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Some effects of reversion virus on the growth and cropping of black currants

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SUMMARY

Black currant bushes of nine varieties were graft-inoculated with reversion virus and compared with healthy bushes in a field trial of eight years' duration. Two virulent and one relatively avirulent strain caused similar flower and leaf symptoms of differing severity.

The first symptoms appeared in the year after inoculation, when they were restricted to a few shoots and yields were unaffected. Thereafter yields declined as symptoms spread to all shoots within four or five years. The characteristically glabrous flowers borne by virus-affected shoots usually developed abnormally early in spring and many abscissed prematurely. Ultimately infection with the virulent strains caused bushes to become virtually barren. Fruits that did develop were small with few seeds, many of which were abnormal. One virulent strain had little effect on bushes previously infected with the avirulent strain, which alone halved yield and caused slight symptoms that spread slowly.

Annually the first-formed leaves subtending the flowers of virus-affected shoots were few, small and pale. Later vegetative growth was abnormally vigorous with many, short axillary shoots. Infection decreased susceptibility to the leaf-spot fungus (*Pseudopeziza ribis* Kleb.) and delayed leaf abscission.

REVERSION is the most important disease affecting the black currant (*Ribes nigrum* L.) in Britain and some other European countries, yet there is little detailed information on its effects. Infection may greatly reduce cropping (Amos and Hatton, 1927; Collingwood and Brock, 1961; Legowski and Gould, 1965), but the occurrence of avirulent strains was long overlooked (Cropley *et al.*, 1964). Nor has it been appreciated that varieties differ in sensitivity and that some shoots of bushes infected with virulent strains behave normally for several years.

In the present experiment the sequence of symptoms and effects on crop were recorded after infecting nine black currant varieties with three strains of reversion virus and with a combination of a virulent and a relatively avirulent strain.

MATERIALS AND METHODS

Experimental design

Healthy two-year-old bushes were planted at East Malling in October 1961. There were 84 bushes 4 ft apart in each of three rows 8 ft apart. A third of each row was planted with one of nine varieties, namely Amos Black, Baldwin, Blacksmith, Boskoop Giant, Cotswold Cross, Goliath, Seabrook's Black, Wellington XXX and Westwick Choice.

Within each variety the following treatments were allocated to individual bushes in a series of four randomized blocks, each containing seven bushes:

V_1 (1962). Inoculated in 1962 with a virulent strain of reversion virus from Cranbrook, Kent.

V_2 (1962). Inoculated in 1962 with a virulent strain from East Malling.

V_1 (1963). Inoculated in 1963 with the V_1 strain.

A (1962). Inoculated in 1962 with a relatively avirulent strain from Harrietsham, Kent (Posnette, 1952; Cropley *et al.*, 1964).

A + V_1. Inoculated in 1962 with the A strain, followed by the V_1 strain in 1963.

O_1. Control bushes inoculated in 1962 from an uninfected source.

O_2 Uninoculated controls.

All inoculations were by grafts made in August, using patches of bark without buds to avoid transferring the gall mite vector of reversion virus (*Phytoptus ribis* Nal.).

Each year the O_1 and O_2 groups of uninfected control bushes behaved and cropped alike, and for simplicity their yields are combined in Figure 3. The same applies to the two groups of bushes inoculated with the virulent strains in 1962.

Observations and records

Symptom development was followed by examining the bushes twice weekly as flowering began and thereafter fortnightly throughout each growing season.

The crop of each bush was picked and weighed separately. Samples of fifty fruits were collected from representative bushes in 1964, 1965 and 1966. The fruits from infected bushes were collected at random from shoots with symptoms. Fresh weights were recorded, and the seeds were then squeezed onto filter paper, counted, washed, dried and weighed.

Flower and fruit abscission was recorded in 1965 and 1966. For each of two contrasted varieties one shoot was selected on each of eight healthy and eight infected bushes. The node and position on the raceme were recorded for 100 flowers per shoot and abscission was recorded fortnightly until harvest.

