Pest control: A survey

Preface

We can no longer afford to lose a large proportion of our resources to other organisms, or to support the misery and costs of insect-borne diseases such as malaria and nagana. In this introductory text I have tried to outline the present methods of dealing with these problems and to suggest some of the techniques of pest control which may be of value in the future. The technology of pest control (as yet, it is hardly a science) is changing rapidly and, because of its impact upon our environment, there should be a general understanding of these changes. Thus, although written as a possible text for students in the biological sciences, agriculture, and related disciplines, the book should be understandable, in the main, to the general reader. The last part of the second chapter does presume an acquaintance with statistical ideas, but this is not essential for a general understanding of the remaining chapters. Here and there some knowledge of biological topics, such as genetics, is required; the lack of this may be remedied by reference to any of the many excellent texts of general biology now available.

No attempt is made to give directions for the control of specific pests. Such information can be found easily in many other places and, in any case, its value would be ephemeral. Various control methods are described, however, with sufficient examples for an estimate to be made of their worth. Most examples are taken from animal pest control, but other harmful organisms, such as weeds and plant pathogens, are also discussed. However neatly pest control can be divided in the classroom, there is no such schism in the field. The insect pests and diseases of fruit trees, for example, are controlled concurrently, and the two routines interact one with the other, and with the rest of orchard management.

I have tried not to give undue weight to one class of pest control, such as biological methods, at the expense of others. An attempt to survey the whole of pest control is, I believe, justified, as the practitioners are now trying to integrate the various methods available to them so that pest control may be carried out economically, with as little disruption to the environment as possible. The technology is thus changing from a collection of unrelated *ad hoc* procedures and is beginning to become an ecologically based science. This is the underlying theme of this book.

The text should be of value in introductory courses on pest control in universities and agricultural colleges; it will also provide background material for courses dealing with conservation, and with the impact of man on his environment.

I would like to acknowledge my debt to the writings of Dr B. P. Beirne and of Dr K. E. F. Watt. Dr Beirne has performed a great service to applied biologists by

his analysis of the aims and methods of pest control, while Dr Watt has convinced me that the most valuable implement in pest control will not be the spray gun, but the digital computer.

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It is impossible to thank individually all the many people whose work has contributed to the preparation of a book dealing with such a wide field; I trust that they will accept this as an acknowledgement of my gratitude and debt to them. Needless to say, any errors are entirely my responsibility, and I would be grateful if my attention could be drawn to them. Finally, I must pay tribute to the staff of the McGraw-Hill Publishing Company in England for their help in bringing this work to a conclusion, despite the difficulties of our antipodean relationship.

Arthur Woods
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Pests and their importance

Some definitions

Pest control concerns everyone. It is the day to day business of a wide variety of professional men, including farmers and salesmen, chemists and biologists, physicians and physicists. Everyone, as a victim of pest attack, or as a consumer of treated produce, is subjected to its effects. Even those of us who pay high prices for food guaranteed unsprayed by chemicals can accumulate significant amounts of insecticides in the body.

Because so many different kinds of people are involved in the business of pest control, its terminology has become confused and any attempt to standardize it must surely fail. Nevertheless, we must, at the outset, define those terms which we are going to use frequently, although we recognize that, for the reason given, these definitions will not always agree with those found elsewhere.

Pest

A pest is an organism which harms man or his property, or is likely to do so. The harm must be significant; the damage of economic importance.

The last statement should be qualified by saying that the damage must at least be thought to be of economic importance. There are many organisms whose importance was not realized till recently and which were therefore not counted as pests. Conversely, a number of accepted pests rarely, if ever, cause damage which passes the economic threshold, but, because they are conspicuous in some way, they have earned the stigma of destroyers.

Most authors further qualify the definition by stating that before we can count an organism as a pest we must be able, at least in theory, to control it, for, otherwise, it is no more a pest, in the economic sense, than is an earthquake, a hailstorm, or unsuitable soil (Beirne, 1967).

In everyday usage, the word pest means some harmful insect or allied form, but here we shall include all those harmful organisms and viruses which are not left to the attention of the physician, the veterinary surgeon, or the food microbiologist. That is to say, our definition will not include those micro-organisms which cause disease in man and his domestic animals and those which damage processed products, but it will cover, besides the noxious arthropods, the nematodes, molluscs, and vertebrates which attack us and our property, the weeds which compete with our plants and those micro-organisms and viruses which cause disease in our crops.

