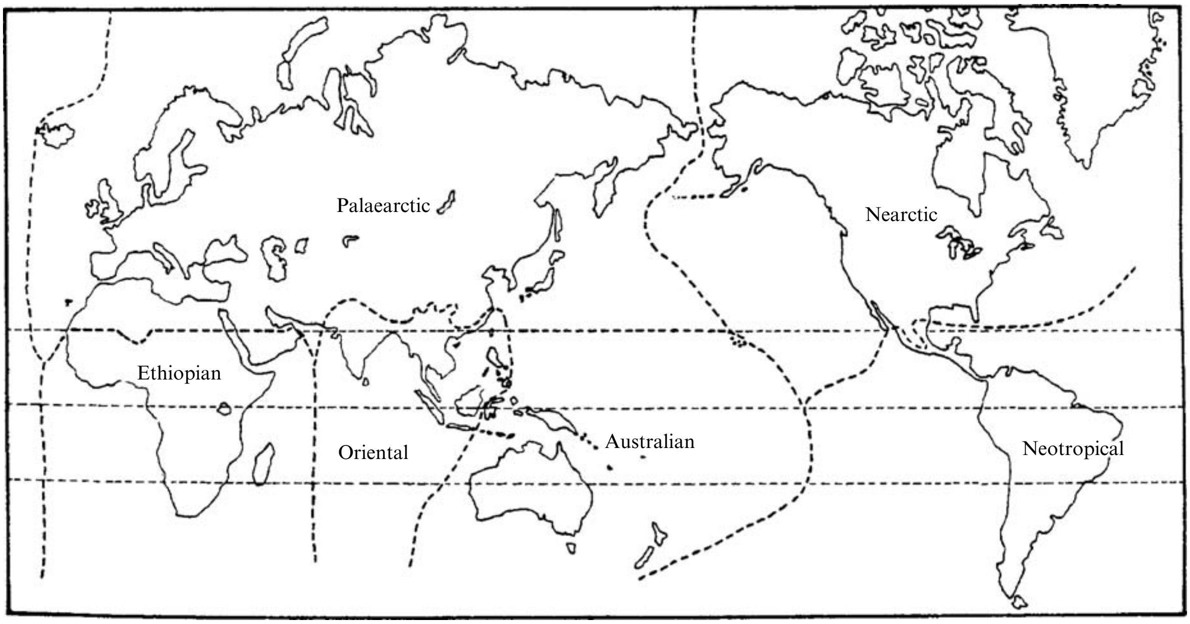


Fig. 7. Zoogeographical regions of the World.



an innate tendency to increase, they display a similar innate tendency to dispersal.

Migration

The movement of animal populations, or individuals, from one area to another on a larger scale than merely a local dispersal, can be defined in three different ways.

(a) Immigration – This is the movement of animals into a region.
(b) Emigration – This is the movement of animals out of a region.
(c) Migration – In the strict sense this applies to a definite double journey, firstly out of one region to another, and then the return to the original region. In the literature the term migration is sometimes incorrectly used to denote just a lengthy dispersal movement. It should be stressed that sometimes it is not clear to what extent a return movement occurs when pest migrations are discussed.

Flying birds, and migratory bats, are clearly in control of their direction of dispersal, although some species appear to prefer to fly into prevailing wind systems, whereas others apparently fly downwind for long distances. Most insects are small in size, and recent research does indicate that even with locusts, which are of moderate size, most movements are completely controlled by prevailing winds. It appears that the insects use their wings primarily to remain in the air and they are then carried quite passively by the wind or air currents to wherever the wind blows; when they stop flying they lose their buoyancy and descend. This is the situation for many long-distance dispersals; local dispersal and food/mate seeking is clearly an active procedure under individual control by the insect(s) concerned.

An interesting short review, titled *Dispersal and movement of insect pests* was published recently (Stinner *et al*., 1983).

Immigration is the movement of a pest population into an area from elsewhere, and in certain parts of the world is a very important source of major pests. In most of the tropics there is little insect migration (apart from locusts) because of the general stability of climate. Migration is typically an animal phenomenon of the colder parts of the world, where animals move away from northern areas after the short warm summer, and before the onset of the long cold winter. There are some tropical migrations, including the spectacular ungulate migrations of eastern Africa, where animals move to new food sources away from arid areas suffering from their annual dry season, they are basically following seasonal rains and the new grass growth that is promoted across part of the continent.

