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THE WOODINESS VIRUS OF THE PASSION VINE (Passiflora edulis Sims).

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SUMMARY.

1. Studies on the epiphytology, symptomatology and transmissibility of the woodiness virus are reported.

2. Initial infections of new plantings are commonly highest in portions adjacent to a diseased source. In unpruned plantations there is no significant difference between the infection rate near a previously healthy vine and that near a diseased vine. Though there is a continuous reservoir of virus infection in the concentrated horticultural districts of south-eastern Queensland, local isolation within the farm may ensure freedom from the virus for 10 months after planting vines.

3. Greenhouse and field studies have shown 13 distinct symptoms to be associated with the virus. These are described. A seasonal variation in the expression of individual types of symptoms has been observed.

4. Apart from occasional high populations of a few species, the passion vine supports a relatively small insect fauna. The known aphid vectors of the woodiness virus do not colonise the passion vine by choice but breed on weeds and other plants in and around the plantation.

5. The virus is readily transmitted in the greenhouse (at mean maximum temperatures from $72.2^{\circ}F$. to $106.4^{\circ}F$.) by mechanical means, by the leaf-grafting technique, or by the insertion of a rectangular piece of leaf under the cambium of the stem.

6. The time taken for the expression of the first symptom (the characteristic terminal reaction) in infected seedlings is governed by temperature. It varies from 7 days at $98.1^{\circ}F$. to 24.6 days at $73.2^{\circ}F$. $-79.5^{\circ}F$.

7. The reactions of other species of Passiflora to infection with the woodiness virus are described.

8. The virus can be transmitted readily from an infected vine to a healthy vine by cutting with secateurs.

9. It has been demonstrated by selective mechanical and leaf graft transmissions in the greenhouse that the relative concentrations of different components of the virus can be altered. The fern leaf symptom was segregated from the virus mixture and maintained free from the typical mottle symptom. It was then shown that the typical mottle is responsible for the production of the characteristic terminal reaction.

10. It is postulated that the woodiness virus as it occurs in Australia exists as a complex of strains and is not a single entity, as previously thought.

HISTORY OF THE WOODINESS VIRUS.

According to Cobb (1901), the woodiness virus of passion fruit was known in New South Wales at least as early as 1891. He reported that the disease appeared to a serious extent about 1897, but that its serious effects were restricted to the County of Cumberland. The epiphytotic incidence of the virus within plantations reported by Cobb over 50 years ago is of considerable interest—"Whole vineyards may suffer so severely that hardly a vine escapes, and most of the vineyards in a given locality may be afflicted . . ."

Over the intervening years the virus has spread rapidly and it is now the greatest disease menace of passion vines in the eastern States of Australia. The decline in productivity in New South Wales from 0.4 bushels per vine in 1913 to 0.2 bushels in 1937 was mainly attributable to the disease (Noble and Noble, 1939). Simmonds (1938) rated woodiness as the most important disease of passion vines in Queensland and reported that it was only since 1931 that the disease had assumed serious proportions in the State. Since that time it has become of universal occurrence in the coastal and mountain plantations of south-eastern Queensland.

Elsewhere, the disease has been recorded in Kenya (McDonald, 1937), in South Africa (Storey, 1940), and, probably, in England (Bewley, 1923), and in Sumatra (Palm, 1922).

Three names have been assigned to this disease by various workers— "woodiness," "bullet" and "mosaic." The self-explanatory "woodiness," referring to the economically important symptom of the woody, misshapen fruit, proposed by Cobb in 1901, was the first name suggested and would appear to be the most suitable.

EPIPHYTOLOGY.

In south-eastern Queensland the passion vine is cultivated on a large percentage of small-crop and fruit farms, both in the coastal areas and on the coastal range country. In the coastal areas passion vines are grown mainly in association with bananas, pineapples, strawberries, papaws, tomatoes, cabbages and cauliflowers. On the coastal range country they are grown together with bananas and pineapples.

Twenty years ago plantations of 10 acres and over were relatively common, but today the areas are small, varying from half an acre to six acres on individual farms, but most commonly about one acre. The smaller areas now farmed to this lucrative crop are the direct result of a persistent complex of diseases, of which the woodiness virus is the most consistently damaging.

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The other diseases of the complex are Fusarium wilt, brown spot (*Alternaria* passiftorae Simmonds) and Septoria spot (Septoria passiftorae Louw). The high number of plantings still persisted with is the result of the appeal of the high return per acre obtainable from the harvesting of one or two crops of fruit before the diseases render the vines totally unproductive.

The majority of growers, then, while reluctant to neglect an opportunity to obtain a good cash return from a small area of vines over a short period, have a philosophical outlook on the future of the planting, and the small plantation receives scant attention from the point of view of disease control. When the existing planting becomes unproductive, a new area is planted, often while the old diseased vines are still in position. Further, these diseased plants frequently remain in position over the whole of the period of the establishment of the seedbed, the planting out, and the early growth of the new vines.

It was observed over the period of these investigations that a high percentage of infection occurred early in the life of new plantings adjacent to old, diseased areas. Infections as high as 100% were recorded in 9- and 10-month-old plantations in 1946 and 1947 when such plantings were adjacent to older diseased areas.

