INAUGURAL LECTURE SERIES

The Ecology of Tropical Plant Viruses

by

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Natural Resources Institute

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the UNIVERSITY *of* GREENWICH

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An Inaugural Lecture Delivered at the University of Greenwich

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Mike Thresh took a first degree in botany at the Imperial College of Science, University of London, in the days of Professors W. Brown and F. G. Gregory. He then spent a year with the plant virologists at Rothamsted Experimental Station as a Colonial Research Scholar. During this period there was an opportunity for field work in East Anglia on the control of sugar beet yellowing viruses using one of the first organophosphorus insecticides to be made available for use in agriculture.

His first overseas assignment was in Ghana and Nigeria on the epidemiology and control of cocoa swollen shoot disease as one of the team of virologists at the West African Cocoa Research Institute. After seven years in West Africa similar studies followed on virus diseases of hop, blackcurrant and other fruit crop species as a plant virologist at East Malling Research Station (now part of Horticultural Research International). These studies and contributions on general epidemiological concepts led to a University of London Ph.D. and D.Sc. and to a Queen's Award for Technological Achievement to East Malling and the Department of Hop Research, Wye College.

Whilst on the staff at East Malling a 3-month FAO assignment in Ethiopia was followed by other consultancies and advisory visits on behalf of FAO, British Council, Overseas Development Administration (ODA), now the Department for International Development (DFID) and International Agricultural Research Centres. This led to an ODA-funded project on cocoa swollen shoot disease and then transfer to a UK-based appointment as Plant Virologist with the ODA Corps of Specialists. East Malling continued to be the base for many overseas forays into Africa and Asia until plant pathology was included in the remit of the Natural Resources Institute and the transfer was made to Chatham Maritime. Quasi retirement and an honorary position as Professorial Research Fellow of the University of Greenwich came after a 5-year contract as Senior Virologist at NRI.

Mike Thresh has been an active member of several scientific societies and has served on committees and councils of the Society for General Microbiology, the Biological Council, the Association of Applied Biologists (AAB), the Federation of British Plant Pathologists, the British Society for Plant Pathology (BSPP) and the International Society for Plant Pathology (ISPP). He has edited/co-edited six books/conference proceedings and been Programme Secretary of AAB, President of BSPP and Chairman of the Virus Epidemiology Committee of ISPP since its inception in 1979.

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INTRODUCTION

In recent decades ecology has become one of the dominant themes of the biological sciences. However, this has not always been so as the subject emerged from the specialist study of plant and animal communities in natural habitats that were often remote and sometimes exotic. It has since become a unifying all-embracing discipline that is of great importance, not only in botany, zoology and microbiology, but also in international affairs in relation to current issues concerning the environment, conservation, pollution, sustainability and the constraints to the growth of human populations and economies.

The current prominence and status of ecology is reflected in the series of Inaugural Lectures of which this is a part. It is concerned with the ecology of tropical plant viruses and Professor Cheke also adopted an ecological approach in his presentation on river blindness. Moreover, Professor Grant dealt with eco-toxicology and Professor Hall has adopted the title of Professor of Chemical Ecology.

My presentation is in four parts. A brief section on the history of tropical plant virology and the prominent role that has been and continues to be played by UK scientists is followed by general comments on tropical environments, crops, viruses and vectors. Six important virus diseases are then considered in some detail as a basis for a more general discussion of some of the main issues raised.

THE ROLE OF UK SCIENTISTS IN TROPICAL PLANT VIROLOGY

UK scientists have played an important and distinguished role in the development of all aspects of tropical agriculture from the earliest colonial days. The first colonial botanists and agriculturalists, who were responsible for some of the original crop introductions, were soon followed by entomologists and shortly afterwards by plant pathologists. These included Marshall Ward FRS (1854–1906) whose pioneering studies on coffee rust in what is now Sri Lanka have been described in graphic detail (Large 1950). This tradition has been maintained and there have since been important contributions on many other fungal diseases including cocoa witches' broom (Wheeler 1987).

Plant virology has a more recent history than the study of fungal pathogens, but viruses were undoubtedly present and causing serious losses in the tropics long before they were studied in detail. Indeed, in 1890 no less a personage than His Excellency H.M. Governor of Fiji wrote at length to the Colonial Office in London on what is now known as banana bunchy top virus disease (Magee 1953). He noted that "in or about 1879 *Musa cavendishii* growing in the island of Moturiki were attacked with a disease" and commented that "at the suggestion of the Kew authorities I am sending them the roots, stems and leaves of a diseased plant preserved in a clear pickle of salt and water, and it is not improbable that the highly trained intelligence at Kew may detect that which is beyond our observation here".

Sugar-cane mosaic is another tropical virus disease to have attracted early attention (Brandes 1919) and UK pathologists and entomologists were involved closely in the study of cotton leaf curl disease and its whitefly vector in Sudan and Nigeria from the 1920s (Bailey 1934, Tarr 1951). At this time H. H. Storey FRS (1894–1969) began his scientific career in South Africa and published one of the earliest papers on groundnut rosette virus disease (Storey & Bottomley 1928). He then transferred to Amani (in what is now Tanzania) and later to Muguga (Kenya) where he remained until his death, apart from a brief period at the Colonial Office in London. The pioneering work of Storey on groundnut rosette, cassava mosaic and other tropical viruses still merits careful scrutiny and two of his elegant papers on the transmission of maize streak virus by its leafhopper vectors have been reprinted as *Phytopathological Classics* (Campbell & Bruehl 1986). The status of Storey's work was fully recognized by his contemporaries and in 1946 he became one of the first plant virologists to be elected a Fellow of the Royal Society.

In 1937, whilst Storey was in East Africa, A. F. Posnette FRS, who was also a member of the Colonial Agricultural Service, was in what is now Ghana. There he was making the transition from plant breeding to plant virology in response to the apparently new threat posed by cocoa swollen shoot disease. Posnette went on to produce a comprehensive and definitive series of papers on the viral aetiology, transmission, ecology and control of the disease before returning to the UK in 1949. Although then concerned primarily with virus diseases of temperate fruit crops he later undertook many other short-term assignments in West Africa and elsewhere, on swollen shoot and other virus or virus-like diseases of tropical crops (Posnette 1980).

Sir Frederick Bawden FRS (1908–72) was another eminent virologist of the same period who took a keen interest in tropical agriculture, even though based at Rothamsted Experimental Station in the UK throughout his distinguished career. He undertook many overseas assignments in India, Sudan, West Africa and elsewhere and had an immense influence as adviser, consultant and through his own research, writing and teaching.