It is difficult to fit into any tidy scheme the larger parasites, such as flukes, tapeworms, and roundworms, which attack man and his animals. Sometimes they are the concern of the physician or the veterinarian who treats the diseases they cause, but often their attacks may be avoided or lessened by techniques very similar to those used in the control of insect pests. When such techniques are available or possible the parasite will be regarded as a pest.

One important difficulty in the application of this definition is, as we hinted above, in deciding whether or not the damage is of economic importance. Two examples, the mangold fly and fruit pests, will illustrate this.

There is no doubt that in some seasons the mangold fly, *Pegomyia hyoscyami* var. *betae*, can reduce the yield of sugar-beet by two or three tons an acre by the mining of the maggots in the young leaves. The spectacular appearance of an attacked crop can be quite misleading, however. Field trials in which beet seedlings at the four- to eight-leaf stage were defoliated with scissors showed that the crop can undergo 50 per cent defoliation with no loss in sugar percentage and only a 5 per cent drop in expected yield. Even complete defoliation led to a loss of little more than a quarter of the normal yield (Jones *et al.*, 1955). It would seem likely that over the years sugar-beet crops have been sprayed many times quite needlessly.

Since the coming of the modern insecticides and fungicides, the public has come to expect, and demand, blemish-free fruit and vegetables. Thus, a number of organisms whose damage does not reduce the yield or nutritional value of fruit are now regarded as pests simply because of our newly won, but possibly impermanent, ability to control them, and as a result of our revision of the threshold of economic damage.

Control

This term rarely stands alone and is usually qualified in some way. Beirne has given much thought to the use of the term and its derivatives, and we shall adopt, in the main, his system (Beirne, 1967).

Beirne restricts the use of the term 'control' to any action which has, as its objective, the amelioration of the harm caused by pests, and in which man plays some deliberate role. Here he differs from many authors in that they also use the term for situations in which man plays no deliberate part, but in which population densities of both pests and non-pest organisms are regulated and kept within fairly definite bounds by environmental factors. Such a situation is called natural control by, among others, Varley (1947), Thompson (1956), Milne (1958), and DeBach (1964). For this kind of regulation of population density Beirne uses the term 'natural regulation'.

This restriction of the term 'control' to cases in which man participates, is useful and should be encouraged as it avoids lengthy qualifying statements when actual pest situations are discussed.

It should be noted that in the above definition of the term 'control' the object is not necessarily the destruction of the pest but rather the amelioration of its damage. The term control, however, implies to most people the actual killing of the pest population, or at least a high proportion of it. In fact, the destruction of the pest may often make nonsense of the real goal, the lessening of the damage. For this reason there is a tendency to substitute for 'pest control' other phrases which show more clearly the real aims of the measures taken. Beirne prefers the term 'pest management' and this, indeed, is the title of his book referred to earlier.

As we said before, the term 'control' rarely stands alone and is almost always associated with some other word or words. Examples are 'governmental control', 'chemical control', 'biological control', 'insect control' and so on. Beirne divided these phrases into nine major groups and for a full discussion the reader is referred to his book. Here we have space to discuss only a few of these categories.

Categories of control The first refers to the way in which the objective, the lessening of the damage, is achieved. In preventive control the aim is to prevent the initiation of an attack, and the pest may or may not be killed. In corrective or curative control the aim is to destroy the organism either by killing it or preventing its reproduction after its attack has started.

The second category deals with the manner of application of the controls and it includes, for example, chemical control by spraying and biological control by the introduction of living material (other than resistant varieties) into the environment of the pest. Cultural control and ecological control are also listed here. The first refers to the adaptation of conventional practices so that the pest is destroyed or harmed. Ecological control has several meanings but here it will be used in the sense of using existing environmental factors so that they either harm the pest directly or benefit their natural enemies.

An obvious category refers to the agents used in control. Thus biological control involves living agents while chemical and physical control, collectively known as technical control, refer to the use of chemical and physical agents respectively.

In this book biological control is reserved for the employment by man of living material for the control of pests. Many authors, including particularly DeBach (1964a), use the term to include the action of organisms which harm the pest and occur naturally in the same environment.

All members of this category can be subdivided. Biological control, for example, may be effected by microbial pathogens, by predators, by parasites, or by the pest itself. The last technique is known as autocidal control.

It is often important to indicate the way in which the particular control measure works. The damage caused by the pest may be minimized by killing the pest outright, by hindering its reproduction, or by affecting its activity or behaviour in some suitable way.