Spray programme and cultural operations

The experimental bushes were raised from selected cuttings in an isolated nursery where endrin was used fortnightly to control gall mites. Thereafter endrin was applied annually at the grape stage, endosulfan three weeks after first blossom and lime sulphur two weeks later. These measures prevented the spread of reversion to uninoculated bushes, and gall mite infestations were slow to appear and increase until spraying ceased in 1968.

Metasystox and DDT were used to control insect pests. The leaf spot fungus *Pseudopeziza ribis* Kleb. was controlled by early zineb sprays and by a post-harvest application of Bordeaux mixture with cotton-seed oil.

The bushes were pruned at planting to leave few buds above ground; thereafter only damaged and interlocking shoots were removed.

The ground was uncultivated throughout the trial and inorganic fertilizers were applied annually. Weeds were controlled by annual winter applications of simazine and tar oil.

RESULTS

Symptom expression

Virulent strains (V_1 and V_2)

Symptoms were not seen until growth began in April 1963. Nine of the 72 bushes inoculated in 1962 then developed flower buds that were glabrous and brightly coloured compared with the hirsute, grey buds of healthy bushes. Symptoms were restricted to the flowers of single nodes alongside grafts.

The first-formed leaves subtending flowers and the basal leaves of extension growth were normal. Subsequent leaves developed symptoms that were inconspicuous and restricted to the inoculated and adjacent branches. The V_1 strain caused vein-pattern symptoms in May, whereas the June leaves were abnormally flat with a small basal sinus and few veins or marginal serrations (Fig. 1). The V_2 strain caused little vein-pattern, and usually the first symptom was the changed shape and venation of the June leaves (Fig. 1).

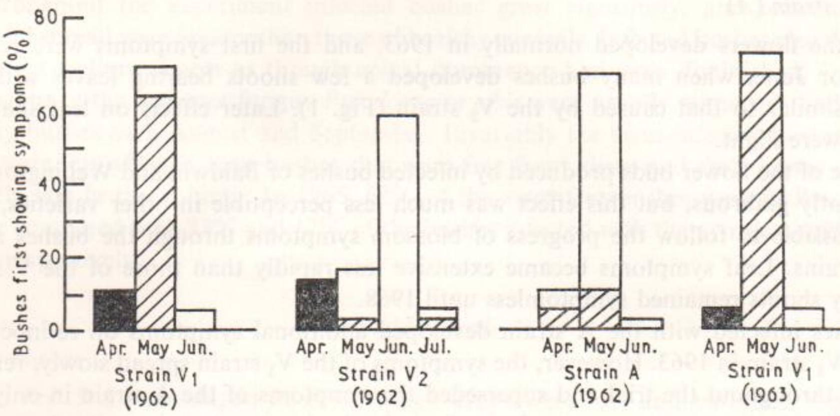

FIG. 1

The type of symptom first recorded in the year after inoculating black currant bushes with virulent (V_1 and V_2) or avirulent (A) strains of reversion virus in 1962 or 1963.
■ Glabrous buds; ▨ Vein pattern of leaves; □ Change in leaf shape and venation.

The bushes with sparse symptoms in 1963 developed conspicuous symptoms in 1964, when all the flower buds were glabrous on a third of the shoots, including all those developing near the inoculated branches. Two-thirds of the shoots developed glabrous flower buds in 1965 and virtually all shoots were affected by 1967 or 1968 (Fig. 2). Leaves with vein-pattern developed only on branches showing symptoms for the first time, whereas all shoots eventually developed leaves of abnormal shape and venation.

There was a similar but slower sequence of symptoms in bushes that were not inoculated until 1963 (Figs. 1 and 2). Only 16% of the shoots carried glabrous buds two years after inoculation and a few shoots were still unaffected after six years.

