

THE RELATIONSHIP BETWEEN INSECT PESTS AND COTTON PRODUCTION
IN CENTRAL AFRICA

by

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ABSTRACT:

The relationship between an insect pest and its host is one of dynamic equilibrium in which each is under the influence of a number of environmental factors. In the natural condition, the population density of the insect is kept in check by climatic factors, by limitations of food and by pathogens, parasites and predators. These checks lead to a situation of relative population stability. However, when a plant species is grown as a crop over an extensive area, available food for insect pests is capable of supporting a much larger population and a state of relative instability is introduced in which the pest can increase and disperse rapidly unless kept in check by other controls. The use of insecticides accentuates this instability by removing many parasites and predators, permitting an almost unrestricted increase of those pests which are not controlled by the insecticide. Eventually other checks will often come into play, limiting further increase in the population but by this stage, the pest may have done a considerable amount of economic damage.

Cotton production in Central Africa has been erratic since the crop was first introduced in the early 1920's. The level of production was regulated by yields and price levels. However, in the first few years after the introduction of cotton to a new area, yield levels were usually relatively good and the red bollworm, Diparopsis castanea was not observed. After a few years, this pest made its appearance, increasing steadily over the years and leading to reduced yields and eventually to reduced production. The jassid, Empoasca spp., the bollworm Heliothis armigera and the cotton stainer, Dysdercus spp. also emerged as major pests during the early years of production. During this period, cotton was a major crop in Malawi, production was at a low, erratic level in Rhodesia and, at times, non-existent in Zambia.

An insect control programme was introduced in 1959. This programme was based on scouting to determine what pests were present in the crop, the choice of the most effective insecticide to control these pests and efficient application of the insecticides. Insect control has resulted in a general improvement in plant growth, increasing its attractiveness to certain pests. In addition, the incidence of certain parasites and predators has been reduced. These two factors, in combination, have led to an increase in oviposition by

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Heliothis moths, although these pests are being controlled by the insecticides. Following the use of organic insecticides, red spider mites, Tetranychus spp. have begun to make their appearance in the crop earlier in the season. This pest can do very serious damage when not controlled.

For many years, the main emphasis in the breeding programme was on resistance to Empoasca. Breeding for insect resistance requires firstly, a knowledge of the characters in the plant which will affect the behavioural pattern of the pest and secondly, the ability to transfer these characters to a commercially acceptable variety. The first requirement can be met through a study of insect responses to specific phenotypes of cotton and through a study of the effect of various chemical constituents of the plant on the insect pest under consideration. The second requirement is complicated by the fact that in many cases, resistance to one pest leads to susceptibility to another, and that the requirement for resistance is often over-ruled by other economic considerations.

Continued control of pests calls for research into improved techniques utilizing insecticides with greater selectivity, attractants and repellants, chemosterilants, agronomic practices which will minimise the severity of insect pest infestations and the breeding of insect resistant varieties. The ultimate objective is the development of a fully integrated pest control programme which will have minimal adverse effects on the overall insect ecosystem. The effectiveness of any pest control programme depends on close co-operation on the one hand between the farmer, the extension worker, and the producers of agricultural chemicals and on the other, between extension workers, the producers of agricultural chemicals and the research workers to ensure that the recommended programme is correctly applied and to ensure that it continues to give satisfactory results without build up of insecticide resistance.

INTRODUCTION:

Estimates indicate that approximately one-third of the world's agricultural products are destroyed annually by pests either in the field or in storage. The economic importance of pest damage is directly related to the crop under consideration. Thus horticultural crops may be rendered unmarketable by a small amount of damage while a similar amount of damage in a field crop will be of little consequence apart from reducing the yield. Similarly, determinate plant types are subject to pest attacks over a far shorter period than plants with an indeterminate flowering habit. Thus the period of insect attack on a crop like coffee or cotton is far more prolonged than on a grain crop. Success in eliminating even a part of the destruction of agricultural products caused by insect pests will be a major contribution in overcoming the present disparity between population growth and agricultural productivity.

The relationship between the insect and its host plant involves the feeding preferences of the adult and its oviposition preferences which, in turn, are related to the feeding preferences of the juvenile forms. This relationship is, therefore, necessarily, a complex one (Gillham, 1964). Dethier (1952) describe the whole drama of changing feeding preferences as a dynamic equilibrium between the two changing systems, the plant and the insect. By its very nature, any agricultural endeavour has a profound influence on this equilibrium. In the first place, a single host plant species is planted without competition over a considerable area, thus providing an abundant and readily available host for its particular pest complex. The natural enemies may be able to regulate the population increase of the insect pest species and so protect the crop plant from excessive damage. However, when natural controls are not sufficient to keep the population density of the pest species at a low level, serious economic damage may result. In these circumstances, therefore, an increase in production becomes a primary factor in the development of plant pests and parasites.

As soon as insecticides are introduced for the control of any insect species which is becoming overabundant, the parasites and predators of this and other species may be destroyed, leaving the way open for high population densities to develop of any species not controlled by the insecticide being used. Such a situation has frequently been reported in the case of the red spider mite, *Tetranychus* spp., where spraying for the control of other species of insect has destroyed its natural controls (Hussein, 1958; McKinlay, 1959; Hassan et al., 1961). This permits the mite population to increase to economically serious proportions at a time in the season when they can do serious damage.