Agents which kill the pest are known as pesticides, but there is an unfortunate tendency to restrict this term to chemical agents. There is a related tendency to call all chemical agents pesticides whether they kill the pests or not. Unless qualified in some way, for example 'biological pesticides' or 'physical pesticide', the term will mean a chemical agent which kills the pest.

Beirne's final category arises from the realization that pest control cannot be fragmented into several distinct techniques, each one of which should be applied for a particular problem, with the exclusion of the others. In the planning of a campaign against a particular pest all possible techniques should be considered, and a combination of those which will give the maximum control of the damage with the fewest undesirable side-effects, should be chosen.

Such approaches to the problem are known as pest management, integrated control, harmonious control or rational pest control. All these phrases mean essentially the same thing, 'to manage pests rationally in relation to their environments by applying controls that integrate with one another and with natural regulatory factors to produce a harmonious system. Or, to select and apply controls logically and intelligently, with commonsense and with foresight, to produce the optimum of good effects and the minimum of bad ones (Beirne, 1967).

Victim

We have defined the main terms to be used, and other necessary definitions will be given later as the need arises. We now have the opposite problem, the finding of a word to fit a definition.

Pests attack a wide range of objects, both living and dead, which are of value to us. There does not seem to be a suitable word in common usage which covers all these objects so, for want of a better term, we shall follow Beirne's suggestion and use the word 'victim' in this sense, although we realize that it will include inanimate objects as well as living ones.

The damage caused by pests

The ways in which pests damage their victims

In exploiting their victims for their own needs pests may damage them directly or indirectly. Unfortunately these terms are used in two different ways.

If the part of the victim which is damaged is the part in which man is interested then the damage is said to be direct, whereas if some other part of the victim is damaged, and not the useful part, except indirectly, the damage is indirect. Thus the larvae of the wheat bulb fly, *Leptohylemyia coarctata* burrow into the young shoots of wheat plants, and reduce the yield of the crop only indirectly. In this case they are said to be indirect pests.

The other use of the term is much commoner and will be employed here. If in exploiting the victim the pest damages it by virtue of this exploitation it is a direct pest. If the exploitation causes little or no damage, but the victim is harmed in some other way as a result of the pest's attentions or presence, then it is damaged indirectly.

Direct and indirect damage can take many forms, and since we have little space here to discuss them fully, the reader is referred to the many textbooks of economic entomology and plant pathology where the damage will be described under the specific causal organisms.

Direct damage usually results from the pest's use of the victim as a source of nourishment. Insects chew the tissue or suck the sap or blood of living organisms. Plant pathogens attack various parts of the plant for the same reason. But direct damage may be caused in other ways, for pests may exploit their victims as sites for egg-laying or shelter. Cicadas, when laying their eggs in young twigs, frequently damage them so severely that die-back follows. The apple twig cutter, *Rhynchites coeruleus*, having laid her eggs within the tissues of a twig, cuts it through just below the oviposition site so that it usually falls to the ground where the egg hatches, and the grub completes its development.

There are a number of beetles which will bore into any suitable hard material, such as wood, to provide themselves with pupation sites, and one species is even credited with the sinking of a wooden ship carrying a cargo of penguin carcases (*Hakluyt's Voyages*, ed. Goldsmid, Edinb. 1890, cited in Busvine, 1951).

The indirect damage caused by pests displays a much wider range of forms. Possibly the most important type is when the pest is a vector or alternative host of some economically important parasite or disease. Plant viruses of many kinds, and of great destructive power, are transmitted by sap-sucking aphids, leaf-hoppers and nematodes, and blood-sucking mosquitoes spread several important human diseases such as malaria, yellow fever, dengue and filariasis, to mention only four. The oriental rat flea, *Xenopsylla cheopis*, carries bubonic plague, essentially a disease of rodents, from the cooling corpses of rats to man. In this case both the rat and the flea are acting as indirect pests of their victim.

As is the case with the dead rat, the pests need not come into direct contact with their victims to harm them. Snails of the genus *Limnaea* do not attack sheep in any way, but they are the intermediate host of the liver-fluke, *Fasciola hepatica*, still an important parasite of sheep and cattle in waterlogged pastures.

