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**VIRUS DISEASES OF QUEENSLAND STRAWBERRIES
AND THE EPIDEMIOLOGICAL EFFECTS OF THE
STRAWBERRY RUNNER APPROVAL SCHEME**

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SUMMARY

Four viruses infecting Queensland strawberry cultivars were identified. Tobacco streak virus (TSV) was isolated mechanically and reinoculated to strawberry plants. It was identified serologically, morphologically and by host range. Strawberry mild yellow edge virus (MYEV), strawberry mottle virus (SMV) and strawberry latent A virus (SLAV) were identified by indicator reactions. SMV was readily transmitted by both *Chaetosiphon fragaefolii* and *Aphis gossypii* but no experimental aphid transmission of MYEV was obtained. No virus-like particles were seen by electron microscope examination of thin sections of material infected by SMV, MYEV or SLAV.

The reactions of *Duchesnea indica* to inoculation with SMV, MYEV and TSV were investigated. This naturalised species is a poor host of these viruses and would have little epidemiological importance. Examination of symptoms on seven indicators showed that the *Fragaria vesca* clones were better indicators than *Fragaria virginiana* clones for these four viruses. Severe symptoms were produced on plants of the main commercial cultivar (Redlands Crimson) by artificial virus complexes of MYEV + SMV and TSV + SMV, but the latter was not severe in the chronic phase. The virtual eradication of strawberry viruses from commercial plantings in Queensland is attributed to distribution of uninfected material and a reduction in vector populations.

I. INTRODUCTION

Except for brief summaries in reviews and one paper by Stubbs (1957) on the mottle group viruses, there are few published data on virus diseases of strawberries in Australia. Few crops have been so universally affected by virus disease as strawberries (Fulton and McGrew 1970) and few virus syndromes are so effectively controlled solely by manipulation of cultural practices.

The sub-tropical environment of the strawberry growing areas of coastal Queensland has resulted in the selection of specially adapted cultivars, most of which are locally bred (Anon. 1970). Severe crinkle and yellow edge diseases were formerly prevalent in these cultivars and prompted rogueing of diseased plants from runner production areas over 20 years ago. However, when leaf-graft testing (Bringhurst and Voth 1956) was begun, strawberry mottle virus (SMV) was found to be prevalent even in symptomless plants (B.L. Oxenham, unpublished data).

Identification of many strawberry viruses is still largely based on their reaction on selected indicated clones (Frazier 1974; Fulton and McGrew 1970; Fulton 1977) and vector transmission characteristics (Frazier and Posnette 1958; Mellor and Forbes 1960). Mellor and Frazier (1970) considered that SMV may actually be a number of conveniently grouped viruses which have low persistence in the aphid vectors and produce mottle symptoms in *Fragaria vesca* L. but do not cause obvious symptoms in commercial strawberries.

Tobacco streak virus (TSV) and the nematode-borne viruses of strawberry have been identified by particle type, host range and serology (Stace-Smith and Frazier 1971; Lister 1970). No morphological characterization of strawberry mild yellow edge virus (MYEV) has been published but there is one report of virus-like particles in *F. vesca* infected with SMV (Kitajima *et al.* 1971). Strawberry crinkle virus (SCV) has been shown to have the distinctive morphology of a rhabdovirus (Richardson *et al.* 1972).

This paper documents the virus disease problems which have occurred in the Queensland strawberry industry and the epidemiological effects of introduction of uninfected material through a runner approval scheme.

II. MATERIALS AND METHODS

Leaf graft indexing

Strawberry virus indicator clones UC1, UC4, UC5, UC10 and UC11 (Frazier 1974) were used for leaf-graft indexing. *F. vesca* plants were grown from seed originating from the Russian strain used by Stubbs (1957). *Duchesnea indica* (Andr.) Focke plants were also grown from seed and propagated from runners. Indicator plants were used only when young, vigorous and well-grown. At least two leaves on each test plant were grafted and an uninoculated control plant maintained in each pot. When indexing field material some known positive SMV and MYEV grafts were included for comparison. Only older leaves were removed before grafting. Further pruning (Frazier 1974) was not found to be beneficial on the young plants used. Except for the indexing of field material, a minimum of four replicates was used for all graft-inoculated tests. Temperatures for all tests were maintained below 25°C.