With the exception of the Soviet Union where cotton production extends to 47°N., the major cotton producing areas of the world are between 35°S. and 37°N. latitude. A wide range of cotton insect pests are found in this area. Hargreaves (1948) lists 1,326 insect species of the world which have been found on cotton of which 482 are recorded from Africa, South of the Sahara. Many of these species are not important. However, a considerable number of species are present in any cotton producing area, presenting a very complex pattern which varies very considerably from season to season and from location to location.

This paper demonstrates how the population level of certain insect pest species have been influenced by the level of production of cotton in Central Africa and how these pests, in turn, have exerted an influence on further expansion in production. It goes on to demonstrate the difficulties of developing an effective programme for the control of all the major pests in the insect complex on cotton. The development of such a programme has exerted a very considerable influence on the level of production which, in turn, has necessitated continued research to maintain the effectiveness of the programme.

The role of extension services and the need for co-operation from commercial agricultural chemical interests is stressed. Host plant resistance has played an important role in cotton production in Central Africa over a number of years but its role is complicated by the range of pests which attack the crop and by the influence which resistance to one pest may have on the prevalence of another. Finally, the paper deals with the need for continued high level research, backed by effective extension services, to prevent indiscriminate use of insecticides which may lead to serious, uncontrollable problems through the development of multiple insecticide resistant strains of the major insect pest species.

FACTORS WHICH INFLUENCE THE PREVALENCE OF INSECTS:

All animals have an innate capacity to increase, the expression of which is regulated by climatic factors, the availability of suitable food, by competition within and between species and by natural enemies. The climatic effect is both a direct effect on the speed of development, fecundity and longevity of the animal and an indirect effect on the availability of food. Temperature, moisture and light are the most important climatic factors while wind may play a major role in the dispersion of certain insects.

All animals have a favourable temperature and moisture range within which they live and multiply. Extremes of temperature and humidity may prove fatal but various mechanisms have evolved which will permit animals to survive through unfavourable periods. On the other hand, most animals can survive in extreme of light and darkness of the intensity found in nature, but they are influenced by illuminance, direction, photoperiod, wavelength and degree of polarization of light. These factors provide the necessary stimuli to those mechanisms which regulate the life cycle and keep it in step with the season. Many insects spend at least part of their life cycle within the structure of a host plant or animal where the temperature, humidity, light intensity and wind velocity may differ markedly from the surroundings. Thus the relative importance of micro and macro climate must be borne in mind (Gillham, 1966:).

Where a limitation to population growth is not imposed by climatic factors, other factors such as the availability of suitable food, competition for the same ecological niche or the prevalence of specific and non-specific predators and parasites may regulate the abundance of a given species. However, even under favourable climatic conditions, in the presence of abundant food and the absence of predators, an upper limit to numbers will be imposed by the influence of density on birth-rate and death-rate (Andrewartha and Birch, 1956). This situation has been studied experimentally but crowding in nature is rare, particularly under the conditions pertaining in the experiments where food was not limiting.

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Insects can be grouped into those which feed on living plant matter, those which feed on dead or decaying plant matter, those which live on live animal matter, those which live on dead animal matter and those which live on both animal and plant matter. A few species have omnivorous feeding habits but most insects have specialised to some extent and phytophagous or plant eating insects may be divided into polyphagous, oligophagous and monophagous groups. The first group has a wide range of host plants, the second a relatively restricted range while members of the third group are highly specialised, restricting their activities to one or two closely related hosts (Gillman, 1966). Gause (1934) stated that two or more forms of animal with the same ecological requirements cannot coexist indefinitely in the same ecological niche because one of them will, in all likelihood, be more efficient than the other and will out-breed and supplant it. This principle is demonstrated by the evolution of increasing specialization from polyphagous to oligophagous to monophagous feeding habits, providing new species with spatial isolation.

The factors regulating the abundance of insects can be well demonstrated on cotton, Gossypium hirsutum (L.). The cotton plant has an indeterminate flowering habit and during most of the flowering period, it carries buds and bolls in various stages of development. Rainey (1948) demonstrated the influence of the stage of development of the cotton plant on its susceptibility to various pests and diseases. Since the plant carries bolls for a fairly prolonged period in all stages of development, it is subject to attack by a range of insect pests over a long period.

A wide range of insect pest species, falling into the polyphagous, oligophagous and monophagous groups, inhabit the temperate and tropical regions of the world where cotton is normally grown as a crop plant. The pattern of attack by any particular insect species is influenced by the stage of development of the host plant, by climatic factors, and by the relative availability and attractiveness of alternative host plants. The species attacking cotton will obviously vary considerably from season to season and from one location to another, but a fairly typical pattern of attack will consist of those species which attack the apical bud early in the development of the plant and which may continue for a prolonged period, followed by leaf sucking and leaf eating species and followed, in turn, by those species which attack the fruiting bodies. There will obviously be a considerable overlap between the various groups, but all are directly and indirectly influenced by climatic factors and all enjoy a certain amount of both spatial and temporal isolation resulting from the part of the plant actually attacked and the timing of the attack. An apparent exception may exist in the case of bollworm species but generally, in areas which have more than one species, the pattern of attack is typified by the predominance of one species at any one time during the season.

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THE INSECT PESTS OF COTTON IN CENTRAL AFRICA:

Cultivated cottons of world belong to four species, two of which Gossypium arboreum and Gossypium herbaceum are known as old world species while the other two, Gossypium hirsutum and Gossypium barbadense, are commonly known as new world species. The American Upland varieties belong to the species Gossypium hirsutum and are by far the most commonly grown throughout the world. All cultivated Central African varieties belong to this species.

