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The Virus Complex Causing Swollen Shoot Disease of Cacao in West Africa

J. M. Thresh and T. W. Tinsley, West African Cocoa Research Institute, Nigerian Substation Moor Plantation, Ibadan, Nigeria

Cacao is grown in many tropical countries and virus diseases have been reported in Ghana, Nigeria, Ivory Coast, Sierra Leone, Trinidad and Ceylon. They may also occur in Java, Sumatra and South America, where suspicious symptoms have been recorded (8). The viruses and the diseases they cause have received little attention except in Trinidad and West Africa, where numerous symptomatically distinct isolates have been made and ascribed to three distinct viruses (9). The cacao necrosis and cacao mottle leaf viruses have a limited distribution and are unimportant. By comparison, the virus complex causing swollen shoot disease is widespread and one of the most important factors influencing yield. The relationships between the swollen shoot viruses form the subject of the present paper. They are complex and equivocal and have parallels with problems encountered in classifying viruses of other crops.

The collection of different isolates

The symptoms on trees affected by swollen shoot disease in West Africa are not always the same, and swellings are common in some outbreaks but rare or even absent in others. The leaf symptoms also differ in type and severity between and within outbreaks. These differences can be caused by the host, but typical isolates from dissimilar outbreaks usually cause equally dissimilar but consistent symptoms on uniform test plants.

More than a hundred symptomatically distinct isolates have been studied and even more could be obtained with increased attention to the finer details of symptom expression. Different isolates from the same outbreaks and localities are most readily distinguished by their virulence in seedlings, as they cause symptoms differing in severity but not in type. By comparison, typical isolates from widely different areas cause symptoms which differ in type and perhaps also in severity (Figure 1). These minor differences between isolates from the same trees and outbreaks and greater differences between isolates from elsewhere are a feature of cacao swollen shoot disease and have parallels with the situation in other crops (3).

Criteria available for classifying isolates

Symptoms are notoriously unreliable for indicating relationships between viruses affecting the same host and attempts have been made to find other criteria for classifying the numerous isolates from cacao.

1. *Physico-chemical properties and serology.* The inability to transmit any of the cacao viruses by sap inoculation means that there is no information on their properties in *vitro* and attempts to produce antisera have failed.

2. *Insect transmission and vector specificity.* The different isolates causing cacao swollen shoot disease are not uniformly transmitted