Animal migrations and dispersal movements are natural phenomena characteristic of all phyla in the animal kingdom and many species now regarded as pests will have generally dispersed during the millenia from their endemic areas (areas of origin). This innate tendency will still be present in all animal populations, but in some cases it operates slowly and may not be at all obvious. Flying insects can effect their own dispersal, influenced by winds and air currents of course. Some of the more novel means of dispersal include riding on floating flotsam (for rats, insects etc.), concealment in the feathers of migrating birds, and aerial transport by typhoon and hurricane. Migration and natural succession was clearly demonstrated on the island of Krakatoa after its total devastation by a volcanic eruption.

Locusts and armyworms (*Spodoptera* spp.) are migratory tropical species of considerable economic importance; they breed in areas of hazardous climate which compels them to disperse on their sometimes lengthy journeys.

The Brown Planthopper of Rice (BPH) (*Nilaparvata lugens*) has recently become established as a major pest of rice in Japan through its migratory behaviour. The climate of S. Japan (Kyushu) is sub-tropical or tropical in the summer, but the winter is cold with snow and ice and the BPH cannot survive the winter. The White-backed Planthopper (*Sogatella furcifera*) is likewise an annual migrant into Japan. These planthoppers (Delphacidae) live along the coastal regions of E. Asia (and elsewhere in India and S.E. Asia) and each spring they migrate northwards, usually entering Kyushu in Japan in the period mid-June to mid-July when they are caught in wind traps along the coast. They then breed on the rice crops and usually have four generations each summer in Japan before dying out in the cooler weather of the autumn after harvest.

Some of the countries most affected by regular pest migrations include Canada, Japan, North China, Fennoscandia, and to a lesser extent the UK. In Canada, particularly, there is quite a large number of insect pests that cannot survive the very cold winter; they arrive in early summer from the USA and breed during the hot Canadian summer/early autumn and then die later in the fall when temperatures plummet.

Pollination

The value of insect pollination of crops to man is really inestimable, although the annual yield of insect-pollinated crops in the USA has been estimated to be in the region of US $5000 million (at present values).

The crops pollinated by insects (entomophilous) include top fruit (e.g. citrus, apple, pear, peach, plum, cherry, almond, mango); bush and cane fruits (e.g. currants, raspberry, blackberry, gooseberry); ground fruit (e.g. strawberry); some Leguminosae (e.g. pulses, clovers); all Cruciferae (brassicas and other vegetables); other vegetables such as Cucurbitaceae and onions; cotton, cocoa, tea, some coffees; most flowers and some trees (e.g. lime).

The crops that are anemophilous (wind-pollinated) are mostly the Gramineae (cereals and sugar-cane), and many trees, particularly the Gymnospermae (pines, spruces and other conifers). A few crop plants are partly entomophilous and partly anemophilous, such as beet, spinach, carrot, parsnip, white mustard, charlock and chrysanthemum. With a surprisingly large number of crops there is apparently uncertainty as to the precise manner of natural fertilization. Some crops are grown in cultivated clones with fruit set by parthenocarpy (e.g. banana, and Smyrna fig), and others are propagated vegetatively like sugarcane and potato. Some crops are self-pollinating, such as *Coffea arabica*, pea, groundnut, some beans and many Solanaceae, but apparently sometimes cross-pollination by insects is effected.

One result of widespread use of chemical insecticides has been the great reduction of insect pollinator populations (mostly bees) in many parts of the world, and at the present time many crops are grown under conditions of inadequate pollination. However, for some crops which are at least partially self-pollinating the precise value of increased insect pollination is not known (Free & Williams, 1977). As mentioned later (page 62), some crops typically over-produce flowers and fruit so increased pollination of these crops may be of little value; but it does seem quite likely that many crops are now suffering from under-pollination. An example of the difference in yield that can be achieved by increased pollination in some crops was shown on red clover in Ohio (USA) where the average yield reported was about 0.1 m^3/ha of seed; after an increase in the local bee population the field yield rose to about 0.4 m^3/ha, and when a plot was enclosed and subjected to maximum pollination by bees the yield was raised to 1.1 m^3/ha.