More recently B. D. Harrison FRS, who is a former student of Bawden, has played a similar role and also made important contributions on the nature and interrelationships of the many viruses of the family *Geminiviridae* that infect tropical and sub-tropical crops. This work has been done at the Scottish Crop Research Institute, Dundee, in projects that have been sponsored, at least in part, by the UK Department for International Development (DFID), formerly the Overseas Development Administration (ODA). Several other UK institutes and universities have also contributed to tropical virology in this way and also provide post-graduate training in plant virology and vector entomology for students from overseas. Moreover, strong links have been established between UK establishments and the various International Agricultural Research Centres.

Studies on tropical viruses done solely in the UK have obvious limitations and there have been several DFID/ODA-funded field-based projects overseas. In the 1970s these included one on virus diseases of cassava, maize and other food crops in Kenya and another on cocoa swollen shoot disease in Ghana. More recently an expanding programme was developed at the Natural Resources Institute (NRI) on rice tungro, cassava mosaic, maize streak and other virus diseases of tropical food crops. This programme was mounted in response to the ODA research strategy developed in the 1980s (ODA, 1989) which was intended to extend and complement the work being done on tropical viruses in the UK at the time and being funded by ODA, EEC, the Rockefeller Foundation and other sources. The current Crop Protection Programme is administered by NR International Ltd on behalf of DFID.

This brief summary indicates the long history and continued involvement of UK virologists in tropical agriculture. Such activities are to the mutual advantage of all concerned and promote the development of plant virology as a whole. UK virologists gain access to a wider range of viruses, vectors and problems than they would otherwise encounter and those overseas can utilize the facilities and expertise that is readily available in the UK and even now seldom available in the tropics. There is obvious scope for the University of Greenwich to become involved and it is encouraging to note that several Ph.D. students have been registered recently for studies on tropical plant viruses or virus vectors. Moreover, there is already an M.Sc. course on Sustainable Agriculture and one is planned on Natural Resources. Both courses are intended to attract students from overseas and will include aspects of tropical virology.

TROPICAL ENVIRONMENTS

The adjective *tropical* is used or mis-used in various ways and often as a synonym for *hot*, *fervid* or even *passionate*. More precisely it relates to the portion of the Earth's surface bounded by the Tropics of Cancer (23' 27' N) and Capricorn (23' 27' S), which delimit the zone over which the sun is vertically overhead for some part of the year. Latitude determines day-length and potential solar radiation levels, and for this reason it is used as a variable in some crop growth models. However, it is not of direct biological importance and there is no clear distinction between environments, crops or pathogens within the tropics and those outside. This is partly because some of the highest temperatures are experienced outside the tropics and many sub-tropical or even temperate areas are very hot for at least some part of the year.

Climatic and vegetation zones

Temperatures are usually adequate for plant growth throughout the year in the lowland tropics where soil moisture is the main limiting factor. This explains why natural vegetation cover and cropping systems are determined mainly by the amount of rainfall and the length of the dry season. The natural vegetation is evergreen rainforest in lowland areas having little or no dry season. Tree, root and tuber crops are important in such areas, although many other crops are also grown in overlapping sequence throughout the year. Grasses, cereals and annuals predominate and growth is markedly seasonal where rainfall is low and there are prolonged periods of drought. Various types of deciduous woodland and savannah and diverse crops occupy the intermediate zones. Such patterns of crops and vegetation are seen particularly clearly in West Africa, where much of the land mass is below 1000 m above sea level and rainfall decreases with increasing distance from the coast. Temperature becomes increasingly important as a factor influencing growth at higher altitudes, and many different temperate crops (including cereals, deciduous fruits, flowers and vegetables) are grown in upland areas of the tropics below the alpine zone.

Tropical crops

The diverse climatic conditions encountered within the tropics account for the very wide range of crops grown. In considering their main features as hosts of viruses it is important to distinguish between indigenous and exotic crops, between those raised from seed and those propagated vegetatively, and also between long-lived woody perennials and herbaceous plants of relatively short duration. These crop characteristics are of great ecological importance and influence the nature and severity of the disease problems encountered and the prospects for control (Thresh 1987).

Some crops, such as cocoa, are entirely restricted to the tropics, whereas many others are also grown widely elsewhere. Any distinction between tropical and non-tropical crops and habitats has been blurred by the increased use of irrigation and various forms of protection to facilitate growth during dry or cool periods. Moreover, some temperate crops have been adapted for cultivation in the tropics and *vice versa*, as seen with cereals such as sorghum and maize from the tropics and wheat from higher latitudes.

Tropical cropping systems

Harlan (1976) lists several important features of the basic types of subsistence agriculture that emerged independently in different regions of the world several thousand years ago:

- many wild and cultivated plants utilized
- crops often grown in mixtures
- diverse landraces or cultivars grown
- landraces themselves genetically diverse
- fields small and often scattered
- human populations mobile and shift periodically
- bush fallow rotations widely practised.

Cropping systems with at least some of these features still occur within the tropics, and elsewhere, and in some areas they predominate. However, in all regions there have been marked trends away from genetic diversity and the exploitation of wild species (Harlan 1976, Day 1977). This has been due to an increased reliance on a limited number of cultivars of a few main crops, often grown in virtual monocultures and not in mixtures. Moreover, the decreased mobility of burgeoning populations has also led to increased pressure on the land and to shorter rotations. These trends are not new, even in the tropics, where export crops including rubber, tea, coffee, sugar-cane, cotton, citrus, oil palm, banana, sisal, tobacco and pineapple have long been grown on large estates under central management. There have also been the large almost continuous stands of crops such as cocoa, coconut or sugar-cane grown by many individual small-scale farmers on contiguous land-holdings. More recently these trends have extended to food crops, associated with the increased use of mechanization and the activities of local or expatriate companies, state farms or other large land owners. Such developments, together with the very diverse habitats found within the tropics and the increased use of irrigation, have led to an extremely complex and continually changing situation. Many different crops and cropping systems are exploited and in some areas basic subsistence agriculture, as practised for centuries, occurs alongside large commercial holdings that are highly mechanized and utilize irrigation, a few modern varieties and the latest technical innovations. Indeed, the same crops may be grown in entirely different ways, as with maize within South Africa, Zimbabwe and Zambia and banana within the Philippines.

There is scope for comparative studies of the pests and pathogens encountered in such contrasting systems. However, few such studies have been undertaken and there is a dearth of information on the epidemiology of viruses in different cropping systems and on the effects of the changes in practices that have occurred. Despite the difficulties involved it is particularly important to determine the effects of growing crops as mixtures of different cultivars or with other species, as still widely practised in many parts of the tropics. Meanwhile, for viruses as for other pathogens, there are *a priori* grounds for assuming that crop diversity and other features of basic subsistence agriculture provide considerable protection from serious attack, and that severe epidemics seldom occur within such cropping systems (Harlan 1976, Buddenhagen 1977, Thresh 1982, Bos 1992). An extension of the argument is that many features of modern agriculture have led to an erosion of natural defence mechanisms and to greatly increased risk of pest and disease problems. However, it should be appreciated that this is a plausible but largely unsubstantiated supposition that merits much more detailed consideration than it has yet received.