Clones of the strawberry cultivars Phenomenal and Majestic, free of SMV, were obtained by heat therapy at 38.5°C ± 1°C of well established plants which had been induced to run by extended day length. After heat treatment for c. 25 days small runners were severed and grown under mist until established. These plants were then indexed four times over a period of 1 year.

Virus isolation and identification

Mechanical transmissions of TSV and SMV were attempted by sap inoculations from newly infected leaves of graft-inoculated plants or from petals to cucumber (*cv. Palmetto*), guar (*Cyamopsis tetragonoloba* (L.) Taub.) and *Chenopodium quinoa* Willd. seedlings.

Sap was extracted either in K₂HPO₄ buffer (0.1 M) to which concentrated thioglycolic acid was added until the pH reached 8.0, or in 2% nicotine. Mortars, pestles, buffer and leaf tissue were chilled to 4°C before use. Host range test plants were checked by back-indexing to cucumber plants.

Materials and procedures used for partial purification, serology and electron microscopy of TSV were as previously described (Greber 1971).

Aphid transmission

Strawberry aphids (*Chaetosiphon fragaefolii* (Cock.)) and melon aphids (*Aphis gossypii* Glover) were collected from field strawberry plants and large apterous individuals were caged overnight on virus-free strawberry plants. Young nymphs produced during a 12 to 24 h period were then transferred carefully to other healthy strawberry plants to start colonies.

For aphid transmission of SMV a 2 to 3-h acquisition feeding period was permitted on detached leaves followed by a transmission feeding period of 12 h on indicator plants. Acquisition feeds for mild yellow edge virus (MYEV) were on potted plants previously infected by leaf-grafting and held in cages. Inoculation feeds were made to plants of the UC4 clone, pruned to two expanded leaves. Groups of 5 to 10 *C. fragaefolii* and 10 to 20 *A. gossypii* were used for each transmission test. Control plants were fed on by aphids without acquisition and the plants on which colonies were reared were indexed by leaf-grafts to indicators.

Sources of virus isolates

The TSV isolate used in tests of reactions on strawberry virus indicators and *D. indica*, was derived by mechanical transmission from a purified preparation of the strawberry M9 isolate. The two SMV isolates used in similar tests were aphid-transmitted from strawberry breeding lines. They produced consistent reactions with no evidence of component separation. The MYEV isolate used was the residual component after heat therapy of the M7 clone of the Redlands Crimson cultivar.

TABLE 1
HOST REACTIONS OF THE M9 STRAWBERRY TSV ISOLATE

Host	Symptoms	
	Inoculated Leaves	Systemic
<i>Carica papaya</i>	ringspots, mottle	epinasty, dark vein banding, necrosis, mottle
<i>Chenopodium quinoa</i>	chlorotic—necrotic lesions	chlorotic and necrotic lesions
<i>Cucumis sativus</i>	chlorotic spot lesions, wilting	mottle on leaves 1 to 3
<i>Cyamopsis tetragonoloba</i>	dark small lesions	..
<i>Macrotyloma lathyroides</i>	chlorotic or reddish lesions	rugose mosaic
<i>Nicotiana clevelandii</i>	chlorosis	necrotic speckle
<i>Nicotiana tabacum</i> cv. Turkish	pale concentric rings	pale necrotic patterns then recovery
<i>Phaseolus vulgaris</i> cv. Bountiful	small dark ringspots	vein browning, red nodes, pod mottle
<i>Vigna unguiculata</i> ssp <i>unguiculata</i> cv. Blackeye	red ringspots	nodal necrosis

III. RESULTS

Identification of viruses present

Graft inoculations and sap and aphid transmissions have shown the presence of at least four separate viruses in Queensland strawberry cultivars.

1. **STRAWBERRY MOTTLE VIRUS.** At the beginning of the work reported here 100 plants of the cvs. Majestic and Phenomenal were leaf-graft indexed to *F. vesca* seedlings and all produced symptoms within the range reported for SMV. The severity of the reaction on the indicator plants was variable in grafts from different plants of the same cultivar but those from cv. Phenomenal were the most severe and usually caused some degree of necrosis. This severity was later shown to be due to the presence of strawberry latent A virus (SLAV) in the Phenomenal clone. Transmission of SMV from symptomless plants of the Majestic and Phenomenal cultivars by both aphid species also produced variable symptoms in indicator plants. Since *A. gossypii* is known to transmit only SMV from strawberries (Carver *et al.* 1965; Frazier 1960) and the different symptom types could be maintained by graft propagation, more than one strain of SMV was probably present at the time when infection of commercial stocks was common.