Cotton is a perennial plant but it is generally cultivated as an annual. The plant is characterised by a main stem with a dominant apical bud. This bud is extremely attractive to a number of insect pests, particularly in the early stages of development of the plant. The aerial portions of all species of the genus Gossypium are characterised by the presence of pigment glands which vary in size, number, distribution and pigmentation in different species. They secrete a volatile oil which is probably responsible for the characteristic odour of the cotton plant (Standford and Viehove, 1918). The pigment gossypol, one of the constituents of the glands, is toxic to a number of pests and pathogens in its free form. Gillham (1965) suggested that the glands may have evolved in this genus as a protective mechanism against the ravages of pests. With the exception of Gossypium tomentosum which is found in Hawaii, all species of the genus are also characterised by the presence of extra-floral nectaries on the under-side of the leaf and on the base of the bracts.

Cotton is normally planted from seed during the spring. It takes from six to eight weeks to the start of flowering. The plant has an indeterminate flowering habit, lasting about 12 weeks. Since it takes about eight weeks for the boll to develop from pollination to maturity, the plant normally carries buds and bolls in various stages of development for most of its flowering period.

Pearson (1958) confined his attention to about 150 species of the 482 recorded by Hargreaves from Africa south of the Sahara. He indicated that most of the others have little or no economic importance. The major pests which are of concern on cotton in Central Africa are listed in Table I.

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TABLE I.

THE MAJOR PESTS OF COTTON IN CENTRAL AFRICA

Order	Genus	Species	Common Name	Plant Part Attacked.
Lepidoptera	Xanthodes	gracilis		Leaf
	Anomis	sabulifera		"
	Cosmophila	flava	semi looper	"
	Spodoptera	littoralis	} Egyptian cotton	"
	Prodenia	litura		"
	Diparopsis	castanea	red bollworm	boll
	Earias	spp.	spiny bollworm	"
	Heliothis	annigera	American bollworm	"
	Pectinophora	gossypiella	pink bollworm	"
Hemiptera	Dysdercus	spp.	stainer	seed
	Empoasca	facialis	jassid	leaf
	Empoasca	lybica	jassid	"
	Helopeltis	schoutedeni	helopeltis	leaf, stem and boll
	Helopeltis	bergroth	helopeltis	" " " "
	Lygus	vosseleri	lygus	terminal bud
	Oxycorenus	spp.	darky stainer	seed
Aphidae	Aphis	gossypii	aphid	leaf
Acarina	Tetranychus	telarius	red spider mite	leaf
Tetranychidae		lombardini		
		ludeni		
		neocaledonicus		

The red bollworm, *Diparopsis castanea* Hmps., confines its activity to the genus *Gossypium* and its close relative *Cienfuegosia* and is the single representative of the monophagous group. McKinley⁽¹⁾ has expressed doubt as to the ability of this pest to feed and breed on *Cienfuegosia*. The oligophagous group which has a number of Malvaceous host species, is represented by the cotton stainer *Dysdercus* spp., the spiny bollworm *Earias* spp., the darky stainer *Cosmophila* spp., and *Xanthodes gracilis*. The pink bollworm, *Pectinophora gossypiella* Saund., is regarded as being oligophagous, having been recorded as

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McKinley⁽¹⁾ D.J. Personal communication.

feeding and breeding on Hibiscus dongolensis as well as Gossypium hirsutum in Rhodesia (Matthews et al., 1965) and on several host plants elsewhere (Shiller et al., 1962). However, outbreaks have been recorded in Malawi without any alternative host plants being found (Matthews et al., 1965). The polyphagous group has a wide range of alternative host plants and forms by far the largest group of cotton pests. The bollworm, Heliothis armigera Hbn., is probably the most destructive of the pests falling within this group. The larvae of various species of this genus function as bollworms in all the major cotton producing areas of the world. They feed on the fruit of a wide range of plants, amongst which maize, Zea mays is a preferred host. The wide distribution of the species of this genus makes it one of the most destructive of all cotton pests. The aphids Aphis gossypii Glor. and jassids Empoasca spp. are also major polyphagous pests on cotton in Central Africa. The Acarina spider mites, Tetranychus spp. have a wide range of host plants and under certain conditions can cause serious damage to the cotton crop.

The pattern of insect attack on cotton in Central Africa, as in other parts of the world, varies considerably from season to season and from location to location. However, taken in sequence in a fairly typical season, some lygus damage can be expected in the seedling stage. Empoasca makes its appearance fairly early and can be present on the crop for a considerable part of the season. Where alternative food sources are not available, Diparopsis and Paria may eat their way into the growing tip and act as stem borers. These two species can be present more or less throughout the season, feeding on the growing tip prior to the onset of flowering and attacking the bolls once these have started to develop. Heliothis feeds mainly on buds and bolls and so moves into the cotton crop during the course of flowering. Dysdercus spp. feed on the developing seed, attacking the cotton plant as the bolls start to ripen and so tend to be late season pests. Aphids may attack cotton virtually at any time during the plant's development, while under natural conditions, Tetranychus is a late season pest if it makes its appearance at all. In certain areas, leaf eating caterpillars Cosmophila flava (F), and the Elegant grasshopper, Zonocerus elegans Thmb., may cause severe damage to young plants (Tunstall et al., 1965).