Tropical viruses

The many different viruses that have been isolated from tropical crops belong to diverse taxonomic groups (Brunt et al. 1990), but they are in no way distinctive or unique. In structure and physicochemical properties they resemble equivalent viruses of temperate crops. Moreover, tropical viruses have no special biological features and they are transmitted in diverse ways. All the main types of vectors are represented, with the apparent exception of nematodes (Table 1). This may simply reflect the limited attention given to nematodes as vectors in the tropics, as many potential nematode vector species occur and several viruses of tropical crops have been ascribed to the nepovirus group, several members of which are transmitted by nematodes. Similarly, there is no great significance in the disproportionate importance of whiteflies and beetles as vectors in the tropics and sub-tropics because these vectors are of limited distribution or activity at higher latitudes.

Many tropical viruses including those of great economic importance listed in Table 2 also occur elsewhere, and the region in which they originated is not always clear. For each of these viruses there are likely to be large differences in epidemiology between temperate and tropical regions. This is because of the very different environments and cropping systems encountered, but a comparative epidemiological approach has seldom been adopted. Some of the important factors to be considered are apparent from a comparison of potato-growing in the subsistence agriculture of the Andean region of South America with that in the technologically advanced temperate areas of Europe and North America (Table 3).

Of the viruses listed in Table 2, tobacco mosaic tobamovirus has no arthropod vector and it has been widely distributed in smoking and chewing tobacco so that it is introduced to crops by workers during handling and cultivation. Several of the other viruses listed have been widely disseminated in seed or vegetative propagules. However, the four planthopper-borne viruses of rice behave differently and are of greater biological interest because they persist in the vector and two are known to be carried far by wind-borne migrants (Thresh 1983). The phenomenon has been studied in greatest detail in parts of northern China and Japan where rice is only grown during the summer months and the planthopper *(Nilaparvata lugens)* vector of rice grassy stunt

Table 1 Representative viruses of tropical crops and their means of spread

Contact-borne	Cassava common mosaic potexvirus (v) Tobacco mosaic tobamovirus
Fungus-borne	Peanut clump furovirus (s)
Mite-borne	Pigeon pea sterility mosaic 'virus'
Aphid-borne: non-persistent	Bean common mosaic potyvirus (s) Papaya ringspot potyvirus Peanut stunt cucumovirus (s) Soybean mosaic potyvirus (s) Sugar-cane mosaic potyvirus (v)
Aphid-borne: persistent	Banana bunchy top virus (v) Citrus tristeza closterovirus (v) Groundnut rosette viruses
Hopper-borne	Maize rayado fino marafivirus Maize streak geminivirus Rice hoja blanca tenuivirus Sugar-cane Fiji virus (v)
Mealybug-borne	Cocoa swollen shoot badnavirus (v) Pineapple wilt capillovirus (v) Banana streak badnavirus (v)
Whitefly-borne	Cassava mosaic geminiviruses (v) Cotton leaf curl geminivirus Tomato yellow leaf curl geminivirus
Thrips-borne	Groundnut bud necrosis tospovirus Tomato spotted wilt tospovirus
Beetle-borne	Bean rugose mosaic comovirus Cowpea mosaic comovirus Okra mosaic tymovirus Rice yellow mottle sobemovirus

s = also seed-borne; v = also disseminated in vegetative propagules

Table 2 Some important viruses of temperate/tropical crops

Contact-borne	Tobacco mosaic tobamovirus
	Tomato mosaic tobamovirus(s)
Aphid-borne	Alfalfa mosaic (s)
	Bean common mosaic potyvirus (s)
	Lettuce mosaic potyvirus (s)
	Maize dwarf mosaic potyvirus (s)
	Peanut stripe potyvirus (s)
	Potato virus Y potyvirus (v)
	Soybean mosaic potyvirus (s)
	Sugar-cane mosaic potyvirus (v)
	Potato leaf-roll luteovirus (v)
	Barley yellow dwarf luteovirus
Thrips-borne	Tomato spotted wilt tospovirus (v)
Hopper-borne	Rice grassy stunt tenuivirus
	Rice hoja blanca tenuivirus
	Rice ragged stunt phytoreovirus
	Rice tungro spherical machlovirus

s = also seed-borne; v= also disseminated in vegetative propagules

Table 3 Contrasting features of potato cultivation in the Andean Region of South America and Europe/North America

Andean Region	Europe/North America
Small irregular fields	Large flat fields
Mixed cropping	Pure stands
Cultivar/species mixtures	Uniform cultivars
'Own' seed	Certified seed
No pesticides/fertilizers	Pesticides/fertilizers
Absent or short rotation	Normal rotations
Natural hybrids grown	Bred cultivars

Jones (1981)

and rice ragged stunt viruses does not survive the winter. These areas are subject to invasion by infective vectors that are swept northwards from tropical areas where rice is grown throughout the year and where infection is endemic (Kisimoto 1976).

Barley yellow dwarf luteoviruses occur in both temperate and tropical regions and they too can be carried far by aphid vectors (Irwin & Thresh 1988). This raises the possibility of long-range movement between tropical and temperate regions, or between highland and lowland areas in response to seasonal factors and the availability of cereal crops and grasses at a suitable stage of growth for colonization by vectors. However, so little is known about the host range and epidemiology of barley yellow dwarf viruses in the tropics and sub-tropics that such possibilities have yet to be considered in the work now being done in such important cereal-growing areas as the Andes, the Himalayas, North Africa and the highland regions of East and Central Africa (Irwin & Thresh 1990).

SIX IMPORTANT TROPICAL VIRUS DISEASES

The six virus diseases selected for detailed consideration here are all mainly or entirely restricted to the tropics.

Cocoa swollen shoot disease

Swollen shoot disease of cocoa (*Theobroma cacao*) was first reported in 1936, in what is now the Eastern Region of Ghana. At the time this was the most important cocoa-growing area in the world and there was an immediate response by the colonial authorities. It was announced that "Government do not intend to run any avoidable risks and steps have been taken to obtain a plant pathologist on loan for six months from Sierra Leone". The comment proved to be overly optimistic as for more than 60 years there has been a continued need for research on swollen shoot virus and its mealybug (pseudococcid) vectors. This has been justified by the magnitude and complexity of the problem. Moreover, the need for a broad-based ecological approach soon became apparent following the detection of wild indigenous tree hosts of swollen shoot virus and the finding that several mealybug vector species occur in association with more than 120 other insect species, including 75 species of ant, 16 species of Hymenoptera and three species of predatory beetle (Strickland 1951, Tinsley 1964, Leston 1971).

The overall research effort on swollen shoot disease has exceeded 250 operational-years in Ghana alone, including a substantial input from vector entomologists and resistance breeders. The commitment has been greater than to any other virus disease of a tropical crop, and yet it is unexceptional when compared with the effort made in recent decades on plum pox disease in Europe, or several other comparable diseases of temperate fruit trees. This is yet another indication of the extent to which tropical diseases are under-researched.