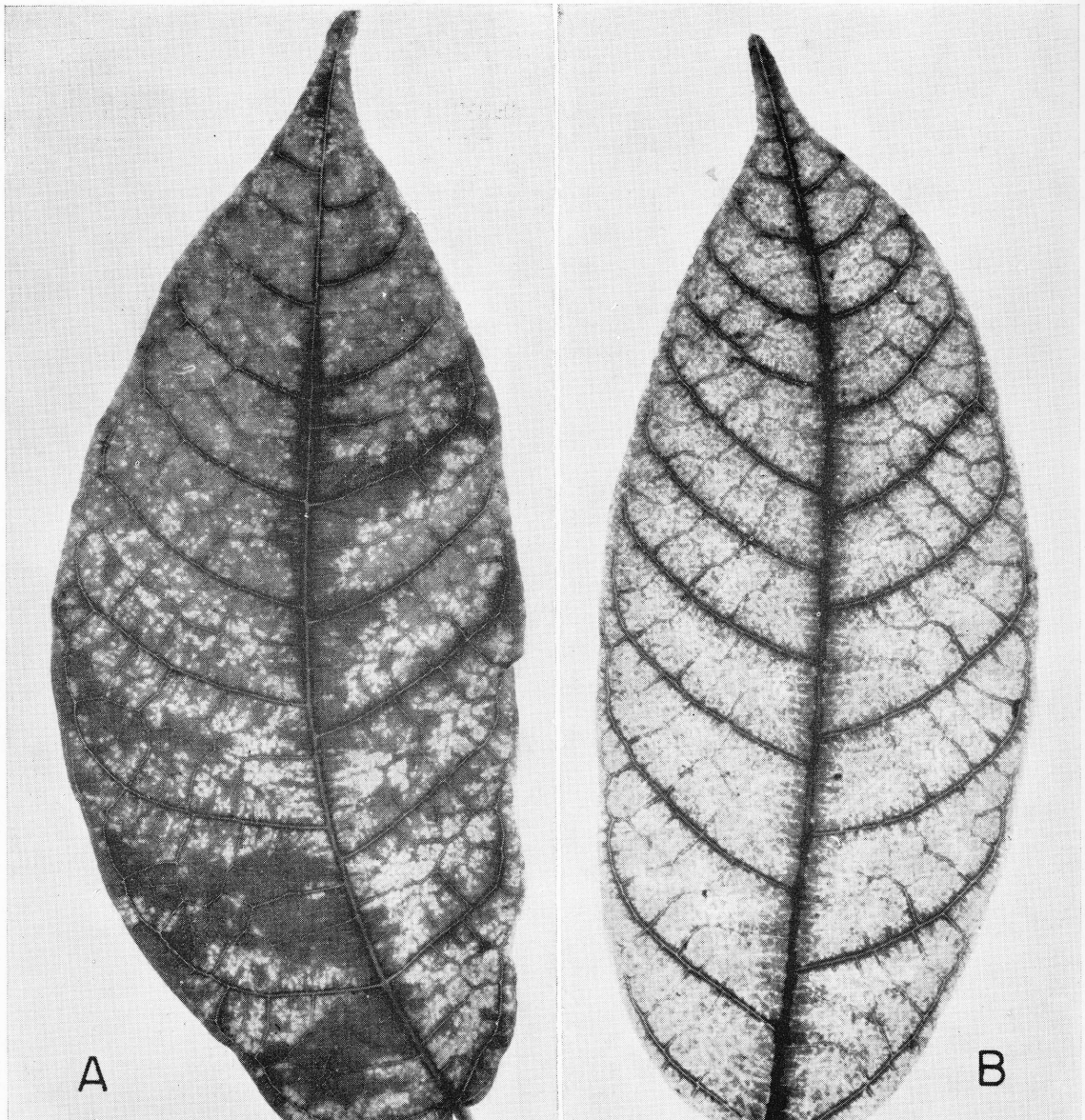

Figure 1. Symptoms caused by different isolates of cacao swollen shoot virus. A. Conspicuous leaf symptoms caused by an isolate from an outbreak found near Abuku in the Ibadan Province of Nigeria. B. Extensive chlorosis caused by an unrelated isolate from Egbeda in the Ibadan Province of Nigeria.

by all the mealybug species which are vectors and this suggests a possible approach to classification, as with other viruses (5). However, only a few of the isolates have been investigated, the key mealybug species are not always readily available and concentration effects may mask qualitative differences between isolates. This makes experiments difficult to standardize and the available results are inadequate. Virus-vector relations as used

to distinguish the viruses of strawberry and other crops are also of limited value and all the isolates yet tested have been transmitted in a similar way.

3. *Host range.* Many viruses and virus strains have been characterized by their host range, but this approach has been limited with cacao viruses which seem to infect only some species in the Tiliales and Malvales.

The New Juaben isolate seems to have the widest host range, which includes all the species known to be susceptible to other isolates (10). These may be grouped according to their ability to infect three key species, but only a limited number of isolates have yet been investigated and large-scale work is difficult. This is because some susceptible species resist or tolerate infection and often show inconspicuous or transient symptoms. Furthermore, mealybugs must be used for the inoculations and to identify virus in suspected hosts.

4. *Protection test.* Plants already infected with one virus are often immune or show no additional symptoms when inoculated with a related strain. By comparison, unrelated strains usually super-infect and cause additional symptoms and effects on growth. Tests using these interference phenomena have given particularly valuable evidence on strain relationships with viruses of many different crops (1).

Numerous tests have been done with isolates from cacao and grafts have been used for most of the inoculations. One difficulty has been to recognize the symptoms of the challenging isolate whenever they occur on plants already infected with the first. This means that the interpretation of the results is equivocal unless the tests are limited to pairs of isolates which cause symptoms differing greatly in type or severity. Furthermore, reciprocal tests are desirable but not always possible, because virulent symptoms can be recognized on plants already infected with a mild strain but not vice versa. Despite these limitations, certain virulent isolates consistently fail to produce additional symptoms on plants infected with a mild strain. Other viruses fail to cause recognizable symptoms on plants already showing the usual symptoms of the first inoculation. However, such instances of interference are rare and most tests have failed to suggest any close relationships between typical isolates from different localities in the Ivory Coast, Ghana and Nigeria. Because of this, it has been suggested that the whole technique should be re-examined and mealybugs used for the challenging inoculations (9). There are also possibilities of using the Holmes test (4) for virus relationships (7). This is based on the observation that unrelated (but not related) pathogens usually have cumulative effects on the growth of their host.