In Fig. 1 the incidence of the virus in a 9-month-old plantation approximately 8 yards from the closest row of a 2-year-old vineyard is plotted. An examination of the position of infected vines in this plantation suggests the spread of the virus from the neighbouring source into the new planting.



Fig. 1.—Incidence of "Woodiness" in 9-month-old vines. (Redland Bay Road, 3.9.46.)

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Three more or less typical farms in the Redlands district (near Brisbane) were selected for detailed observations on the incidents of the virus within plantations. The data have been statistically examined, tests made for departure of the distribution of the infected vines from randomness, and the association of later infections with earlier infections determined.

Plantation A.

The incidence of the virus was plotted on September 2, 1946, when the vines were nine months old, and subsequently in October and November when the typical foliage mottle and the malformed fruit symptoms were well expressed. With the reappearance of the foliage mottle in April 1947, the occurrence of the virus was plotted then and again at the beginning of June and towards the end of August, by which time all vines (then 17 months old) in the planting were infected. There were uncultivated areas on the northern and eastern sides of this vineyard and a plantation of bananas on the western side; the area was bounded on the south by a plantation completely infected with woodiness when plotting commenced.

At the time of the first plotting the initial infections were not randomly distributed, the percentage infected being higher in the southernmost three rows (i.e., in the rows nearest the disease source), mainly due to the higher percentage infected in the lower south-western area. Fresh infections to November 27, 1946 showed no significant departures from randomness, but



total infections to that date showed some indication of a departure from randomness, the percentage infected increasing from the northern end of the planting to the southern end (i.e., the percentage infected was highest in the areas closest to the diseased source).

The difference between the infection rates near a healthy vine and near a previously infected vine was not significant.

The disease incidence map of this plantation is shown in Fig. 2.

Plantation B.

In this plantation the incidence of the virus was plotted in September and October of 1946 and subsequently in July 1947, by which time all vines were infected. This planting was bounded on the western and eastern sides by an uncultivated area and a banana plantation, respectively; on the southeastern side five chains away was a source of the virus in 2-year-old infected plants; and on the northern end a few yards away was an infected planting of 2-year-old and 9-month-old vines.



Fig. 3.-Field Plan, Plantation B. Pinklands.

The incidence of the virus in this plantation is shown in Fig. 3.

Analysis of the data from this plot showed that there was some indication of a progressive increase in the percentage infected from the southern to the northern side of the planting (i.e., the percentage infected appeared to be higher in the vines closest to the nearest diseased source). No test of neighbour infection was carried out in this planting.

Plantation C.

In this plantation the virus incidence was plotted in September, October and November, 1946, and subsequently in June 1947, at which time every vine was infected.

This planting was bounded by an area of pineapples, a banana plantation, an uncultivated area, and, on the north-eastern side, a 2-year-old passion vine plantation infected with woodiness (Fig. 4).



Fig. 4.—Field Plan, Plantation C, Thornlands.

Examination of the data from this plantation showed that the initial infections were not randomly distributed. The percentage infected increased progressively from the western to the eastern side of the planting; the western half showed a significantly lower percentage infected than the eastern half. The percentage infected was higher in the north-eastern quarter of the plot than in the other quarters (i.e., the vines nearest to the source of infected vines showed a higher proportion of infections). Fresh infections up to November 27, 1946, and total infections to the same date showed a marked increase in the proportion infected from the western side to the eastern side of the plantation.

The vines not diseased on September 2, 1946, were subdivided into two classes—those near healthy vines and those near an infected vine. Each of these classes was later subdivided into two classes—healthy and infected at

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27/11/46. The classifications were carried out along the rows, the end plants being classified according to the nature of the adjacent vine in the same row. The X² test showed that the difference between the infection rates near a previously healthy vine and near a previously infected vine was not significant.

The vines in these examples were not mechanically pruned, and mechanical transmission by this method can be ignored. However, the extent of seedbed infection prior to planting out cannot be overlooked, or in these examples, actually assessed.

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·	Grower.		Percentage Infection.	Presence of Olde Vines or	or Abs r Infect 1 Prope	ence ted rty.	Other Crops Growing in Immediate Vicinity of Young Vines over 10-month Period.					
No. 1			100	Present			Passion vines : lettuce.					
No. 2	2 \ldots 61			Present			Passion vines					
No. 3							Passion vines; bananas; pineapples					
No. 4			21	Present			Passion vines ; bananas					
No. 5			17	Present			Passion vines					
No. 6			0 ·	Absent			Bananas; cabbages; tomatoes					
No. 7		0					Tomatoes					
No. 8	No. 8 0						Bananas; custard apples; papaws tomatoes					

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While there is a continuous reservoir of virus infection present in the concentrated horticultural districts of coastal south-eastern Queensland, it has been determined that local isolation within a farm will give early freedom from infection in a new planting. This freedom from the virus may persist over 10 months. An examination of eight 10-month-old plantations in the Thornlands district was made in September 1946; the results are shown in Table 1. Growers 5–8 used a common source of seed—from No. 5. The extent of infection after 10 months is of particular interest, as it would appear to be associated with the presence or absence of older infected vines on the property.

SYMPTOMATOLOGY.

There is great variation in the symptoms produced by the woodiness virus, and in addition, there is seasonal variation in the expression of individual types of symptoms. The complete series of symptoms produced has not previously been described.