Since very few weeds are directly parasitic on their victims, their main damage is indirect. Most importantly they compete for space, light, water, and nutrients, and some, such as couch grass, *Agropyron repens*, secrete substances which inhibit the growth of their rivals. Another form of indirect damage resembles that caused by the vectors and intermediate hosts mentioned before. Many weeds serve as alternative hosts for insect pests and pathogens, frequently carrying them over periods when the normally attacked crops are absent (Duffus, 1971). Thus several weeds support populations of aphids before potato crops are ready for attack. Some weeds, indeed, are obligate, or almost obligate, alternative hosts for pests. Barberry, *Berberis vulgaris*, is essential for the completion of the life cycle of black stem rust of wheat, *Puccinia graminis*, while, in British climatic conditions, few black bean aphids, *Aphis fabae*, overwinter except as eggs on spindle, *Euonymus europaeus*, and a few other shrubs. These aphids, incidentally, as well as being vectors of plant viruses, produce, like many other aphids, a copious sugary honey dew which coats the plant leaves, serving as a medium for sooty mould fungi. Although these do not attack the plant they do severely restrict its photosynthetic efficiency. The dried honey dew is also very difficult to remove from the paintwork of motor cars left standing under aphid-infested trees.

Returning to the indirect damage caused by weeds, a number of them are found to be troublesome stock-poisoners, the outstanding example in Europe being the common ragwort, *Senecio jacobaea*. In non-fatal poisoning a complicating feature is the craving which the victims, both stock and children, sometimes develop for the guilty plant which, on the first opportunity, they will actively seek out. This is useful in that in the cases where the offending plant has not been identified, the animal itself carries out its own diagnosis, but it does mean that the stock has to be excluded from the pasture in question. With children it is a little more difficult. The list of such plants includes, among others, laurel, rhododendron and woody nightshade, *Solanum dulcamara*.

Less serious, but still of economic importance to the farmer, is the tainting of milk and flesh by ramsons, *Allium ursinum*, and other members of the same genus growing in pastures.

Bartels and Cramer have published a valuable survey of poisoning by weeds, and of similar side-effects of plant diseases and animal pests on the health of animals and man (Bartels and Cramer, 1966). In this survey they also discussed the effects of pests on the quality of harvested products.

Many plant pathogens produce toxic principles in the crops they attack and they effect the health of the consumers of the product. Outstanding among these is the fungus known as ergot, *Claviceps purpurea*. The active principles of this pathogen are used in medicine for the relief of migraine and for the excitation and contraction of the muscles of the uterus. The alkaloids stimulate the involuntary muscles and paralyse the sympathetic nervous system. The ergots are most often found among rye grains but fortunately, with modern screening methods, their presence in human food is now quite rare. The most recent serious outbreak of human poisoning took place in the small French village of Pont St Esprit, about twenty miles north of Avignon, in 1948. In this case the entire population of the village suffered from ergotism, the source of the infection being traced to a black-market supply of rye used by a village baker. The hallucinations and visual abnormalities arising in this case and others may explain the stories of witchcraft and other manifestations when, in the Middle Ages, whole districts obtained their bread from one source.

Ergot also infests certain pasture grasses, especially rye grass in Europe and paspalum in Australia. People that have walked through badly infected pastures sometime show mild ergotism, and stock feeding on the grasses display typical gangrenous symptoms in the tail, the hooves, the lips, and the tip of the tongue, all due to the constriction of the smaller blood vessels.

The various rusts of cereals have also been implicated in outbreaks of disease but few plant pathogens, if any, have such serious effects as ergot. In recent years, however, there have been widespread deaths among turkeys in England resulting from their being fed with peanuts and peanut meal infected with certain strains of *Aspergillus flavus*. Subsequent experiments showed the fungus can be toxic to other animals. The symptoms of poisoning included hepatitis, tissue necrosis and kidney damage. It is also probable that the active principles, which are referred to as aflotoxins, are carcinogens. The toxic nature of this fungus appears to have been long recognized by a native tribe in Guyana who used ground-nuts for the execution of offenders against tribal laws (Moody and Moody, 1963; Bartels and Cramer, 1966). Other fungi, such as *Aspergillus parasiticus* and *Penicillium puberulum*, produce aflotoxins identical with, or similar to, those of *A. flavus*.

Sweet clover is occasionally infected by certain moulds which convert the coumarin present in the hay into oxycoumarin or dicoumarin. Oxycoumarin inhibits the formation of prothrombin in the blood, and since this is necessary for the coagulation of the blood, animals eating the spoiled hay may die from internal haemorrhage.

A number of animal pests infesting crops and stored products are troublesome because of their allergic effects on sensitive people. House mites have been implicated, for example, in many cases of asthma. The dust arising from the remains of insects in stored products is also responsible for many allergic conditions. It is also possible that, because of their content of quinones, these remains, if consumed, would be carcinogenic.

