THE VIRUS DISEASES OF TREES IN TWO CONTINENTS

Recent work on the Swollen shoot of Cacao in the Gold Coast in the light of recent work on the tree viruses in the U. S. A.

Noel F. Robertson

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THE VIRUS DISEASES OF TREES IN TWO CONTINENTS

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In 1946 the writer was sent by the Colonial Office on a visit to Canada and the U. S. A. to study the work in progress there on the virus diseases of crop plants. Particular attention was paid to the virus diseases of trees and tree crops since the opportunities for studying these in Britain are small. In January, 1947 the writer was sent to work at the West African Cacao Research Institute on the Swollen shoot virus of Theobroma cacao L. In this essay an attempt will be made to discuss the particular problem of Swollen shoot of cacao in the light of the generalisations made from a study of many viruses in the U. S. A. The problem in West Africa is very different from any single problem in the U. S. A. The whole structure of the agriculture of the area is different, the people are mainly illiterate and the administrative difficulties are great. Nevertheless the Swollen shoot virus problem shows many facets which are present singly or in combination in other tree virus problems and a comparison of this virus with its analogues in the U. S. A. brings out these similarities. The writer believes that, in the absence of any formal teaching of plant virus pathology in Britain, such an educational visit as he was allowed to make is a valuable teaching method ; the success of this essay will in some measure depend on its ability to convince the readers that this is so.

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THE IMPORTANCE OF FRUIT-GROWING IN THE U. S. A.

Fruit growing is one of the major industries of the U. S. A. Approximately 1/60 of the arable acreage is devoted to fruit growing (International Institute of Agriculture, 1938) and between 1931 and 1936 fruit was the third largest item in the agricultural exports ; the U. S. A. supplied 31.6% of the world's apples, 17.6% of citrus fruits and 18.9% of raisins, in those years (Bacon & Schlaemer, 1940).

Citrus fruit in the States finds its greatest concentration in Florida and California. Oranges, lemons and grapefruit are the principal crops grown. The industry is highly capitalised, costs are high and in normal times the crop is sold in a fiercely competitive market. The producers can then only stay in business by achieving maximum efficiency. This efficiency is largely dependent upon sound advice on pathological matters, for in the words of one grower "Once the citrus crop is planted its future is all pathology".

Peaches are grown throughout the country with areas of concentration in New York State, North Carolina, South Carolina, Georgia, California and in some of the dry valleys of Washington and British Columbia. Peaches are probably a more flexible crop than citrus fruits ; the peach tree comes into economic bearing when four years old and in its early years can be inter-planted with potatoes or some vegetable crop. The peach crop is extremely perishable and reaches a high peak of delivery all at once. On this account its market value may often slump badly. It is, however, a crop which is always in demand and the different areas come into production at different times and do not compete for the market to the same extent as do the citrus areas. Moreover there is always a steady demand on the canning market.

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Cherries and plums behave in much the same way as peaches, on the market, but they are less flexible crops coming into economic bearing much later in life and continuing to bear for a much longer period. Their distribution is in the areas of reasonable rainfall on both coasts.

Apples and pears are occasional crops throughout the U. S. A. and Canada but their greatest concentration is attained in the Ontario Peninsula, the New England States, New York and in Washington and British Columbia both in the wetter coastal areas and in the dry inland valleys under irrigation. They are high cost crops but they can be kept under conditions of gas storage and released on a favourable market.

The soft fruits are of local importance, being grown for the fresh fruit market in the neighbourhood of towns and for local canning enterprises.

Grapes come in a class by themselves, they are expensive to grow and are mostly grown under contract for wineries and are assured of a stable market.

The question as to whether the crops mentioned above are grown for export or under conditions of irrigation, or both, is of importance in evaluating the importance of disease in their production. When the crops are grown for export it is important that as many as possible of the fruits should be unblemished and of high quality. Similarly where the costs of irrigation are to be added to normal costs it is important that maximum production combined with maximum efficiency of production be achieved.

<u>THE IMPORTANCE OF DISEASES IN THE VARIOUS CROPS AND THE EXTENT OF THE DAMAGE AND LOSS THEY CAUSE</u>

The fungus and bacterial diseases attacking fruit trees in the U. S. A. and Canada are very similar in their effects to those in Britain and Europe. They are mostly seasonal in

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their incidence and cause the loss of fruit locally. In some instances they kill out trees but usually only to a limited extent. Much of the loss caused is by a depreciation in quality, as, for example, in the Scab disease of apples (Venturia inaequalis) where the fruit affected is totally unsaleable. Limited depreciation of quality in such a crop as peaches may not be of great economic importance. These fruits have a high and sharp peak in reaching the market and heavy culling under such conditions is often completely compensated by a rise in the market price. Reduction in quality in crops which mature evenly over the season and for which the demand is constant and steady is a more serious matter. Loss of quality in citrus fruit due to Brown Rot (Phytophthora citrophthora) or to the Stubborn virus is a serious matter because of the severe grading to which oranges are subjected. The Phony disease of peaches, a virus disease which reduces crop and quality, in its early overall incidence of about 2% had a negligible effect on the economics of peach production, although where it affected individual orchards at a high percentage its effects were much more serious.

In general the effect of virus diseases is to reduce productivity or to kill the tree. Both effects are of the greatest consequence to a grower who is competing in difficult market. Moreover there are cases where the virus reduces the quality of all the fruit on a tree and spreads rapidly throughout an area so that none of the fruit is worth harvesting ; this is happening in British Columbia. In the Sweet Cherries of the Kootenay area of Lake Okanagan a virus called "Little Cherry Virus" has appeared and has spread rapidly, affecting every tree in the area. The crop is worthless on the fresh fruit market but fortunately it can be used in the manufacture of processed "Maraschino Cherries". Many of the fruit virus diseases are quite lethal but perhaps the most spectacular case

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of a lethal plant virus, which spreads rapidly, is to be seen in the Phloem Necrosis virus of Elms. This disease is spreading very rapidly down through the Mid-West States, as far south as Jackson, Mississipi and as far west as Kansas City, it is destroying the very valuable shade trees of towns where summer shade is almost a necessity of life. In Columbus, Ohio, which the writer visited, 10,000 elm trees are dying every year. The town began with a population of 125,000 elms and it has already lost half of them. It was an unpleasant experience to drive down avenue after avenue with only the skeletons remaining of what had once been some of the loveliest ornamental groves in temperate regions. This is, in the writer's eyes, the supreme example of the potential destructiviness of the virus diseases of planted tree crops. The great difficulty in controlling this disease lies in the fact that the "incubation period", the time between infection and the expression of symptoms is a very long one of twelve months or more and so eradication of trees showing symptoms does not remove all of the infection reservoir. When the incubation period is short and spread is slower a very lethal disease is easily controlled because it either kills itself out or is readily noticed and eradicated. An example of such a disease is the Rosette disease of peach which occurs sporadically in the Virginias and Carolinas.

Perhaps the most serious aspect of tree virus diseases in the U.S.A. is to be seen in those viruses which reduce efficiency while themselves remaining unnoticed by the grower and often by the plant pathologist. A good example of such a disease is the "Cherry Yellows" disease of Sour (Montmorency) cherries (Keitt & Clayton, 1943) which occurs very frequently around Wisconsin and Michigan and may affect upwards of 50% of the trees in an orchard without the grower being aware of anything other than a very severe reduction in yield which

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cannot be mitigated by cultural methods. The disease shows evanescent symptoms and is therefore extremely uncertain to diagnose ; it cannot be confirmed with absolute certainty by any easy inoculation technique and is thus a worry to both grower and pathologist. It may go on for years reducing the productivity of an orchard and when a grower in spite of every cultural practice gets one quarter to half a crop he cannot hope to remain in business in a market with a narrow margin of profit. It would be tedious to deal at length with individual diseases on individual crops and a list of bulletins giving such information is included in the bibliography. It is hoped in the remainder of the essay to extract some general information on the effectiveness of disease control measures, research methods and results, from the whirlwind tour of research centres and the miscellaneous impressions and information obtained on that tour.

THE EFFECTIVENESS OF CONTROL MEASURES FOR THE VIRUS DISEASES OF TREES

(a) Eradication of infected crop plants

The eradication of infected plants (or their effective segregation) is the obvious empirical approach to the control of communicable disease. It has had wide applications and success in the control of bacterial and virus diseases of animals, including man. In the control of plant diseases it has proved useful against certain slow moving fungus pathogens in which the gradient of the epidemic curve is small (e.g. *Armillaria mellea*) and in Britain has been successfully used as a method of obtaining and maintaining healthy stocks of potatoes. It has been generally successful against virus diseases in the smaller clonally propagated plants, raspberries, strawberries, etc. and this may be because the plants can be grown on a nursery scale and closely scrutinised before being

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placed in the field. Once in the field they can be maintained in a fair state of health for a year or two and then the crop is replanted. Such a method of "control" could hardly be counted successful if used against fruit trees and yet it is being used there and one can see it whittling away orchards until there is nothing left but a group of trees of all ages with continual removals and continual replacements. Used against fruit tree virus diseases in the U. S. A. this method has had as many failures as successes.

Peach Mosaic was observed in several separated places in the U. S. A. from 1931-33 (Hutchins, Bodine and Thornberry, 1937) and immediate eradication measures were taken against it. Success has been achieved in those areas with a high peach population such as the San Bernardino and Riverside counties of California. No compensation was offered to growers for the removal of their trees and the cost to individual growers must have been enormous. Nevertheless the officials in the area believe that the stringent procedure of the early days has been well worth while. The insect vector (if any) of peach mosaic is not known but the disease apparently shows up the first year after infection and in certain varieties it shows up in the early spring as petal breaking. Thus in concentrated peach areas spring inspection, where the variety is suitable, and early summer inspection where it is not, combined with immediate eradication cuts down the length of time the trees are dangerous as sources of inoculum and controls the disease adequately.

In contrast to the success of eradication in California it was found in Texas and Colorado to be impossible to give adequate inspection of the scattered peach holdings and eradication has been dropped as an impracticable and uneconomic policy. In these areas the disease has been allowed to take its course and the result has been rather a surprising one. The severe strains of the disease have been eliminated by

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the growers themselves or have died out and there has been a gradual selection towards the milder strains and the majority of the trees are now carrying a mild strain which protects against any of the severe strains which may arise. Moreover for such low cost areas these peaches are moderately productive.

The administration of the eradication project (never an easy job) is of some interest. The Federal Officers were responsible for instigating the campaign and the carrying out of it was by gangs under Federal control. These gangs asked for permission to eradicate and if this was given the trees were inspected and cut and pulled free of charge. If the grower refused to allow the removal of the trees the orchard was inspected, infected trees marked and the State authorities were informed. In California (and in Georgia where much the same procedure is used against Phoney Peach disease) the State is empowered to remove diseased trees, a removal gang does the job and then the State charges the cost to the grower. The legality of these actions have been proved in the law-courts and it is now generally realised by the growers that it is safer to give permission at the beginning.

Eradication has been used against the Phoney Peach virus in Georgia and the neighbouring states. Its success in practice has been less than its success on paper. The officials of the Bureau of Entomology and Plant Quarantine show one a map on which through the years there has been a gradual shrinking of the northern boundary of the area occupied by the disease. When one visits the area it becomes apparent that there is no natural spread in the areas where eradication is effective and in the areas where natural spread occurs the eradication programme is very far from controlling the disease. It did in fact seem to be reasonably successful up till 1945 for till then the recurrent percentage of diseased trees had been around 2-3%. In 1945 however the percentage jumped considerably

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and for some years back it had been showing individual cases of large increases which were not shown in the overall percentage. The situation has continued serious in 1946 and the overall incidence which was about 8% in 1945 seemed to be about the same figure. In local areas the disease was devastating. In one orchard observed by the writer the grower had lost 500 trees for two years running out of an original total of 4,000 trees and it seems as if the disease will continue to take the same toll until there is no orchard left.