Symptoms.

As the result of field and greenhouse studies on the virus, the following 13 types of symptoms are now recorded:—Malformed fruit; typical foliage mottle; yellow spot mottle; terminal bunchiness; translucent areas; foliage ring spot; fruit ring spot; stippled fruit; fern leaves; tip chlorosis; stem mottle; vein hypertrophy; seedling terminal reaction. The first 11 symptoms occur in the field. The last two have been observed only in the greenhouse.

Table 2.

Www.off.	Type of Symptom.							Winter.				Spring.		Summer.	
Type of Sympton	J	an.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sep.	Oct.	Nov.	Dec.		
Translucent Areas in	Termin	al											}		
Leaves	•••	••	+	+	+	+	+	+	+	+	+	+		+	
Terminal Bunchiness	•••	••	-	+	+	+	+	+	+	+	+	+	+	+	
Typical Foliage Mottle				—	+	+	+	+ .	+ -	+	+	+	+	—	
Yellow Spot Mottle					-	+	+	+	+	+	+	+	+	+	
Foliage Ring Spot			-	_		_	+	+	+	+	+	+	+		
Stippled Fruit					-			+	+	+	+	+	+		
Malformed Fruit			_			-		+	+	+	+	+	+		
Fruit Ring Spot			-	_	-		_		_	+	.+	+	+	+	
Tip Chlorosis			-		_		-		-	+.	+	+			
Fern Leaves					-		-	_	_	-	+	+	+	+	
Stem Mottle		.	-	-	-			-	-		+	+			

FIELD SYMPTOM TYPES AND THEIR SEASONAL OCCURRENCE IN SOUTH-EASTERN QUEENSLAND

The seasonal occurrence of the symptoms in the field is shown in Table 2. This summary is based on numerous observations carried out in south-eastern Queensland during the years 1946, 1947 and 1948.

1. Malformed Fruit.

This (Fig. 5) is the economically important symptom, consisting of more or less grossly misshapen fruit (with abnormal thickening and hardening of the tissues of the pericarp and reduced pulp cavity), which are produced on infected vines from June to November in south-eastern Queensland. Outside this period the fruit on infected vines are not grossly misshapen, but they are smaller in size than healthy fruit, are not perfect in shape, and have a thicker pericarp.

Woody fruit are detectable by their uneven shape when the fruit measure only $\frac{1}{4}$ in. to $\frac{1}{2}$ in. along their longest dimension. A mottle on the calyx accompanies the fruit symptoms.

2. Typical Foliage Mottle.

This is a broad bullate mottle with the dark-green areas localized on the raised or blistered portions of the leaf (Fig. 6). The blisters are raised from the top surface of the leaf. The leaf colour between the dark-green, raised areas is yellow-green. The leaves present a puckered apparance and are frequently misshapen. This mottle can be readily detected from March until November, but its expression is most marked during the winter and spring months. A fleeting mottle can be seen in the summer months just behind the terminals.



Fig. 5. Deformed Fruit with Thickened Pericarp and Reduced Pulp Cavity.

The yellow spot mottle may be associated with the typical mottle. Occasionally a leaf may be seen with both of these mottles present but with each distinctly confined to definite areas of the leaf.

3. Yellow Spot Mottle.

This mottle is produced by numerous small yellow spots on the leaf (Figs. 7 and 8). Occasionally the spots may be few in number, discrete, and occur unmixed with any other leaf mottle. The yellow spots are generally circular in shape, but when large are irregular in outline and occasionally have a necrotic centre. This mottle occurs on the vines from April to November. It is commonly associated with the typical mottle and may also occur on fern leaves. It is best expressed on older leaves.



Fig. 6.

Typical Bullate Foliage Mottle. Normal plant at right.

4. Terminal Bunchiness.

This symptom is a lack of growth at the terminal accompanied by a bunchiness of harsh-textured terminal leaves. It may be detected on systemically infected vines in any month of the year but is best expressed in winter, when the terminal leaves are markedly downcurled along the axis of the main vine,

5. Translucent Areas.

Infected vines show a vein clearing in the terminal leaves accompanied by translucent or cleared areas. This symptom may be detected at any time of the year.

6. Foliage Ring Spot.

This is a relatively rare symptom. Ring spots are associated with the yellow spot mottle (Fig. 8) and are caused, apparently, by the rearrangement of the yellow spot mottle into rings. Tissue bounded by the rings is green and does not become necrotic.

7. Fruit Ring Spot.

Ring spots (Fig. 9) may occur on normal fruit or on fruit that are misshapen and have hardened and thickened pericarps. They may occur as circular, green, discrete ring spots with a purple centre, up to $\frac{3}{4}$ cm. in



Fig. 7. Yellow Spot Mottle.

diameter, and as small as 3 mm. in diameter. They may fuse during development to give large, irregularly shaped outlines. They can occur on all portions of the fruit but may be confined to one half of it. Frequently their occurrence is more intense on one side of the fruit.

As the fruit ripen and shrivel the ring spots gradually become obscure. When ring spots occur in fruit which are still green, their centre remains a "greasy green" as the fruit ripens in place of the purple in a riper fruit. In this case, as the fruit ripens the ring spots again become obscure and the final result is the presence of a number of larger or smaller greasy-green dots or spots on the normal green of the fruit. Such fruit may ripen normally.