Bee destruction in Japan has been serious since World War II due to the very intensive nature of agriculture there, and in some orchards, by 1980, growers had to resort to hand-pollination – both time-consuming and labour-expensive. It had been estimated that about 25% of labour-time in fruit orchards in Japan was spent on pollination of the crop. An interesting development in Japan has been to use mason bees (in particular *Osmia cornifrons*) in fruit orchards for pollination. Artificial nest sites (usually consisting of small bundles of open canes or narrow tubes, about 5–6 mm diameter) are manufactured and situated in suitable sheltered locations in the orchards, often under the eaves of the house and buildings. These sites are readily colonized by the mason bees. Research has shown the *Osmia* bees to be good pollinators; they forage in Japan from 08.00 h to 18.00 h daily, visiting some 15 flowers per minute. A local population of 500–600 bees per hectare will give adequate pollination without recourse to outside pollinators, and there will be a 50% fruit-set within 65 m of the nest site (Maeta & Kitamura, 1980).

The main groups of insects responsible for flower pollination are:

(a) Hymenoptera
Apidae – Honey Bee (*Apis mellifera*), cosmopolitan
– Other Bees (*Apis* spp.), pantropical
– Bumble Bees (*Bombus* spp.), native to the Holarctic only (now in New Zealand)
Megachilidae – Leaf-cutting Bees (*Megachile* spp.)
– Mason Bees (*Osmia* spp.)

(b) Diptera
Syrphidae – Hover Flies
Muscidae – House Fly, Bluebottles, etc.

Some Lepidoptera (butterflies and moths) may be of importance, but mostly for ornamentals with flowers having a long tubular corolla. A few beetles and some thrips pollinate some crops, and a few somewhat bizarre tropical plants (e.g. orchids) are pollinated by humming-birds or bats.

The most important wild pollinators are probably bumble bees and flies, but *Bombus* is mainly Holarctic in distribution. In the tropics, honey bees, Megachilidae and flies are probably the most important pollinators, but flies (Muscidae) can only pollinate the open-type flowers such as in the Cruciferae. In the cooler temperate regions *Apis mellifera* is domesticated and kept in hives which are easily handled and may be transported to orchards specifically for crop pollination. In the tropics however *Apis mellifera*, although domesticated and kept in 'hives', also occurs widely as wild colonies nesting in hollow trees, etc.

A fairly recent spectacular crop pollination success was made by C.A.B. International (1982). Oil Palm, native to West Africa, has been grown in plantations in Sumatra and Malaya since about 1930, and now is planted throughout S.E. Asia. But here the natural pollination was inadeuate and yields were low. To compensate the growers had to resort to hand pollination with an annual labour bill of about US $11 million. In 1978 C.A.B.I. sent entomologists to West Africa and they discovered a complex of pollinators of which weevils of the genus *Elaeidobius* appeared to be the most important. *E. Kamerunicus* was imported into Peninsular Malaya and is now widely successfully pollinating the oil palms with a consistent yield increase of about 20% and no need for hand pollination - making an overall annual saving of some US $115 million.

After the early catastrophes, when insecticide spraying in orchards and crops in flower resulted in large-scale bee destruction, most chemical companies are now including toxicity testing against bees as part of their regular pesticide screening programmes, and in the UK there are elaborate arrangements made to ensure that apiarists (bee-keepers) are warned before any major local insecticide applications are made. Also care is taken to avoid spraying particular crops in flower, so that bumble bee populations are safeguarded. In the tropics, however, there is seldom any warning given prior to spraying, but in these regions the majority of bees are wild anyway.

In the UK work on plant pollination is being conducted at Rothamsted Experimental Station, Herts., and from a bibliographical point of view by the International Bee Research Association (for example see Crane & Walker, 1983). An interesting review paper is by Kevan & Baker (1983).

3 *Principles of pest control*

Definition of the term 'pest'

Before contemplating taking any control measures against an insect species in a crop, the species must be correctly identified; then, presuming its biology is known, it should be clearly established that the species in this particular context is a pest, and that it could be profitable to attempt population control.

In this section the various terms used to describe pests are defined. It should be noted that some terms are more or less synonymous, but they are all well established in the literature. For example a *major* pest is very often a *serious* pest, and all *economic* pests are serious.