Eradication in this case would seem to have failed completely, although he would be a brave man who would recommend its cessation at the moment. If we look for the reason for the failure of the eradication campaign we can find it in some recent data on the virus host relationships. It has been found that there is an incubation period of a year between the time of inoculation (by grafting) and the appearance of symptoms. It seems reasonable to assume that there will be a similar interval between natural infection and the onset of symptoms (the problem is complex and many other factors enter which will not be discussed). If trees in the orchard are carrying a full load of the virus or at least sufficient to infect another tree without themselves showing symptoms then the futility of eradicating trees showing symptoms becomes obvious.

As a general principle it can be concluded that eradication methods only pay when the symptoms of the disease show up quickly after inoculation and where spread is correlated with the regular spread of an insect vector.

There is one special case where eradication except as a purely horticultural operation does not pay. This is in the Pierce disease of grapes (Hewitt _et al._ 1943) where one method of spread is by the migration of infected leaf-hoppers _Cicadella circellata_, (Baker), which alight in an area, feed on the plants, infect them and then rise in a swarm and pass on.

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Obviously when the insect vector does not occur normally in this area, and it rarely does, eradication of diseased plants as a control measure would be both uneconomic and useless.

Eradication as an effective measure should only be employed where there is adequate knowledge of the insect-virus relations, the behaviour of the virus in the plant and the bionomics of the vector.

(b) <u>Eradication of infected wild hosts and symptomless carriers</u>

The presence of reservoirs of virus in infected wild hosts, either showing symptoms or acting as carriers, and in cultivated varieties which are symptomless carriers is an important factor in the spread of many diseases.

Wild hosts which are carriers of virus are of importance in at least three serious plant diseases in North America.

The Pierce disease of grapes, which is causing so much concern in California at the moment, is carried by three groups of leaf-hoppers. The most important vector in the north coastal area (Napa Valley) is <u>Draeculacephala minerva</u>, Ball. This lives naturally in the vegetation of stream banks and it has been found that certain of the components of this vegetation are carriers of the virus and the incidence of the disease is highest in those areas directly adjoining the stream bed. The virus is also carried by grasses and it causes a severe disease, "Alfalfa Dwarf" in Lucerne. The leaf-hopper <u>Cicadella circellata</u> which feeds on grasses and lucerne carries the virus to adjacent vineyards and such vineyards are often completely decimated. In these cases it is impracticable to eradicate the alternative host and the method of control used at present is the passive one of avoiding these areas for planting. Experiments are in progress to test the possibility of spraying the areas inhabited by the leaf-hoppers with D.D.T.

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to control their spread.

In the state of New York the Eastern X disease of peaches became very important about 1934. It is still an important disease but a method of control has been developed which depends on the fact that the wild choke-cherry (Prunus virginiana) is infected with the disease and is a source of inoculum for the neighbouring peach orchards. It has been found that there is no spread of the disease from choke-cherry to peach when the former is at least 500 feet from the peach.

Methods have been worked out for the simple eradication of the choke-cherry by chemical methods using sodium chlorate ($\frac{3}{4}$ lb. to a gallon) or ammonium sulphamate at the same concentration. The quantity used is between one and two gallons per 100 sq. ft. (see Hildebrand, Berkely and Cation, 1942).

The third case of spread from wild to cultivated hosts is the Mottleleaf virus of cherry where the natural host is Prunus emarginata Walp., the Bitter Cherry of the north-western Pacific states. Thickets of the wild host, which is generally symptomless, occur in the foot-hill canyons. When cherries are grown in these areas the incidence of the disease is generally severe.

In certain cultivated plants varieties exist which are tolerant carriers of a virus which affects very severely other varieties of the same species. Thus in strawberries the variety Huxley's Giant is a symptomless carrier of the yellow-edge and crinkle complex of viruses (Harris and King, 1942) and healthy stocks of Royal Sovereign strawberries can become infected when grown next to apparently healthy stocks of Huxley. Royal Sovereign reacts very severely when infected with the yellow-edge-crinkle complex (Harris & Prentice, 1946).

The general conclusion can be drawn that it is necessary to have detailed knowledge of the host range and symptomatology of any virus before attempting to control it.

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(c) <u>Plant quarantine and the inspection of nursery stock.</u>

In consequence of the severe epiphytotics caused by imported fungi plant quarantine (legislation, inspection and embargo) has been extensively developed in the U. S. A. It has had moderate success against foreign fungi and insect pests. Inter-state quarantine regulations are very variable, in some states, such as California, they are very stringent and in others free passage of all plants is allowed. The administration of an embargo against fungi, bacteria and insects is a comparatively easy matter when compared with the difficulties of enforcing the exclusion of viruses, where the symptoms may be fleeting or completely non-evident. Theoretically inspection for viruses is made whenever any plants are imported and some attempt is being made to inspect nursery stock moving between the states of the Pacific north-west. What the effect of these measures is it is difficult to say. Indeed, when one considers the multiplicity of guises which the symptoms of virus diseases can assume, it seems the only safe quarantine regulation would be complete embargo against all living plants.

When we come to consider the inspection of nursery stock before distribution to the trade we are on surer ground. It is gradually coming to be recognised in the U. S. A. that the use of infected budwood by nursery men is one of the major sources of viruses in orchards to-day. In California the dissemination of the Psorosis virus of citrus fruits can be blamed entirely on the use and distribution of unhealthy budwood from one of the original Navel-orange trees (Professor Fawcett in conversation). The leaf symptoms of this disease have only recently been recognised and their connection with the bark lesions which give the name has only recently been proved. With the understanding of the nature of the disease control measures have taken the form of a voluntary inspection scheme. Any tree which a nurseryman wishes to have certified as free

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from disease and suitable as a source of budwood is inspected for two years, at various stages of growth, and if it shows no signs of the disease is registered as disease free. The trees which are budded from it are inspected and samples examined to see that no disease has been missed.

The recent technique invented by Wallace (1947) for hastening the onset of foliage symptoms may in future be used as a method of indexing the budwood parent trees and may supplant the present laborious and lengthy method. In Wallace's technique pieces of scraped leaf are implanted under the bark of healthy orange seedlings and leaf symptoms show up in from 15 days to 28 days.

Dissemination of disease by means of budwood is relatively common among the slow-moving viruses and those in which the symptoms are obscure. The Stony-pit disease of pear (Kienholz, 1939), Peach wart disease (Blodgett, 1943) and Apricot ring-pox (Bodine & Kreutzer, 1942, Reeves, 1943) are all transmitted solely (as far as known) in this way. The cherry disease called Mottle leaf (Reeves, 1941) is carried without symptoms by some cherry varieties. Often these varieties are used as pollenators of the commercial Bing and Royal Ann varieties and are top worked on the orchard trees for this purpose. The cherries carrying the pollenator scions are very frequently affected by the Mottle leaf disease. The writer has seen whole orchards infected by Mottle leaf and the spread could be attributed entirely to the top-working of pollenators. Mr. E.L. Reeves who has had extensive experience of this condition believes that top-working of pollenators on commercial cherries should be condemned out of hand for the danger it holds of transmitting virus diseases.

A group of diseases which are not viruses but which often simulate virus symptoms are spread in this way. These diseases are believed to have their origin as bud sports. They are difficult to detect except after much experience and

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the source tree for budwood in a nursery may be infected and used year after year without the nurseryman being aware that it is diseased. The conditions known as Crinkle and Deep Suture of Sweet cherry where the leaf looks rougher and less regular than normal, where fruiting is severely depressed and the fruit is rough and bumpy and often "deep-sutured" are of this nature. These conditions are not easily diagnosed by the nurseryman and often whole nursery lots are budded from an affected tree and the buyer may find out too late that all his trees are unproductive and of undesirable types. Still worse the poor trees may pass unnoticed and the grower (who is unable to take an objective view of his own farm) carries the burden of an unproductive orchard and wonders at his ill-luck when he finds himself a bankrupt.

It is of some interest to record that when working at East Malling after a visit to the U.S. the writer kept a watch for some of these obscure conditions. It is easy to imagine one sees them but in the case of Stony-pit of pear the symptoms seen by the writer were confirmed by Dr. Prentice as being caused by a transmissible virus. Dr. Prentice had observed the condition in previous years and had performed inoculations which fully confirmed the virus nature of the disease. The symptoms of Stony-pit resemble those of the obscure British disease known as "Dimple".

THE SEARCH FOR INSECT VECTORS OF THE VIRUS DISEASES OF FRUIT TREES

Most of the fruit-tree viruses spread naturally in the field and by analogy with the viruses of herbaceous plants it is believed that insect vectors are the responsible agents. But in only one case has it been definitely shown that an insect is the vector of an American fruit tree virus. In 1933 Kunkel showed that the leaf-hopper, Macropsis trimaculata carried the virus of Peach yellows. Since then despite repeated efforts

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no relationship has been demonstrated between any of the American fruit tree viruses and an insect. This prompts the question as to whether there is some inherent difficulty in demonstrating such a relationship or whether there is no connection between these viruses and insect vectors and their spread is by some mysterious and hitherto unknown means. Work in the U. S. A. has been concentrated on the Phony Peach disease, Peach Mosaic and Phloem necrosis of Elm and although in the first two cases work has been in progress for about 15 years no insect has been shown to be a vector. The workers on Phony peach and Phloem necrosis believe that they have now got indications of the vector responsible but it will be some time before they can be sure.

Certain criticisms of the methods employed in the search for insect vectors in the U. S. can be made while at the same time realising the enormous difficulties of the task. Firstly the problem is not treated with the amount of respect due to it. The authorities do not seem to be aware of the over-riding importance of finding the responsible vectors. The search for and study of vectors would seem to the writer the first step in the study of a virus disease. The relative apportioning of workers in this and other branches of the study of fruit-tree viruses seems altogether wrong. Each disease has one entomologist, or perhaps two, working exclusively on the insect problem. It might be better if all the entomologists who at the moment are spread over many vector problems were concentrated on one, when a reasonably quick solution might be hoped for. The search for an insect vector demands considerable routine work and too often the entomologist finds his time taken up with tying bags, catching insects, potting plants and generally doing all but direct the search for the insect in the right direction. It seems very necessary to concentrate a large team of entomologists with adequate

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technical assistance on such a job.

At the moment in America all the inoculations are on seedling trees of a year or more or on budded trees. Wherever it is possible the use of very young seedlings seems to offer much greater facilities for a quick turn over, a saving in space, speeding up in symptom expression and the carrying on of work at all seasons of the year. At the moment when year-old trees are used there is an interval of at least a year before symptoms show up. There are of course certain difficulties in the way of using seedling trees, in the case of elms, for example, the seeds (when fertile) only germinate for a short spell after maturing and again in the following spring.

In Pierce's disease of grapes we have a disease where the search for the insect vector has been successful. So far three principal vectors have been discovered, Draculocephala minerva, Ball, Carneocephala fulgida, Nott., and Cicadella circellata, (Baker) and, since the last publication on the subject several other vectors which seem to be less important in general have been discovered (Hewitt in conversation). In the study of the biology of the vectors appears to lie the key to the control of the disease. It has been found that the Cicadella inhabits the vegetation of stream banks and canyons and like locusts it will go on migratory flights. The local movements of the leaf-hoppers and their migrations coincide with the main spread of the virus and it is by an attack on the insects in their breeding places that it is hoped eventually to actively control the disease. Dr. Hewitt told the writer that it is proposed to spray the river beds with D.D.T. from helicopters, as an experimental measure, in the hope that it may prove a practical method of control.

When an insect is suspected of being vector of a virus and when no clues are known to its identity generalised cover sparying is often adopted in attempt to save a particularly

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valuable tree or group of trees. It is a wholly uneconomic measure but it is being used in an attempt to save some of the elm trees in the mid-western states from the ravages of Phloem necrosis disease. The principle is to keep the trees sprayed with a D.D.T. insecticide in the hope that any vectors will be killed before infecting the tree. To spray a tree 100 feet high with a oil-water emulsion containing D.D.T. is very expensive business even when the types of power sprayers used are capable of throwing an effective dose to that height. A type of mist-blower is being developed which it is hoped will throw an atomised suspension of D.D.T. in kerosene to this distance and will cut the costs of laying on the large supplies of water necessary in the present method. Mr. Parker the entomologist at Columbus was very enthusiastic about this machine ; the writer did not see one so was unable to judge its performance. Cover spraying will probably become a useful means of protection when the period of activity of the insect vector is more exactly known and a quick acting insecticide can be used. Conversely cover spraying at specific times can be used as an experimental procedure for finding out the period of activity of the vector and thus narrowing the search to those insects known to be actively feeding at this time.