Groups of *A. gossypii* transmitted SMV from cv. Phenomenal to 8 of 10 *F. vesca* seedlings, on which symptoms first appeared after 10 days. Groups of *C. fragaefolii* rarely failed to transmit SMV and this species was obviously an efficient vector. For example, in one series of transfers 21 of 22 plants were infected. When two consecutive 12-h transmission feeding periods were allowed, transmission occurred only during the first feed. This confirmed the low persistence of this type of strawberry virus (Stubbs 1957).

SMV was readily removed from Phenomenal, Majestic and Redlands Crimson clones by heat therapy. Removal from the first two cultivars was confirmed by leaf-graft indexing. Because the untreated M9 clone of Redlands Crimson was also infected with TSV, the removal of SMV from this clone was confirmed by aphid transmissions.

Attempts were made to transmit SMV in sap from leaves of freshly infected strawberry plants to cucumber and *C. quinoa* plants. No transmission was obtained. Thin sections of SMV-infected leaves were examined in the electron microscope but no virus-like particles were seen.

2. **STRAWBERRY LATENT A VIRUS.** After heat therapy treatment for 5 to 6 weeks some clones of cv. Majestic were apparently free of virus, but all cv. Phenomenal plants still produced symptoms similar to SLAV when leaf-graft indexed.

Most indicators show no symptoms with SLAV alone (Mellor and Fitzpatrick 1961). However, a transient epinasty and some necrosis were consistently produced in seedlings of the strain of *F. vesca* used in this work, provided plants were young and in rapid growth and the temperature after grafting was maintained at about 20°C. SLAV was not transmitted experimentally by *C. fragaefolii* even when reared on infected plants, nor did this virus spread to other cultivars in the field during many years of joint propagation.

No bullet-shaped particles were seen by electron microscope examination of negatively stained sap preparations from infected petals although SLAV has been presumed to be a strain of SCV (Frazier and Posnette 1958). Petals of a freshly infected *F. vesca* plant were also examined after embedding in Spurr's medium and thin sectioning, but no virus-like particles were seen.

3. STRAWBERRY MILD YELLOW EDGE VIRUS. The severe yellow edge disease (SMV + MYEV) occurred commonly in field planting of the Phenomenal and Majestic cultivars before SMV was removed by heat therapy from mother clones used for commercial propagation. MYEV was evidently transmitted from these older cultivars to the newly-bred Redlands Crimson cultivar while it was still being evaluated.

Two similar clones (M7 and M9) bred at Redlands Horticultural Research Station were combined in a trial release as cv. Redlands Crimson. This release was subject to severe degeneration in the first season in the field. Symptoms resembling severe yellow edge disease developed in up to one third of the plants on some farms by the end of the season. Testing the two constituent clones separately by leaf-graft indexing showed that both gave severe, but different, virus reactions on *F. vesca* seedling and UCI indicators. Both clones were then subjected to heat therapy. One clone (M7) subsequently gave no reaction when indexed to *F. vesca* over a period of several months and was multiplied in preparation for commercial release. However, further testing on *F. vesca* seedlings and UC4 clone indicators over the following year gave reactions typical of MYEV. After removal of this MYEV by meristem propagation a significant increase in yield was demonstrated (M. Herrington, R. Drew, R. Greber and F. Duncalfe, unpublished data).

C. fragaefolii from two different colonies failed to transmit the M7 isolate of MYEV to any of 20 UC4 or 6 *F. vesca* seedling indicator plants, using acquisition feeding periods of 12 to 24 h and transmission feeding periods of 2 days. Transmission attempts were also unsuccessful using acquisition from strawberry plants infected with MYEV + SMV, MYEV + TSV, MYEV + SLAV and MYEV alone from *D. indica*.