Pest. The definition of a pest can be very subjective, varying according to many criteria; but in the widest sense any animal (or plant) causing harm or damage to man, his animals, his crops or possessions, even if just causing annoyance, qualifies for the term pest. From an agricultural point of view, an animal or plant out of context is regarded as a pest (individually) even though it may not belong to a pest species. Thus a deer on a farm is a pest, but next-door in a game park it is not, and is in fact a valuable national asset there. Similarly, volunteer cabbage plants growing in a field with onions have to be regarded as 'weed' pests.

Many insects belong to generally accepted *pest species*, as listed in chapter 10, but individual populations are not necessarily always pests; that is, of course, not necessarily *economic pests*.

As pointed out by Norton & Conway (in Cherret & Sagar, 1977), we are often somewhat over-preoccupied at the present time with the state of the 'pest' population, whereas probably the most important aspect of a pest species is the damage (or illness) caused by the pest and the value placed upon these consequences by human society.

Economic pest. On an agricultural basis, we are concerned when the crop damage caused by insects leads to a loss in yield or quality, resulting in a loss of profits by the farmer. When the yield loss reaches certain proportions the pest can be defined as an economic pest. Clearly the value of the crop is of paramount importance in this case, and it is difficult to generalize, but as a general guide for most crops it is agreed that most species reach *pest status* when there is a 5–10% loss in yield. Obviously a loss of 10% of the plant stand in a cereal or rape field (note that this is not the same as a 10% loss in yield!) is not particularly serious, whereas the loss of a single mature tree of *Citrus*, apple or peach is important.

Economic damage. This is the amount of damage done to a crop that will financially justify the cost of taking artificial control measures, and will clearly vary from crop to crop according to its basic value, the actual market value at the time and other factors. In practice, many peasant farmers engaged in subsistence farming feel that they cannot justify use of pesticides at all.

Economic injury level (EIL). This is the lowest population density that will cause economic damage, and will vary between crops, seasons and areas. But it is of basic agricultural importance that it is known for all the major crops in an area.

Economic threshold. It is desirable that control measures be taken to prevent a pest population from actually causing economic injury. So the economic threshold (Stern *et al*., 1959) is the population density of an increasing pest population, at which control measures should be started to prevent the population from reaching the economic injury level (see fig. 2).

Pest complex. The normal situation in a field or plantation crop is that it will be attacked by a number of insects, mites, birds and mammals, nematodes and pathogens which together form a complicated interacting *pest complex*. The control of a pest complex is complicated and requires careful assessment, especially as to which are the *key pests*, and careful integration of the several different methods of control which may be required. This, of course, makes the process of evaluation difficult, and generally, in the past, much money was wasted on uneconomic pest control, either through carelessness or lack of knowledge.

Pest spectrum. This is the total range of different types and species of pests recorded attacking any particular crop, and especially of concern in one particular area. The total number of insects (and mites) recorded from the major crop species are considerable; these records, incidentally, are of insects feeding or egg-laying on the plant, and do not include casual observations when the insect might just be resting, or when, for example, caterpillars have crawled up on to the plant just to pupate (e.g. Large White Butterfly). Simmonds & Greathead (in Cherrett & Sagar, 1977) listed the numbers of pest species, on a world basis, recorded from sugarcane as 1300, cotton 1360, coffee 838, and cocoa 1400. Fortunately, for the practising entomologist, and the farmers, these numbers reflect the situation globally and many of these pests are restricted geographically to one part of the world. For example, wherever apple is grown it will be attacked by a tortricid complex (Lep., Tortricoidea) but the actual species differ from region to region. Only a few major pests are completely cosmopolitan (e.g. *Myzus persicae*, *Agrotis ipsilon*) or pantropical (e.g. *Maruca testulalis*) in distribution (in point of fact, their widespread distribution is one reason for their being regarded as major pests).

Pest load. This is the actual (total) number of different species (and numbers of individuals) of pests found on either a crop or an individual plant at any one time, and, as already mentioned, this would usually be a pest complex, but could also be a monospecific population, although this would be rare.