8. Stippled Fruit.

Markings occur on the fruit in the form of an irregular dotted and stippled pattern below the epidermis. On green fruit the pattern appears, in contrast, as a grey colour. When they are small, the swellings may be roughly circular but they are generally fused to give an irregular pattern.



Fig. 8. Foliage Ring Spot Accompanied by Yellow Spot Mcttle.

9. Fern Leaves.

Fern leaves are distorted leaves, the individual leaf lobes being filiform and having irregular or serrated margins (Figs. 10–12). In the field and in the greenhouse the typical woodiness mottle is not found associated with fern leaves, but yellow spot mottle may be associated with this symptom (Fig. 11). In the field, fern leaves are produced over the period September to December.

10. Tip Chlorosis.

The terminal leaves are chlorotic, with a trace of green vein banding. Associated with the tip chlorosis is the stem mottle described below. Small, brown, necrotic, slightly depressed lesions appear on the stem near the terminal, and the terminal leaves and tendrils die back. Tip chlorosis is present in the field during the months of August, September and October.

11. Stem Mottle.

A light-green mottle may occur on the stems and petioles of infected plants, and is prominent in the field in September and October. The stem mottle may be produced in the greenhouse in the winter months.



Fig. 9. Fruit Ring Spot.



Fig. 10. -Fern Leaf Type.

Fig. 11. Fern Leaf Accompanied by Yellow Spot Mottle.

12. Vein Hypertrophy.

This consists of a raised main vein, which commonly pursues a zigzag path. The symptom is not infrequently encountered in the greenhouse, but has not been observed in the field.

13. Seedling Terminal Reaction.

This is the first symptom shown in the greenhoute by seedling passion vines after inoculation with the woodiness virus. The terminal reaction consists of a marked downcurling of the first unfolded terminal leaflet, followed by spiral twisting, and the cupping-under of the leaflet edges (Fig. 13). Vein



Extreme Forms of Fern Leaves Produced in the Greenhouse. Normal leaf at top left.

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clearing occurs and translucent areas appear. All these symptoms may appear also in the second unfolded leaflet, while in the third unfolded leaflet marginal waving is commonly the only symptom present.

SUMMER SYMPTOMS OF WOODINESS IN THE FIELD.

Even over the period of least expression of the virus during high summer temperatures, infected vines may be detected in the field by the presence of the following symptoms. Growth is less than in a healthy vine; it may actually cease in some laterals, and a bunchiness of the terminal leaves occur. The texture of the older leaves is harsh, and while fruit



Fig. 13.

Seedling Terminal Reactions. Left, downcurling of first and second unfolded leaflets along axis of main vein. Right, spiral twisting of first unfolded leaflet. Both 12 days after mechanical inoculation.

produced at this time are not obviously deformed they are not perfect in shape and tend to be thickened in the pericarp. A fleeting mottle may be detected in the leaves just behind the terminal leaves. Translucent areas occur in the terminal leaves; they are shown by a clearing of the normal light-green colour in the vicinity of the veins.

Symptoms again become well expressed in March with the appearance of the prominent typical foliage mottle.

INSECT POPULATIONS OF THE PASSION VINE.

Noble and Noble (1939) demonstrated transmission of the virus by Myzus persicae (Sulz.) and by Macrosiphum gei Koch, together with two unnamed species of aphids. Magee (1948) showed that Aphis gossypii Glov. is also a vector.

It was observed early in these investigations that, apart from occasional high populations involving a few species, the passion vine normally supports very few insects. In order to determine the extent of the insect populations on passion vines in Queensland, sampling was conducted at fortnightly intervals over a period of 13 months on four plantations located at Victoria Point, Cleveland and Ormiston. Net sweeping of the passion vine foliage, apart from rendering difficult the recovery of mites and thrips, was found

relatively ineffective, and a sampling method was adopted, taking 20 flowers, 20 terminals, and 20 leaves at random into separate containers on each of the four plantations. In the laboratory, ether was placed in the canisters and the leaves and flowers were shaken over white paper and then brushed with a camel-hair brush. It was then found necessary to examine the leaves and flowers with a binocular microscope and to remove the mites and small insects with a camel-hair brush.

The results obtained are shown in Tables 3-6.

Aphids were found present from March to September but their population on the vines throughout the 13 months was very low. Species detected were *Aphis gossypii*, *Macrosiphum gei* and *Aphis rumicis* L.