Relationships between isolates causing swollen shoot disease

Protection tests provide the only reliable evidence on relationships between the numerous isolates causing swollen shoot disease and can be used to distinguish numerous groups. Isolates in the different groups do not interprotect, have cumulative effects on growth and cause dissimilar leaf symptoms. By comparison, the isolates within each group interprotect, do not have cumulative effects on growth and cause symptoms of a similar type. They may, however, differ greatly in the severity of their effects. For example, some isolates cause only mild symptoms and have barely detectable effects on growth, whereas others cause conspicuous swellings and leaf mosaic, resulting in severe stunting and perhaps death. This emphasizes the misleading nature of a classification based on the ability of the different isolates to cause stunting, swellings and the various leaf symptoms. This approach was attempted but has now been abandoned.

In Ghana, most attention has been given to the group of interprotecting isolates collected from the New Juaben district of the Eastern Province. These isolates also interprotect with others collected from more distant localities near Konongo and Sedi Nkawie in Ashanti and from Kongodia in the Ivory Coast. Numerous other isolates have been made from Ghana and the Ivory Coast and these do not usually protect against those from New Juaben or against each other.

There have been few experiments with different isolates from adjacent trees and localities and the available results of protection tests may give a false impression of heterogeneity. However, isolates which do not interprotect have been collected from adjacent trees at Mamfe and similar results have been reported from the Western Province, where the situation is particularly complex. This may be due to the frequent spread of virus from indigenous hosts, in which mutation and selection may have occurred for many years.

Groups of interprotecting isolates also occur in Nigeria and the one from Egbeda includes several which cause symptoms differing in intensity and virulence. Other isolates which interprotect have been collected from outbreaks near Offa-Igbo and a further group from Abaku. The two isolates from Olanla and one collected 65 miles away at Ilesha form an additional group. These localities are the only ones to have been investigated in detail. Elsewhere in Nigeria many other isolates are known to be immunologically distinct and additional tests on material from the field will probably reveal that they too have numerous related strains.

Protection clearly indicates close relationships and the isolates within each group are most conveniently referred to as related strains. The status of the many different groups is more equivocal. Failure to protect may mean that some or all of them should be referred to as distinct viruses. Alternatively, the protection tests may be taken to indicate only the closest affinities between the strains of related viruses. This is certainly a convenient assumption, because all the groups cause virtually the same disease and it would be unreasonable and misleading to give them separate names. For this reason, swollen shoot disease is considered to be caused by a complex of closely related cacao swollen shoot viruses, which have a similar host range, cause similar symptoms in cacao and are unusual in having mealybug vectors.

Analogies with viruses of other crops

The classification of the cacao swollen shoot viruses has been made particularly difficult by the failure to produce antisera and by the limited results from protection tests. The situation with many other viruses is similar. For example, the viruses causing curly top of sugar beet in the Americas also occur in numerous immunologically distinct groups, cause virtually the same disease and have similar leaf hopper vectors. Furthermore, sugar beet in the Americas and cacao in West Africa are exotics and may have been infected recently by the spread of virus from indigenous hosts.

There are several serologically unrelated tobacco necrosis viruses, but they have not been given separate names because they all cause similar diseases and have similar physicochemical properties. They may be analogous to the complex of swollen shoot viruses and the ring spot viruses are also comparable. Several of these cause distinct diseases, are unrelated serologically and are given separate names. Nevertheless, they may be transmitted in the same way and have similar properties. Each virus also occurs in numerous distinct strains and only the most closely related ones in each group will interprotect (3). As with the swollen shoot viruses, related strains usually come from nearby localities, with greater differences between those from elsewhere.