THE SEARCH FOR RESISTANCE

Whenever a new and destructive plant virus is recognised there is an immediate search for a variety of the crop plant attacked which will show resistance to the disease. It is of considerable interest and importance to discover how far resistance has been found useful in combating the spread of the fruit-tree viruses of the U.S.A.

We are up against the difficulty at the outset of the varying conception of resistance. In its original sense the word means that resistant plants do not become infected by the virus. There are very few cases of such total resistance,

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probably the best case is the U. S. D. A. seedling potato no. 41956 (Schultz et al., 1934). Mostly when resistance is talked of a tolerant reaction to infection with reduced multiplication of the virus is implied but it is often difficult in the literature to discover just what a writer means by "resistance". In conversation it appeared that most of the American workers mean tolerance when speaking of resistance.

There seems little doubt that the development of varieties of sugarbeet "resistant" to the Curly Top virus (i.e. beets showing no symptoms when attacked by the disease and having a reduced virus concentration and thus a reduced inoculum potential) has enabled the sugarbeet industry to survive in the foothill areas of the Pacific west coast. In peaches, a similar situation occurs with regard to Peach mosaic although no practical use has been made of it. Certain of the Clingstone varieties (e.g. Orange Cling, Hutchins, Bodine & Thornberry, 1937) are practically symptomless carriers of Peach mosaic. The reason that no use has been made of this tolerance is that an eradication campaign was begun to save valuable varieties such as J.H. Hale which show severe symptoms and it would have been administrative suicide to encourage at the same time the growth of symptomless carriers.

No resistance or tolerance to Phoney peach disease nor any resistance to Eastern or Western X. disease has been observed in cultivated varieties but in Peach Yellows although all cultivated forms are visibly affected, certain wild Prunus sp. are symptomless carriers.

The question of the advisability of using symptomless carriers or conversely of inoculating susceptible varieties with a mild virus strain and thus "immunising" them (Price, 1932) divides American workers. In many areas the use of tolerant varieties has been successful, notably so against sugar beet Curly Top virus. In other areas the use of a sort of natural

immunisation ...../

immunisation by eradicating severe strains of the virus and leaving the milder strains has been brought about through force of circumstances ; in Colorado and Texas where the eradication campaign broke down the growers themselves have removed the severe strains of the Peach mosaic and an area of universal infection with mild virus strains is being produced unintentionally.

The great danger of encouraging the use of tolerant varieties or inoculation with mild strains of the virus is that the large number of virus particles present in the area increases the chance of mutation of the virus and the production of a strain with really devastating effects. The question is one which lends itself to biological philosophising and the probability is that by eradication of severe strains and the encouragement of symptomless carriers we are following a normal evolutionary sequence with no more danger than ever occurs when growing a large mass of plants permanently in one place. But when opinions were collected from American workers no unanimity could be found. For example Clayton and McKinney believe that the Ambelino type of tolerance-resistance is the only worthwhile type of resistance to Tobacco Mosaic virus to develop in tobacco while with equal vigour Valleau puts forward the view that the hyper-sensitive type of resistance obtained from Nicotiana glutinosa is the only right one. It seems that we have not had sufficient experience of different types of immunity to plant viruses to formulate any principles for their use in plant protection.

An interesting and special case of immunity was seen in Washington where the Red Raspberry Mosaic is combatted by the use of strains of raspberries which for physical reasons (probably degree of hairiness) are distasteful to the vectors of the virus. The vector is Amphorophora rubi and it has been found that it will not thrive on certain raspberry varieties all of which have Lloyd George variety as one parent (Huber & Schwartze, 1938). The curious thing is that the aphid thrives

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quite happily on Lloyd George and its progeny in Britain.

THE USE OF CHEMOTHERAPY AGAINST PLANT VIRUS DISEASES

In view of the extreme seriousness of the plant virus diseases and the frequent failure of the well-tried methods of control it seemed to the writer that any reports of new methods of control should be carefully followed up. With this end in view a special visit was paid to Dr. Zentmeyer at the Univeristy of California citrus Experiment Station and to Mr. Stoddard and Drs. Dimond and Horsfall at the Connecticut Agricultural Experiment Station. The earlier published work in the subject was in abstracts in Phytopathology and was difficult to evaluate. After his visit the writer was convinced that very close attention should be given to this work. The results so far obtained are backed by only meagre experimental studies but there seems little reason to doubt that further work may substantiate the present findings. The most striking results have so far been obtained in the control of the Dutch Elm disease a fungus disease (hadromycosis) caused by Ophiostoma ulmi. A number of compounds related to the quinones (quinone, pyrogallol, p-nitrophenol, 8-hydroxyquinoline sulphate etc. see Horsfall & Zentmeyer 1943) have reduced the severity of symptoms and in some cases seemed to have effected a permanent cure. It seems that the effect of these substances may be to antidote the toxin produced by the fungus which is responsible for the wilting and death of the tree. There are difficulties in the way of introducing these chemicals into the tree and when it is found possible to introduce them by means of soil applications this seems the most suitable method. Dr. Horsfall told the writer that he believed that soil applications of oxyquinoline sulphate would probably prove effective against the disease. Experiments on standard elms are in progress at the moment but owing to the nature of the trees and the necessity of

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using pairs of trees, treated and untreated and observing them in an infected area for several years, it will be some time before the results are fit for scrutiny. So far very definite evidence of recovery has been obtained in the year when symptoms were observed but it cannot be definitely stated that this recovery persists in the next and succeeding years. It is in the protective action of this chemical that the Connecticut workers put their faith and that cannot be decided until some time has elapsed.

Stoddard working in the Connecticut laboratory has attempted to cure the Eastern X disease of Peach with various chemical treatments. His earlier work made use of the method of soaking the diseased buds in chemical solutions and then placing them in healthy trees and observing the amount of disease transmission. With this method 50% of his diseased buds were cured but the scope of the experiments were not such that the results can be accepted as statistically valid although there is no reason for doubting that with repetition similar results would be obtained. The method he now uses is to inoculate healthy seedlings with diseased buds and then to apply his therapeutic substances as injections or by the soil. The most effective chemical he has used so far has been iso-quinolinium bromide which applied by the soil has given a cure of 80-90%. It is difficult to judge the value of this work without seeing the statistical layout of the experiments and that could not be easily ascertained in conversation.

Promising as the results may seem the whole approach is very unsatisfactory in its blind empiriscism. In the disease used as experimental material there is no precision in the methods of infection, infection is by budding and the introduced dose or mass of the virus cannot be easily controlled. Moreover the method is slow with only one experiment being possible each year and the method of introducing the therapeutic

agent .../

agent, whether by the soil or by injection or by soaking the buds must be open to great variation and no account can be taken of the dose required. Without some information as to the behaviour of these supposed therapeutic agents in the plant it is difficult to have any other method of testing new chemicals other than by trial and error and this is very wasteful of time and material.

The ideal approach would be the purely fundamental one of the physiology of virus multiplication within the plant. There is no doubt that this will have to be done but for the practising plant pathologist faced with a serious problem to which an immediate solution must be found some compromise is necessary. The writer suggests that quickness with certainty can be obtained by cutting down the experimental variation to a minimum, standardising the methods of infection (preferably using insect vectors and a constant source of virus), using materials in active growth (in large numbers and growing under controlled conditions) and by using standard doses of the therapeutic agent. If, for example, it was desired to search for a drug which would cure the Swollen shoot disease of Cacao the writer suggests that the following procedure might be followed. To begin with it would be necessary to have a detailed knowledge of the insect vector so that standard doses of the virus might be introduced into the plant. This could be followed by growing large numbers of Cacao seedlings in standard nutrient solutions with added standard doses of the therapeutic agents being tested. It would be more satisfactory still if it were found possible to grow cambial tissue cultures infected with the virus and to add the therapeutic agents to the nutrient solutions. If any graded measurements of the effects of the different chemicals is to be made it would be necessary to devise some means of measuring the quantity of virus present and to do this it

would ...../

would be necessary to develop some quantitative test for the virus such as a precipitating test, if an anti-serum can be produced against the virus.

Chemotherapy for plant virus diseases may seem a long way from realisation and indeed it may never be realised. But with the very poor methods of control available against fruit tree viruses at the moment it seems very important to probe thoroughly such a promising line.

SOME COMMENTS ON METHODS OF INOCULATION

In the absence of a bacterial or fungal pathogen the first step in the demonstration that a pathological condition is associated with the presence of a virus is the graft transmission of the condition from diseased to healthy trees. Grafting is possible only at a limited season and is a laborious business. Bud transmission with its longer season and ease of performance has long been used where possible but in many cases it gives a low percentage of takes or may even fail to demonstrate the transmissibility of the virus. In such cases chip budding in which a piece of wood containing a bud is fitted into a suitable bed in a branch is used (see fig. 1).

Fig 1.

Or else spur budding in which a whole spur is used in place of the normal bud is used (see fig. 2).

Fig 2.

In elm trees it has been found difficult to bud or graft in the normal way and a patch graft has been found successful. An oval patch of bark and cambium is fitted to a tree where a patch of the same size has been removed. Union takes place but it is rarely permanent, the connection is however maintained long enough to allow of the passage of the virus.

Wallace's method (1947) of placing a piece of scraped leaf under the bark of seedling orange trees has

proved ..../

proved a successful means of hastening the appearance of foliage symptoms in the study of the Psorosis disease of oranges.

Where budding and grafting fail it has been found possible to achieve transmission by means of Dodder (Cuscuta sp.) a parasitic flowering plant which forms vascular connections with its host. If it is trained on two hosts, one of which is infected with a virus then in a certain proportion of cases transmission of the virus to the new host occurs.

COMPLICATING FACTORS IN THE STUDY OF VIRUSES

This visit to the U. S. A. provided an object lesson in the complications which can ensue when latent viruses are present in the supposed healthy plants used for virus testing or in the Dodder used in transmission studies. In peaches a virus called Ringspot is very commonly present and is seed transmissible in a number of cases. In any event infection of the young plants quickly takes place. When infected plants are used in transmission experiments or when the plants being tested are infected with ringspot as well as with a recognisable virus then immense confusion may result in the attempts to systematise the virus nomenclature. The workers in the Californian peach area seem to be aware of the necessity for caution in describing as new, pathological conditions which are due to the presence of the Ringspot virus and another virus which would give different symptoms if it occurred alone. The workers in the east do not seem to be aware of this necessity for caution and they are in some considerable confusion about the results of their inoculations and experiments.

The complication in Dodder has been demonstrated by Bennett (1944) who has found a latent virus present in his Dodder plants and has shown that it can give rise to false conclusions when ignored.

In ..../

In connection with inoculation procedure the system used at St. Catherine's in Canada, where suspected virus material is budded on to a host series laid out in comparable rows seems a good one. Mostly no straightforward comparison is made, data on symptoms is collected from trees growing all over the orchard and the host range tried is a matter of the trees available when the inoculations are done.

SOME INTERESTING THEORETICAL DISCOVERIES

It is impossible to list all the theoretical points which became clear to the writer during the course of his tour but four of the recent discoveries appealed to him as of major importance.

1. The demonstration by Dr. L.M. Black of the transmission of the virus of Clover Club disease through the eggs of an Agallian leaf hopper. This confirms Fukushi's (1934) earlier work which has long been a matter of dispute. Black's work has not been published at the time of writing.

2. The demonstration by Giddings (1945) of the "mass action effect" in the infection of sugar beet plants with curly top virus.

3. The finding that the strains of peach mosaic virus from different areas do not protect against one another while those from the same area do (Dr. L.C. Cochrane in conversation).

4. The discovery that the psorosis virus of citrus shows primary symptoms for ten to twenty years and then suddenly gives secondary symptoms of bark scaling. That seedlings inoculated from trees with primary (leaf) symptoms show primary symptoms first and then (by inference) the secondary symptoms after the extended time interval but that seedlings inoculated from the secondary lesions show immediate secondary symptoms followed by death. One wonders if the virus in the lesions has mutated and whether the virus is induced to mutate by environmental circumstances or whether it is a case of a

virus ...../

virus showing a time controlled mutation.