THE INFLUENCE OF COTTON PRODUCTION ON THE RED BOLLWORM DIPAROPSIS CASTANEA:

Cotton was grown on a limited scale in Malawi from 1905 and in Rhodesia from the early 1920's. By the mid-1920's, Empoasca spp. had emerged as a major pest. By reducing the efficiency of the foliage of the plant and causing actual defoliation, yields were being reduced and the quality adversely affected to such an extent that future production appeared doubtful. Despite this, Cameron (1927) considered that Dysdercus spp., were to be feared far more than Empoasca. Hamilton and Peat (1927) observed that Empoasca would definitely

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come within the control of the plant breeder, but that Heliothis was undoubtedly the most serious pest. They went on to record that Parias spp. did some slight damage while Diparopsis did not appear to be present. The breeding programme for the development of Empoasca resistant varieties will be discussed in a later section of this paper. In this section consideration will be given to the developing importance of Diparopsis with increased production.

During the 1926/27 season, the bollworm attack was extremely small and consisted almost entirely of Parias spp. In that year there was virtually no Heliothis damage throughout the country, possibly due to the late arrival of the first rains and there was no Diparopsis activity (Peat, 1928).

The following season, shedding due to bollworms on the Research Station at Gatooma was once again slight and mainly due to Parias. A few Heliothis were observed on the crop, but once again, no Diparopsis were recorded although they were reported to be present in cotton in the Bulawayo and Mazoe Valley areas. At the time, it was considered that a comparison between the flora of the Gatooma and Mazoe areas may give some indication of the reason for the presence of the bollworm on cotton in one area and not in the other. It was also decided to establish a small plot of ratooned cotton on the Research Station for the study of bollworm and stainer attacks (Peat, 1929).

In the 1928/29 season, a very severe attack of Heliothis occurred. However, on the ratooned trap crop in a collection of 180 bollworms, the ratio of Diparopsis to Parias to Heliothis was 4.6 to 1.3 to 1. In a later collection, 22 Diparopsis were found, 10 Parias and 1 Heliothis. Thus Diparopsis formed 76% of the total bollworms collected from the raton trap crop in that year, the first time this species had been recorded on cotton on the Research Station. In contrast, although Diparopsis were recorded on the annual crop, they formed only 0.001% of the recorded bollworm population in the annual observation plot. In this plot, 3.1% of the bollworms collected were Parias while 96% were Heliothis (Peat, 1930).

By 1930, Heliothis was considered to be the most serious problem and Cameron (1931) considered that it was imperative that every effort should be made to counter the activities of this pest. The 1929/30 season was completely dominated by a more or less continuous attack of Heliothis from the beginning of March into May. However, by comparison with the figures for the previous year, the proportion of Heliothis collected between February and the end of May fell to 72% while Diparopsis rose to 9% and Parias to 19%. For March the percentages were 83% Heliothis, 2% Diparopsis and 15% Parias and for April 75%, 12½% and 12½% respectively.

The larvae of Heliothis are very active, attacking buds, flowers and bolls and are capable of destroying a considerable proportion of the potential crop in a relatively short time. By contrast, Diparopsis larvae

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tend to move into a boll and remain there until it is eaten out. Thus, Heliothis was considered to be the most serious pest, since a given number of larvae are capable of doing far more damage than an equivalent number of Diparopsis larvae. The lateness of the Heliothis attacks suggested that it may be possible to escape serious damage by forcing an early crop through breeding and through agronomic practices. The same could not be said of Diparopsis. It was considered important to develop prolific strains which produced large numbers of small bolls rather than strains producing small numbers of large bolls (Peat, 1931).

The 1930/31 season was characterised by severe drought and losses due to insect attacks were secondary to those caused by climatic conditions. However, in contrast to previous years, Diparopsis became a major pest on annual cotton on the Research Station. This was considered to be serious and disturbing but it was felt that despite this, Diparopsis was not to be feared as much as Heliothis because of the differences of the proportion of damage done by individuals of each species (Peat, 1932).

The following season was considered to be the best during the first seven years of the Station's establishment. Heliothis made its appearance early and was the principal pest. However, the incidence of Diparopsis was prolonged and moderately severe from the beginning of January to the end of the season. Farias was not at any time as severe as in previous seasons but it was present throughout the whole season (Peat et al., 1933).

The 1932/33 season was described by Cameron (1934) as being lop-sided with too much rain at the beginning and not enough later on. The Heliothis infestation was relatively small but there was a heavy and continuous attack of Diparopsis throughout the season. The Heliothis attack in the 1933/34 season was fairly similar to that experienced in previous years. The period of attack varied according to the earliness or lateness of the crop and, generally speaking, late planted cotton suffered most. Serious Diparopsis damage was experienced in the latter part of the season. This came on top of the Heliothis attack and led to serious losses of the mature bolls which remained. Peat (1934) stated that it was believed that the attacks had increased largely by a build up from year to year of an endemic Diparopsis moth population. The knowledge gained concerning this species indicated that ratooning would be a highly inadvisable practice in infested areas since the population would breed up on the ratoon crop and would then make devastating attacks on annual cotton later on in the season.

These reports indicate that between 1923 when Diparopsis was not observed on cotton on the Research Station and 1933, this species had become a major cotton pest. The history of cotton production in Rhodesia from 1920-1959 was one of fluctuating production. The precise reasons for this cannot be ascribed to any particular cause. Nevertheless, over a period of years, increased seed cotton prices led to acreage expansion until price

recessions or reduced yields resulting from a build up of insect pests caused a reduction in acreage. The pattern of increasing importance of Diparopsis was repeated on many occasions. For various reasons, a district would go out of cotton production for several years. When it came back to cotton, Diparopsis would not be found on the crop for the first year or two and yields would be reasonably good. In succeeding years, Diparopsis would increase steadily and yield levels would decline. The most recent occurrence of this type was in the Mazoe Valley where interest in cotton increased rapidly following the introduction of the insect control programme in 1959. For the first two or three years, no Diparopsis were found on cotton crops in the area but then they began to make their appearance and spread steadily in succeeding years. Their importance has, on this occasion, been kept in check by effective application of the insect control recommendations.