Date.	Thrips tabaci.	Thrips imaginis.	Taeniothrips kellyanus.	Thrips app.	Haplothrips froggatti.	Aphis gossypii	Macrosiphum gei.	Aphis rumicis.	Aphis spp.	Acarina.	Miscellaneous.
21 - 8 - 46	40	19				2	2				1 Phalacridae
10 - 9 - 46	84	26	1	1			1				
2 - 10 - 46	15	9									2 Coccinellidae
16 - 10 - 46				2							3 Entomobryidae
30-10-46	66			• • •			•••				
13 - 11 - 46	41	••••				• •	· • •				
11 - 12 - 46	4										
8 - 1 - 47	6										
5 - 2 - 47					•••					•••	
19 - 2 - 47		•••		••	•••	••	• •			•••	1 Siphanta acuta
13 - 3 - 47	1				••	••	•••			5	Eggs of Caedicia
27 - 3 - 47				••••		6				12	2 Pheidole megacephala; 2
9-4-47									1	5	Psocoptera; 2 Pseudococ- cidae
				• •		••		••		Ű	1 Coccidae
23 - 4 - 47			2	4		••	•••			18	3 Psyllidae ; 2 Psocoptera
7-5-47				1		1		••	1	8	2 Miridae ; 1 Coccidae
22 - 5 - 47	1	• •		••	•••	••	••	•••	••	2	1 Chalcidoidea ; 1 Psocoptera
4-6-47	7	• •			•••	••	•••	••		••	2 Psocidae ; 3 Formicidae
19 - 6 - 47		• •			••	••	•••	•••	•••	••	2 Psocidae ; 2 Neophysopus sp.
4-7-47	1	•••	••	••	•••	•••		2		1	1 Delphacidae
23 - 7 - 47	9			••	•••	••	••	••	2	••	
6 - 8 - 47	4	•••		2	•••	••	•••	••	•••	••	2 Hemiptera
25 - 8 - 47	79		•••	9	•••	••	••	••		1	2 Psyllidae ; 2 Neophysopus sp. ;
	ļ		} .								2 Coleoptera ; 5 Homoptera
12 - 9 - 47	99	• •	3	•••	•••	••	••	••		••	2 Hemiptera
24 - 9 - 47	71				2	••	•••	•••	•••	11	Scores of Lepidopterous larvae ;
											3 Corticaria australis
Total	528	54	6	19	2	9	3	. 2	4	63	la suo anno 1995. Ny INSEE dia mampina

 Table 3.

 INCIDENCE OF INSECTS ON THE PASSION VINE—PLANTATION 1, ORMISTON.

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A number of nymphal aphids were found to be present, indicating that some breeding was, in fact, occurring on the vines. However, from the numbers found it would appear unlikely that the aphids breeding on the vines were the major agents in the extensive infections with the virus recorded in vineyards over the period of the investigations.

Apart from the regular samplings in these four plantations, observations were made for aphid vectors elsewhere. *Myzus persicae, Aphis rumicis* and *A. gossypii* were found present on young passion vines in the Redland Bay and Victoria Point areas in April and May of 1946. In June 1946, small

Date.	Thrips tabaci.	Thrips imaginis.	Taeniothrips kellyanus.	Thrips spp.	Haplothrips froggatti.	Aphis gossypii.	Macrosiphum gei.	Aphis rumicis.	Aphis spp.	Acarina.	Miscellaneous,
2-9-46	52										2 Rhizobius spp.
10 - 9 - 46	63	19							7		11
2-10-46	14	8	•••			••		••	••		4 Nitidulidae; 2 Chrysomel- idae; 2 Pheidole mega- cephala
16 - 10 - 46	14	6				· •					2 Lathridiidae
30 - 10 - 46										.:	
13 - 11 - 46	68										1 Nitidulidae
27 - 11 - 46	2			<i>'</i>							,
11 - 12 - 46											· · · ·
8-1-47	7			1							1 Pheidole megacephala; 1
5-2-47	2		•••		••	••	••			••	I Pristhesancus papuensis ; 1 Coccinella transversalis
19 - 2 - 47						• •					
27 - 3 - 47					••						
9-4-47									1	6	
23 - 4 - 47									2	1	1 Psocoptera
7-5-47				1					1	7	
22 - 5 - 47						••			1	6	
4 - 6 - 47				1				5		·	2 Neophysopus sp.; 2 Coleoptera
19 - 6 - 47				••	•••	••		••		••	3 Lepidopterous larvae; 2 Neophysopus sp.
4 - 7 - 47		·		2				1			2 Agonoscelis rutila
23 - 7 - 47										2	0
6 - 8 - 47				2				••			8 Neophysopus sp.
25-8-47	10		· · .	••		2		••	••		2 Neophysopus sp.; 2 Psocop-
12-9-47	72		4	4					•••		4 Nezara viridula ; 2 Corticaria australis
24-9-47	14	• • •	•••		•••	•••	•••	•••	••	••	
Total	318	33	4	11		2	• • •	6	12	22	

Table 4.

INCIDENCE OF INSECTS ON THE PASSION VINE-PLANTATION 2, REDLAND BAY ROAD,

CLEVELAND.

Τá	ъЫ	le	- 5.
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INCIDENCE OF INSECTS ON THE PASSION VINE-PLANTATION 3. THORNLANDS. gossypii. rumicis. Thrips tabaci Taeniothrips kellyanus. Thrips imaginis. Haplothrips froggatti. Macrosiphun gei. Thrips spp. spp. Date. Miscellaneous. Acarina A phis 1 Aphis Aphis : 10 - 9 - 4656 6 1 1 2 - 10 - 468 1 9 2 Chrysomelidae • • •• . . 16-10-46 104 Pheidole megacephala; 201 Entomobryidae 30 - 10 - 4635 $\mathbf{2}$ 1 3 Psocidae 13 - 11 - 46 $\mathbf{2}$ 621 4 Psocidae ; 2 Nitidulidae 27-11-46 1 Chalcidoidea; 1 Psocidae 1 11 - 12 - 46. 8 - 1 - 47. 5 - 2 - 47 $\mathbf{2}$ 1 19 - 2 - 47. • • 13 - 3 - 471 2 Psocidae • • 9 - 4 - 471 $\mathbf{2}$ 4 Psocoptera; 1 Neophysopus sp. 23 - 4 - 471 5 Psocoptera; 1 Neophysopus 14. sp.; Lepidopterous eggs 7 - 5 - 471 Psocoptera 1 . . 9 : 22 - 5 - 471 7 1 Braconidae • • . . 4 - 6 - 472 4 • • 19 - 6 - 47. . 1 3 Psocidae Total .. 191 $\mathbf{26}$ $\mathbf{2}$ 7 1 . . 1 35