The value of the stimulus of seeing the inception and growth of such theoretical work to a young plant pathologist cannot be over estimated.

GENERAL IMPRESSION DERIVED FROM THE TOUR

The extreme geographical delimitation of the virus diseases of fruit trees in the U. S. A. is borne upon one by amount of travelling required in order to see them. The diseases of the east coast are in general different from those of the west and, very often, each fruit growing valley has its own special brand of virus. There is great need, as the Americans themselves realise, for some central co-ordinating station which would examine the viruses as they are discovered, and preferably before they are reported, and decide whether they are related to existing viruses or not. At the moment, for example, nobody knows if Eastern X disease of peaches, Western X diseases of peaches and the Buckskin disease of cherries are the same or not. None of the areas in which any one of these diseases occurs is willing to import the others for comparative tests and it seems that the station will have to be well isolated and under heavy quarantine control. Apparently a small station on these lines has been established in Texas but so far its scope and powers are not great enough. There are many new viruses described which are in all probability old ones under a new name. The dangers of confusion are lessened when the worker has an opportunity to travel and compare notes with others. Since virus diseases, unlike fungus diseases, cannot be studied by the interchange of dried specimens the necessity for travel is even greater and travel and visits to other virus workers should certainly be required of all pathologists who are working with virus diseases.

The ..../

The continuing and increasing severity of the virus diseases of standing fruit trees and the small success in controlling them achieved by individual workers suggests that when a new disease appears and shows signs of becoming important a concentrated attack should be made on it by a number of workers. Experience in America has shown that this is the only safe method of attack. Practical research designed for the immediate solution of a problem with the minimum of systematic and fundamental work has failed to control these diseases in a spectacular and disturbing fashion. Only a thorough and fundamental approach (with at the same time a realisation of practical needs) can hope to achieve success. No longer is it possible to treat a fruit tree virus as a mere curiosity which, when its graft transmissibility has been demonstrated by a pathologist in his spare time, can be easily controlled or relagated to the ranks of the inocuous uncontrollables.

The great need in America is for good virologists acquainted with the whole complexity of the subject and prepared to devote themselves to years of patient and systematic work, good pathologists are needed too with a sound conception of the economic problems set by virus diseases but these are more easily found in the U. S. A. where pathology has long been on a dollars and cents basis.

The writer left America with a great appreciation of the pathological extension work in that country besides which the advice available in Britain seems very inadequate and completely uninspired, with gratitude for the unfailing hospitality of American pathologists, and with real pride in British academic research in mycology and plant viruses. Perhaps the most important contribution which a trip to the U. S. A. can make to the education of a plant pathologist is to let him feel that plant pathological problems are of

overwhelming ...../

overwhelming importance in such a fruit industry as that of the U. S. A. for in this country the young would-be-pathologist has often to ask himself what his function is when an increase in any of our arable crops (under conditions of pre-war economics) was a hindrance rather than a help to the farmer and required the setting up of complex systems of quantity regulation such as the potato marketing board.

THE SWOLLEN SHOOT DISEASE OF CACAO IN WEST AFRICA

The account which follows describes the history of Swollen shoot disease in West Africa, the research work on it and the control measures against it. In following the logical development of this work the writer does not keep to the order of treatment in the generalised account and it is hoped that the correspondence with the generalisations of that account as well as the departures from these will be obvious to the reader. In the last section of this essay an attempt is made to sum up the comparison of this virus of cacao with its congeners in the U. S. A. The work on the details of the virus vector relationships is the author's own as is that on the alternative hosts of viruses C and M. The other work discussed is that of Posnette and Todd.

GENERAL BACKGROUND

The introduction of Theobroma cacao to the Gold Coast took place about 90 years ago (Paine, 1945) but the first record of its planting and subsequent multiplication is of 1879 when the almost legendary Tetteh Quarshie is believed to have brought the first pods from Fernando Po. Further introductions were made by Governor Griffiths at Aburi ; he introduced a yellow podded variety like the present day Amelonado variety, from San Thome in 1891. From these small beginnings the cacao

was ...../

was multiplied and fitted into their system of subsistence farming by the peasants and has now grown to be an export crop of the first magnitude on which the wealth and prosperity of the individual farmers and of the Colony are completely dependent. In 1936 cocoa represented 98 per cent by value of all agricultural exports and 65 per cent of total exports. In Nigeria the development of cocoa production has had a similar history. The first introductions are said to have been from San Thomé in 1874 (Howes, 1947). The speed of development in Nigeria has however been slower, whereas in the Gold Coast the production rose from 730 tons in 1899 to 31,000 tons in 1934, in Nigeria the yield rose from 158 tons in 1900 to 9,000 tons in 1945 (data supplied by Dr. D.W. Goodall, W.A.C.R.I.).

In the world cocoa market West African Cacao has taken an ever bigger place. In 1936-37 the exports from the Gold Coast and Nigeria were 56 per cent of the world total. In its early days the West African cocoa was of poor quality and was generally used as a filler by the manufacturers while the high grade Criollo cocoas from the West Indies were used for flavour. Nowadays owing to improvements in the home product and technical advances in manufacture the need for fine grade cocoas is not so great. (Imperial Economic Committee, 1932).

The cacao in the Gold Coast and Nigeria is entirely peasant owned and it is grown on small farms varying from a fraction of an acre to about five acres in extent. In the Gold Coast the cacao is almost universally grown under the shade of secondary forest, the cacao occupying the small tree and shrub layer described by Foggie, 1947. This forest may be of any age varying from early secondary forest to secondary forest of such age as to be approaching the natural climax forest. The degree of shading varies greatly too. In Nigeria the cacao is not grown much under shade and in some of the marginal lands the life of a plantation is a short one. In the Gold Coast the cacao trees are grown close together and their tops

interlace ...../

interlace in a continuous canopy. In some parts of Nigeria the trees grow separately in an orchard formation.

Throughout the area the farms were held in the beginning on an occupational basis, the lands as a whole belonging to the tribe and certain lands, the Stool lands, being directly under the control of the Stool (i.e. the chief and his elders). The permanent and profitable nature of cacao has brought changes in the system (Nowell, 1938) many lands have become permanently appropriated as family lands and many of these and the stool lands have been sold to strangers. Sub-division of these lands in inheritance may take place and in extreme cases a man may own many lands in different areas ; he may never visit the land to farm it himself, employing labourers or relations to do this for him for monetory recompense or for a share of the crop. These cocoa-farms are often heavily mortgaged and the whole system of cocoa buying and brokerage encourages indebtedness on the part of the farmer. This was particularly the case before the advent of the Cocoa Marketing Board (1947) since cocoa is sold on a narrow market in New York and London which is open to marked fluctuation (Nowell, 1938).

THE ADVENT OF SWOLLEN SHOOT AND BEGINNING OF CUTTING OUT

This then was the country to which swollen shoot disease came, a country of rapidly expanding cocoa production, of fluctuating economic life, of a rising standard of living and of great agricultural ignorance. Deterioration of the cacao of the Eastern Province of the Gold Coast has been known for some time. The earliest reports (Paine, 1945) are those of the people of Nankese who state that the cacao was observed to die shortly after the 1918 influenza epidemic; Paine, reporting this, deduces that if the disease was Swollen shoot it had been present almost as long as the cacao. Paine gives an account of several such anecdotal reports throughout the

twenties .../

twenties. In 1930 there was a definite report by Hay of the dying of cocoa to the East of the Nankese - Amanhia road. At this time the dying became so obvious that an enquiry into its cause was begun. H. A. Dade visited the Gold Coast to advise on the problem in 1937. That it was a difficult problem can be appreciated from the fact that both he (1937) and Voelcker and West (1940) (who were cacao experts and well acquainted with cacao in the field) were convinced that the cause was a compound of soil factors, drought and Capsid damage. The first recognition of the "Swollen shoot" condition was by Stevens (1936). The transmission and virus nature of the disease was first demonstrated by Posnette (1940) and thereafter there was a slow recognition by the agricultural administration of the nature and implications of the disease. Great credit must go to Posnette for the vision with which he treated the problem and his early experimental demonstration of the nature of the spread of the disease and of the value of the removal of infected trees as a means of reducing the spread of infection (Posnette, 1941). He showed that the spread was of two kinds a simple extension of the boundary of an outbreak and the occurrence of new outbreaks distant from the others and initially smaller. He also showed that the annual loss from Swollen shoot at the Cacao Research Station at Tafo could be reduced by two thirds by a policy of cutting out diseased trees and one ring of contacts. In 1937 the Gold Coast Department of Agriculture did a small amount of cutting out at Akwadum (near Koforidua) but when the extent of the disease was known the campaign was dropped. In 1941, on the basis of Posnette's work at Tafo cutting out was started at Kwaben and extensive cutting out took place between 1941 and 1943 when war-time difficulties caused the campaign to cease. A good deal of the cutting out was around Nkawkaw and to the West of the Atewa Range (it was hoped that the Atewa Range would act as a barrier to the main spread of Swollen shoot). The results of this

cutting .../

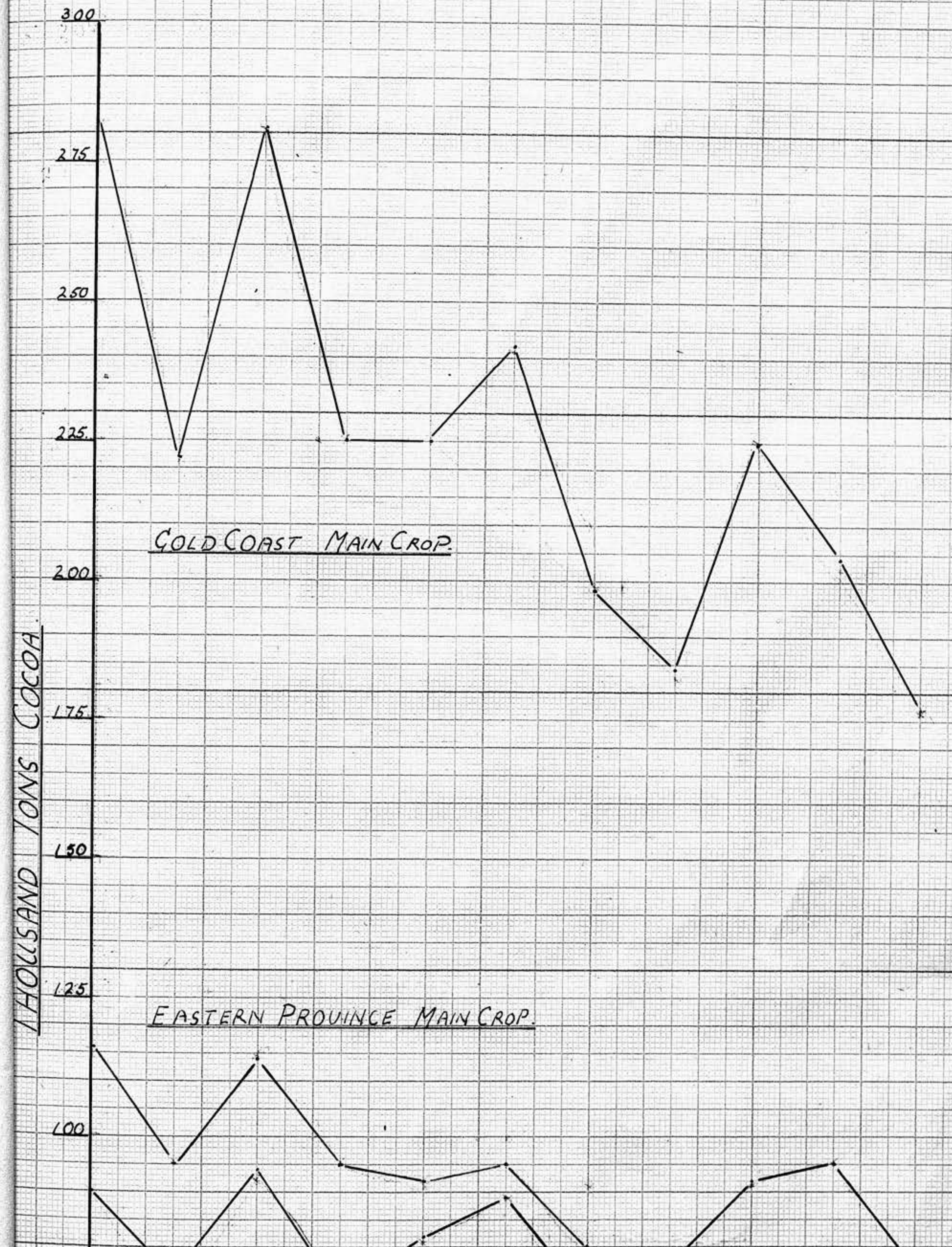
300
275
250
225.
200
175.
150
125
100
75
50
THOUSAND TONS COCOA
GOLD COAST MAIN CROP.
EASTERN PROVINCE MAIN CROP.
ASHANTI MAIN CROP.
19 36/37
37/38
38/39
39/40
40/41
41/42
42/43
43/44
44/45
45/46
46/47.
YEAR