Diparopsis has a very limited host range, being confined mainly to Gossypium and its close relative Gienfugosia. The former is found wild in Rhodesia while the latter is not. Similar patterns of a steady increase in the prevalence of pests with a limited host range associated with an increase in production of a host plant can be traced in many cases. In Rhodesia, the pink bollworm, Pectinophora gossypiella was probably present on its wild host, Hibiscus dongolensis, in the South Eastern part of the country for many years. Cotton was introduced to the area as a commercial crop in 1957 and by 1959, Pectinophora was an established pest on this crop (Whellan, 1960, Matthews et al., 1965). Stringent control measures kept further expansion in check for a number of years, but an increase in cotton production in the area could very well lead to this pest becoming established. In Malawi, a severe outbreak of Pectinophora occurred in 1959 but the pest was not found on any wild host plants. Matthews et al., (1965) expressed the opinion that this outbreak was the result of a steady increase in population density during a period of two years when the closed season for cotton was not adequately observed. Rose et al., (1957b) reported a similar situation in the Sudan where the increase in Pectinophora attack was related to a steady increase in standover cotton. The relationship between the prevalence of an insect pest with a limited host range and the increase in production of a host plant is far easier to trace than that of a pest with a wide host range, since it is a direct relationship in the former whereas in the latter, the population density of the pest is influenced by a number of factors relating to the whole of its host range. Thus the increases in Diparopsis population densities described can be directly related to cotton production whereas Heliothis population densities cannot.

The influence of increased productivity of a host plant on the incidence of an insect pest can take several forms. Diparopsis and Pectinophora were probably present in wild host plants in Rhodesia when the cotton crop plant was introduced. In time, the pest transferred onto the cultivated plant where the population density steadily increased with increased

production. The converse occurs when a crop is already established and a new pest is introduced to the area, often without its predators and parasites. The introduction of the European corn borer, Pyrausta nubilalis, to the United States and its subsequent spread onto new hosts through vast areas is an example of this type of situation. This pest feeds mainly on Artemisia vulgaris L. in its native habitat in Europe. It was first observed near Boston, Massachusetts, in 1917 on sweet corn. It spread rapidly and by 1952, was present in 37 states east of the Rocky Mountains, becoming a major pest of maize, Zea mays, in the U.S. corn belt. A third situation occurs when a new crop plant is introduced into a rotation, closing a gap in the food cycle of a pest which is already in the area, and while not economically damaged itself, the new crop enables the pest to reach epidemic proportions on other crops already in the area. A good example is provided by the lygus, Lygus hemerus Knight, in California/^{which} overwinters on lucerne (alfalfa), doing very little damage to this crop but migrates onto neighbouring annual crops such as cotton where it may do very serious damage (Storn et al., 1964). Finally, the practices employed to control one pest may destroy the parasites and predators of another, permitting it to establish itself as a major pest. The establishment of red spider mite, Tetranychus spp. following the use of insecticides for the control of other pests has been widely reported (Husselne, 1958; McKinlay, 1959; Hasson et. al., 1961).

THE DEVELOPMENT OF THE INSECT CONTROL PROGRAMME IN CENTRAL AFRICA :

Pfadt (1962) defined integrated insect control as control of pests which combines and integrates chemical methods with natural and biological control. Chemical control is applied as necessary and in a manner which is least disruptive to natural and biological control. This is the ideal aimed at by economic entomologists. However, the attainment of the ideal is difficult in a crop like cotton because of the complex pattern of insect attack in which the control practices necessary for one insect species directly influence other species in the complex. Nonetheless, every effort must be made to minimise the disruptive effects of the insect control programme on the over-all insect ecosystem.

The Cotton Pest Research team was established in Central Africa in 1956 with the prime objective of developing control measures for Diparopsis. By this time, despite the ravages of the Heliothis, Diparopsis was recognised as the major pest limiting further development of cotton production in the area. The research programme developed by this team covered a complete study of Diparopsis, including the thorough study of the biology of the pest with particular reference to the mechanisms involved in initiating and breaking the diapause of over-wintering pupae, a study of the sex attractants of the female moth, a study of the possible utilization of chemosterilants for the control of the pest and finally, a study of chemical means of control. Efforts were also

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made to study the parasites and predators of this and the related species, Diparopsis watsoni (Roths.) in North Africa, Diparopsis techrogramma B.-B. in Angola and Sacadoses pyralis Dyar. in South America.

Because of the incidence of other insect pests on cotton, the main emphasis was placed on the development of effective chemical control measures to cover the whole of the insect complex. The initial programme covered the screening of insecticides against the major pests in the laboratory, the field testing of the most promising insecticides and finally, extension trials throughout the territory to study the effectiveness of the insect control recommendations under a wide range of environmental conditions (Matthews 1966a, 1966b, 1966c; Tunstall and Matthews, 1965).