Surveys of the cocoa-growing areas of Ghana and other West African countries in the 1940s established that swollen shoot disease was far more widespread than the first reports from Ghana had indicated. However, infection was most prevalent in Ghana, where countless millions of infected cocoa trees had been killed. More than 190 million other cocoa trees have since been removed by the authorities in attempts to control or at least contain spread by enforcing the biggest and most ambitious eradication campaign ever mounted against a plant disease (Thresh & Owusu 1986). The campaign was based on the early results of Posnette (1943), who followed the pattern and sequence of disease spread and demonstrated the effectiveness of eradication measures, especially when used to treat small outbreaks whilst still at an early stage. Outbreaks are initiated by incoming wind-borne mealybugs (mainly small first instar larvae) that can be blown over considerable distances (Cornwell 1960). Subsequent 'radial' spread is mainly local by mealybugs walking short distances between the interlocking canopy branches of adjacent trees to give slowly expanding patches of disease that ultimately coalesce and form large 'areas of mass infection' (Thresh 1958). The two types of spread were illustrated by Vanderplank (1963) in a general discussion of the initiation and subsequent progress of plant disease outbreaks.

Cocoa swollen shoot virus is now so widespread in cocoa that other hosts are of limited epidemiological importance. They are known to include the baobab *(Adansonia digitata)*, silk cotton *(Ceiba pentandra)* and several other indigenous tree species of the lowland rainforest or adjoining savannah. Infected baobab and *Cola chlamydantha* trees have been detected in forest reserves or other areas far from the nearest cocoa and also in circumstances suggesting that they were the initial sources from which virus spread to nearby cocoa (Posnette 1981). This suggests that indigenous trees were the original hosts of swollen shoot virus and that spread to cocoa occurred after the crop was introduced from the Neotropics to West Africa at the end of the 19th century. Spread from indigenous trees to cocoa was greatly facilitated by the varieties and cropping practices adopted by farmers in Ghana, Nigeria and elsewhere in West Africa. They planted mainly in the rainforest areas after selectively thinning the original forest vegetation so that cocoa was often established beneath or alongside indigenous hosts of swollen shoot virus and its vectors. Moreover, once the virus became established in cocoa it could spread readily to neighbouring farms as these were often established in contiguous arrays of small holdings, with little or no separation between them (Thresh et al. 1988a).

The most extensive tracts of cocoa were in the Eastern Region of Ghana, where conditions were particularly favourable for crop growth. This area has always been the one most seriously affected by swollen shoot disease and infection is now more prevalent there than ever before. Only limited attempts are being made to contain its spread, although use is now being made of partially resistant varieties (Thresh et al. 1988b). There is also scope for replanting in compact blocks that are provided with at least some isolation from existing infected stands (Ollennu et al. 1989). However, it is difficult to change traditional practices and adopt this approach because of the generally small size and irregular shape of the farms.

Cassava mosaic disease

The disease known as cassava mosaic, or in some publications, as African or Indian cassava mosaic disease, was first reported in Tanzania in 1894. It has since been recorded in Sri Lanka and India and in all the main cassava-growing areas of Africa and the adjacent islands. However, the whitefly-borne geminiviruses that are responsible have not been reported outside Africa and the Indian sub-continent and the mosaic disease of cassava in South/Central America has a completely different aetiology (Thresh et al. in press). This has led to the conclusion that cassava mosaic geminiviruses are indigenous to the areas where they occur and that spread to cassava occurred from some other host(s) after the crop was introduced from Brazil to Africa in the 16th century and to the Indian sub-continent in the 18th century (Fauquet & Fargette 1990). The original hosts are not known, but more than one species may have been involved because the virus strains that predominate in West and Central Africa differ markedly in serological properties from those collected east of the Great African Rift valley and from the strains in India (Swanson & Harrison 1994). Whatever their origins, African cassava mosaic viruses are now widespread and prevalent and in a recent economic assessment they were ranked as causing the most important vector-borne disease of crops in Africa (Geddes 1990). This was not the situation in the 1920s and 1930s when there were the first reports of mosaic in parts of southern Nigeria, Ghana and other West African countries where the disease had not been reported previously. Problems were also reported in eastern and southern Africa and the major epidemic that occurred in Madagascar and caused serious losses in the 1940s has been particularly well documented (Cours et al. 1998).

Cassava mosaic was one of the first diseases to be studied by Storey in Tanzania and it has since received considerable attention in other countries, including Madagascar, Kenya, Nigeria, Côte d'Ivoire and most recently Uganda. Much epidemiological information has been obtained but it provides an inadequate base for developing effective control measures when considered in relation to the vast area of cassava in Africa (latest FAO estimate 8.35 million ha), the different virus strains that occur and the many different environments and cropping systems in which the crop is grown. The limitations of the available information became apparent in Uganda in 1988 when a severe epidemic was reported in areas where for some years mosaic had not been a serious problem (Otim-Nape et al. 1997). The varieties affected by the epidemic were so vulnerable to infection that they sustained very severe damage and their cultivation was largely abandoned. Food shortages ensued in the many areas where cassava was the main staple food and of particular importance in times of drought. This necessitated a greatly increased research and extension programme to develop and promote effective means of control.

Two different strategies of mosaic disease control have long been apparent (Storey 1936, Thresh & Otim-Nape 1994, Thresh et al. 1998). One is to develop varieties that are in some way resistant or tolerant of infection. The alternative, or in some circumstances complementary, approach is by sanitation. This involves the use of mosaic-free planting material and the removal (roguing) of all known sources of infection. Sanitation is only likely to be effective where the occurrence of mosaic is due mainly to the use of infected cuttings and *not* to spread by the whitefly vector *(Bemisia tabaci)*. This is known to be the situation from experiments done in Kenya, in parts of southern Uganda and at some sites in the Guinea savannah zone of Côte d'Ivoire. By contrast, spread by whiteflies is usually rapid in the lowland rainforest zones of Nigeria and Côte d'Ivoire and in the epidemic areas of Uganda where roguing is of limited effectiveness unless highly resistant varieties are grown.

The association between rapid spread by whiteflies and high rainfall that is apparent in West Africa does not necessarily apply elsewhere, and until recent years spread in Uganda was much slower in the humid coffee and banana-growing areas around Lake Victoria than in the hotter and somewhat drier savannah areas to the north. This emphasizes the complexity of the situation and the need for additional studies to explain the results obtained and to determine the most appropriate control strategy to adopt in the many parts of Africa where little epidemiological information has been obtained. Meanwhile, cassava mosaic continues to cause serious losses and, considering the continent as a whole, only limited attempts are being made to control the disease by sanitation or by using resistant varieties (Thresh et al. 1997).