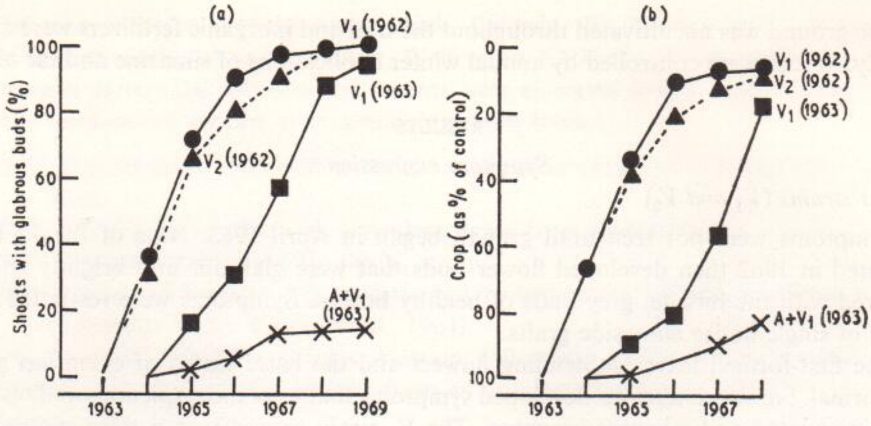

FIG. 2

The percentage of shoots with glabrous blossom (a) and the decrease in crop (b) caused by infection with virulent (V_1 and V_2) strains of reversion virus in 1962 or 1963. Half the bushes inoculated in 1963 were previously inoculated with the avirulent strain (A) in 1962.

Avirulent strain (A)

All the flowers developed normally in 1963, and the first symptoms were recorded in May or June, when many bushes developed a few shoots bearing leaves with vein-pattern, similar to that caused by the V_2 strain (Fig. 1). Later effects on leaf shape and venation were slight.

Some of the flower buds produced by infected bushes of Baldwin and Wellington XXX were slightly glabrous, but this effect was much less perceptible in other varieties, and it was impossible to follow the progress of blossom symptoms through the bushes as with the V strains. Leaf symptoms became extensive less rapidly than those of the V strains, and many shoots remained symptomless until 1968.

Bushes infected with the A strain developed additional symptoms on re-inoculation with the V_1 strain in 1963. However, the symptoms of the V_1 strain spread slowly, remained localized throughout the trial and superseded the symptoms of the A strain in only a few shoots. Shoots that were symptomless when the bushes were re-inoculated eventually developed typical symptoms of the A strain and continued to bear fruit.

Varietal differences in symptom expression

The different varieties reacted similarly to infection and produced similar flower and leaf symptoms. However, the normal flower buds of some varieties were less hairy or more brightly coloured than those of others and were little affected by virus infection. 'Double' flowers with extra petals instead of stamens did not occur, although they have been reported in continental Europe and once in England (Hatton and Amos, 1917).

Diagnosis by leaf symptoms is complicated by varietal differences in leaf form. For example, normal leaves of Westwick Choice have few marginal serrations, those of Seabrook's Black have little basal sinus and those of Raven and Tor Cross are unusually flat. The eeffcts of virulent strains are so great, however, that their diagnosis is seldom complicated

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by such differences between varieties. It is much more difficult to distinguish the inconspicuous effects of avirulent strains, particularly those seldom causing vein-pattern. The flower symptoms also tend to be unreliable for routine identification, because they are inconspicuous in some varieties and may be obscured by discolouration caused by frost damage.

Effects on growth and appearance

The flowers and first-formed leaves of virus-affected shoots developed abnormally early each year, except in 1967 when all growth was retarded by unusually cold weather.

Annually the leaves subtending the glabrous flower buds of virus-affected shoots were conspicuously pale, small and few. However, the spring pallor is of limited diagnostic importance, because it is not obvious in all varieties and is easily overlooked unless the bushes have been infected for several years (*pace* Swarbrick and Thompson, 1932).

