FURTHER EVIDENCE OF POPULATION SHIFT IN THE GUMMING DISEASE PATHOGEN IN MAURITIUS

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ABSTRACT

After an epidemic of gumming disease in Mauritius in 1964, due to the appearance of a new strain of the bacterium, several new varieties which had been tested and found resistant, were brought under cultivation to replace highly susceptible ones which had been earmarked for eradication. Some of the former subsequently showed high susceptibility and this has been attributed to further changes in the bacterial population.

Differences in pathogenicity between the old strain, present on noble canes, and the new strain, responsible for the epidemic, have been confirmed experimentally on three type varieties. Furthermore, a strain × variety interaction was found, indicating differences in virulence between the two strains and the existence of vertical resistance to the old strain in variety M 147/44. Such differences have not been found between isolates from varieties recently affected by the disease, including those obtained from infected M 147/44.

The problem of population shift in the pathogen is discussed in terms of recent concepts and the implications in the variety selection programme are outlined.

INTRODUCTION

Gumming disease of sugarcane (Xanthomonas vasculorum (Cobb) Dowson) reappeared in epidemic form in Mauritius in 1964, after it had been absent from commercial fields for nearly 20 years, through a sustained policy based on the cultivation of resistant varieties only (Antoine,1 Antoine and Pérombelon3). The epidemic was due to the appearance of a new strain of the pathogen which led to changes in the resistance of several important varieties, one of which, M 147/44, occupied, at the time, a considerable area. The susceptible varieties were earmarked for eradication after a reasonable delay, taking into account that a cane cycle occupies on an average 8 to 10 years in Mauritius. The whole problem has already been extensively reviewed (Antoine,1 Ricaud11).

The existence of differences in strains of the pathogen in the territories of the Western Indian Ocean area had previously been reported (Antoine and Hayward,8 Hayward7), and the differential behaviour of certain varieties in these countries was thus accounted for.

Two phases of the disease should be distinguished: foliar infection and systemic infection, the latter being the one which may lead to economic loss (Hughes8). Varieties which are highly susceptible to foliar infection, may or may not be tolerant to systemic infection (North,9 Ricaud13). However, the danger of cultivating susceptible but tolerant varieties, especially in an area where climatic conditions may often be favourable to rapid spread of the disease (e.g. cyclonic wind-swept rain), had been stressed (Antoine and Ricaud,4 Ricaud13). Such varieties maintain a reservoir of the pathogen from which new strains may evolve and affect previously resistant varieties.
The method of testing for selection of resistance to the disease, which was originally developed in Australia and has been used in Mauritius since 1931, has recently been described by Ricaud. It is based on the infection of test varieties, under natural conditions of dissemination of the pathogen, from adjacent inoculated rows of a susceptible variety. For reasons stated above, consideration has to be given, in Mauritius, to resistance to foliar as well as systemic infection. Since 1964, varieties have been tested with both old and new strains of the pathogen, in different localities, and testing has been operated at earlier stages in the selection programme (Antoinel).

Further changes in varietal resistance are reported in this paper. The problem of changes in the bacterial population, and its implications in variety selection and the control of the disease, are discussed.

EVIDENCE OF CHANGES IN VARIETAL RESISTANCE

Of 8 varieties released since 1964, 3 have shown susceptibility after a few years of multiplication. The cases of M 377/56 and M 351/57 deserve special mention. Variety M 377/56 was approved for wide scale planting in 1967 after having been multiplied gradually in several plots. It had been rated resistant in a trial with the old strain, and in 2 trials with the new strain, in which the level of infection was particularly severe, 18% and 47% of varieties in the trials being rated susceptible and the control plots of M 147/44 showing the highest infection recorded for this variety. Towards the end of 1967, signs of severe foliar infection were observed in M 377/56, in a few isolated plots and, in 1968, a few cases of systemic infection were found (Ricaud). In 1970, after favourable conditions for disease development had occurred, severe cases of systemic infection and widespread foliar infection were detected (Ricaud). The variety has proved less tolerant than M 147/44, judging by the severity of symptoms of systemic infection, and its propagation has been prohibited. A large area of the variety is still disease-free but heavy foliar infection has been observed in 15% of the plantations. In resistance trials, laid down more recently, wherever infection has been severe, the variety has confirmed its high susceptibility. Furthermore, of 1 000 individual stools derived from cuttings submitted to gamma irradiation and tested in a trial, not a single one escaped infection.