numbers of Macrosiphum gei, A. gossypii and A. rumicis were found on vines in the Springbrook area, and in July 1947, M. persicae was again collected from passion vines. Aphis rumicis on one occasion (9/6/48) was found colonising passion vine terminals in the Thornlands district. In August 1947, in an infected plantation in the Rochedale area the insect population was found to consist of relatively high numbers of thrips on the flowers, terminals and leaves (Thrips tabaci Lind., T. imaginis Bagn., Haplothrips froggatti Hood) and a number of other insects (including Triphleps australis China, Pheidole megacephala (F.), and Lathridius sp.). No aphids were present on the vines. On the weeds within the plantation, however, Macrosiphum gei and Aphis rumicis were found to be present in some numbers.

Species of thrips were the insects most constantly present on the vines and they showed peak populations from August to November. The species numerically strongest were Thrips tabaci Lind. and T. imaginis Bagn.

Jassids were found to be infrequent visitors to the passion vine. They were not detected over the period of these samplings, but it must be noted that the method of sampling was not suitable for the collection of jassids.

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Table (б.
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INCIDENCE OF INSECTS ON THE PASSION VINE-PLANTATION 4, VICTORIA POINT.

	Thri	Thrips imagi	Taeniothr kellyan	Thrips spp	Haplothrips froggatti.	Aphis gossy	Macrosiphun gei.	Aphis rumic	Aphis spp.	Acarina.	Miscellancous.
21-8-46	54	4			4				4		2 Lathridiidae
10 - 9 - 46	34	3									
2 - 10 - 46	19	16									1 Chalcidoidea
16-10-46	26	2]			2 Chalcidoidea
30-10-46	12						• • •	1			
13-11-46	51										
27 - 11 - 46	1										
11-12-46	7										
8-1-47	7		• • •								
5 - 2 - 47											
19 - 2 - 47							• •				
13 - 3 - 47	1		•••								1 Empoasca sp.
27 - 3 - 47						••	•••			8	2 Pseudococcidae
9-4-47					1	••				13	1 Psocoptera; 1 Myceto- philidae
7-5-47				1						4	-
22 - 5 - 47	1	1						1		2	Lepidopterous larvae; 1 Dip-
	-										tera; 1 Anthocoridae
4-6-47	7		1	1		2	1	2			1 Psocidae ; 2 Miridae
19 - 6 - 47	4			2			·				2 Plectoptera ; 2 Phalacridae
4-7-47	7		'							1	
23-7-47	4						1			2	4 Triphleps australis
6 - 8 - 47				2							2 Diptera ; 6 Hemiptera
25 - 8 - 47	21										2 Coccinellidae
28 - 8 - 47	1										2 Triphleps australis ; 2 Nysius
											vinitor
12 - 9 - 47	59									2	6 Triphleps australis
24 - 9 - 47	32							• •	•••	•••	2 Coccinellidae
Total	347	25	 	5	5	2	 	2	 4	32	

Empoasca terra-reginae Paoli was collected in April and July of 1946 from several areas and *Peregrinus maidis* Ashm. was found on passion vines at Rochedale.

It is concluded that apart from the occasional incidences in epidemic form of pests such as Rutherglen bug (*Nysius vinitor* Berg.), green vegetable bug (*Nezara viridula* (L.)), Queensland fruit fly (*Strumeta tryoni* (Frogg.)) and the passion vine mite (*Tenuipalpus californicus* Banks), the passion vine supports a relatively small insect fauna. While known aphid vectors have been found on the vines, it is concluded that they do not colonise this plant by choice but that they breed on weeds and horticultural plants in and around the plantation. It would therefore appear that infection must be spread by itinerant visits by the vectors concerned.

TRANSMISSION OF THE VIRUS.

In the greenhouse the woodiness virus is readily transmitted mechanically by the glass spatula-carborundum dusting technique at mean maximum temperatures ranging from 72.2°F. to 106.4°F. This technique was employed in the mechanical transmissions referred to in this paper. Inoculum was prepared by macerating infected tissue in water with a mortar and pestle.

In grafting transmissions, the leaf grafting technique of Nattrass (1944) was exclusively employed. In this technique the petiole of the infected leaf is cut wedge-shaped and slipped into a longitudinal cut in the cambium of a healthy seedling. The area is then bound with tacky rubber. The passion vine is very amenable to this treatment and only rarely does a grafted leaf fail to survive. The method is conservative of material, and has the advantage that if in 24 hours the grafted leaf is turgid the success of the graft is then known. Individual leaves infected with the typical mottle (Fig. 14), or with fern leaf (Fig. 15), persisted, grafted to healthy seedlings, for 11-16 months in the greenhouse.