Samples collected in March 1966 and analysed by Dr M. Allen revealed no significant differences in the amounts or relative proportions of N, P, K, Ca or Mg in samples of the developing stems, leaves and flower buds collected from normal and discoloured growth.

Throughout the experiment infected bushes grew vigorously, and ultimately their height and spread were greater than those of healthy controls. Infected bushes also developed many short axillary shoots as though apical dominance had been diminished.

Lesions of the leaf-spot fungus *Pseudopeziza ribis* were usually numerous and obvious on many bushes each August and September. Invariably the virus-infected bushes of each variety were less affected than bushes that were free from virus, and their leaves abscissed unusually late in the autumn. In 1965, 62% of the virus-free bushes were leafless by 25th October compared with 33% and 12% of the bushes infected with the avirulent and virulent strains, respectively.

Yield records

Healthy bushes

The first fruits developed in 1963, when crops were low and variable. Yields were higher in 1964, and those obtained in 1965 were the highest recorded because subsequent crops were reduced by spring frosts (Fig. 3).

Virulent strains

There was a close relationship between yields expressed as a percentage of the uninfected controls and the proportion of shoots with blossom symptoms ($r = -0.96$, $P < 0.001$). Yields were unaffected by virus in the year after inoculation and then declined as symptoms became more extensive (Fig. 2). Crops had become negligible by 1966, when such fruits as did develop were mainly restricted to the Amos Black bushes, which had an average crop of 1.5 lb per bush.

The V_1 strain had a less rapid effect on bushes inoculated in 1963 (Fig. 3). Yields were first affected in 1965, but they were not greatly diminished until 1967 and only became negligible in 1968.

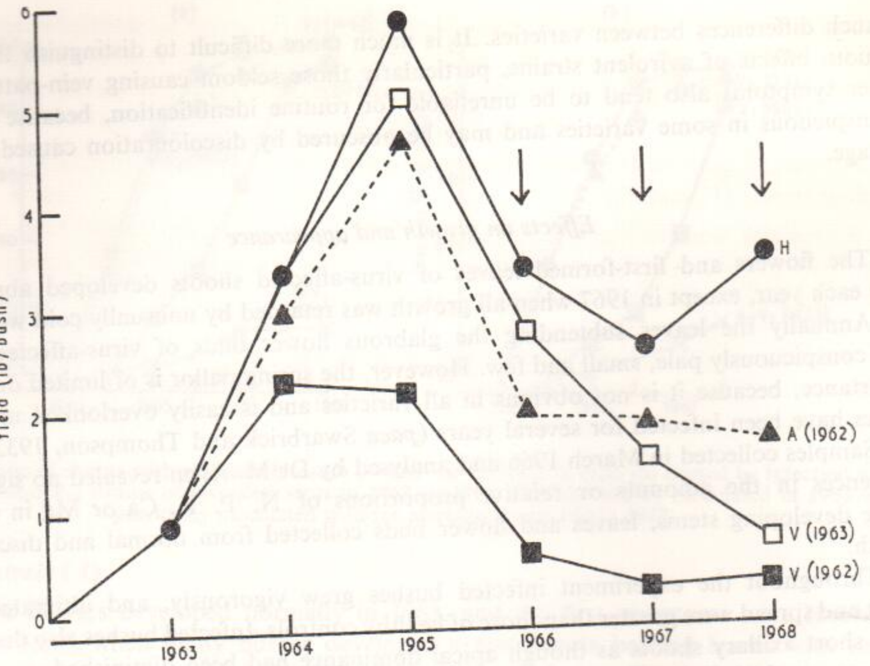

FIG. 3

The effect of virulent (V) and avirulent (A) strains of reversion virus on the yield of black currant bushes inoculated in 1962 or 1963.
Arrows indicate years in which yields were seriously affected by spring frosts.
A yield of 1·6 lb per bush is equivalent to 1 ton/acre.