The results of the initial screening programme indicated that no single insecticide was sufficient in itself to control all the insects in the complex attacking cotton. It also indicated that the effective control of Diparopsis depended on the first instar larvae coming into contact with the insecticide between hatching and entrance into the boll. Similarly, effective control of Heliothis also depended on control of the first instar larvae since the larvae are not exposed to the insecticide once they enter the boll and older larvae become increasingly difficult to kill. The effectiveness of the insect control programme, therefore, depended not only on finding suitable insecticides but also on ensuring a thorough coverage of the plant. The initial investigations had to be backed up by research into the most effective means of applying insecticides under practical field conditions. The first stage in this development was the modified knapsack sprayer which has proved extremely effective, particularly under peasant agricultural conditions (Tunstall et al., 1961). This was followed by the application of the tailboom used on the modified knapsack for ox-drawn and tractor-mounted ground spraying equipment for use on more extensive acreages (Tunstall et al., 1965). Finally, comparisons were made between the ground spraying equipment developed and aerial applications of insecticide since this form of application has advantages under certain conditions (Matthews and Tunstall, 1965; Johnstone and Matthews, 1965). Finally a system of scouting had to be developed so that the incidence of the various pests in the crop could be assessed. This assessment forms the basis for the choice of insecticide and the timing of spraying (Tunstall et al., 1966).

Large scale trials were conducted to test the effectiveness of the spray programme developed under field conditions in the three Central African territories. The overall mean yields in sprayed and unsprayed trial plots in the three territories in 1960 and 1961 were 1,480 and 585 pounds of seed cotton per acre, respectively.

Matthews and Tunstall (1963) found that there was an increase in Heliothis oviposition on sprayed cotton. They considered that while reduced mortality as a result of fewer parasites and predators was one of the main causes of this, increased attractiveness of the plant was also an important factor. They stressed that once spraying had commenced, the importance of scouting was accentuated since increased oviposition on unprotected plants could lead to very serious crop losses.

BREEDING FOR HOST PLANT RESISTANCE:

Host plant resistance is the ideal method of pest control. Painter (1951) defined insect resistance as the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect populations. Parnell *et al.*, (1949) showed that even a low level of resistance resulted in a significant reduction in the population of Bemisia spp. in cotton.

Host plant resistance may be due to any one or any combination of three inter-related mechanisms. These are classified as preference or non-preference defined as the group of plant characters and insect responses which lead to or away from the use of a particular plant for oviposition, food or shelter, antibiosis defined as the tendency to prevent, injure or destroy insect life and tolerance defined as the ability of a plant to reduce or repair injury to a marked degree in spite of supporting an insect population approximately equal to that damaging a susceptible host (Painter, 1951).

Cotton is attacked by a complex of insect pests the composition of which varies, as has been indicated, from season to season and from location to location. The development of varieties carrying resistance to all the major pests would, therefore, be a very difficult task if indeed it could be accomplished at all. However, resistance to any one pest, even at a low level, could have a profound influence on the overall pattern of insect control.

In Rhodesia, cotton was first produced in the early 1920's but by the middle of that decade, jassid threatened to put an end to future production (Peat, 1928). The situation in Malawi was not so clear cut but nonetheless, this pest was a problem (Ducker, 1930). Parnell *et al.*, (1949) demonstrated the relationship between leaf hairiness and the incidence of Bemisia. The development of Bemisia resistant varieties was the sole method of control and made continued cotton production possible over thousands of acres in Africa for some thirty years, until the introduction of other methods of control.

Investigations were initiated in 1960 into possible sources of resistance to the bollworm, Heliothis zea in North Carolina and Heliothis armigera in Rhodesia. The approach was that proposed by Stephens (1957) in which the objective was to determine the influence of specific plant characters of cotton on the behavioural pattern of Heliothis. This was strictly a study of insect preferences. The characters under study were red and green leaf colour, the presence and absence of glands, the presence and absence of extra-floral nectaries and the presence and absence of leaf hairs. The glandless, red leaf and plant hairiness phenotypes were chosen as variants from normal which could influence the sensory perception of Heliothis, while the nectariless variant was chosen for its possible adverse effect on the longevity of the Heliothis imago through the removal of a possible food source.

The results of these investigations indicated that the Heliothis imago prefers a hairy plant to a smooth plant for oviposition. Survival rates on the glandless variant appeared to be higher than on normal cotton. Apart from the influence on Heliothis, the glandless variant was attacked by a wider range of pests than the normal plant. The different characters studied are being combined on a common background for continued investigations.

Working with similar genetic strains, Lukefahr et al. (1965) demonstrated in the laboratory and in field cages that the glandless and nectary free cotton plants had lower populations of bollworm Heliothis zea (Boddie); the tobacco budworm, Heliothis virescens (F); the pink bollworm, Pectinophora gossypiella (Saunders); the cabbage looper, Trichoplusia ni (Hubner); and the cotton leaf worm, Alabama argillacea (Hubner). They followed this up with field experiments in which significantly fewer larvae of the bollworm and the cotton fleahopper, Psallus seriatus (Reuter) were found on a glabrous and nectary-free strain than on normal cotton (Lukefahr et al., 1966). The expression of the nectary free character in reducing insect populations is very sensitive to plot size and is, therefore, difficult to test under field conditions.