It was also determined that the virus may be transmitted by inserting a small rectangular piece $(\frac{1}{2} \text{ in. } x \frac{1}{8} \text{ in.})$ of infected leaf into a cut in the cambium of the stem of a healthy seedling and binding with tacky rubber. Within a month callus tissue is laid down around the area and transmission of the virus has occurred.

A single attempt to obtain evidence of soil transmission failed. Stem and leaf tissue from infected vines added to soil growing healthy seedlings failed to produce the disease.

Magee (1948) reported that the woodiness virus is identical with cucumber mosaic virus. It was not possible, however, over the course of the investigations, to transfer mechanically various cultures of the woodiness virus in *Passiflora edulis* to tomato (*Lycopersicon esculentum* Mill.), *Datura stramonium* L., cucumber (*Cucumis sativus* L.), *Lupinus mutabilis* Sweet, or tobacco (*Nicotiana tabacum* L.). Eleven separate attempts were made, involving 51 indicator plants over a range of temperatures from 79.0°F. to 100.6°F., the majority of the attempts being made at the higher temperature. At the times of such failures to obtain a response with any of these species, the inoculum used produced the usual reactions on *Passiflora edulis* and *P. alba* Link & Otto.

Temperature Relationship with Expression of Terminal Symptoms.

The bending downwards of the first and second unfolded leaflets along the axis of the main veins in seedling passion vines shortly after they are inoculated with the woodiness virus is a familiar symptom to workers with this virus.



Fig. 14.

Bunching of Terminal and Cessation of Growth Following Leaf Graft with Typical Bullate Mottle. 44 days after grafting. Healthy plant at right.

Employing Passiflora edulis and P. alba as healthy seedlings, and using various isolates of the virus in P. edulis as inoculum, it was found, both by leaf graft and by mechanical transmissions, that the time taken for the appearance of the terminal symptoms is governed by temperature.



Fig. 15.

Left, plant grafted with typical bullate mottle (note terminal reaction). Right, grafted with fern leaf (note absence of terminal reaction). Both 12 days after grafting.

The terminal symptoms may be expressed in as short a time as six days, with a mean of seven days, when the mean maximum temperature is $98\cdot1^{\circ}F$. (in November). When the mean maximum temperature drops to $83\cdot2^{\circ}F$. (April), the mean time for appearance of terminal symptoms is extended to $8\cdot8$ days, while in the coolest months (May, June, July), when the mean maximum varies from $73\cdot2^{\circ}F$, to $79\cdot5^{\circ}F$, the mean time taken for terminal symptoms to appear is $24\cdot6$ days.

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REACTIONS OF OTHER SPECIES OF PASSIFLORA TO THE WOODINESS VIRUS.

In the course of these investigations the reactions of other commonly occurring species of *Passiflora* to the woodiness virus were determined.

P. suberosa L.—In the field *P. suberosa* may be observed showing in the older leaves a fleeting light-green mottle with which large light-green spots may be associated. There may also be very slight rugosity on some of the young leaves. On several occasions during the summer and winter months, inoculations from such material failed to produce symptoms in *P. edulis* L., *P. foetida* L., *P. edulis* Sims forma *flavicarpa* O. Degener, or *P. alba*. Conversely, attempts to infect *P. suberosa* with virulent cultures of woodiness virus in *P. edulis* failed. Finally, to determine whether masking of the virus occurred in the last-mentioned tests, the symptomless *P. suberosa* plants were inoculated to *P. alba*; no response was obtained.

P. edulis f. *flavicarpa*.—This species reacts readily to inoculation with the woodiness virus. In the cooler months it produces symptoms similar to those shown by *P. edulis*, with the exception that the yellow spot mottle has a special affinity with this species. Twenty-seven days after inoculation with *P. edulis* material showing the typical mottle and yellow spot mottle, the young terminal leaves of *P. edulis* f. *flavicarpa* show vein clearing and are downcurled; the yellow spot mottle is conspicuously shown on the older leaves, with the yellow spots large and discrete. The petiole mottle on this species is more marked than in *P. edulis*.

Over the spring months the new growth on infected *P. edulis* f. *flavicarpa* plants is relatively normal, but there may be some asymmetry of leaves. In early summer, the plants again show the typical terminal symptoms accompanied by conspicuous discrete yellow mottle on the older leaves, unaccompanied by rugosity.

P. foetida.—Marked reaction of this species to the virus of the typical mottle is shown (Fig. 16). Infected seedlings may die within 33-53 days after inoculation during the winter months. Fourteen days after inoculations made in the cooler months the last three unfolded leaves show a violent spiral twisting accompanied by downcurling along the main veins, and a prominent green veinbanding and yellowing of interveinal areas occurs. Green veinbanding occurs also in the older leaves. Twenty-six days after moculation the leaves become bright yellow with a filigree of green veins.

P. alba.—This species is highly susceptible to woodiness. It is a small, easily-grown plant that can be repeatedly pruned and is an excellent species for greenhouse work with the virus.

When the mean maximum temperature varies from 91.5° F. to 106.4° F. (October to March), symptoms are masked in the new growth of systemically infected *P. alba* p'ants. However, if inoculations are made to seedlings of



Fig. 16. Terminal Symptoms in *Passiflora foetida* 14 days After Inoculation. Healthy plant at right.