FIG. 3.

cutting out campaign were carefully studied by the West African Cacao Research Institute in 1944 (just then set up in place of the Central Research Station and financed by funds from the war-time cocoa marketing system) and it was confirmed that the cutting out of infected trees could successfully control the spread of disease. The Gold Coast Government accepted the W.A.C.R.I.'s recommendation and legislation was enacted so that cutting out could be enforced (Gold Coast Government 1948). The campaign has been very slow in getting under way - mostly because of shortage of staff and in the meantime the disease is slowly decimating the country's cacao. If the radial spread alone is considered it can be seen that even although the spread is slow the radial linear rate of spread approximately doubles for each year and so it will become ever faster and faster (Posnette, 1944). That is why delay at the moment is of such a serious nature. At the same time as the linear spread doubles the areal spread increases as the square of the radius.

The seriousness of the situation can also be observed in the statistics of cocoa production in the Gold Coast. Swollen shoot, in its most serious form is confined to the Eastern Province and in Ashanti where a good deal of cocoa is comparatively young it is circumscribed. The figures for cocoa production in Ashanti and the Eastern Province show a marked falling off in yield in the Eastern Province as compared with Ashanti (Fig. 3. Data of Dept. Agriculture, Gold Coast). The loss for 1947 is estimated at 60,000 tons, a loss of £4,500,000 at present day prices. Many other factors might, of course, be associated with such a decline, namely soil deterioration and age of the trees, but since in the period between 1930 and 1947, 47,000,000 trees are estimated to have become infected with the disease, and, since the life of a tree after infection is about 18 months (Gold Coast Government, 1948), a large proportion of these trees are now dead, the correlation of yield figures with Swollen shoot does not seem unreasonable.

THE .../

THE PART PLAYED BY DROUGHT AND SOIL DETERIORATION

From the earliest days drought and soils have been implicated in the deterioration of the Gold Coast cacao. Dade (1937) maintained that the deterioration in the cacao was due principally to progressive deforestation of the cocoa areas, this, he suggested, is leading to a change of climax dominant from forest to grass and that of course implies a consequent lessening of the rainfall. At the time when Dade was writing it was widely held that deforestation did in fact interfere with rainfall. The present point of view is that there are areas in the world where rainfall is determined by physiographic factors and trade winds and that in such areas when the forest is removed and the area left, forest climax re-asserts itself. In other areas of gentler precipitation where the trees may act as condensers and the forest litter regulate run-off from the catchment area, then deforestation may lead to the lessening of rainfall and effective rainfall (F. R., 1947). It would seem in the light of later experience where farms killed by Swollen shoot Disease are rapidly reverting to bush and young forest that it was not a deterioration in climate which was affecting the cacao. Moreover Voelcker and West (1940), were very careful to draw a distinction between "true drought die-back" of cacao in the drier areas of the Gold Coast and die-back in the wetter areas which they at the time attributed to Capsid bug attack.

Associated with the idea of climatic deterioration was the idea of soil failure. It is well known that tropical soils owe much of their fertility to the humus layer derived from the forest cover and when this disappears some soils become barren. Charter (1947) has analysed the soils of the Gold Coast into "Good and bad cacao soils" and he has shown that some of the sandy soils, shallow soils and heavy clay soils at the base of a catena will often allow the cacao to die out in dry weather and that on such soils once the fertility

accumulated .../

accumulated by the forest is exhausted it is useless to try to re-establish cacao. Many of the red clay - clay loams at the top of a catenal sequence and derived from granites and dark igneous rocks are capable in his opinion of maintaining cacao indefinitely without deterioration.

THE ETIOLOGY, SYMPTOMS AND PROGNOSIS OF SWOLLEN SHOOT DISEASE

The virus nature of Swollen shoot disease was demonstrated in grafting experiments by Posnette (1940). The disease was observed at first in the Eastern Province and later was reported from wide spread areas throughout West Africa (Posnette personal communication). It soon became apparent that the virus from these areas differed from one another and Todd (unpublished) derived a method of distinguishing the different viruses by following their Symptomatology in the sequence of leaves and flushing which follow inoculation of healthy Amelonado seedlings. About 30 viruses (clearly differentiated) on symptomatology are present in the Gold Coast (Todd personal communication). The symptoms of these viruses resemble one another very closely and it is not yet clear how many of them can be considered as strains of the others (Crowdy and Posnette, 1947) or as separate viruses.

The virus which is of the greatest importance in the Gold Coast at the moment is the virus 1A, the New Juaben Virus. This is the virus which is widespread in the Eastern Province of the Gold Coast and which is threatening the Gold Coast Cocoa industry. This virus gives characteristic symptoms consisting of swellings of the branches and a leaf pattern, the detailed analysis of which is complex, but which in essence is a yellow vein clearing of the fourth order veins followed on later leaves by a general distribution of small areas of clearing in minute blocks which give to the leaf a "peppered appearance". In older leaves there may be a restriction of the symptoms to an area ~~ability~~ abutting on to the secondary and tetiary veins and this gives an appearance of a fern pattern. The pods are also

affected ...../

affected, being smaller and almost spherical in shape and they have a dark green mottle ~~after~~ often overlaid with a reddish colour and persisting as a green mottle in the ripe pod (Posnette, 1947a). The prognosis for any tree affected by this virus is certain death within a period of not more than two years. The leaves became progressively smaller, mature, senescence and fall off earlier. Finally the apical bud dies and die-back proceeds down the tree. A number of axillary buds are stimulated and die in their turn.

The writer has been particularly concerned with two of the milder strains of the virus and they do not show the same progression of symptoms as does the New Juaben Virus. In the virus M which was discovered at Mampong in 1945 by John Paine (9th Quarterly Report W. A. C. R. I.) the symptoms show up in the flush after inoculation and then the following flushes are symptomless, later a first flush may show symptoms and the symptomless flushes appear again. In virus E no swellings have been observed and the typical symptoms in the leaves are of a yellow mottle in between the secondary veins leaving a broad green band along the secondary veins and midrib (Posnette, 1947a). Both these strains are mild strains in that they do not kill the tree. We have no data on the effect of yield on the Mampong Virus but Crowdy & Posnette (1947) have shown a 50% reduction in yield with virus C in 3 years. The rate of spread of virus C is, they find, very much less than that of virus A.

THE VECTORS OF THE SWOLLEN SHOOT VIRUSES

The first record of transmission of the Swollen shoot virus (virus A) is that of Cotterell (1943), the conditions of this experiment were not however rigorous. Box (1945) reported definite transmissions of members of the Swollen shoot virus complex by Pseudococcus exitiabilis, Laing (syn. Ps. njalensis, Laing, Hall, 1945). This and the fact that the Psyllid,

Mesohomotoma .../

Mesohomotoma tessmanni, Aulm and the Aphid *Toxoptera coffeae*, Mietner are not vectors was confirmed by Posnette and Strickland (1948). These authors have also worked out the experimental technique for the transmission of the virus and Posnette (1947b) has perfected a method of feeding the mealybugs on the embryo cacao bean. The testa and one cotyledon are dissected away and the insects are placed on the remaining cotyledon, this with the plumule and radicle acts as the test plant.

THE VECTOR-VIRUS RELATIONSHIPS

Posnette and Strickland (1948, in the press) have already investigated the relationships between vectors and infection. Posnette's demonstration that dissected cacao beans are good test plants for cacao virus-vector work (1947a) has enabled more detailed investigations to be made ; now a considerable reduction in the variability of results has been achieved and the insect can be manipulated to give any desired degree of infection with the principal viruses and when anomalies occur a quantitative estimate of the probability of their being due to chance can be made.

The virus sources have been standardised and for most of the work infected seedlings of not more than 40 days old are used as source plants. *Pseudococcus njalensis* Laing, "crawlers" (1st and 2nd instar larvae) are used as the standard vectors. Large populations of these crawlers can be obtained by colonising young plants between 20 and 30 days old with grand females of ? *Ps. njalensis* from the field, colonies of young insects are fit for use about seven days after the original colonisation. Most of the work has been done with viruses C and M which do not occur in the field at Tafo and any contamination of insects from the field with virus A can be easily seen. where The work has been thought of practical importance it has been repeated with virus A.

THE .../

THE EFFECT OF INSECT NUMBER ON TRANSMISSION RATE

The effect of insect number has been investigated for its practical applications and for the theoretical interest of discovering if there is any "mass action" effect in mealybug transmission of the virus i.e. whether the effect of a large number of insects infecting a plant is greater than the sum of the effects of individual insects. The table given below shows for virus A and Ps. njalensis the totals of infections caused by varying numbers of insects in an experiment replicated six times. In the same table can be seen the expected numbers calculated from the probability of infection by one insect. The figures in both columns agree very closely and the "goodness of fit" has a probability of 0.9-0.95 in the table of X^2. There is thus no mass action effect.

Table 1

No. of insects	No. of infections out of 60 Observed	Calculated	X^2
1	6	6.18	0.0052
5	32	25.15	1.8657
10	42	39.77	0.1250
15	48	48.25	0.0013
20	54	53.18	0.0126
25	57	56.04	0.0164
30	57	57.70	0.0081

X^2 total = 2.0343.

The probability of successful infection by one insect is .103 and using 30 insects the expected probability of success is .9617.

THE ../

THE EFFECT OF AGE OF TEST PLANT AS INFECTION RATE

For practical reasons it is not always possible to use embryos as test plants. Discrepancies between the expected rate of infection and the actual rates when seedlings were used as test plants led to an experimental consideration of the effect of age of plant. Plants of ages from 0 to 6 weeks were colonised in a randomised fashion with 30 crawlers each, of Ps. njalensis carrying virus A. The treatments and the total number of infections out of 48 trials (six blocks of eight plants per treatment) are listed in table 2.

Table 2

Age	Appearance when inoculated	Total No. infections
0 weeks	Fresh beans laid on soil	36
2 weeks	Cotyledon emergent	39
3 weeks	Cotyledon and young plumule	40
4 weeks	Leaves expanding	25
5 weeks	Leaves maturing	20
6 weeks	Leaves mature	22

In the analysis of variance the results fall into two groups, plants up to three weeks of age show a significantly higher rate of infection than those of four to six weeks. The difference between totals required for significance is 9.529.

It has been found in routine experiments using mature plants and cuttings that about 50% infection is obtained using 30 crawlers per plant and this figure agrees with that for four to six weeks old plants in the experiment above. It is not possible to say yet whether the differences are real differences in the susceptibility of the tissue of young plants (mostly cotyledon) or whether the differences are related to mechanical difficulties of mealybug feeding in the older plants.

When .../

When suspected alternative hosts are being infected as beans on dissected embryos it sometimes happens that it is not easy to remove one cotyledon as is done in the cacao controls, or the removal of one cotyledon may seriously hinder the growth of the plant e.g. Cola chlamydantha K. Schum. The comparison of dissected and undissected beans makes a considerable difference in the infection rates. When whole beans of Theobroma bicolor Humb. et Bonp. are compared with whole beans of T. cacao there is no statistical difference between the infection rates but if whole beans of T. bicolor are compared with dissected beans of T. cacao, the T. cacao gives a significantly higher rate of infection (P = .05) than the T. bicolor.

