The reaction of different cacao types to infection with swollen-shoot virus

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SUMMARY

Graft tests were used to investigate the reaction of different cacao types to infection with swollen-shoot virus. Budlings of all the clones in Nigeria were infected with virulent isolates so that the sequence of symptom expression could be followed.

All the Amelonado and Morona clones and most of the Trinitarios were affected severely. They showed extensive, conspicuous leaf symptoms and large stem swellings. The Upper Amazon cacaos reacted less uniformly. The Scavina clones developed conspicuous symptoms, whereas those produced in the Nanay and Iquitos types were often slight and sometimes transient. Many Parinari clones and hybrids of Parinari parentage showed an extreme reaction: a veinal necrosis which often caused complete collapse of affected leaves and sometimes extended to the stem and growing point. Tests on progenies derived from crosses of sensitive with tolerant parents suggested that the sensitive reaction was dominant.

These results are discussed in relation to the present plant breeding programme and to the possibility of releasing high-yielding hybrid progenies for replanting the extensive and heavily infected areas of Nigeria, within which control measures have been stopped.

INTRODUCTION

The viruses causing swollen-shoot disease of cacao in Nigeria have been found in all the major producing areas of the Western Region, where they are an important factor influencing productivity. Eradication of infected trees is the only control measure which can be practised on a large scale to check the spread of infection and it has been attempted by the government since 1947. However, efforts to eradicate swollen-shoot disease from the Region failed and have been abandoned in two large areas involving a total of over 1000 square miles. Within these areas virus has spread unchecked and the cycle of infection is maintained by continuous replanting on many small holdings (Lister & Thresh, 1957; Thresh, 1959).

There are no immediate prospects of obtaining cacaos immune or highly resistant to infection and the alternative of using tolerant types has been considered in Ghana and rejected (Posnette & Todd, 1951). This was because attempts were then being made to eradicate the disease and the presence of tolerant trees would have increased the difficulty in identifying infected trees. These considerations do not apply in the

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areas of Western Nigeria where control measures have been abandoned and tolerance studies were resumed to seek high-yielding types that would not be severely affected by virus infection. The present paper describes preliminary tests for tolerant types suitable for use in a breeding programme and in field trials.

Inoculation techniques

MATERIALS AND METHODS

All transmissions were made by grafting, which is the simplest and most reliable method available. In preliminary experiments buds of the clones under test grew and showed symptoms rapidly when grafted on to saplings which had been infected with a virulent virus isolate for 2 years. This method revealed consistent differences in behaviour between different clones: some grew vigorously, almost without symptoms, whereas others were stunted. However, infected saplings grew slowly to the stage at which they could be budded and were too few for the main experiments. In these, healthy buds of the clones under test were grafted on to 6-month-old healthy Amelonado seedlings at about 6 in, above soil level. The stocks were cut back to just above the bud after 3 weeks, when union had occurred. The stocks were then grafted with patches of bark from Amelonado seedlings infected with a particularly virulent isolate of swollen-shoot virus. One isolate, collected originally from Egbeda in Western Nigeria (Thresh, 1961), was used throughout the main experiments and additional isolates from Abaku, Olanla, Offa-Igbo and Ondo were compared in one series of tests. Symptoms usually appeared in the budlings within 2 months and records were made frequently for 6 months to follow the full sequence of symptom expression. The practice of budding on to highly sensitive Amelonado cacao may have slightly exaggerated the symptoms shown in the scion. Tests with rooted cuttings indicated that this effect was unimportant and there was no evidence that any of the symptoms recorded were from incompatibility between stock and scion.

Cacao material available

Most cacao breeding in West Africa has been done in Ghana, where selections have been made from the local Amelonado and Amelonado-Trinitario populations (Posnette, 1943) and from Amazon and Imperial College (I.C.S.) selections collected in Trinidad (Posnette, 1951; Knight & Rogers, 1955). The Trinidad introductions were made as pods and form the T series, of which numbers 1 to 59 were the result of natural pollinations. Progenies 60 to 102 were mainly the result of hand pollinations involving Parinari, Nanay, Iquitos and Scavina Amazons. Particular parents are referred to in the text by the codes used in Trinidad: Pa, Na, I.M.C. and Sca, respectively.