Weeds, and other kinds of pests, can make farming and forestry operations more difficult and costly. Cleavers, *Galium aparine*, and stem borers such as the wheat stem sawflies *Cephus pygmaeus* and *C. cinctus*, as well as various plant pathogens, cause the lodging of cereal crops, with consequent difficulties in harvesting. The cabbage aphid, *Brevicoryne brassicae*, by virtue of the sticky waxy nature of its colonies makes the harvesting of brassicas unpleasant and their preparation for market more difficult.

A similar form of damage is the contamination of stored products and packaged goods by the dead bodies and exuvia of insect pests and the faeces of insects, birds, and rodents.

Rodents, especially rats, cause considerable trouble by their gnawing of various materials in their search for food. This can cause serious structural damage to buildings, and may even be the cause of a quarter of the fires of unknown origin in the United States of America (Dykstra, 1967).

The cost of pest damage

While nobody denies that pests are costly, both in terms of money and in human suffering, no one has calculated exactly how expensive they are on a global basis. Good estimates have been made in some of the more advanced countries, notably the USA and the United Kingdom, and extrapolations have been made from these to cover other parts of the world. These are, however, countries with advanced agricultural and public health techniques who suffer a smaller proportionate loss than, for example, some of the Asian, South American, and African states. On the other hand, because of their generally higher yields per acre and greater total production, the larger advanced countries probably suffer more in absolute terms through pest damage to crops and stored products.

It is also difficult to find a suitable unit in which to express crop losses. A monetary unit is unsatisfactory because of the elasticity of prices. In times of shortage resulting from pest attack, a product will command a high price on the market, much greater than it would fetch in times of glut when pests are few. To measure pest damage in terms of the higher value would give an inflated estimate. There is also the difficulty of converting values from units in one country's currency to those of another.

Expressing the damage in terms of lost yield, either absolutely or as a percentage, does not allow for losses in quality of the product, a disadvantage not shared by the monetary measure. Nor does it take into account the costs of pest control operations and research, whether these be successful or not.

In the literature, the percentage loss can be expressed in two ways, either as a fraction of the yield actually obtained or as a percentage of the yield which would have been obtained in the absence of the pests. Unfortunately, some authors do not state which method they are using. Another difficulty which is usually glossed over is how one determines what the yield would be in the absence of pests – a crop without its troubles is probably even rarer than a man in perfect health.

Ordish has tried to circumvent some of these difficulties by the introduction of a new unit, the untaken acre (Ordish, 1952). This is, simply, an extra acre of the crop which must be grown to, as it were, satisfy the pests; an acre, incidentally, which, in the absence of pest damage, could be devoted to something else.

This method does avoid one pitfall into which agricultural economists sometimes fall, that of double counting. In adding up the losses in a crop it is easy to forget that an individual plant or fruit can only be destroyed once, even if it is suffering from the attentions of several pests. Similarly a man can only die once even if he is suffering from both malaria and sleeping sickness. It was this sort of error that led an official of the US Department of Agriculture to conclude, facetiously, that the USA harvested no wheat or maize at all in 1944 (Ordish, 1952).

The trouble with Ordish's measure is that it is only meaningful with respect to the particular area and time under consideration. It is difficult to 'translate' India's untaken acres of wheat into English ones because of the greater productivity of the English fields. In Europe and other advanced areas there has been a steady increase in yields per acre of most crops over the last century, thus a straight comparison of the untaken acres of the 1860s with those of the 1960s would be meaningless.

This general increase in productivity causes another difficulty. It is obviously more meaningful to express pest losses as an average over a period of say, ten years, than to express the losses in terms of what happened in a single season. If the yield has increased through the use of better fertilizers, increased irrigation, new varieties, more efficient crop protection techniques and so on, the interpretation of the average becomes difficult.

One of the most ambitious attempts at counting the costs of pests in agriculture has been made by Cramer (1967). He has surveyed much of the world's literature on the subject and arrived at a total cost of between seventy and ninety thousand million American dollars a year. This estimate is based on the prices paid to the growers in the various countries, the data being taken from the Production Yearbook of the FAO (1965).

To this total must be added a large part of the annual value of world production of pesticides, about one thousand million dollars. Cramer estimates that without these pesticides world food prices would be between fifty and one hundred per cent higher than they are now.

His estimate for the percentage losses are, as a fraction of the actual production, 55 per cent and as a fraction of the potential production, 35 per cent. The latter figure can be broken down as follows: Insect pests, 13·8 per cent; Diseases, 11·6 per cent; Weeds, 9·5 per cent.