Avirulent strain

The A strain reduced yields slightly in the second year after inoculation and to a greater extent in subsequent years. Crops were halved when all shoots bore symptoms (Fig. 3). The virulent strain inoculated in 1963 had little effect on the yield of bushes that had been previously inoculated with the A strain.

Effects on fruit number and fruit set

Invariably the infected bushes produced as many flowers as the healthy ones. However, most of the glabrous flowers affected by the V strains and many of those affected by the A strain abscissed. The symptomless flowers of partially affected bushes behaved normally and many formed fruit, even though some were on shoots that developed leaf symptoms later in the same season. The symptomless shoots of partially affected bushes did not produce more or larger fruits to compensate for the losses caused in other branches.

Flower and fruit abscission were recorded in detail for varieties with contrasted flowering habits in 1965. All the healthy flowers had opened by 14th April, but during the next fortnight some died and abscissed from the tips of the persistent pedicels; relatively few of the fruitlets fell later. The final set was similar all along the short racemes of the Goliath bushes but decreased from 70–80% near the base of the long racemes of Blacksmith to 40–50% near the apex.

Bushes infected with the V strains flowered a few days earlier than normal, but they developed similar numbers of flowers per node and shed similar numbers during and shortly after blossoming. Many other flowers then failed to develop further and eventually fell (Fig. 4).

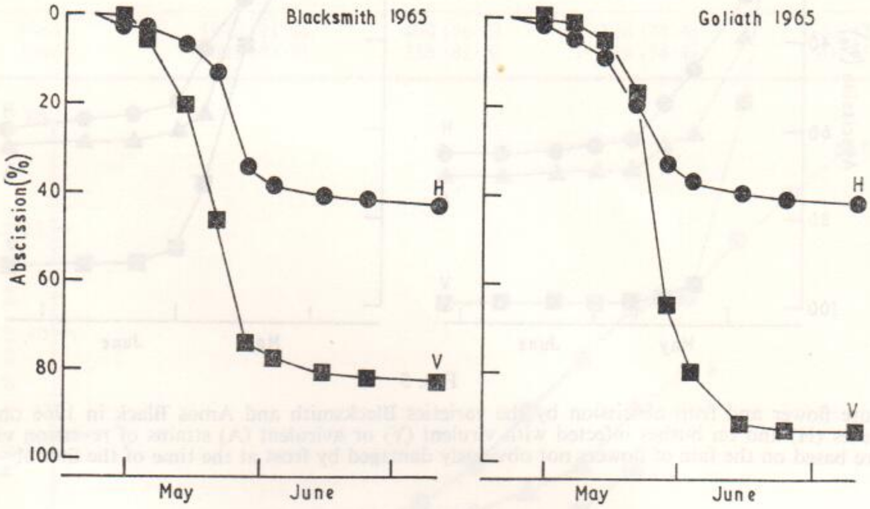

FIG. 4

Premature flower and fruit abscission by the varieties Blacksmith and Goliath in 1965 on healthy bushes (H) and on bushes infected with virulent strains (V) of reversion virus.
Data are based on the fate of all the flowers produced by representative shoots.

A sensitive variety, Blacksmith, and a partially tolerant variety, Amos Black, were observed in 1966 when growth began unusually early and many flower buds were severely damaged by frosts beginning on the night of 14th March. Almost half the flowers on healthy Blacksmith bushes became discoloured and necrotic within a few days, whereas healthy Amos Black bushes were much less advanced and only 10% of their flowers were damaged. Within each variety losses were greater on the reverted bushes than on the healthy ones, on which the flowers were less forward and better protected by hairs and subtending leaves.

Frost-damaged flowers soon withered and fell; approximately 60% of the apparently undamaged flowers remaining on the healthy bushes had also abscissed by 23rd May. The losses were even greater on virus-infected bushes, particularly those infected with the V strains (Fig. 5).

The Amos Black bushes had shown some tolerance to infection in 1965, and the bushes infected with the V strains again developed some fruits in 1966, whereas the bushes of other varieties were even more severely affected than in 1965 and were virtually barren.