The most promising representatives of each type and the parents used in the production of a special series of hybrids have been given W.A.C.R.I. clone numbers (C I to C85). Many representatives of this series established as cuttings or budlings in Nigeria were used in the present investigations. Additional material used included introductions from Trinidad growing at the Gambari Experimental Station and hybrids growing in the two series of W.A.C.R.I. variety trials in Nigeria. The first series is intended to under contrasted cli Amazon × Amelonad standards (Glendinni

Amelonado clones

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Parinari Amazons

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series is intended to obtain information on the performance of different Amazons under contrasted climatic conditions. The second series compares the growth of Amazon × Amelonado and Amazon × Trinitario hybrids with Amazon and Amelonado standards (Glendinning, 1962).

Amelonado clones

RESULTS

The Amelonado clones developed conspicuous symptoms when infected with the Egbeda virus. When they were budded on to infected root-stocks, the first formed leaves became discoloured and crinkled and many fell before reaching maturity. The surviving leaves showed extensive interveinal chlorisis (Pl., fig. 1) large stem swellings appeared and growth was stunted. Budlings on healthy stocks which were infected later showed a similar but less severe reaction and most plants passed eventually into a relatively mild chronic phase in which the leaf symptoms tended to be restricted to the areas alongside the main veins.

Some clones sometimes showed chlorotic flecks as a preliminary symptom, limited to the third- and fourth-order veins, which sometimes became necrotic. This necrotic reaction rarely affected the main veins and did not spread into the shoot.

Because of the very limited variation within the Amelonado type of cacao in West Africa it is not surprising that most of the clones reacted similarly. Indeed, the few that showed relatively inconspicuous symptoms reacted more severely when retested. Our experience is consistent with previous observations on the apparent sensitivity of Amelonado cacao to other swollen-shoot isolates (Posnette & Todd, 1951). This is an unfortunate feature, because the large, uniform bean size and flavour of Amelonado cacao are desirable attributes and several clones have been used as parents in the production of hybrid seed.

Trinitario clones

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Most of the available Trinitario clones were hybrids with local Amelonados and they behaved very like the Amelonados in their reaction to the Egbeda virus. Crinkling and abscission of the leaves, severe chlorosis and large swellings were noted in the most sensitive types. These included a Nigerian selection T(N) 38, Criollo cacaos and T 39 seedlings obtained by the natural pollination of I.C.S. 6, a clone which tolerates virus infection in Trinidad (Baker & Dale, 1947). Other Trinitarios produced less conspicuous leaf symptoms, but these were often accompanied by very large swellings. Clones C 23 and C 26 showed very slight leaf symptoms and the swellings were slow to appear. Symptoms were even slighter in seedlings of T9 derived from an outstanding Costa Rican clone introduced to Trinidad as Costa Rica Red. These limited tests suggest that the variable Trinitario cacaos may include very tolerant individuals also suitable in other ways for use as parents of hybrid seed.

Parinari Amazons

The cacao of the Parinari tributary of the Upper Amazon is represented in West Africa by some pure-bred types and others derived from natural and controlled pollinations with other cacaos, notably the Nanay group. The effect of the Egbeda

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isolate was not the same in all clones and the most sensitive types gave a striking necrotic reaction which has not been reported previously (Pl., fig. 2). Symptoms appeared first as chlorotic flecks along the third- and fourth-order veins, which later became necrotic. Usually the necrosis then spread along the main veins and petioles, so that whole leaves wilted, and abscissed. The necrosis sometimes spread along the stem to the growing point and stopped growth. The axillary shoots which developed subsequently often showed a similar sequence of necrotic symptoms. The most severely affected plants died, and survivors passed into a chronic phase of infection with inconspicuous clearing and banding of the veins. The Parinari reaction was noted in the parent clone Pa₇, and in all its hybrids with Pa₃₅, Nanay and Iquitos trees. The Trinidad clone Pa₃₅ showed conspicuous symptoms without the necrosis, which occurred in some Pa₃₅ × Nanay hybrids.

When seedlings of the W.A.C.R.I. Series II progenies, derived from crosses between Amazon (Parinari × Nanay) hybrids and selected Amelonado or Trinitario trees, were infected, a proportion showed the Parinari necrosis whenever T79 (Na32×Pa7) trees were parents. A similar segregation occurred in progenies derived from intercrossing T63 (Na32×Pa35) trees which gave a necrotic reaction. Additional tests involved five groups of seedlings resulting from intercrossing Parinari×Nanay hybrids. Each group showed an apparent segregation of the Parinari necrosis and the less conspicuous Nanay reaction. The ratios involved are being investigated and a larger sample of the valuable Parinari population is being studied to select less sensitive types for further breeding.

Morona Amazons

Cacao from the Rio Marañon is poorly represented in West Africa and tests were limited to the open-pollinated progeny of two trees in Trinidad. Infected clones grew badly, produced very large swellings, and developed vein-clearing and chlorosis of the leaves.