Key pests. In any one local pest complex it is usually possible to single out one or two major pests that are the most important; these are defined as key pests, and are usually perennial and dominate control practices. A single crop may have one or more key pests, which may or may not vary between areas and between seasons. It is of course necessary to establish economic thresholds for these key pests in order to be certain when to apply control measures, for it has been often observed that the mere presence of a few individuals of a key pest species in a crop may cause undue alarm and lead to unnecessary pesticide treatment. Key pests owe their status to several factors, including their usually high reproductive potential, and the type of damage they inflict on the host plant (e.g. Codling Moth on apple; Boll Weevil on cotton).

Serious pest. This is a species that is both a major pest and an economic pest of particular importance, being very damaging and causing considerable harm to the crop plants and a large loss in yield. It almost invariably occurs in large numbers.

Major pest. In this book these are the species of insects and mites that are either serious pests of a crop (or crops) in a restricted locality, or are economic pests over a large part of the distributional range of the crop plant(s). Thus the species here regarded as major pests usually require controlling over a large part of their distributional (geographical) range, most of the time. As mentioned in chapter 1 however, some species of insects have been included as 'major pests' in this book because of their widespread and frequent occurrence, biological interest, wide range of host plants, or other aspects of academic interest. In any one crop, in one location, at one time, there is usually only a rather small number (say 4–8) of major pests in the complex that actually require controlling. For example, although the pest spectrum for cotton worldwide is 1360 species, on any one cotton crop there will probably only be about five species requiring population control. Usually for most crops in most localities the major pest species remain fairly constant from year to year, but several entomologists have commented recently that in some areas they have observed that the major pest species complex has been gradually changing over a long period of time. Soehardjan (1980) reported that in Indonesia the 8–10 major pests of rice have largely changed over the period of time 1929–79, although there are some differences within different parts of the island of Java. As mentioned already, the Brown Planthopper (BPH) of rice has risen in 10 years from obscurity to becoming the most serious pest of rice in most parts of Asia. And it is reported from IRRI that there are now two new major rice pests in tropical Asia (Pathak, 1980): the Sugarcane Leafhopper and Rusty Plum Aphid. So over a period of some 10–50 years it is expected that the complement of major pests for a crop may change. It must be remembered that evolution continues all the time, though it is not often obvious, and that in an artificial environment, such as agriculture, it can be expected that evolution will be accelerated.

Minor pests. These are the species that are recorded feeding or ovipositing on the crop plant(s) but usually do not inflict damage of economic importance; often their effect on the plant is indiscernible. They may be confined to particular crop plants or may prefer other plants as hosts. Many (but not all) pests listed as minor pests are potentially major pests (viz. BPH of rice). Many species that are major pests of one crop will occur in a minor capacity on other crops. And sometimes a major pest of a particular crop in one part of the world (e.g. Europe) will be a minor pest on the same crop in a different part (e.g. Australia or the New World).

Potential pest. This term is used occasionally in the literature and refers to a minor pest species that could become a major pest following some change in the agroecosystem. Only a relatively small proportion of the species listed as minor pests are really potential pests in this sense, because of their basic biology.

Secondary or sporadic pest. Defined by Coaker (in Cherret & Sagar, 1977) as a species whose numbers are usually controlled by biotic and abiotic factors which occasionally break down, allowing the pest to exceed its economic injury threshold.

Pest populations. A most important point to remember is that an insect is only an actual pest (in practice) at or above a certain population density, and most control measures are aimed only at reducing this population to a lower level. So insect pest population studies are vitally important, and although mentioned here briefly the topic is included in chapter 2 (page 5), as an aspect of pest ecology.

Pest species accumulation. Long-term stable habitats generally exhibit an extensive species diversity, both in host plants and in phytophagous arthropods. This is shown typically in old forests, and also some plantation crops such as cocoa, rubber, sugarcane and tea (Banerjee, 1981). The pest species accumulation in the monocultures is in part a reflection of the area under cultivation; other important factors are the type of plant, the geographical location of the habitat (area) and its natural species richness, and the age of the actual plants and of the community (crop). It appears that in some cases the age of the plant community is not particularly important, but Banerjee observed that in tea plantations (from the Old World tropics, excluding China) age appeared to be a major factor and pest species saturation was apparently reached (in plantations in N.E. India) at the plantation age of about 35 years. After this age there was no further increase in pest species numbers.