It is not proposed that binomial nomenclature should be introduced for cacao viruses, but the strains and groups of the swollen shoot complex may correspond or be at least analogous to the varieties and species of higher organisms. On this terminology the complex itself becomes a genus and this grouping of related viruses may indicate phylogeny. It is certainly convenient to assume that the swollen shoot viruses have had a common origin, perhaps in indigenous hosts, long before cacao was introduced to West Africa. This cannot be proved but cacao viruses which do not interprotect are now known to occur in *Cola chlamydantha* K. Schum. growing in different parts of remote forest reserves in the Western Province of Ghana (11). Furthermore, interference between strains within the New Juaben group does not always result in complete protection (6). This indicates different degrees of relationship and related strains

may eventually diverge until interference is no longer detectable.

Comparable evolutionary trends could explain the development of the ring spot viruses from a common source ; similarly with viruses causing cucumber mosaic, and aspermy disease. These groups and the tobacco necrosis and beet curly top viruses may be conveniently referred to as genera and many others may be proposed. However, as Bawden (1) has stated, their arrangement into the equivalent of families and orders is at present obscure and may have to await further physical or chemical techniques. Alternatively, other features such as mode of transmission and particle morphology could be employed (2). For example, many workers have already stressed the apparent similarities between the leaf hopper transmitted viruses causing diseases of the "yellows" type. Similarly, Bawden has stressed the affinities between potato virus Y, henbane mosaic virus, tobacco etch and soybean mosaic viruses and others which do not persist in their aphid vectors. A further group could comprise the viruses which have spherical particles and which can be crystallized. These also resemble each other in physicochemical features, are inactivated in the same way and cause diseases including turnip yellows, turnip crinkle, bean southern mosaic and squash mosaic.

Summary

Cacao necrosis and cacao mottle leaf viruses have limited distributions in West Africa and are unimportant. By comparison, the cacao swollen shoot viruses are widespread and occur in numerous symptomatically distinct forms. There are usually only minor differences between isolates from the same outbreaks and localities, with greater differences between isolates from dissimilar areas. The isolates may differ in host range and are not uniformly transmitted by all the mealybug species which are vectors.

Isolates from the same trees, outbreaks and localities usually protect against each other but not against isolates from elsewhere. This suggests that isolates in the swollen shoot complex can be arranged into groups, within but not between which the strains interprotect and are closely related.

The situation with the cacao swollen shoot viruses resembles that with viruses of certain other crops, in which similar difficulties have been encountered in developing suitable criteria for classification.

LITERATURE CITED

1. BAWDEN, F. C. 1950. *Plant viruses and virus diseases*. Chronica Botanica Company, Waltham, Mass., U.S.A.

2. BRANDES, J. and C. WETTER. 1959. Classification of elongated plant viruses on the basis of particle morphology. *Virology* 8 : 99-115.

3. HARRISON, B. D. 1958. Relationships between beet ringspot, potato bouquet and tomato black ring viruses. *Journ. Gen. Microbiol.* 18 : 450-460.

4. HOLMES, F. O. 1956. A simultaneous infection test for viral interrelationships as applied to aspermy and other viruses. *Virology* 2 : 611-617.

5. POSNETTE, A. F. 1950. Virus diseases of cacao in West Africa. VII. Virus transmission by different vector species. *Ann. Appl. Biol.* 37 : 378-384.

6. POSNETTE, A. F. and J. M. TODD. 1955. Virus diseases of cacao in West Africa. IX. Strain variation and interference in virus 1A. *Ann. Appl. Biol.* 43 : 433-453.

7. THRESH, J. M. 1960. Virus research. *Ann. Rep. W. Afr. Cocoa Res. Inst.* 1958-1959.

8. THRESH, J. M. and T. W. TINSLEY. 1958. Viruses of cacao ; the world situation. *Proc. 6th Inter-American Cacao Conference, Colombia.*

9. THRESH, J. M. and T. W. TINSLEY. 1959. The viruses of cacao. *Tech. Bull. W. Afr. Cocoa Res. Inst.* 7.

10. TINSLEY, T. W. and A. L. WHARTON. 1958. Studies on the host ranges of viruses from *Theobroma cacao* L. *Ann. Appl. Biol.* 46 : 1-6.

11. TODD, J. M. 1951. An indigenous source of swollen shoot disease of cacao. *Nature*, Lond. 67 : 952-953.