Table 3

T. bicolor unsplit	T. cacao unsplit	T. bicolor unsplit	T. cacao split
5	4	5	8
1	2	1	3
2	2	7	7
8	2	2	8
5	4	4	9
21	14	19	35

This effect is a purely mechanical one, the insects can find feeding sites more readily on the split beans.

BIOLOGICAL RACES OF MEALYBUGS

It was at one time suspected that some of the discrepancies and failures in transmission might be due to the occurrence of non-transmitting biological races of Ps. njalensis. Accordingly nine colonies from single gravid females were established, from widely separate areas of the environs of Tafo and were tested for their ability to transmit virus M, in the first, second and third generations. All transmitted the virus

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at approximately the same rates. It seems from these observations and from the reproducibility of routine results obtained in the laboratory where many hundreds of sources of Ps. njalensis have been used in experiments and have given consistent transmission rates, that the occurrence of non-transmitting strains of Ps. njalensis (for virus M), if they occur, is not of such frequency as to vitiate the reliability of transmission studies. No such detailed studies of virus A and Ps. njalensis have been made but routine transmissions do not suggest the presence of biological races of different transmitting powers. Pseudococcus citri Risso is easier to breed from single insects, and nine separate collections from Tafo and one pooled collection from Kpeve have been tested thoroughly for their ability to transmit viruses A, M & C. All have transmitted viruses A and M and all but one, virus C. This strain I 41/78 has consistently failed to transmit virus C. In a series of replicated experiments control Ps. citri transmitted virus C. 17 out of 55 times with five insects per plant and Source I 41/78 transmitted virus C not at all. Specimens of the mealybug have been submitted to Mr. Strickland for identification and he informs me that it falls well within the normal range of variation of Ps. citri in West Africa.

HOW THE INSECT INFECTS THE PLANT

Most of the insects which carry plant viruses have relatively short stylets and the time taken to reach the feeding site is short, of the order of a few minutes. The time taken to infect the host is also short, although the amount of infection increases appreciably when the insects are left on the plant for periods of hours. Not much is known of the feeding habits of the Coccidae and the long slender stylets penetrate deeply into the plant. It was thus of interest to examine the feeding behaviour of these insects in some detail.

In order to determine the feeding sites serial sections of insects feeding on young cacao leaves were cut. The stylets and stylet tracks (which show up well when stained with Safranin) take an intracellular course through the cells of the cortex. In the stele the tracks often branch and if single take such a tortuous course as to make the definition of their endpoint extremely difficult. Many of these tracks pass through the phloem and appear to end in the xylem and others pass through the xylem to the phloem. Other tracks do not reach either tissue, but it is not possible to assess whether such a track is a mere trial penetration by the insect or whether it represents the stylet track of a successful penetration from which feeding resulted.

The feeding mechanism has been studied in more detail by allowing the insects to feed on blocks of 3% cleared agar a method suggested by the work of Dr. Walter Carter. Rings of solid agar were cut from poured Petri plates and removed to a glass slide, a number of adults or crawlers of Ps. njalensis were then placed in the centre of the ring of agar and a cover glass placed on top. The slide was placed in the dark for 30 minutes and then examined under the microscope. When an insect was settling to feed the following series of events took place. The rostrum, which lies about the centre of the ventral surface, makes tentative thrusts at the agar surface and finally becomes apressed against the agar surface. The tip of the stylets then enters the agar. Thereafter the rostrum retracts and advances with a rapid, pulsating motion and the stylets more into the plant at what appears under low power magnification to be a steady rate. Under a higher magnification the tip of the stylets can be seen to move with short discrete movements, each forward movement is preceded by the secretion of a droplet of saliva from near the tip of the stylets, these retract a little before moving through the

salivary .../

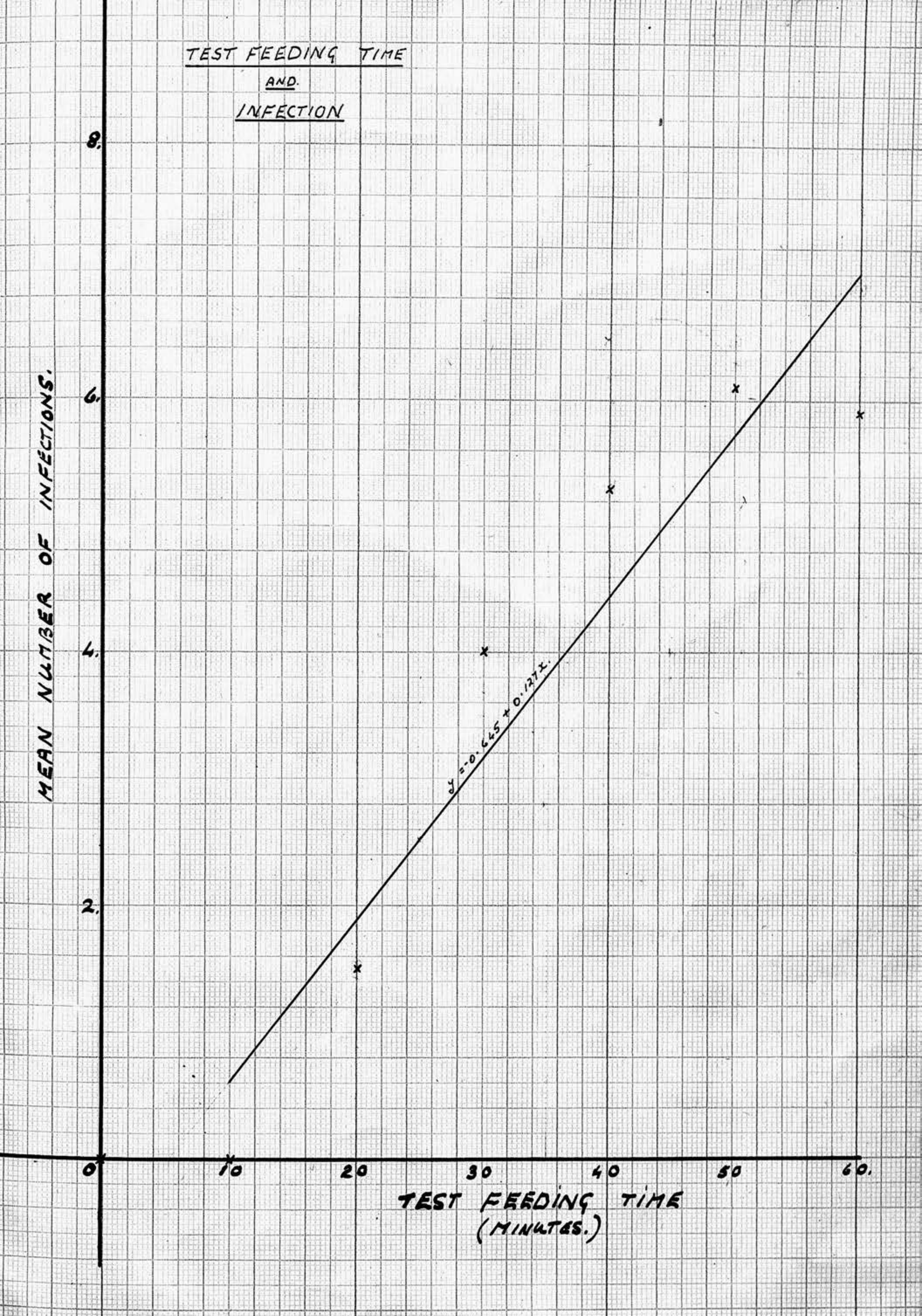
TEST FEEDING TIME
AND.
INFECTION
MEAN NUMBER OF INFECTIONS.
8.
6.
4.
2.
0
10
20
30
40
50
60.
y = -0.645 + 0.127x.
TEST FEEDING TIME
(MINUTES.)

FIG. 4.

salivary droplet and moulding a tube, the feeding tube thus comes to be composed of a series of droplets with a straight tube through the centre. Under low magnification the tube has a laddered appearance.

The stylets move inwards at a rate of about 0.5 μ per second, there is no difference between adults and crawlers in the rate of penetration but the differences in stylet length are such that the crawlers penetrate to their greatest extent in about 15 minutes while adults may take up to 30 minutes after settling. The stylets do not always continue to more V inwards but may stop or they may be partially withdrawn and branch off again at another angle. In sections of leaves and on agar many short terminal branches may arise from one main stylet track.

The feeding behaviour described above is reflected in the results of experiments on the effect of length of time of test feeding. When this was determined for virus M for periods of 1, 2, 4 & 12 hours in a series of six replicated experiments there was found to be no significant increase in numbers of infections after one hour. The increase in infection rate for periods within an hour are shown in the following table. ~ Fig 4.

Table 4

Test feeding time minutes	Mean No. infections out of ten
10	0
20	1.5
30	4.0
40	5.3
50	6.2
60	5.9

The data is best fitted by a linear regression line of formula $y = -0.645 + 0.127X$.

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THE LOSS OF VIRUS BY STARVED INSECTS

When removing vectors from source plants to test plants there is a choice between insects actually feeding and insects which have fed and are walking about. It is therefore important to know if there is any falling off in infective powers of insects after short periods of starvation. It is also important to know how long the crawlers of Ps. njalensis remain infective on prolonged starvation since Strickland has shown (1948) that the crawlers of mealybugs can be carried some distance by the wind. Many experiments on starvation of crawlers of Ps. njalensis up to 12 hours have shown no falling off in the infective ability of insects carrying the virus M and several longer experiments up to 74 hours (the crawlers will generally remain alive and active up to about 40 hours but under exceptionally favourable conditions they may remain active longer) have shown that infection does not persist after a period of 36 hours. One such experiment as shown in table 5.

Table 5.

Hours starved	Infection out of 10	Hours starved	Infection out of 10
0	2	20	8
2	6	22	2
4	4	24	0
6	4	26	3
8	5	28	4
10	6	30	1
12	2	32	1
14	2	34	1
16	2	36	0
18	3	38	0
		40	0

Similar results have been obtained with young adults in less extensive tests.

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HOW THE INSECT PICKS UP THE VIRUS -

(a) Starved insects

When crawlers of Ps. njalensis which have been previously starved for 12 hours are placed on the leaves of infested plants C. ? they do not immediately feed. The numbers of insects feeding increases more or less linearly until six hours and then becomes constant. The number of infections obtained from insects feeding on these leaves at first increases in a similar ~~number~~ manner but instead of becoming steady at six hours continues to rise until it reaches a maximum between eight and ten hours. A sharp fall takes place at 12 hours. The data on which this statement is based were obtained in a series of six replicated experiments in which starved Ps. njalensis crawlers were fed on young leaves of month old plants infected with the Mampong virus, for periods up to 12 hours at two hour intervals. The figures are given in table 6.

Table 6

Time on plant (Hours)	Mean no. insects settled out of 50		Mean no. of infections out of 10	
	Actual	Calculated	Actual	Calculated
X				
0	0	1.198	0	.19
2	18.5	14.858	2.16	1.05
4	18.3	21.424	2.66	2.73
6	23.1	23.321	3.86	4.58
8	23.3	22.962	5.66	5.94
10	23.3	22.763	6.85	5.97
12	24.6	25.146	3.50	4.13

From the analysis of variance of the observed data the difference between infection means required for significance is 2.522. The calculated values are obtained by solution of the best fitting cubic regression equation for the appropriate values of x.