No virus-like particles were seen when stained thin sections of fixed and embedded leaves of UC4 plants with early chlorotic symptoms of MYEV were examined in the electron microscope.

4. TOBACCO STREAK VIRUS. Following heat therapy of the M9 clone of the original Redlands Crimson release, a necrotic reaction occurred very quickly (5 to 7 days) after treatment ceased, although no severe symptoms were observed on the field material before treatment began.

Mechanical transmission to cucumber seedlings from leaves of the plants showing initial necrotic, epinasty or mottle symptoms was achieved in about one-third of attempts using either 2% nicotine base or phosphate buffer with thio-glycollic acid additive as extracting medium. Transmission was more reliable from petals of freshly infected plants and infection of at least two cucumber plants in each pot was obtained in all five separate attempts from this source. TSV was also isolated directly to guar and *C. quinoa* from strawberry petals. After increase by further propagation in cucumber plants, the virus was transmitted to a host range similar to that of TSV isolates obtained from other sources (Greber 1971). The strawberry isolate consistently produced severe red-node symptoms (Mink *et al.* 1966) in Bountiful bean and also infected papaw (*Carica papaya* L.). A few papaw seedlings developed terminal necrosis and died, others developed epinasty, dark-green vein-banding and mottle symptoms, but these symptoms eventually disappeared from new growth. Re-isolation was successfully performed for all hosts as shown in table 2, but was most readily achieved soon after symptoms appeared. In contrast to TSV isolates from other Queensland sources, no leaves with dentate margins were produced in chronic infections of tobacco (*Nicotiana tabacum* L.) cv. Turkish (Greber 1971).

TABLE 2
REACTIONS OF STRAWBERRY INDICATORS TO FOUR VIRUSES

Indicator	SMV	TSV	MYEV	Latent A
<i>Fragaria vesca</i> seedlings ..	epinasty, mottle, stunting	epinasty, petiole stunt, chlorosis	older leaf mottle	epinasty, young leaf necrosis
UC 1	epinasty, chlorotic mottle, stunting	epinasty, petiole stunt, chlorosis	older leaf mottle	nil or epinasty
UC 4	epinasty, chlorotic mottle, stunting	epinasty, leaflet asymetry, stunting, chlorosis	vein and leaflet necrosis, downcurl	Nil
UC 5	epinasty, chlorotic mottle, stunting	epinasty, asymetry, petiole stunt, chlorosis	vein and leaflet necrosis, downcurl	Nil
UC 10	nil or mild	epinasty, petiole stunt, rugosity	mild chlorosis	Nil
UC 11	nil or mild	petiole stunt	mild chlorosis	Nil
cv. Majestic ..	nil	epinasty, petiole stunt, ringspots or mottle	nil	Nil
<i>Duchesnea indica</i>	yellow mottle	epinasty, rugosity, chlorotic veinbanding	mild chlorosis	Nil

Note :—(a) Some of the symptoms listed are transient

(b) The necrotic symptoms produced by TSV are variable and may be absent

Average time for first reactions at 20 to 22°C: SMV, 9 days; TSV, 9 days; MYEV, 22 days; SLAV, 12 days.

The strawberry isolate of TSV was partially purified from *Nicotiana cleve-landii* Gray leaves harvested at the time systemic symptoms appeared. The charcoal/citric acid/centrifugation method (Greber 1971) gave a preparation of high infectivity when assayed on guar cotyledons. After glutaraldehyde fixation, particles c. 25 nm in diameter were seen in purified preparations negatively stained with potassium phosphotungstate and examined with the electron microscope.

Gel-diffusion serology gave confluent lines of precipitation between the strawberry isolate and an *Ageratum* isolate of TSV (figure 1a), when used against one antiserum homologous with the latter and another provided earlier by G. I. Mink (Greber 1971; Mink *et al.* 1966).