In developing a breeding programme for host plant resistance, the breeder requires a thorough knowledge of the life history of the insect and the nature of the damage caused. This knowledge forms the basis for selecting possible sources of resistance for further study among related varieties and species of the host plant. The nature of any resistance must be identified and it must be shown that it is transmitted to the progeny (Gillham, 1963). Stephens (1957) stressed that in the absence of a thorough knowledge of the nature of the resistance the breeder has a difficult task because of the small number of plants in a segregating population which possess the correct gene combination to confer resistance and because of the difficulty in identifying resistant plants. Wessling (1958) demonstrated this situation in population mixtures between Pilose plants which had some resistance to the boll weevil and susceptible plants. The incidence of weevil on Pilose plants was higher when they were grown in mixtures than when they were grown in pure stands. Similarly, the nectariless character of cotton only influences insect population density when nectary free plants are grown over a large area.

Research on host plant resistance is necessarily of a long term nature. Planning must take this into account since success can lead to maintained or increased yields at lower cost. Even a low level of resistance can have a profound influence on the overall insect control programme.

DISCUSSION:

The relationship between the host plant and its pests is one of dynamic equilibrium in which each influences the other and is, in turn, under the influence of a number of environmental factors. In natural conditions,

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this equilibrium reaches a status of relative stability in which the population density of the pest is kept in check. The introduction of agriculture may introduce instability by removing the check imposed on the insect population growth by limitations of available food. Equilibrium will eventually be restored. If this occurs at a low population density as a result of an increase in natural and biological controls, little economic damage will result. However, equilibrium may only be reached when the pest population density has reached a level where there is serious economic damage, in which case some means of control other than natural and biological control may be necessary.

Instability in the equilibrium may result directly from an increase of the pest species due to the increase in available food. On the other hand, it may arise indirectly from the transfer of a pest from a wild host onto a cultivated host, through the closing of a gap in the food cycle as a result of the introduction of a new host plant or as a result of the destruction of biological controls of one pest by the control measures used on another.

This paper refers primarily to insect pests. However, the principles involved apply equally to other pests. As an example, the three main races of the Red-billed Quolea finch occupy the savannah areas of Africa. The southern race, Quolea quolea lathamii extends from the Cape to Malawi and from southern Angola to Mozambique. Other races occur in East and West Africa. Within each race, the population is in a continuous state of flux, responding to various factors, of which seasonal variation is the most important. Human intervention in the form of destroying breeding grounds or creating new feeding ground is also important.

The Quolea breeding grounds are normally in areas of dense bush. Breeding has to coincide with the setting of seed of various annual and perennial grasses and is, therefore, governed by rainfall. When the breeding is over, the birds move away from the breeding grounds onto farm lands if these are handy or grass seed is scanty.

Quoleas were particularly numerous in Rhodesia in the early 1950's, but thereafter, they moved into South Africa in vast numbers due to large acreages of farm land in the highveld providing suitable weed and small grain seeds. Conditions were sufficiently favourable for the birds to stay on and breed in poplar and Eucalypt plantations. This was previously completely unknown.

Intensive control measures were applied over a four year period. Initially, although about 85% of the known population in South Africa were killed each year, the population density the following year was unchanged due to immigration from neighbouring territories. Eventually, however, control measures in South Africa drastically reduced the overall population of the southern race.

Throughout the range of the Red-billed Quail, control measures have been necessary because of the depredations of small grain crops which form the staple diet of peasant populations. Full investigations of the presence of this and other potential pests is necessary before any new agricultural development programme is undertaken (Flowers⁽²⁾).

There are numerous cases where the increase in the population density of a pest has been checked by biological controls. The introduction of the ladybird beetle Rodolia cardinalis (Muls.) into South Africa, California and elsewhere to control cotton-cushion scale, Aspidiotus perniciosus Comstock, in citrus is a classic example (Sweetman, 1936; Lounsbury, 1900). Sweetman (1936), Steinhaus (1947), Wigglesworth (1965) and many others have described biological control, involving parasites, predators and pathogens of various kinds. However, when biological control is not sufficient to prevent serious economic destruction, other means of pest control are necessary.

The pattern of biological control in cotton varies very considerably from location to location. Whitcomb and Bell (1964) found overwhelming evidence in Arkansas that predators frequently prevent outbreaks of bollworms, aphids and spider mites. By contrast, Wene and Skeets (1962) reported that in the Salt Valley area of Arizona, the predator complex was unable to bring the Lygus infestation below the destructive level and a high predatory insect complex did not prevent a severe outbreak of either salt marsh caterpillars, Pastinaca aerea or the cotton leaf perforator, Bucculatrix thurbericella. In Central Africa, biological control of cotton pests has not, as yet, been sufficient to keep the major pests, Heliothis, Diparopsis and Dysdercus in check. In the absence of insecticides, it has checked Aphis and Tetranychus while Empoasca has been checked by host plant resistance.

Knipling (1962, 1964) has described the use of chemosterilants or irradiation as a means of control by sterilizing individuals for subsequent release into the population to compete with normal individuals. This principle has been successfully used in the control of the screw-worm Cochliomyia hominivorax (Coq.) Research into the use of chemosterilants for the control of Diparopsis is progressing but has not reached the point of practical application.

et al.,
Keller et al., (1962) and Maxwell (1963) demonstrated the presence of a powerful feeding arrestant and stimulant for the boll weevil, Anthonomus grandis Boh., in various parts of the cotton plant. These substances were classified as arrestants and stimulants (Dethier et al., 1960) since no apparent attraction existed unless the insect came into actual contact with them. Subsequently, Keller et al., (1962) extracted an attractant to Anthonomus. This was followed by the extraction of a repellent. Maxwell et al., (1963) speculated that a dynamic balance exists between the repellent and the attractant which determines the pattern of insect responses through the season.