(b) Unstarved insects

In a parallel series of experiments with unstarved crawlers of Ps. njalensis the number of insects feeding again

rose ...../

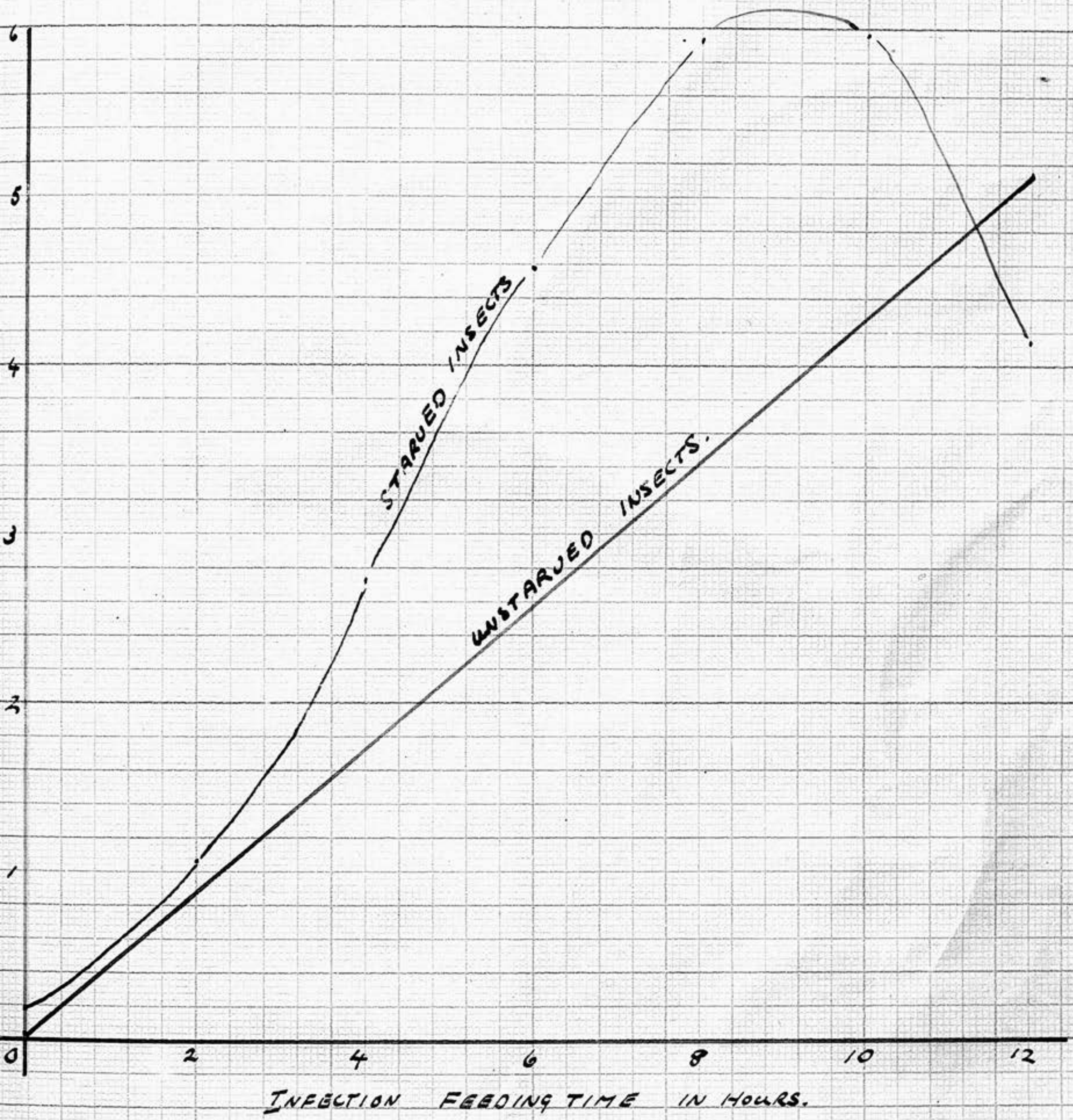

FIG. 5. REGRESSION DATA OF TABLES V & VII.

COMPARISON OF EFFECT OF TIME ON INFECTION FEEDING OF STARVED AND UNSTARVED CRAWLERS OF *Ps. NATALENSIS.*

rose approximately linearly between 0 and 6 hours but the gradient of the plotted line was less steep. A similar flattening out between 6 and 12 hours wea apparent but the numbers settled were consistently less than in the starved insects. The numbers of infections increased linearly from 0 to 12 hours but did not reach the maximum of the starved insects at 8 and 10 hours. ~~at 12 hours.~~ At 12 hours it did not show any sign of the sudden drop exhibited by the infection rate of the starved insects. The figures in table 7 are derived in the same way as those of table 6. See also fig 5.

Table 7

Time on plant (Hours)	Mean no. insects settled out of 50		Mean no. infection out of 10	
	Actual	Calculated	Actual	Calculated
X				
0	0	-0.312	0	.02
2	6.66	6.716	0.16	.87
4	10.66	11.942	1.83	1.72
6	16.33	15.366	3.50	2.57
8	17.50	16.988	3.33	3.42
10	16.33	16.803	4.83	4.27
12	14.83	14.826	4.33	5.12

THE SEARCH FOR ALTERNATIVE HOSTS

Cacao differs from the fruit trees of temperate and sub-tropical climates in the fact that in West Africa it is wholly propagated by seeds. There has thus been no opportunity for the virus to build up in vegetatively propagated stocks. For the same reason it seems unlikely that the virus could be introduced from outside West Africa unless it is seed-borne. Posnette (1947a) has shown that this is not the case and we have two alternatives for the origin of the virus. It may have arisen de novo but no other well authenticated case of such a virus origin is known and it seems most logical to look first among the wild relatives of cacao for alternative hosts. This work was initiated by Todd and Posnette in the Eastern Province in 1946. They began by attempting to correlate small outbreaks of the virus with the presence of forest trees but with no results. Attempts were also made to infect relatives of cacao by graft transmission but the difficulty of assessing the degree of "take" of the buds and the impermanence of such buds as did take made the results of doubtful value. The first positive and encouraging result was when Todd found a coppiced plant of Cola chlamydantha, K. Schum., in an outbreak near Wiawso in the Western Province, which showed yellow vein banding. Insect transmission from this plant to cacao produced virus symptoms in the cacao directly comparable with those in the cacao at Wiawso. Another such coppiced tree was found by Todd, Posnette and the writer in January, 1947. Thereafter Todd and Posnette have made extensive surveys in the Western Province and have found the group of Western Province viruses to be widespread in Cola chlamydantha. Todd has shown, moreover, that C. chlamydantha, remote from cacao, in a forest reserve, carries one of these viruses.

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The next encouraging step was when Posnette successfully transmitted virus A from cacao to Cola cordifolia, R. Br. The uncertainty of insect transmission however made negative results suspect. The writer's work on insect transmission reported above has allowed more certainty in the method. Where seed and insect supplies have allowed twenty or more seedlings or fleshy embryos of the plant under test have been colonised with 30 viruliferous crawlers of Ps. njalensis each, an equal number of cacao beans have been colonised as controls. Where insects feed well and a high rate of transmission is obtained in the cacao controls it is assumed that if no infection as judged by symptoms and back transmission to cacao, is obtained in the plant under test, it can be considered not to be an alternative host.

Using this method a number of the Sterculiaceae and Bombacaceae have been examined and the results are presented in the following table.

H o s t	Virus C	Virus M
Sterculia rhinopetala, K. Schum.	+ symptoms	+ symptoms
Sterculia tragacantha, Lindl.	-	+ no symptoms
Adansonia digitata, Linn.	+ symptoms	+ no symptoms
Cola cordifolia, R. Brown	+ no symptoms	?

Todd and Posnette have shown that virus A can infect

Cola cordifolia

Adansonia digitata

Ceiba pentandra, Gaertn.

Bombax buonopozense, P. Beauv.

Our knowledge of possible alternative hosts is all the time increasing but the study of these hosts in the field is proving extremely difficult. For example Sterculia tragacantha shows ..../

shows no symptoms and the virus has been difficult to recover from plants later than 55 days from the time of infection. When the writer visited the outbreak of the virus he found that a Sterculia tragacantha tree was associated with nearly every one of the delimited outbreaks. But tests of the trees were all negative. Todd has shown that Ceiba pentandra plants will yield the virus when tested with insects but only at a low rate. Other plants e.g. Adansonia give rates of transmission comparable with cacao seedlings. Where the rates of transmission are low e.g. in Ceiba one wonders what degree of testing will be necessary before it can be shown whether a 200 feet high Ceiba tree with a girth of 10 feet ~~comes~~ carries the virus or not. Work at the moment is concentrated on this problem and it will be some time before results are forthcoming.

What will be the importance of the hosts if they do carry the virus, in low concentration, in the field ? The chances of cacao plants being infected from them will be much less than from infected cacao plants but over the country where such trees are parts of the forest under which the cacao is grown, the chances of new centres of infection arising are high and once a virus of the virulence of virus A is established in cacao the disease will spread again. It is certain that for the implementation of the cutting out campaign and the maintainance of healthy cacao in the future by inspection, a very full knowledge of the importance of these alternative hosts is required. What administrative measures will be required, whether removal of alternative hosts or inspection of cacao in their vicinity will depend on the results of these investigations.

THE SEARCH FOR RESISTANCE

As soon as the extent of the Swollen shoot disease was realised a search was began for resistance. Trees which remained ~~alone~~ alive and apparently healthy in outbreaks were propagated at Tafo

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and these and certain introductions were tested extensively by graft inoculation at Tafo and Akwadum. It appears from this work that many of these trees are infected with an "attenuated" or mild form of the virus and are in this way "immune" to infection with more virulent forms of the virus. This type of immunity is of course non-sterile. Some of the plants notably the clone CU 85 do not carry a mild virus but show tolerance to the severe strains of the virus. It is not yet clear whether this tolerance can be compared to the tolerance-resistance of the Sugar beets where there is a reduction in the amount of virus present in an infected plant and fewer plants become infected with the same "dose" of virus. No differences have shown up in the graft inoculation work and the writer is at present testing the reactions of these clones to insect infection to find out if they show any differences in susceptibility.

It may be asked whether the possibility of using the mild strains as a protection against the virulent strains has been considered. It has, but more information is being sought on the effect of these mild viruses on yield and on the protection they afford in the field before any decisions are reached. It is obvious that it will not be a comfortable decision to recommend the dispersal of any virus no matter how mild throughout an area as large as the Gold Coast cacao belt.

POSSIBILITY OF THE USE OF CHEMOTHERAPY

The Swollen shoot disease has become a national issue in the Gold Coast and there is considerable real opposition to the cutting-out campaign from the farmers and from political groups who wish the support of the farmers. These people in the press and on their own farms have one great cry, "Why can't you give us a medicine for ~~own~~ our cacao ?" This very natural request sets a large task to the research worker. So far it has been judged best to concentrate on identifying and classifying

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the viruses, collecting data on their rate of spread, finding their vectors, giving precision to experimental transmission and studying alternative hosts and control by rogueing in the field. With a method of control evolved and depending now on administration it seems reasonable to examine the possibility of chemotherapy in case the cutting out policy should fail by faulty administration.

Two methods are proposed to be used, the method of sifting through chemicals which are already suspected of having chemotherapeutic effects against plant viruses and the more satisfacotry method of studying the drift of the principal metabolites of cacao in the developing plant, infected and not infected with the disease. It may be possible from the last method to discover that some of these metabolites are related to the build up of the virus and by using enzyme blocking groups as therapeutic agents to stop the build up of the virus. The cacao plant is an excellent subject for these studies since for the first two months of its life it depends almost entirely on its cotyledons for food. One essential step for detailed study is to be able to grow the embryos of cacao without the presence of the cotyledons. This has been achieved in a synthetic medium with the addition of a small quantity of cotyledon extract.

DISCUSSION

When we compare the Swollen shoot virus with the tree viruses in the U. S. A. we see many similarities and two main differences. The first difference is that Swollen shoot disease spreads by extension of the periphery of the outbreak, each tree becoming infected from a neighbouring tree ; this is very different from most of the American fruit-tree viruses, where the spread is extremely scattered and irregular. This peripheral spread is accompanied by an incubation period which

varies..../

varies from three months to more than a year but which in practise is generally less than a year. The second main difference is that the insect vectors are known. That together with the fact that there is no close season for cacao virus work makes it possible that we may get a more complete picture of this tree virus than of any other so far studied.