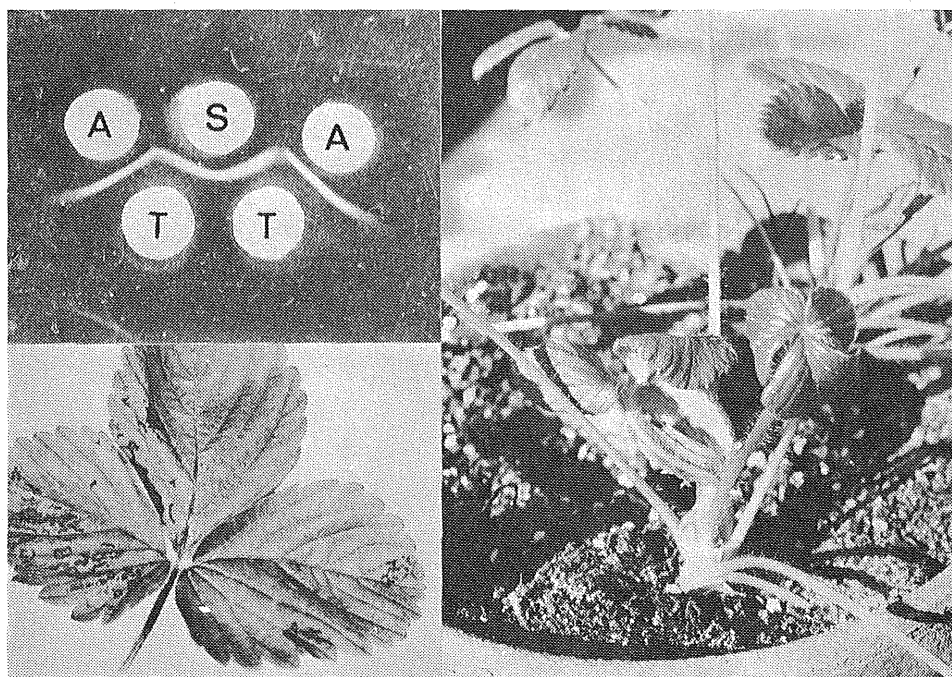


Figure 1. (a) (Top left) Gel-diffusion serology reaction between partially purified strawberry (S) and Ageratum (A) isolates of tobacco streak virus (TSV) and a TSV antiserum (T) obtained from *G. I. Mink*, Prosser, U.S.A. (b) and (c) Strawberry M9 isolate of TSV mechanically inoculated to *cv. Majestic* plants showing epinasty reaction and necrotic line-pattern.

Mechanical inoculation of healthy runners of *cv. Majestic* and *F. vesca* seedlings with either infective cucumber sap or purified virus produced a shock reaction within 7 days. This consisted of leaflet epinasty (figure 2b) and petiole stunting. Some necrosis, either on the tips of expanding leaves or in a pattern of fine dark etched rings and lines on the leaf surface (figure 2c) also occurred. After 3 weeks, the new growth of *cv. Majestic* showed pale green line patterns, semi-ringspots and an indistinct mottle. All symptoms eventually faded but there was a tendency for seasonal reappearance. In *F. vesca* seedlings, symptoms at one month consisted of short petioles, inter-veinal chlorosis and some veinal necrosis. Leaves of *F. vesca* seedlings remained small for a long period. Shock symptoms could be reproduced by leaf-graft propagation even from symptomless mechanically-infected strawberries.

Comparisons

Symptoms and transmission characteristics of the four viruses and their experimental complexes are compared below.

Simultaneous leaf grafts from MYEV, TSV, SLAV and SMV sources were made to UC1, UC4, UC5, UC10, UC11 and *F. vesca* seedling plants, using four replicates. Results are shown in table 2. Times to first symptoms for SMV and TSV were similar at 6 to 12 days. SLAV took *c.* 12 days and MYEV 3 to 4 weeks. The *F. vesca* clones were more useful than *F. virginiana* clones as indicators for these viruses. UC4 showed the most obvious and distinctive symptoms for SMV, TSV, and MYEV.

Leaf grafts from the original Phenomenal clone (SMV + SLAV) produced an initial necrotic reaction on *F. vesca* seedlings which was followed by development of small mottled leaves. Grafts of SMV alone to *F. vesca* seedlings produced a moderate mottle without necrosis. When plants of the UC1 clone were grafted with an SMV source (aphid-transmitted isolate) and compared to UC1 plants grafted with both SMV and SLAV, a slightly more severe reaction was noted in the latter.