(2) Flowers, D.C.H. . Personal communication

Many insects are subject to olfactory stimuli to find suitable feeding and oviposition sites and to bring the male and female together for mating. Odour baited lures may, therefore, be used in traps, or to cause confusion, preventing mating, or leading to oviposition on unsuitable sites. Many attractants, particularly sex attractants, are species specific and can be used in conjunction with insecticides or sterilants to control a particular species without affecting other insects in the area. Specific attractants can also be used in traps as a means of detecting the spread of a pest (Jacobson et al., 1964). Diparopsis is one species in which the female imago has a powerful sex attractant. This is the subject of intensive research (Tunstall⁽³⁾).

The presence of olfactory stimuli in the plant opens the way for the plant breeder to develop varieties which are not attractive to the pest and so provide a non-preference type of host plant resistance to specific pests. Many successful host plant resistance breeding programmes have been carried out without a fundamental knowledge of the biological and biochemical inter-relationship between the insect and its host. However, this basic knowledge is considered essential if rapid progress is to be made (Beck, 1965).

In several crops, spectacular successes have been achieved in breeding for insect resistance. These include resistance to the hessian fly, Phytophaga destructor (Say), and the wheat stem sawfly, Cephus cinctus (Norton) in wheat, the spotted alfalfa aphid, Therioaphis maculata (Buckton) and the pea aphid, Macrosiphum vici (Kalt) in lucerne (alfalfa), to the European corn borer, Pyrausta nubilalis (Hübner) and the corn earworm, Heliothis zea (Boëdic) in maize, to the chinch bug, Blissus leucopterus (Say) in sorghum and to various leaf hoppers in cotton. Many other examples of breeding for host plant resistance could be cited but these serve to demonstrate the contribution which can be made in the field of pest control by the plant breeder (Jenkins et al., 1965).

Host plant resistance is an ideal method of pest control since it provides the farmer with increased yields at no extra cost. However, the development of insect resistant varieties is complicated by the fact that in many instances, the factors which provide resistance to one pest, increase susceptibility to another or are unacceptable commercially. Thus leaf hairiness provides resistance to Lyropassa in cotton but is often accompanied by low quality lint (Rose et al., 1957a), and it increases susceptibility to Aphis and white fly, Benisia tabaci (Dark and Saunders, 1958) and to Heliothis (Gillham, 1963). Furthermore, Matthews (1966b) found that there was a positive correlation between leaf hairiness and the effectiveness of insecticide applications. This resulted from reduced run off of the insecticide on a hairy surface and from increased wandering time by newly hatched larvae. The difficulty can be minimized if all genetic material

(3) Tunstall, J.P. Personal communication

in a programme is screened for non-preference, tolerance and antibiosis. The likelihood of a breakdown of resistance is reduced if two or more forms of resistance can be combined.

Stephens (1957) considered that the disruptive effect of insecticides imposes a limitation on their use but that an additional limitation is imposed by the patience and financial ability of the farmer to carry an insect control programme through to its conclusion. A poorly executed programme of insect control may be more harmful than no control at all. However, in many cases, for the immediate future, insecticides are and will remain an essential part of agricultural production.

All the pests in the insect complex on a crop are not necessarily controlled by the same insecticide. Effective control depends on treating the insect when it is at its most sensitive to the insecticide. Thus efficient insect scouting must form an essential part of any insect control programme since this forms the basis of selecting the most suitable insecticide for control of the particular pests in the crop and of correct timing of applications. Scouting also provides an index of the effectiveness of the programme and may give an early warning of a possible development of insecticide resistance. The importance of timing cannot be overstressed (Matthews and Tunstall, 1963; Mistic, 1964; Lincoln and Leigh, 1957). Many cases of insecticide resistance have been recorded (Brazzel, 1963; Brazzel, 1964; Chapman and Coffin, 1964; Eldefrawi *et al.*, 1964; Lowry and Berger, 1965) but frequently, the apparent failure of a recommended insecticide to control a particular pest is due to incorrect timing and poor execution of the application. This has been observed in crops with a heavy infestation of *Tetranychus* in which physiological processes in the plant have been affected by the mites to a point where the effectiveness of systemic insecticides is seriously impaired. Laboratory tests in mites collected under these conditions in Rhodesia have given no indication of resistance so far (McKinley⁽¹⁾).

Extension services to maintain a close liaison between research and the farmer and to ensure that control recommendations are being efficiently carried out with effective results are essential to the success of the programme. The need for scouting and the need to use different insecticides to combat the various pests in the complex opens the way for abuse through the temptation to use mixtures of insecticide on a routine basis. This practice is condemned both on economic and biological grounds. Nonetheless, it has considerable appeal to the farmer and can only be counteracted by an extension service which is free of commercial ties.

Pest control has probably been the major factor in the American agricultural revolution. This has increased yield levels and enabled a small proportion of the population to raise more than enough food to satisfy the needs of the nation. There is little doubt that many agricultural development programmes will run into difficulties with insect and other pests. Insecticides will be necessary, often as the major means of pest

(1) McKinley, D.J. Personal communication

control. The ultimate objective of research into pest control must be the ideal of integrated control. In the meantime, deleterious effects to the insect ecosystem must be minimized by avoidance of indiscriminate use of insecticides through the timely application of the most suitable insecticide to control the particular pests damaging the crop. Failure to accomplish this can lead to increasingly difficult problems of pest control. Success can lead to increased productivity in many areas which can be a major contribution in closing the food gap existing in the world.

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