Maize streak disease

Maize streak disease was first reported in 1901 in South Africa. It has since been recorded in many other African countries and adjoining islands (Rose 1978). The disease has not been confirmed elsewhere, although a somewhat related strain of the hopper-borne geminivirus that causes maize streak has been isolated from a perennial grass *(Digitaria sanguinales)* in Vanuatu (Dollet et al. 1986).

Storey used maize streak virus in his classic studies on the mechanisms of transmission by leafhopper vectors of the genus *Cicadulina* (Campbell & Bruehl 1986). The virus was studied later in Kenya in collaboration with laboratories in the UK. However, the epidemiology of streak disease received little attention outside South Africa until field-based studies began in Zimbabwe (Rose 1974, 1978) and later in Nigeria, Zaire (now Peoples Democratic Republic of Congo) and Uganda. It is unclear whether the initial neglect was because the disease was overlooked or of only limited economic importance. Whatever the previous situation, serious epidemics are known to have occurred in many parts of Africa in the early 1980s, and streak is now recognized as an important constraint on yield, especially in late-planted and irrigated maize. Nevertheless, only limited attempts have been made to elucidate the epidemiology of the disease. This is likely to be very complex because of the many host and vector species involved and the many different environments in which maize and other graminaceous hosts are grown. They include forest and savannah areas in the lowlands and also at mid-elevations. Moreover, maize is grown in very diverse cropping systems which range from mixed smallholder plantings of open-pollinated seed retained from previous crops to large commercial fields using hybrid seed, fertilizers and irrigation. In some areas maize is grown throughout much of the year and sometimes with the benefit of irrigation, whereas in many other areas crops are seasonal and may alternate with wheat or other winter cereals which are also hosts of streak virus and *Cicadulina* vectors.

The complexities that can arise are apparent from experience in Zimbabwe where some crops are irrigated and vectors disperse between wild and cultivated grasses, maize and other cereals depending on seasonal factors influencing the suitability of the different hosts for colonization and reproduction. The main flight period is during the cool, mainly dry months of the southern hemisphere winter between April and September. During this period there is extensive movement from the drying grasses and short-bodied migrant forms of the *Cicadulina* spp. predominate (Rose 1972). They fly considerable distances and give rise to scattered infestations of irrigated grasses and spring-planted maize. Maize streak can be dispersed far and spread is mainly into and not within plantings. The situation is very different during the moist summer months when long-bodied non-migrant forms predominate and spread is mainly local. Steep gradients of infection and edge effects are apparent and isolation is effective as a control measure, whereas it is ineffective during the main flight period (Rose 1974, 1978). Such detailed epidemiological studies are only now being undertaken elsewhere in Africa where the altitudes and agro-ecologies are very different from those in Zimbabwe. Meanwhile, the main approach to control has been through the development of resistant varieties (Efron et al. 1989). These have been produced at the International Institute of Tropical Agriculture (IITA) in Nigeria and elsewhere and have been effective in many parts of Africa. They are now being used widely by farmers or as parents for local adaptation in national breeding programmes.

Rice yellow mottle disease

Rice yellow mottle disease was first reported in 1966 when crops around Lake Victoria, Kenya, were affected. A sobemovirus was isolated from infected plants and shown to be transmitted by species of chrysomelid beetles, including *Chaetocnema pulla* (Bakker 1974). The area originally affected in Kenya was part of a new irrigation project which had led to an increase in rice cultivation due to the availability of water for sequential plantings throughout the year. Yellow mottle disease has since been found in similar circumstances in many of the other African countries where rice cropping practices have been intensified. Detailed observations in south-eastern Nigeria suggested a build-up of infection associated with the introduction of irrigation, new varieties and year-round cultivation (Rossel et al. 1982).

Some of the worst epidemics of yellow mottle disease have been in the Republic of Niger where the irrigated area increased 15-fold between 1974 and 1986 (Reckhaus & Adamou 1986, John et al. 1986). The disease was not noted in Niger until 1982, yet it was prevalent in almost all the irrigated areas in 1984. The main variety grown at the time was introduced from Asia and the overall incidence of infection exceeded 25 per cent. Farmers in Niger were advised to plant synchronously and to withhold irrigation water between plantings to provide a rice-free period and so restrict the build-up of inoculum and vector populations. They were not advised to use chemicals against the beetle vector because of the health and environmental risks involved. However, there are good prospects of utilizing the resistant varieties being developed at the International Centres in West Africa.

Many of the worst outbreaks of rice yellow mottle disease have been in introduced lowland varieties from Asia, whereas local African types have been less severely affected. Indeed, many upland accessions of the African rice *Oryza glaberrima* and local upland types of *O. sativa* are very tolerant. They sustain little damage, support low concentrations of virus and are being used to develop improved varieties (John et al. 1988). Attempts are also being made to use a wild species *O. barthii* that seems immune to infection.

These findings, the apparent absence of rice yellow mottle virus from other continents and its detection in a wild rhizomatous species *(O. longistaminata)* in Mali and Niger (John et al. 1984) are all consistent with the view that the virus is indigenous to Africa and to which local rices have become adapted (Fomba 1988). As with rice hoja blanca virus in Central America the apparent equilibrium established between host and pathogen seems to have been disrupted by the introduction of exotic varieties and an intensification of cropping practices (Thresh 1989).

Rice tungro disease

Rice tungro disease was first described in 1965 following outbreaks in the Philippines and successful transmission experiments with the rice green leafhopper *Nephotettix 'impicticeps'* (now known as *N. virescens)* (Rivera & Ou 1965). What is likely to have been tungro disease had been reported much earlier in the Philippines, Malaysia, Thailand and Indonesia under different local names. The earliest reports were in 1859, although no transmissible pathogen was implicated at the time, or until much later studies and the symptoms were for long attributed to unfavourable soil conditions (Ou 1984).

Tungro is now known to be widespread and sometimes prevalent in all the main rice-growing areas of South-East Asia where it appears to be indigenous. Severe epidemics occurred at the time of the 'green revolution' in the late 1960s in India, Indonesia, Malaysia, Philippines, Sri Lanka and Thailand, soon after the release of the first International Rice Research Institute (IRRI) varieties. There have also been more recent epidemics in these countries and elsewhere in Asia (Chancellor & Thresh 1997). An unexplained feature of tungro is that the disease can suddenly become prevalent and cause serious losses throughout whole regions. Consequently, it has attracted considerable notoriety and politicians and administrators as well as agriculturalists are well aware of the serious consequences of devastating epidemics that cause famine and hardship and change substantial areas from being net exporters to net importers of rice. Such considerations explain the current allocation of large budgets for research and extension activities in attempts to combat tungro disease. These include the NRI/IRRI collaborative project begun in 1990 (Chancellor et al. 1996). Moreover, disease and vector monitoring and survey operations have been mounted by several National Programmes in efforts to determine damage thresholds and reliable methods of forecasting. There has also been widespread and in some instances misguided and irresponsible use of insecticides to control the leafhopper vectors.