This survey only follows the crop as far as the harvest. Further heavy losses follow during the storage and transport of the products, from the depredations of such organisms as rodents, insects, and fungi. On a world basis these losses are probably, in absolute terms, just as great as those suffered before harvest. In the Congo, for example, insect attack during the course of one year led to a loss of weight of 50 per cent in stored sorghum, 20 per cent in beans, and 15 per cent in ground-nuts.

In Sierra Leone stored paddy rice lost a quarter of its weight in one year from insect attack. What remained was not all rice. A large part of what was left in this stack, and in those of the Congo, consisted of the living and dead bodies of insects, and frass (Herford, 1961).

Fruit, of course, suffers particularly badly from rotting when stored and during transport. A 25 per cent loss of stone fruit and imported pineapples was, till the late 1950s, regarded as normal by fruiterers in the USA, and the familiar green mould of oranges, *Penicillium digitatum*, used to destroy 12 per cent of the Australian domestic supplies, though new chemical treatments have reduced this loss considerably (Turner, 1959).

It is impossible to overestimate the importance of the disease-carrying pests. Mosquitoes, as vectors of malaria, have influenced the course of history. Much of Rome's strength lay in the surrounding malarious marshes where besieging armies were weakened by the disease. Plague, always endemic among the rodents of eastern Asia, has frequently erupted out of China and may yet do so again. Aided by the Oriental rat flea it brought the Black Death and possibly the end of the Feudal system in Europe, though this is probably an over-simplification.

The tsetse flies, vectors of sleeping sickness and nagana – a Zulu word meaning the sickness of cattle – halted the northward trek of the Boers with their oxen-drawn waggons. The flies still hold sway over some 6·3 million square kilometres of Central Africa, and the economic atlases show little overlap in the distribution of tsetse and cows.

Tsutsugamushi disease, or scrub typhus, a disease long said by the Japanese to be passed on to man by the 'akamushi' or 'dangerous bug' and now known to be transmitted by larval trombiculid mites, probably incapacitated more Allied soldiers in the Pacific area than did the Japanese. The same war nearly finished with a typhus pandemic and would have done so if the Allies had not deloused the entire population of Naples with the then new insecticide DDT. Typhus is the companion of war but for an account of its history the reader cannot do better than consult Hans Zinsser's classic, *Rats, Lice and History*, fortunately recently reprinted.

To measure the human suffering caused by these and other arthropod-borne diseases in terms of money is both impertinent and well-nigh impossible, but something must be said about the economic effects of the diseases. It is sometimes argued, ethical considerations being left aside, that these diseases help to slow down the population explosion and, untreated, would allow us a little more time to catch up with food production. In reality most of these diseases take a considerable time to kill their victims, who may be made incapable of working for years but who, while awaiting their deaths, still need food, clothing, and fuel. All too frequently the victims are children who die before they can begin their productive life.

Malaria is such a disease. Although it kills two and a half million people a year (Metcalf, 1965) this is a small number compared with the total number of people suffering from the disease. Malaria and many other diseases also deny the use of vast areas of otherwise productive land. Nagana is an outstanding example of a disease of this kind.

How pest problems arise

Of the two or three million organisms in existence probably not more than a few thousand are pests. If we are to avoid creating new pest problems and if we are to control efficiently those pests which we have inherited, it is obviously important to know how these exceptional species became harmful.

As Edwards and Heath have pointed out, there are both long- and short-term factors which control the transition of populations of organisms from the innocuous state to the harmful condition. The long-term factors are those evolutionary pressures which alter the pest population so that it exploits its victims more efficiently. These arise from the interplay of mutations and natural selection. The short-term factors are changes in environmental resistance to population growth. This environmental resistance is composed of abiotic and biotic factors, but they cannot be clearly separated since they interact with each other. Climatic conditions, for example, have a direct effect on both the pest species and on the various parasites, predators, and pathogens which attack it (Edwards and Heath, 1964).

Without a doubt, one of the most important causes of an innocuous population changing into a damaging one is the provision of an almost unlimited food supply by man. Since Neolithic times man has grown his food on comparatively large areas in more or less pure stands, and has stored what he does not immediately use. This has provided organisms, which previously depended on scattered specimens of their victims, with food in such large quantities that their population densities could increase rapidly. There could be little danger of the food supply running out and the population starving, nor could there be much chance that most of the offspring would perish in a vain attempt to find a host. Such pest organisms have subsequently