We have seen that the Phoney Peach disease has an incubation period of a year and for that reason is not responding to the eradication campaign. It differs from Swollen shoot disease however in that the spread is irregular and suspected incubating trees cannot be delimited and removed. The control of Swollen shoot disease by simple eradication of infected plants, the reinspection of the contact areas at three monthly intervals and the removal of fresh infection with such a relatively slow moving and confined virus is theoretically practicable. Posnette has shown that it can work in practice and the various experimental farms maintained by the West African Cacao Research Institute in the midst of devastated cacao further corroborate this. The history of the attempt to control the virus in the Gold Coast is not, however, one of unqualified success. The difficulties have been great because the people themselves cannot be convinced of the seriousness of the disease or of the need for cutting out the diseased trees. They will agree to the cutting out of the dead or nearly dead trees but during the two years or so in which the tree shows symptoms and gradually declines, since even moribund trees may ~~have~~ carry ~~been~~ a limited amount of fruit, they resent the attempts at cutting out very much. A very great deal has been done by the setting up of a cacao survey section of the agricultural department which has mapped out the cacao areas and the areas of virus infection. Twenty European cacao survey officers are now being recruited to supervise the cutting out gangs, but this number considering the sickness rate and the difficult

country ..../

country in which the work has to be done, hardly seems sufficient. Many Africans are employed in administrative and supervisory positions in the cutting out campaign but the dangers of ~~consumption~~ corruption are such that adequate European Supervision is essential. Cases have already came to light of African Supervisors reveiving money from farmers and for this consideration neglecting to cut out the diseased cocoa. Such cases no matter how rare and cases of inconsiderate cutting out became magnified in the public mind and create opposition to the campaign. A start has been made on the cutting out campaign but only a small fraction of the trees requiring cutting have been removed. The recent political unrest in the country has been associated in part with the cutting out campaign and this has been temporarily suspended. The longer the infected area is left the more it will spread and the quicker it will spread.

The fact that we know the insect vectors and these vectors spread, mostly, very slowly from tree to tree might suggest that an attack on the insect vector would ~~save~~ solve the problem of Swollen shoot disease. There are several complicating factors however. The cacao trees grow with an interlacing canopy in wild country which would be difficult of access to spraying machines. For insecticides such as nicotine sulphate suitable water supplies for making up the mixtures would be difficult to find. A further complication is that the mealybugs are themselves attended by ants which build on the colonies carton tents of earth which adequately protect the mealybugs from heavy tropical rainstorms and also from any sprays. Mr. Strickland is at present working on the biology of ants and mealybugs in an attempt to find some means of controlling them. He has shown that the "crawlers" of the mealybugs can be wind distributed and has thus explained certain anomalous cases of scatter spread which have occurred. This method of spread is important in the extension of new areas of

Swollen ..../

Swollen shoot disease but ~~do~~ does not affect the fact that ~~the fact that~~ the main spread is by peripheral ~~spread~~ extension. The scatter spread by wind dispersal is however important in direct relation to the size of the main outbreaks ; the bigger these are the more chance there is of the mealybugs which are blown being viruliferous. This is one more reason for hastening the cutting out of the main area of infection.

In the U. S. A. the alternative hosts have held the key to the solution of the problems of Eastern X virus, Pierce's disease of grape vines and Mottle Leaf virus of sweet cherry. The part played by alternative hosts in the Gold Coast is not yet clear. All of the trees infected with virus A except Firmiana barteri, K. Schum. have shown symptoms but with viruses C and M about half the plants tested have shown no symptoms and such symptomless carriers would if proved important field resevoirs be very troublesome. All the hosts so far found have been forest trees related to cacao but Mr. O. J. Voelcker informs me that in the Nigerian cacao farms such trees are rare and it will be necessary to look elsewhere for the alternative hosts. Perhaps, as in the case of Pierce's disease some of the herbaceous weeds may carry the virus. The importance of alternative hosts to Gold Coast cacao would appear to lie in the renewal of outbreaks which might build up over long periods of time and become threats once more. The actual effect of these alternative hosts on the day to day increase of Swollen shoot disease, when 50 ~~milder~~ million cacao trees are also acting as hosts is probably negligible. They will be of interest in the differentiation of the virus and they will also be of interest if the different viruses can be shown to occur in distinct wild hosts in the field.

In West Africa the cacao widely grown is the West African Amelonado which shows a high degree of genetic uniformity and reacts uniformly to infection by showing symptoms. Other varieties and introduced forms may include symptomless carriers

vide .../

(vide supra CU 85) and it is very necessary to test any such varieties or hybrid progeny before releasing them in the Gold Coast. Until symptomless carriers occur and until cacao comes to be grown as vegitatively propagated varieties no form of internal quarantine seems necessary. No cases have been reported of any spread of the viruses, by human agency or accident, outside of their known geographical areas. Port quarantine against all imported cocoa is of course maintained and any importations if not grown first at Kew are kept under quarantine at Accra 20 miles of "desert" from the nearest cacao.

Whenever a serious virus disease of fruit-trees occurs it generally threatens economic ruin to a large number of people. Time and again the old agriculture axiom of distribution of enterprise over several departments has been shown to be an absolute necessity in fruit farming. It looks as if the Gold Coast will have to learn that the hard way. As yet there is no sign of any crop being developed which could replace cacao or be grown as an alternative to it. Swollen shoot is now a great pathological problem but it is also the product of 50 years of agricultural neglect. The responsibility for this neglect cannot be pinned to any one group of persons, the men on the spot mostly work as hard as the climate and sickness will allow them but they are very few and they haven't much money for research work. Perhaps all this is past and we are entering a new era, a Canaan overflowing with agriculturists and plant pathologists.

My thanks are due to Mr. O.J. Voelcker, Director, West African Cacao Research Institute, for permission to submit this essay and to Messrs. A.F. Posnette, J.M. Todd and A.H. Strickland for permission to quote their unpublished work. The views expressed and generalisations made are my own entirely and they should in no way be identified with the opinions of the West African Cacao Research Institute nor should they be published or quoted.

REFERENCES

Bacon, L.P. & F.C. Schlaemer. "World trade in agricultural products". International Institute of Agriculture. Rome, 1940.

Bennett, C.W. Latent virus of dodder and its effect on sugar beet and other plants. Phytopath., 34 77-91, 1944.

Blodgett, E.C. Peach wart. Phytopath., 33 21-32, 1943.

Bodine, E.W. & W.A. Kreutzer. Ringspot of apricot. Phytopath., 32 179-181, 1942.

Box, H.E. Insect transmission of the 'Swollen shoot' virus in West African cacao. Nature, Lond., 155 608-609, 1945.

Charter, C.F. Cacao soils good and bad. West African Cacao Research Institute. (Mimeographed), 1947.

Cotterell, G.S., Entomology Section, Rep. on Central Cocoa Res. St., Tafo, 1938-43 (Ed. M. Greenwood) Gold Coast Printing Dept. Accra.

Crowdy, S.H. & A.F. Posnette. Virus diseases of cacao in West Africa. II. Cross immunity experiments with viruses 1A, 1B, & 1C. Ann. Appl. Biol., 34 403-411, 1947.

Dade, H.A. Swollen shoot of cacao. Rept. on Mr. H.A.Dade's visit to the Gold Coast. Sess. Paper Legis. Counc. Gold Coast Colony No. 5 of 1937.

Foggie, A. Some ecological observations on a forest type in the Gold Coast. J. Ecology 34 88-106, 1947.

Fukushi, T. Multiplication of virus in its insect vector. Proc. Imp. Academy Japan, 11 301-303, 1935.

Giddings, N.J. Mass action as a factor in curly-top-virus infection of sugar beet. Phytopath., 36 53-56, 1946.

Gold Coast Government. Interim report of the committee of enquiry to review legislation for the treatment of the Swollen shoot disease of cocoa. Accra, Gold Coast, No. 1 of 1948.

Hall /

Hall, W.J. The identity of a mealybug vector of "Swollen shoot" virus disease of cacao in West Africa. Bull. Ent. Res. 36 305-313, 1945.

Harris, R.V. & Mary E. King. Studies in Strawberry virus diseases V. J. Pom. & Hort. Sc. 19 227-242, 1941-42.

Hewitt, W.B., N.W. Frazier, H.E. Jacob & J.H. Freitag. "Pierce's disease of grape vines". Univ. Cal. College Agric., & Agric. Expt. St. Circ. No. 353, Nov. 1943.

Hildebrand, E.M., G.H. Berkley & D. Cation. "Handbook of virus diseases of stone fruits in North America". Michigan Agricultural Experiment Station Misc. Publ. May, 1943.

Horsfall, J.G. and G.A. Zentmeyer. Chemotherapy for vascular diseases of trees. Proc. Nat. Shade Tree Conference, U.S.A., pp. 7-15, 1941.

Huber, G.A. & C.D. Schwartze. Resistance in the Red Raspberry to Mosaic vector Amphorophora rubi, Kalt. J. Agric. Research 57 623-633, 1938.

Hutchins, L.M., E.W. Bodine & H.H. Thornberry. "Peach Mosaic, its identification and control". U.S.D.A. Circ. 427, 1937.

Imperial Economic Committee. Report of the Imperial Economic Committee, 22nd report, 1932. H.M. Stationery Office, London.

Internation Institute of Agriculture. "Yearbook of Agricultural Statistics, 1937-38", Rome, 1938.

Keitt, G.W. & C.N. Clayton. A destructive virus disease of sour cherry. Phytopath., 33 449-468, 1943.

Kienholz, J.R. Stony Pit, a transmissible disease of ~~popons~~ pears. Phytopath. 29 260-267, 1939.

Kunkel, L.O. Insect transmission of Peach Yellows. Contr. Boyce Thompson Institute, 5 19-28, 1933.

Nowell /

Nowell, W. Report of the Commission on the marketing of West African cocoa. H.M. Stationery Office, Lond., Command 5845, 1938.

Paine, J. "The History of Gold Coast Cocoa", Rept. Agronomy Div. W.A.C.R.I., 1945 (Unpublished).

Posnette, A.F. Transmission of Swollen shoot. Trop. Agriculture, Trin. 17 98, 1940.

Posnette, A.F. Swollen shoot virus disease of cacao. Trop. Agriculture, Trin. 18 87-90, 1941.

Posnette, A.F. The diagnosis of Swollen shoot disease of cacao. Trop. Agriculture, Trin., 21 56-58, 1943.

Posnette, A.F. The use of seeds in the insect transmission of some plant viruses. Nature, Lond., 159, 500-501, 1947a.

Posnette, A.F. Virus diseases of cacao in West Africa, I. Cacao viruses 1A, 1B, 1C, & 1D. Ann. appl. Biol. 34 388-402, 1947b.

Posnette, A.F. & A.H. Strickland. Virus diseases of cacao in West Africa. III. Technique of insect transmission. 1948, in the press.

Prentice, I.W. & R.V. Harris. Resolution of Strawberry virus complexes by means of the aphis Capitophorus fragariae. Ann. Appl. Biol. 33 50-53, 1946.

Price, W.C. Acquired immunity to Ring Spot in Nicotiana. Contr. Boyce Thompson Inst. 4 359-403, 1932.

F.R. Forest water catchments. Forestry Abstracts 9 1, 1947.

Reeves, E.L. Mottle leaf, a virus disease of cherries. J. Agric. Res. 62 555-572, 1941.

Reeves, E.L. Virus diseases of fruit trees in Washington. Bull. No. 1 Washington State, Dept. of Agriculture, 1943.

Schultz, E.S., C.F. Clark, Reiner Bonde, W.P. Raleigh & F.J. Stevenson. Resistance of potato to mosaic and other virus diseases. Phytopath. 24 116-132, 1934.

Swingle, R.U. Phloem necrosis, a virus disease of American Elm. U.S.D.A. Circ. 640, 1942.

Stevens /

Stevens, W.F. A new disease of cocoa in the Gold Coast.
Gold Coast Farmer 5 122, 144, 164-165, 1936.

Voelcker, O.J. & J. West. Cacao die-back. Trop. Agriculture, Trin. 17 27-31, 1940.

Wallace, J.M. The use of leaf tissue in graft transmission of psorosis virus. Phytopath., 37 149-152, 1947.