There is considerable information on the two viruses involved in tungro disease and on the mechanisms of virus transmission by the leafhopper vectors (Hibino & Cabunagan 1986). Until very recently much less was known about the epidemiology of the disease, on the pattern, sequence and distance of spread into and within plantings and on the role of weed hosts (Chancellor et al. 1996). This has been a serious limitation of attempts to achieve control and the main emphasis has been on the use of vector-resistant varieties and insecticides. Little attempt is made to isolate or protect seed beds or to plant away from known sources of infection and the possible benefits of such measures are only now being assessed (Holt et al. 1996). However, farmers are encouraged to plant synchronously, to allow a break between successive plantings and to avoid very late planting. In Indonesia they are also advised to adopt recommended sowing dates so that plants are not exposed to infection when they are most vulnerable to incoming vectors (Manwan et al. 1985, Sama et al. 1991).

The need for varieties resistant to tungro and its main vector *N. virescens* became apparent at an early stage of the IRRI breeding programme, and routine screening tests have been made since the late 1960s (Khush 1977). With one exception all the IRRI varieties released since 1966 were rated as having at least some degree of vector resistance in the Philippines at the time they were introduced. Such varieties tend to escape infection (Heinrichs & Rapusas 1983) and they have played a major role in decreasing the losses that are otherwise likely to have occurred due to tungro disease. Indeed, it seems that tungro does not become a problem where vector-resistant varieties predominate, even though they are unable to withstand high inoculum pressure. This suggests that epidemics occur only where susceptibles are grown, or when vector populations have become adapted to previously resistant varieties.

Problems due to the emergence and build-up of vector populations able to thrive on previously resistant varieties have been less acute than those encountered with the rice brown planthopper *(Nilaparvata lugens)*. Nevertheless, there have been various reports of tungro epidemics associated with marked shifts in the behaviour of varieties that were originally regarded as virus and vector-resistant (Dahal 1988). Thus, previous views on the apparent durability of resistance to *N. virescens* (Khush 1984) have been changed and it is now accepted that populations are likely to adapt to resistant varieties within a few years of their general release (Ruangsook & Khush 1987). This explains the current interest in mechanisms of resistance, gene deployment and breeding strategies to provide varieties with more effective and durable forms of resistance, not only to the vector but also to the tungro viruses (Hibino et al. 1988).

Banana bunchy top disease

Banana bunchy top disease was first reported in the 1880s, when it caused serious damage in Fiji. The disease has since caused problems in many other parts of the Pacific region and South-East Asia, including the Philippines, Taiwan, India and most recently, Pakistan. Bunchy top is much less prevalent elsewhere as it is now under control in Australia, of limited distribution in Africa and the Middle East and absent in the Americas (Dale 1987). Plants that are severely affected by bunchy top disease are worthless but the disease also causes indirect losses. These are due to the costs of adopting eradication programmes and virus-free planting material and the need for routine applications of insecticide to control the aphid vector *(Pentalonia nigronervosa)*. There are also serious constraints on the movement of germplasm and other plant material between continents, as required by commercial companies and for breeding programmes. This has led to elaborate and expensive quarantine procedures involving 'third-country' transit and testing centres (Frison & Putter 1989).

Despite the great economic importance of banana, research on bunchy top disease has been seriously neglected and until recently there was uncertainty on the nature of the virus or viruses responsible (Harding et al. 1991). There is a continuing lack of information available on epidemiology and control and the most important findings have been made in sub-tropical areas of New South Wales, Australia (Allen 1983). There banana is an introduced crop of limited importance and it is grown in scattered plantings, mainly along hillsides to avoid frost damage. The climate and growing conditions are very different from those in the tropical areas of the Pacific region where banana and bunchy top disease are indigenous and prevalent. For example, in parts of the southern Philippines many smallholder plantings, large plantations owned by export companies and wild *Musa* spp. all occur in close proximity. Bunchy top disease is a problem in both types of cropping system and unusually there is an opportunity for comparative epidemiological studies. However, detailed information is only now being obtained, despite dissatisfaction with the existing methods of control involving eradication and the use of insecticides (Smith et al. 1998). There is a similar lack of information from elsewhere, although hosts other than *Musa* spp. are known to occur in Taiwan and are being removed as part of the continuing eradication programme on the island (H. J. Su, personal communication).

In Taiwan and elsewhere there has been considerable interest in the possibility of mild strain protection which could be an effective control strategy in those parts of Asia and the Pacific region where bunchy top is largely out of control and eradication is ineffective or impracticable. This is not the situation in Burundi and other parts of Central Africa where bunchy top occurs but does not seem to spread rapidly. However, action is required because the current benign situation could change, as happened in Israel where citrus tristeza virus was present for many years before it began to spread rapidly and cause serious problems (Bar-Joseph & Loebenstein 1973).

DISCUSSION

The six virus diseases considered in the foregoing sections include four of the five given the highest priority in the 1980s ODA research strategy (ODA 1989), but they were chosen primarily for their biological interest and great economic importance. They are not truly representative because they are far more widespread and have received much more attention than other tropical virus diseases, many of which have been seriously neglected or ignored. Nevertheless, the diseases selected are used here as a basis for discussing several important issues of general relevance.

The neglect of tropical virology

Other than cocoa swollen shoot the diseases considered have received inadequate attention in relation to their prevalence and importance and insufficient information is available on which to base effective control measures. This reflects the overall neglect of tropical plant virology and the lack of local facilities and expertise. The situation is particularly acute in the tropical countries of sub-Saharan Africa where the virologists now in post at the Cocoa Research Institute of Ghana still represent a substantial proportion of the total number employed for research on all crops in the entire region.

The inadequacies of the current approach are also apparent by comparing the overall effort on maize streak, groundnut rosette or cassava mosaic diseases in Africa with that given to maize dwarf mosaic or virus diseases of groundnut or potato in the USA or Europe. There is a similar disparity when the great amount of research on virus diseases of rice in Japan, or on cereal yellow dwarf in developed countries, is compared with that on virus diseases of rice and other cereals in the tropics. The problem is acute but beyond detailed consideration here. To a large extent it has arisen because the rapid development and expansion of plant virology in recent decades has been mainly in developed countries. It has involved a greatly increased commitment of resources, an increased specialization of staff and the use of sophisticated electron microscopes and other facilities that are seldom available in the tropics. The work of Storey in East Africa in the 1930s and of Posnette in Ghana in the 1940s was at the time at the forefront of virology, whereas now there is a large and increasing disparity in the amount and type of work being done in the tropics compared with temperate regions.