Leaf graft-induced complexes of TSV + MYEV in meristem-propagated Redlands Crimson plants were without severe chronic symptoms, but shortened petioles and occasional development of young leaf mottling persisted after the initial epinasty reactions. Artificial complexes of SMV and MYEV produced the typical severe yellow edge disease in cool conditions, but complexes of SMV + TSV were not severe in the chronic stage.

Duchesnea indica

This species was tested as an indicator for some strawberry virus isolates by Maasen (1959). It is readily propagated from seed and also from runners. Petioles are thinner than some of the standard indicator clones and are consequently a little more difficult to graft. It is a poor host for *C. fragaefolii* and this aphid did not colonize *D. indica* although it fed adequately to allow virus transmission tests.

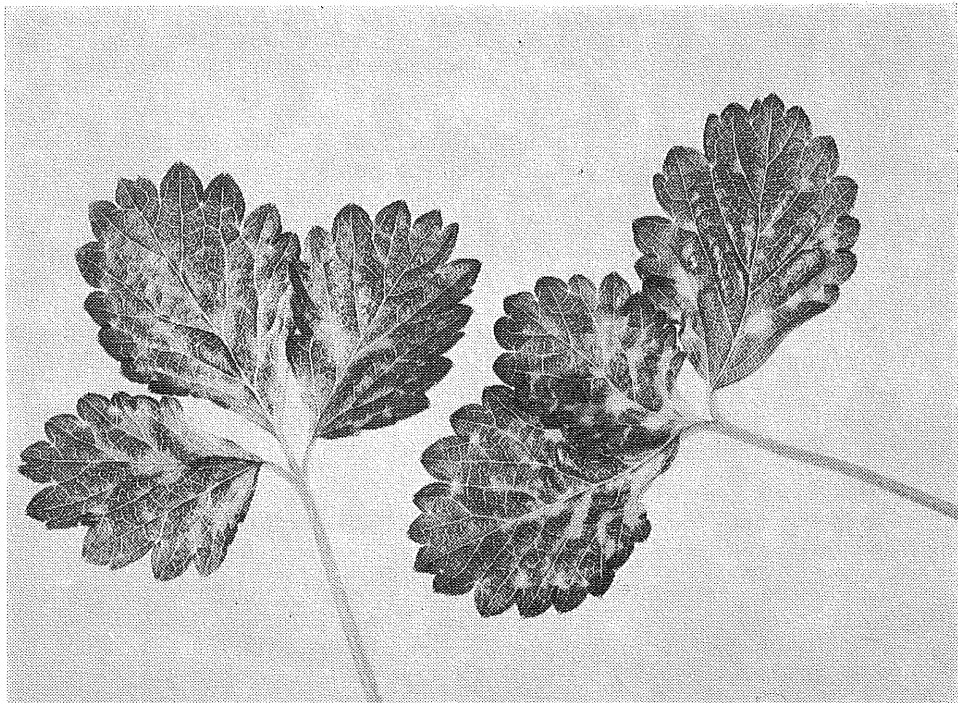


Figure 2 . Yellow mottle symptom on *Duchesnea indica* after infection with a strawberry mottle virus isolate by *Aphis gossypii*.

D. indica plants readily produced symptoms following leaf-graft inoculation with SMV or TSV, but only a very mild chlorosis followed inoculation with MYEV. Surprisingly, MYEV was the only one of these three viruses which consistently reproduced symptoms when leaf grafts were made back from graft-inoculated *D. indica* to UC4 plants.

Two aphid-transmitted isolates of SMV produced a severe chlorotic mottle in the young leaves and flower bracts of all of 10 *D. indica* plants *c.* 10 days after leaf-graft inoculation. These severe symptoms gradually faded and after 2 months most of the new growth appeared normal. In only one of ten attempts were SMV symptoms reproduced in UC4 plants when grafted with *D. indica* leaves showing severe mottle symptoms. Similar mottle symptoms were produced by *D. indica* when inoculated with SMV by using either *C. fragaefolii* or *A. gossypii* (figure 3). The latter was more efficient (6 of 6 plants) and was able to weakly colonize this host. In none of 12 attempts was SMV returned to UC4 from *D. indica* using aphids.

Although MYEV was returned to UC4 from *D. indica* in all of 8 attempts using leaf-grafts, no aphid transmission to UC4 was obtained using *C. fragaefolii* from *D. indica* as an acquisition source.