Scavina Amazons

The Scavina Amazons were collected from Ecuador and are believed to have originated from the Napo tributary of the Upper Amazon. They have distinctive features, including great vigour and resistance to witches' broom disease in Trinidad (Holliday, 1955). The few clones in West Africa were derived from a single openpollinated pod (T 12) collected from one of the few original introductions to Trinidad. Not surprisingly, the different clones reacted to infection differently and our results differed from those obtained with Scavina material in Ghana (Blencowe, 1961). None of the five clones tested showed any evidence of tolerating the Egbeda isolate. Leaf symptoms and stem swellings were conspicuous and some clones reacted necrotically like the Parinari material. The young leaves of several clones showed large red patches and became mottled as the leaves hardened and developed chlorotic or translucent areas.

Progeny A of the Series I field trials is a hybrid between two of the Scavina clones and some seedlings became necrotic, whereas others produced only a conspicuous chlorosis.

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Nanay and Iquitos .

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The most tolerant hybrid derived from clone grew vigorous banding and chlorot symptoms were very Egbeda in sensitive parentage to C 77 we symptoms. This evid sensitivity is dominan of seedlings obtained with an Amelonado.

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Nanay and Iquitos Amazons

Similar cacaos were collected from the Nanay tributary of the Upper Amazon and nearby from an island off Iquitos. They are represented in Trinidad and in West Africa by some pure-bred types and hybrids derived from natural and controlled pollinations with other cacaos. Most clones at least partially tolerated infection with the Egbeda isolate and leaf symptoms were inconspicuous and limited, with few large swellings. In most clones early red-banding was followed by fine clearings of the third- and fourth-order veins, merging in some to form a faint reticulum over the whole leaf (Pl., fig. 3). A few produced more conspicuous symptoms with interveinal chlorosis and crinkling from the unequal growth of the veins and the tissues between.

The chlorotic vein-banding produced in the secondary or chronic phase of infection was often indistinct and confined to the third-order veins. These symptoms differed from those produced at a comparable stage in Amelonado cacao, where the vein-banding is much more obvious and often conspicuous along the main veins.

Seedlings produced by natural pollination of Nanay trees were less tolerant than the pure Nanay types and most produced symptoms typical of the Amelonados or Trinitarios. Open-pollinated Iquitos trees of the T16 and T17 progenies did not respond uniformly to infection, although most reacted less severely than the Nanays. As in Ghana (Dale, 1957), some produced only limited leaf symptoms sometimes accompanied by slight swellings. The Series I progeny F is derived from a cross between two T17 trees selected by Dale and some seedlings produced extensive speckled leaf clearings and large swellings, whereas others were more tolerant. The Series II progeny D is a hybrid between a T16 tree and a tolerant Trinitario. Vigorous seedlings of this parentage have shown only slight symptoms in field trials.

The most tolerant clone in the whole series of tests was C77, a T85 Nanay × Iquitos hybrid derived from a cross between the Trinidad trees Na34 and I.M.C.60. This clone grew vigorously when infected and produced slight often transient red veinbanding and chlorotic specks in the leaves (Pl., fig. 4), without swellings. These symptoms were very similar to those caused by a particularly avirulent isolate from Egbeda in sensitive Amelonado cacao (Thresh, 1961). Other clones of similar parentage to C77 were much less tolerant and the infected parents showed obvious symptoms. This evidence and the results of the Nanay × Parinari crosses suggest that sensitivity is dominant, a conclusion supported by the sensitive reaction of two groups of seedlings obtained by crossing C77 with a sensitive Nanay × Parinari hybrid and with an Amelonado.

The reaction of representative clones to infection with other Nigerian isolates

Many symptomatically distinct isolates of virus have been obtained from outbreaks of swollen-shoot disease in and around the abandoned areas of mass infection in Nigeria. Some isolates are considered to be closely related strains because they are antagonistic in protection tests, but others show no such evidence of close relationship (Thresh & Tinsley, 1960; Thresh, 1961). There is a similar situation in Ghana and the development of tolerant varieties would be complicated if the numerous strains differ in their effects on the various types of cacao.

Budlings of representative Nanay, Scavina, Nanay × Parinari, Trinitario and Amelonado clones were inoculated with virulent isolates of virus from five different locations in Nigeria. The Amelonado and Trinitario clones reacted severely on infection with the Egbeda virus and with each of the other isolates, including those which are thought not to be closely related. The Amazon clones were less severely affected by each virus and least of all by that from Olanla, which affected the Amazons slightly but caused swellings and conspicuous vein-banding in the Trinitarios.