The problem has been recognized but not resolved satisfactorily. One response has been to establish plant virology laboratories and to appoint internationally recruited staff at several of the International Agricultural Research Centres (Bos 1976). These have made substantial contributions and also provide training and support for scientists from National Programmes. However, the total build-up of staff and resources has not been great, research programmes are limited and even in aggregate the overall effort in virology is less than at any one of the major institutes in UK or elsewhere in Europe. Another approach has been to utilize the expertise and facilities available in the UK and other temperate countries for work on tropical viruses. As indicated earlier this has been successful and to mutual advantage. However, it has led to the paradoxical situation that more is known about the structure and properties of some tropical viruses than about the behaviour of the diseases they cause. For example, the nucleotide genome sequences of strains of maize streak and African cassava mosaic geminiviruses have been obtained, yet important features of their epidemiology remain obscure. A further indication of the unsatisfactory situation that has arisen is that only 20 of the 180 contributors to a recent treatise on viruses of tropical plants (Brunt et al. 1990) were based at laboratories in the tropics. Moreover, no information whatsoever is presented on the ecology or control of many of the viruses that are otherwise considered in great detail.

Clearly, research done at International Centres or in temperate countries should complement and support rather than supersede that done by national scientists in the tropics. However, there are great practical difficulties in implementing a solution to this somewhat idealistic comment. A sustained commitment of substantial funds and technical support is required on a national or regional basis. There are few signs that they will be made available by national governments, international organizations or multinational donors and the problem has been exacerbated in recent years by a substantial diversion of funds from 'applied' biology to biotechnology. Meanwhile viruses continue to cause substantial losses and few tropical countries are able to utilize the advances in plant virology being made elsewhere.

Quarantine

Some consider it to be inevitable that all pests and pathogens will eventually become established in all the areas where environmental conditions are suitable for their survival. This pessimistic and defeatist view is supported by experience with several tropical viruses that have been widely distributed in seed stocks or vegetative propagules (Tables 1 and 2). However, many other examples can be cited to show the advantages of adopting effective quarantine procedures in attempts to maintain the present limited distribution of viruses and their vectors. Indeed, several of the viruses considered earlier are largely or entirely restricted to certain continents. For example, rice yellow mottle virus seems restricted to Africa, rice tungro viruses to Asia and rice hoja blanca virus to the New World.

The importance of quarantine is generally recognized and several comprehensive texts are available setting out general principles and techniques (Hewitt & Chiarappa 1977, Kahn 1989). These are now being supplemented by detailed guidelines for specific crops that are being drafted at specialist workshops convened by the Food and Agriculture Organization of the United Nations (FAO) and the International Board for Plant Genetic Resources (now the International Plant Genetic Resources Institute). The problem is to implement such recommendations satisfactorily and to ensure that effective procedures are adopted, despite the vagaries of human behaviour and the ever-increasing traffic in plants and plant produce in world trade and agricultural development, and also for research purposes. Bulk consignments or the large batches of genetically diverse material required by breeders, agronomists and horticulturalists present particular difficulties. These problems are not easily resolved and are exacerbated when relief operations are mounted at times of famine, insecurity or other crises. Moreover, even amongst agricultural scientists there is a tendency to regard quarantine as a routine and uncongenial chore that requires no great commitment of resources or expertise. In reality the situation is very different and quarantine personnel must have the capacity and expertise required to handle a wide range of crops, pests and pathogens with which they may have had limited opportunity to become familiar and which may be growing in very atypical conditions.

In view of the many difficulties encountered and from past experience it is likely that further spread of viruses and vectors will occur. Nevertheless, there are clear advantages in setting up and maintaining adequate quarantine facilities to preserve the *status quo* for as long as possible and so delay the occurrence of new problems and the inevitable losses that would occur.

Disease incidence and crop loss assessment

There have been frequent references in this text to diseases that are 'prevalent', 'serious' and cause 'substantial' losses. However, such terms are qualitative and subjective and give no reliable indication of actual disease incidence or crop loss. This reflects the lack of quantitative information, which is a serious limitation in developing overall research strategies and in setting priorities. A disease such as cocoa swollen shoot in Ghana must have had a great economic, social and even political impact, yet there have been no reliable estimates of crop loss or economic significance and the status of the disease in relation to the serious damage caused by cocoa mirids or to other constraints on yield is uncertain. Similarly, there are few data to support the widely held view that tungro is the most important virus disease of rice in South-East Asia. The disease is certainly one that has a high political 'profile', mainly because of the occasional severe epidemics which can devastate whole areas and necessitate massive imports to maintain food supplies. Such outbreaks cause great hardship and may lead to the widespread use of insecticides to control vectors. However, they should be considered within the overall context of the huge areas of rice grown in such countries as India (currently *c.* 41.2 million ha), Indonesia (*c.* 10.9 million ha) and Philippines (*c.* 3.4 million ha) and the limited number of reports of serious losses. Even when data are available there may be serious difficulties of interpretation because many relate simply to 'areas affected', which indicate the presence or absence of tungro disease in the fields sampled and *not* disease incidence.

The losses caused by tungro or other virus diseases cannot be estimated readily as it is necessary to obtain survey data on the incidence of infection at different stages of crop growth and over several cropping seasons to obtain truly representative data. Information is also required from field experiments designed to assess the effects of typical virus strains on the main varieties grown when inoculated at different stages of growth and in different cropping systems. Both types of data are difficult to obtain on an adequate scale, especially for important crops that are grown widely and in very diverse conditions. The methodology is available (Bos 1982), but few experiments or surveys have been done with tropical crops and this is another manifestation of the overall shortage of facilities and personnel.

The lack of quantitative data on disease incidence and crop loss make it difficult or impossible to draw any definitive conclusions on possible long-term trends. Nevertheless, it is widely assumed that losses have increased as cropping systems have become more intensive, as fallow periods have shortened, and through the increased use of fertilizers, irrigation and exotic new varieties (Thresh 1982, Bos 1992). It is important to appreciate that this remains a plausible assumption, even though it has been used to support a more holistic ecological approach, not only to plant virus diseases but also to other plant protection problems (Bos 1993).

Serious epidemics have undoubtedly occurred in the past, as evident from the early reports of cassava mosaic, groundnut rosette and maize streak in Africa, of banana bunchy top in the Pacific region and of tungro in Indonesia. Whether the situation has since deteriorated or there is now a greater awareness of pest and disease problems as a consequence of improved communications and an increase in the overall scientific effort is unclear. The issue is of crucial importance in relation to any future attempts to increase crop production by changes in cropping practices or through technical innovations. Attempts at retrospective analysis, interpretation and explanation that are made only after serious disease problems have been encountered have serious limitations. There is a great need for definitive base-line data so that the effects of any further innovations or changes in cropping practices can be assessed and an appropriate response can be mounted.

Comparative epidemiology

Attention has been drawn in this paper to the various opportunities for studying the comparative epidemiology of the same diseases in contrasting cropping systems or environments and in different agro-ecologies. Such studies have rarely been undertaken and there is seldom epidemiological information of any type. This undermines current approaches because an understanding of the pattern and sequence of virus spread into and within crops can be expected to facilitate the development of control measures.