Effects on fruit size and seed content

The fruits collected from healthy bushes in 1964, 1965 and 1966 were large with many seeds (Tables I and II). In 1965 there was a highly significant relationship between varietal

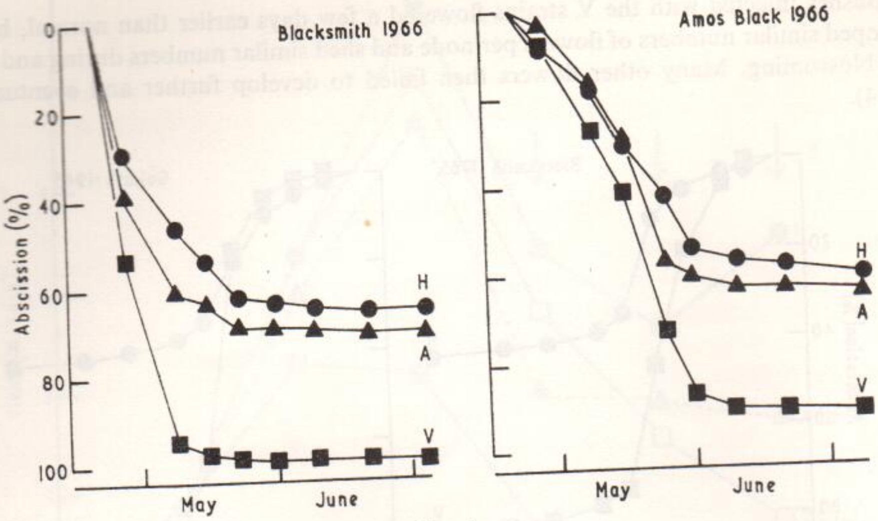

Fig. 5

Premature flower and fruit abscission by the varieties Blacksmith and Amos Black in 1966 on healthy bushes (H) and on bushes infected with virulent (V) or avirulent (A) strains of reversion virus. Data are based on the fate of flowers not obviously damaged by frost at the time of the first observation.

Table I

The mean fresh weight (g) of samples of 200 fruits from healthy and reversion-infected black currant bushes

Season	Healthy bushes	Bushes infected with		Standard error
		A strain	V strain	
1964	166·9	—	119·3	±18·1
1965	113·2	71·9	48·0	±13·3
1966	124·3	78·6	53·8	±13·9

yields and seed content ($r = +0.818$, $P < 0.001$) similar to that found in Germany (Neuman, 1955). There was no such trend in 1966 when some varieties were severely damaged by frosts.

In all years the size of fruit on the healthy bushes increased with seed number (Fig. 6). Small fruits with few seeds occurred at the tips of the long racemes, where the greatest abscission of developing fruitlets occurs (Teaotia and Luckwill, 1956). The seeds were of uniform size and appearance, and only a few were very small, malformed or immature (Table II).

The few fruits produced by reverted shoots were small with few seeds (Tables I and II). Many seeds were very small, malformed or immature, and the remainder were unusually large. Fruit size was positively correlated with seed number, although the fruits contained fewer seeds than fruits of similar size from healthy bushes (Fig. 6). Fruit size and seed number were less variable than on healthy bushes, and there was also less variation according to position on the long racemes of some varieties.

TABLE II

The mean number of seeds (with the percentage of good seeds in parentheses) in samples of forty fruits from healthy and reversion-infected black currant bushes

Season	Healthy bushes	Bushes infected with		Standard error
		A strain	V strain	
1965	1070 (91·1)	409 (86·0)	128 (74·4)	±96 (2·2)
1966	1091 (93·8)	358 (81·8)	118 (74·1)	±104 (3·0)