The Scavina and Nanay × Parinari clones showed an initially severe necrotic reaction to infection with the Egbeda isolate and an unrelated one from Offa-Igbo. Thus the ability to cause necrosis is not confined to a particular group of viruses and it is likely to be an indication of extreme host sensitivity.

Nanay clone C 64 was obviously affected by each isolate. The virus from Offa-Igbo caused a fine banding of tissues alongside the tertiary and quaternary veins. The Ondo virus caused more severe symptoms, a chlorosis of the leaf resulting from localized speckled clearings in the mesophyll. The isolate from Abaku is the only one that never caused swellings in any clone tested.

The Nanay \times Iquitos hybrid C₇₇ showed very slight and sometimes transient leaf symptoms and no swellings on infection with the isolates from Egbeda and Olanla. The Offa-Igbo virus caused slight leaf symptoms usually accompanied by swellings.

The results of these preliminary experiments suggest that clones tend to react in a similar way to infection with different virulent isolates, even though these seem to be unrelated and were collected from widely separated localities. If this is confirmed and clones which tolerate infection with one isolate also tolerate others, it would greatly simplify the breeding programme.

DISCUSSION

Most of the cacao in West Africa has been grown from seed of the Amelonado type derived from a few introductions made at the end of the 19th century from the islands of San Thomé and Fernando Po. The uniform population which has since developed with little conscious selection is characteristically small-yielding. Consequently, many farmers in Ghana and Nigeria recently have been planting the Amazon material selected by W.A.C.R.I. from the extensive introductions made from Trinidad in 1945. It is W.A.C.R.I. policy to continue the present practice of issuing seed rather than clones and the next development will be the introduction of hybrid progenies derived by crossing selected Amazons with Amelonado or Trinitario trees. Such hybrids have shown outstanding vigour, producing large crops of beans acceptable to the manufacturers.

Our tests were limited to the small proportion of the W.A.C.R.I. breeding material established in Nigeria. Nevertheless, they emphasize the extreme vulnerability of the present Amelonado population and suggest that the introduction of Amazon and hybrid material will lead to a much less uniform response to infection. This is because virus effects have been largely ignored in selection, which has been based primarily on

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agronomic features and flavour assessments. Hence the prevalence of the vigorous Parinari, Scavina and Nanay types in the Amazon selections, despite the sensitivity of some to infection.

Attempts to eradicate swollen-shoot disease will be complicated by the planting of many seedlings derived from mixed stands of Upper Amazon trees. Some of these are growing in the neighbourhood of Amelonados and the varied reaction to infection will make it impossible to see symptoms in some trees. Those which tolerate infection are likely to be overlooked by the survey parties and will remain as potential sources of infection. Similar problems will be encountered on the release of the present series of hybrids, which our tests suggest will have a varied but generally severe reaction to infection.

The particular situation in the large areas of Nigeria where control measures have been abandoned presents an opportunity of using the tolerant reaction to advantage. However, our results suggest that extensive reselection, recombination and perhaps new introductions will be necessary before a consistently tolerant behaviour can be obtained in vigorous hybrids producing beans of acceptable size and flavour. If the apparent dominance of the sensitive reaction is confirmed, then it is unlikely that Amelonados can be used as at present to contribute bean size and flavour. Perhaps the most promising approach would be to cross outstandingly tolerant Nanay or Iquitos types with the best Trinitarios. The Series II progeny D is the only one of this type yet produced and tested. Significantly, it has grown well despite infection and it has been much more tolerant than crosses involving an Amelonado parent.

A series of other similar hybrids has been produced and their reactions to different virus isolates are being investigated. The evidence indicating that mealybugs do not readily acquire virus from tolerant trees is being reinvestigated. If this is confirmed, then virus is likely to spread slowly in a tolerant population. The results of these investigations will facilitate a full appraisal of the possibilities of using tolerant varieties where swollen-shoot is prevalent.

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EXPLANATION OF PLATE

Fig. 1. Severe interveinal chlorosis in Amelonado cacao, caused by the virulent Egbeda isolate.

Fig. 2. Chlorotic flecks and necrosis in Parinari cacao caused by the virulent Egbeda isolate.

Fig. 3. Clearings of the third- and fourth-order veins in Nanay cacao, caused by the virulent Egbeda isolate.

Fig. 4. Slight clearing of the minor veins in Nanay-Iquitos clone 77, caused by the virulent Egbeda isolate.



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