The advantages of a comparative epidemiological approach are apparent from experience with the six diseases considered here. Cocoa swollen shoot is an archetypal 'crowd' disease that does not spread quickly or far to any considerable extent and for this reason can be controlled by isolation and sanitation (Thresh et al. 1988a). By comparison, cassava mosaic in the lowland rainforest areas of West Africa and in the epidemic areas of Uganda behaves as a 'vagile' disease. It is spread quickly and far by its whitefly vector and is not amenable to control by isolation or sanitation (Fauquet et al. 1988, Otim-Nape et al. 1997). Maize streak differs in that it behaves as a 'crowd' disease in some circumstances or at certain times of year and as a 'vagile' disease in others (Rose 1974, 1978). Comparable information on the behaviour of tungro and yellow mottle diseases of rice and on banana bunchy top in the tropics and the areas to be treated and approaches to be considered in mounting effective control measures is only now being obtained.

There are large differences between the six diseases in the epidemiological significance of their wild hosts. For cassava mosaic they are considered to be of little or no importance now that infection is so prevalent in cassava (Fauquet & Fargette 1990). The situation is similar with cocoa swollen shoot disease, although wild hosts are of some importance in initiating outbreaks in certain areas (Posnette 1981). Maize streak behaves very differently as grasses are of great and continuing importance as sources of virus and vectors from which spread occurs to maize and other cereals (Rose 1978). There is only limited information of this type on rice tungro, banana bunchy top and rice yellow mottle diseases, which is a further indication of the extent to which the epidemiological approach has been neglected.

The underlying causes of epidemics

Many factors influence the development of epidemics and it is simplistic to assume that there can be any single underlying cause of the serious epidemics of diseases such as those considered here and elsewhere (Thresh 1980a). Nevertheless, for many diseases one particular factor seems to be of crucial importance. This is illustrated by experience with four diseases that are largely or entirely restricted to Africa: cocoa swollen shoot, maize streak, cassava mosaic and groundnut rosette. These diseases can be categorized as being of the 'new encounter' type (*sensu* Buddenhagen 1977). In each instance the main host is an introduced crop that has been affected as a consequence of the pathogen spreading from indigenous hosts. Thus problems were almost inevitable once these crops were exposed to infection when grown on a large scale in Africa.

An additional contributory factor in at least some instances is likely to have been the extreme vulnerability of the introduced germplasm of exotic species that had no previous exposure to African viruses. For example, the rapid expansion of cocoa growing in West Africa which occurred early in the 20th century was based largely on the Amelonado cultivar which was found later to be one of the most susceptible to swollen shoot virus (Posnette 1981, Thresh et al. 1988b). Similarly, recent South American introductions of cassava soon succumbed to cassava mosaic virus when grown in conditions where locally selected types from much earlier introductions were far less severely affected (Hahn et al. 1980). It is also notable that many outbreaks of rice yellow mottle disease are associated with the introduction of exotic Asian varieties to replace the indigenous African ones grown previously (Thresh 1989).

Banana bunchy top and rice tungro diseases differ greatly from the four African ones in that they are mainly important in crops at or near their centre of origin. A crucial factor in the epidemiology of bunchy top is that banana is propagated vegetatively. Growers have only limited access to virus-free planting material and much use is made of infected stocks. This has led to the widespread dissemination of banana bunchy top virus and provides initial foci from which there is further spread by aphid vectors. Thus the cycle of infection is maintained and it is not readily broken. Particular difficulties are encountered by small-scale banana producers who have little opportunity to use virus-free material, roguing or isolation, or to develop regular planting and roguing schedules as practised on commercial plantations (Smith et al. 1998).

The problems posed by rice tungro disease are also closely associated with the cropping systems adopted. Pests and diseases now have far greater opportunities to thrive in the main irrigated rice-growing areas than in the original wild stands, or in the earlier seasonal, mainly rain-fed agriculture. Definitive evidence is lacking, but the apparent increase in the losses due to tungro and other rice diseases has been associated with the increased use of fertilizers, irrigation and short-duration varieties (Thresh 1989). These innovations have led to more intensive cropping patterns due to the shorter interval between successive crops and the wider latitude in planting dates.

Serious losses due to viruses as experienced in rice in South-East Asia, and to a lesser extent in South/Central America and Africa, are likely to occur increasingly with maize, cassava and other staple crops as attempts are made to increase food production in the tropics. This emphasizes the magnitude of the problems now facing applied biologists in attempting to devise means of exploiting the benefits of new varieties and other innovations without increasing the losses due to pests and diseases. Virologists have an important role to play in the continuing debate on the issues involved and in developing improved control measures that can be integrated with those adopted against other pathogens and pests. However, virology is currently under-represented compared with other crop protection disciplines and it is essential that the deficiency should be redressed if much progress is to be made.

CONCLUDING REMARKS

This consideration of the current status of tropical plant virology has arrived at somewhat pessimistic conclusions, but this was largely inevitable. Studies to date have been so limited and are at such a rudimentary stage of development compared with equivalent research in many temperate regions that many more viruses are likely to be present than have yet been described. Moreover, many of the tropical viruses that have been reported have been studied inadequately and there is little information available on their epidemiology or control. A further difficulty is that cropping systems continue to change and influence the status of pests and pathogens as new crops, varieties and practices are introduced and as farmers attempt to increase production and react to changes in the environment and to economic and social factors.

Clearly the overall effort that has been and is being made in tropical virology is totally inadequate in relation to the magnitude of the problems encountered. There is an obvious need for a far greater allocation of personnel and resources if these problems are to be addressed and if food production is to increase to meet the ever-increasing demand. The need is great and there are scientific, economic, political, social and humanitarian grounds for ensuring that it is met.

In this lecture one of the main objectives has been to demonstrate the substantial contribution that has been made by UK scientists to tropical plant virology. The achievements have been substantial and exemplary and have set a trend for other countries to follow. Nevertheless, much remains to be done and I believe that UK virologists and vector ecologists have a continuing and increasing role to play. Staff of the Pest Management Department of NRI, University of Greenwich, are particularly well placed to do so. This follows the decision taken in the late 1980s to recruit plant virologists and epidemiologists and to divert some of the entomological and modelling expertise that was already available within the Institute to the study of plant virus vectors and disease control strategies. Moreover, it was possible to utilize the experience gained and the contacts made in previous entomological studies in the tropics. Field-based projects were mounted in Africa and in Asia on cassava mosaic, rice tungro, maize streak and several other diseases. These studies have recently been extended to groundnut rosette and rice yellow mottle and there is great scope for further extension because there are few other comparable groups operating in Europe or elsewhere. Inevitably there will be a need to adopt an ecological approach, the merits of which have long been apparent from the early studies discussed here and previously (Thresh 1980b, 1981).

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