Variety M 351/57 has so far shown resistance in 4 trials, in 3 of which the infection level was very high. It is still resistant in most areas where it is planted, except in a locality isolated by mountains where a heavy inoculum is provided by fields of M 147/44 which have not yet been uprooted. Cases of systemic infection have been found in M 351/57 there.

Both varieties, M 377/56 and M 351/57, have shown high susceptibility in their first year out of quarantine in Réunion where gumming disease prevails in epidemic form (d'Emmerez and La Giroday). A few other varieties, released in Mauritius after the 1964 epidemic, have been found severely infected in Réunion, while they have remained resistant in Mauritius.

While some varieties have shown such changes of reaction, a few others have proved quite stable. For example variety M 31/45 has always reacted as resistant in all trials established since 1964, in which it has been included as a standard.
NATURE OF CHANGES IN BACTERIAL POPULATION

Changes in the behaviour of the varieties could be due to any of the following factors: (i) an incorrect assessment of resistance at the time of testing, (ii) changes in climatic conditions affecting the inoculum pressure of the pathogen, or (iii) changes in virulence or aggressiveness in the bacterial population. The first 2 assumptions could be rejected in the present cases, considering the high level of infection registered in the trials where resistance was assessed, and also the high degree of foliar infection that can now be observed on the varieties, especially M 377/56.

The problem of variation in plant pathogens in relation to disease resistance in plants has recently been reviewed (Van der Plank,17 Watson18). Strains of plant pathogens can differ in aggressiveness, or virulence, or both. Differences in virulence imply a strain/variety specificity, strains and varieties interact differentially. In the case of differences in aggressiveness such differential interaction does not exist.

A technique recently developed by Ricaud and Delanoé16 for testing varietal reaction to gumming disease, which involves inoculation of detached leaves under controlled conditions, was used to study strain/variety relationships. Results of a test comparing old and new strains are shown in Table 1.

<table>
<thead>
<tr>
<th>Strain</th>
<th>Origin of Isolate</th>
<th>Varieties</th>
<th>55/1182</th>
<th>M 147/44</th>
<th>M 31/45</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old</td>
<td>55/1182</td>
<td>Infection* Index</td>
<td>Field† Reaction</td>
<td>Infection* Index</td>
<td>Field† Reaction</td>
</tr>
<tr>
<td>New</td>
<td>M 147/44</td>
<td>6,6 HS</td>
<td>1,0</td>
<td>R</td>
<td>0,3</td>
</tr>
</tbody>
</table>

* Total extent of infection from points of inoculation for each leaf, determined by microscopic observation.
† Resistant
HS = Highly susceptible
‡ Lower index obtained in all other tests.

Differences between strains and varieties were highly significant and so was the variety × strain interaction. Increased infectivity of the new strain in M 147/44 was not accompanied by greater infectivity in the noble cane 55/1182. Indeed, in another test with the new strain, the noble cane showed a significantly lower infection index than M 147/44 as follows: M 147/44 — 7,9, 55/1182 — 4,1. These results, which have been confirmed, indicate that the 2 strains differ in virulence and that resistance in M 147/44 is vertical, according to the definitions of Van der Plank.17 Similar tests with several isolates from varieties affected by the epidemic: M 147/44, M 377/56 and M 351/37, have not shown any consistent difference in pathotype.

The old strain of the pathogen has survived for many years in a very small collection of noble canes; isolates from this population can be expected to be
quite stable, well adapted to these varieties and with little variation. On the other hand, isolates of the new strain responsible for the epidemic can be expected to consist of a great number of variants, owing to the rapid multiplication in the population (Ricaud13). These variants are in the process of being selected by varieties in cultivation. Differences which exist between them are, however, so small that they cannot be shown experimentally by techniques so far available; they cannot therefore be classified into distinct strains. They only show up by their ability to infect new varieties in the field.

In a study of the bacterial population of the gumming disease epidemic in Réunion, Rat19 confirmed that it was very heterogeneous. Thirteen different groups could be sorted out on the basis of antibiotic sensitivity tests and bacteriophage typing; unfortunately, no correlation was made with pathotype.

On the basis of Van der Plank's concept, such slight differences between isolates of the new strain would be an indication of difference in aggressiveness but not in virulence. A more precise study would be essential to confirm this.