Leaves from a commercial strawberry cultivar which had been mechanically inoculated with a partially purified strawberry TSV isolate were grafted to *D. indica* plants. A transient epinasty of younger leaflets followed by a crumpled leaf symptom was eventually replaced by symptomless growth. All attempts to transmit TSV back to UC4 indicators from *D. indica* by grafting were unsuccessful.

Epidemiology of strawberry viruses in Queensland

The virtual demise of the strawberry aphid in commercial crops, as indicated by observations over a 15-year period, has been a feature of the changed epidemiology during the past decade. Transmission of SMV within field plantings of the first release of the Redlands Crimson cultivar which contained the two components of yellow edge disease in separate clones, was probably due to the vector activity of *A. gossypii*. This possibility was confirmed by experimental transmissions. *A. gossypii* can still frequently be found colonizing all cultivars of commercial strawberries, but the input of 'clean' material from the runner production scheme has apparently outstripped the ability of this vector to maintain SMV in the field.

During a nine-year period, only about one quarter of each year's commercially planted runners were derived from the scheme. Nevertheless random indexing each year of 20 plants from commercial plantings not directly derived from the scheme, showed that SMV has become rare and indeed SMV has not been detected in the field in recent years except in breeding lines maintained on a research station. The infection of new varieties during early field assessment can be attributed to the presence of these infected breeding lines. Nine of sixteen breeding lines were found to be virus-infected at a time when only virus-free material was being used by commercial runner growers, but this problem has since been eliminated.

IV. DISCUSSION

Strawberry crinkle virus has not been mentioned so far in this work. Although symptoms of severe crinkle disease were formerly prevalent, it has not been found in recent years. It is not known whether SCV has been eradicated or whether the removal of the SMV component of the severe crinkle disease has made its detection difficult.

The effects of heat therapy on the two composite virus infections in the M7 and M9 clones could be summarized as follows:

M9 clone	(SMV + TSV)	$\xrightarrow{\text{HT}}$	TSV
M7 clone	(MYEV + TSV)	$\xrightarrow{\text{HT}}$	MYEV

These differential effects imply SMV being removed more readily than TSV and TSV being removed more readily than MYEV.

The failure to achieve experimental aphid transmission of MYEV in these tests parallels the difficulty experienced by several other workers (Mellor and Forbes 1960; Frazier and Posnette 1958). However, transmission did take place in the field as evidenced by infection of the original M7 clone of the Redlands Crimson cultivar while still being evaluated before release. The experimental isolate was derived from this clone after it had been subjected to repeated heat therapy and some modification inhibitory to aphid transmission may have occurred.

The origin of the TSV infection in the two original Redlands Crimson clones is unknown. TSV is known to be seed transmitted in some plant species and the virus could have been acquired from parental material if it is also seed transmitted in strawberries. However TSV is not uncommon in other hosts in Queensland and could have spread from these to strawberries in the breeding plots. It appears likely that both the M7 and M9 clones were of similar original derivation and that their differentiation during preliminary selection was due to the acquisition of different aphid-borne viruses in addition to the basic TSV component.

Because they regularly produce red node symptoms in bean, but no notched leaves in tobacco, our strawberry TSV isolates appear to be closer to the red node strain (Mink *et al.* 1966) than the isolates reported from weed species in Queensland (Greber 1971). In contrast to the failure by Stace-Smith and Frazier (1971), manual reinoculation back to strawberry was achieved, although inoculum of high infectivity was required.

D. indica is widely grown as an ornamental species and is a naturalized weed plant in some locations in south Queensland. No other wild strawberries are present and commercial strawberries are not grown as a perennial crop, although a small proportion of plantings is carried over as ratoons. Under these circumstances it was thought that virus persistence in *D. indica* could have some importance in the epidemiology of the diseases and help to subvert the displacement of infected material by healthy material from the runner scheme. This investigation has shown this is unlikely as *D. indica*, although a host of strawberry viruses, is a poor acquisition source for either *C. fragaefolii* or *A. gossypii*.

The data presented in this paper indicate the probable eradication of strawberry viruses from Queensland if the present action on distribution of uninfected material is continued and the practice of growing only locally derived cultivars and planting material is maintained.

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