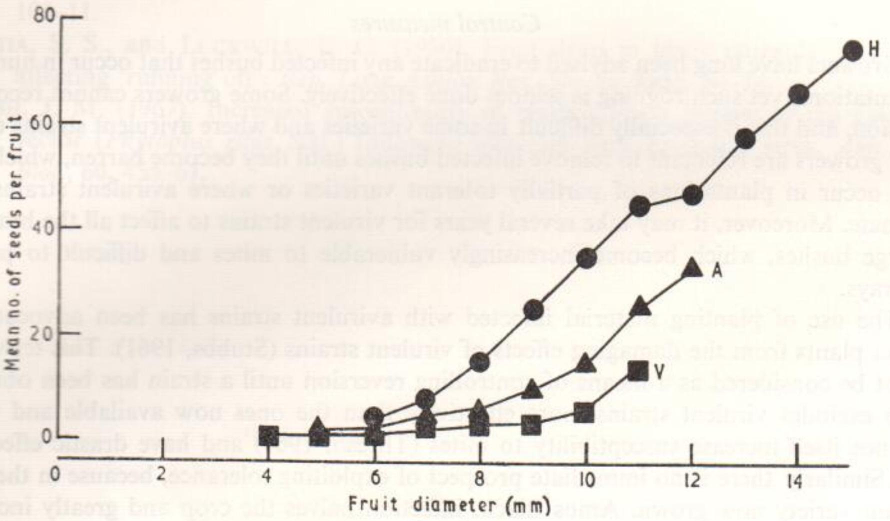

FIG. 6

The relationship between the size and seed content of representative fruits of the variety Goliath collected in 1965 from healthy bushes (H) and bushes infected with virulent (V) or avirulent (A) strains of reversion virus.

DISCUSSION

Effects of reversion virus

When reversion disease was first recognized, the changed appearance of affected bushes suggested that they had 'reverted' to an ancestral type. The changes, now attributed to virus infection, are even greater and more numerous than previously realized.

Some effects of reversion are likely to be interrelated because they are due to sterility, the underlying causes of which are not known, except that the main effect is on the ovules and not on the pollen. Indeed, pollen from infected bushes set a normal crop when used to pollinate healthy bushes, whereas infected bushes set virtually no crop irrespective of the pollen used (Amos and Hatton, 1927; Biggs, 1963).

Reversion causes no obvious changes in the number or appearance of the chromosomes at mitosis (Darlington, 1927), but effects on meiosis have not been considered. Nor have pollen-tube development and fertilization been compared in healthy and infected bushes, although infection causes many embryo sacs to degenerate prematurely (Biggs, 1963).

The few fruits produced by reverted bushes resemble the fruits produced at the tips of long racemes on healthy bushes, as would be expected because small fruits with few seeds are found wherever there is much seed abortion and abscission of developing fruit. It is premature, however, to suggest that fruit size and abscission on healthy and reverted bushes are determined by similar factors. If they were, it would be difficult to explain why the distribution of fruits on reverted bushes was not obviously related to position along the raceme, or why fruits on reverted bushes contained even fewer seeds than fruits of similar size from healthy bushes.

Control measures

Growers have long been advised to eradicate any infected bushes that occur in nurseries or plantations, yet such roguing is seldom done effectively. Some growers cannot recognize reversion, and this is especially difficult in some varieties and where avirulent strains occur. Other growers are reluctant to remove infected bushes until they become barren, which may never occur in plantations of partially tolerant varieties or where avirulent strains predominate. Moreover, it may take several years for virulent strains to affect all the branches of large bushes, which become increasingly vulnerable to mites and difficult to protect by sprays.

The use of planting material infected with avirulent strains has been advocated to protect plants from the damaging effects of virulent strains (Stubbs, 1961). This technique cannot be considered as a means of controlling reversion until a strain has been obtained which excludes virulent strains more effectively than the ones now available and which does not itself increase susceptibility to mites (Thresh, 1967) and have drastic effects on crop. Similarly there is no immediate prospect of exploiting tolerance, because in the most tolerant variety now grown, Amos Black, infection halves the crop and greatly increases susceptibility to mites (Thresh, 1967).

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