SELECTION OF MORE AGGRESSIVE VARIANTS

D'Emmerez de Charmoy4 reported what he interpreted as a progressive increase in susceptibility of varieties after a few years of cultivation. This would appear to support our recent observations in Mauritius, although they should be interpreted in a different way, in the light of recent concepts. The variants that are able to infect new varieties occur in a very low proportion in the bacterial population. Under conditions conducive to high infection, new varieties may be infected by such variants. If infection remains foliar, the more aggressive inoculum is destroyed in dead leaves after harvest. Any new infection must again come from other susceptible varieties in which the disease is well established, with systemic infection, and the inoculum will have the same low proportion of the more aggressive forms. However, if infection becomes systemic in a new variety, stools with systemic infection, whether in ratoon or in plant cane derived from infected setts, will constitute the source of inoculum (Hughes,8 Ricaud13) and such inoculum will be made up solely of the form which is more aggressive in the given variety. By this selection process, the more aggressive form will gradually become dominant as the variety is multiplied and, although the variety does not become intrinsically more susceptible, it will be increasingly more vulnerable. Under these circumstances, the replanting of a new variety in which systemic infection has been detected should be envisaged with extreme caution.

IMPACT ON THE VARIETY SELECTION PROGRAMME

Such changes in the resistance of new varieties have had many repercussions on the selection programme. In resistance trials, varieties are being tested with respect to the strain that is dominant at the time of testing and it is difficult to tell whether they will subsequently remain resistant. In order to overcome, to some extent, these difficulties, varieties are now tested in 3 localities, 2 tests being with the new strain and the other with the old (Ricaud14); furthermore, promising varieties are retested over 3 or 4 years to confirm their reaction. At least 3 varieties are included in the contaminating row in the trials in order to ensure the establishment of the different isolates which are inoculated. These isolates are taken from various localities and different varieties.
The new testing technique which was developed in order to avoid discrepancies in field testing, that could be due to variation in inoculum pressure as a result of varying climatic conditions, may also prove useful for testing with different isolates simultaneously (Ricaud and Delanoe16).

The greatest problem that could arise with changes in resistance is that varieties that become susceptible may prove to be quite intolerant. There is evidence that resistance to foliar infection and tolerance to systemic infection are genetically independent (North9); the tolerance of a variety that shows resistance to foliar infection in a trial cannot be assessed. Thus variety M 377/56 which had shown resistance to foliar infection, later proved less tolerant than M 147/44.

CONCLUSIONS

The changes in resistance of new varieties indicate that the control of gumming disease cannot be based solely on the production of resistant varieties when an epidemic prevails. Emphasis must be laid on sanitation as well. The rapid removal of sources of inoculum provided by the susceptible varieties in which systemic infection has developed and from which more aggressive mutants of the pathogen may arise and pass on to new varieties, is an important corollary measure.

A paradoxical situation arises with the present procedure for the selection of resistance in that a great number of potentially good varieties are being rejected on account of their susceptibility (Ricaud14) while the ones which are kept may not later prove to be safer. If an integrated system combining selection for resistance and proper sanitation could be adopted, a slightly less vigorous selection for resistance could be envisaged with caution, at least with varieties that have reached the higher stages in the breeding programme when their rejection may be more costly. Greater emphasis may be laid on tolerance, or some form of horizontal resistance as defined by Van der Plank.17

A better understanding of the differences between new forms of the pathogen and of the genetic basis of resistance is also desirable in order to improve methods of selection for more stable resistance.

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REFERENCES

EVIDENCIA ADICIONAL SOBRE EL CAMBIO DE POBLACION EN EL PATOGENO DE LA ENFERMEDAD DE LA GOMOSIS EN MAURITIUS

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RESUMEN

Después de una epidemia de gomosis en Mauritis en el 1964, debido a la aparición de una cepa nueva de la bacteria, varias variedades nuevas que habían sido probadas y encontradas resistentes, han sido traídas bajo cultivo para reemplazar variedades altamente susceptibles que habían sido marcadas para su erradicación. Algunas de las variedades mencionadas arriba han mostrado ser posteriormente altamente susceptibles y el problema es atribuido al cambio adicional en la población bacteriana.

La diferencia en patogenicidad entre la cepa vieja presente en cañas nobles y la cepa nueva responsable de la epidemia ha sido confirmado experimentalmente a tres variedades tipo. Además, se encontró una interacción entre cepa y variedad indicando que hay diferencias en virulencia entre las dos cepas y la existencia de resistencia vertical a la cepa vieja en la variedad M. 147/44. Tales diferencias no han sido encontradas entre varias aislaciones de las variedades recientemente afectadas por la enfermedad, incluyendo aquellos obtenidos de la M. 147/44 infectada.

El problema del cambio en población en el patógeno es discutido en términos de los conceptos recientes y están bosquejadas las implicaciones en el programa de selecciones de variedades.