P. alba over this temperature range, terminal symptoms will appear in 9-11 days; they consist of vein clearing in the first or first and second unfolded leaves, wilting of the petioles, downcurling of the leaves along the main veins and the appearance of a yellow green mottle.

When such plants are held in the greenhouse, and the mean maximum temperature drops to 79.0° F., they suffer from a crippling disease. There is a marked reduction in the growth of laterals and terminals, the majority of leaves on the plants are cupped downwards along their main veins, and individual leaflet lobes 'have their margins cupped under along the main veins. The leaves have a prominent yellow or yellowish-light-green mottle, with the lighter areas occurring in patches interveinally to produce a light-green veinbanding. These symptoms persisted until September (mean maximum temperature 81.2° F.).

From October to March (mean maximum temperatures 91.5° F. to 106.4° F.), the symptoms were masked in new growth; in the following April (mean maximum temperature 83.2° F.), translucent areas reappeared in the first unfolded leaflets accompanied by vein clearing. The symptoms of the previous winter were then repeated, accompanied by violent clearing and leaf distortion in the new growth. Stipules or leaf sheaths show similar mottle to the leaves.

The yellow spot and ring spot mottle may occur when P. alba is inoculated with suitable material. The symptoms first appearing after inoculation vary considerably in intensity, depending on the isolate of

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woodiness virus used (e.g., the typical woodiness mottle produces a more severe reaction than fern leaf material). A virulent culture of the typical woodiness mottle produces a more severe clearing of the first and second leaves which may involve the greater portion of the leaf. Older leaves may also show marked downward cupping of the leaflet lobes along the main veins, accompanied by a curling-under of the leaf margins. The leaf mottle may be so intense as to produce an almost yellow leaf.

Fern leaves on P. alba have not been observed in nature. Several isolates of the woodiness virus from P. edulis, however, produced fern leaves in P. alba in the greenhouse.

Passiflora alba, P. foetida and P. suberosa occur wild throughout south-eastern Queensland. Of these, P. alba is a common component of the flora of the mountain and hill country. It is almost universally infected with the woodiness virus and is considered to be an important natural reservoir of infection.

MECHANICAL TRANSMISSION BY SECATEURS.

During pruning operations in the field many successive cuts are made on the laterals of one vine before proceeding to the next vine. As populations of the known aphid vectors seemed inadequate to explain the epiphytotic incidence of the virus in plantations in which pruning was carried out, two tests were made to determine the extent of transmission of the virus by pruning with secateurs.

Test No. 1.

A typically infected passion vine was taken from the field in June 1947, and with this material two tests were made in the greenhouse.

1. Three infected terminals were bunched together and cut six times with the secateurs, which were then used to cut the terminal of a healthy passion vine seedling. This test was repeated five times.

2. Typically mottled leaves were ground in water to produce a thick extract. The secateurs were dipped in this extract and a cut was then made across the terminal of a healthy plant. This test was repeated four times.

The plants were maintained in the greenhouse for four months without any alteration to the above figures.

Test No. 2.

This was carried out on March 23, 1948, and as evidence obtained prior to this date indicated that the fern leaf component in combination with the yellow spot and ring spot mottles differed from the typical mottle in the same combination two distinct cultures of the virus were employed—the typical and the fern leaf.

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Forty-one 4-month-old passion vines were treated in the following manner:---

- (1) A healthy passion vine received one cut with secateurs after one cut had been made on the stem of a seedling infected with the typical woodiness (Plant 89). This test was repeated 20 times.
- (2) A healthy passion vine received one cut with secateurs after one cut had been made on the stem of a seedling infected with fern leaf type (Plant 88). This test was repeated 21 times.

The results obtained are shown in Table 7 and illustrated in Fig. 17.

Sympton		Ter	ninal	Reac	tion.	Bullate Mottle.	Fern Leaves.			No Symptoms.	
Days after Inco	ulation.	7	13	16	37	90	90	130	155		
Source.	Number Inoculated.										
Typical	20	1	10	11	11	11	0	0	1	9	
Fern Leaf	· 21	0	1*	0	2	3	1	6	7	11	

Table 7.												
NUMBER	OF	PLANTS	SHOWING	Symptoms.								

* Terminal reaction not present on 16th day.

Ninety days after the secateur transmissions were made the symptoms displayed by the plants in the ex fern leaf and the ex typical were quite different. The ex typical showed no fern leaves but exhibited a prominent bullate mottle, with the green colour confined to the raised areas and the remaining areas of the leaves light-green or cleared. Three plants of the ex fern leaf showed similar symptoms to the ex typical, but one of the other ex fern leaf plants had produced five fern leaves uncontaminated with the typical mottle. The ex typical were producing new growth slowly while the ex fern leaf (with the above exceptions) remained green and grew relatively normally.

At 130 days after inoculation, six of the ex fern leaf plants had produced fern leaves in the first and second leaves, while there were no fern leaves present in the ex typical.

At 155 days after inoculation, seven of the ex fern leaf plants were consistently producing fern leaves in the new growth and the yellow spot mottle was present on the older leaves. Vein clearing occurred in the terminal leaves but the plants were generally green in colour and making reasonably good growth. At this time 10 of the 11 infected plants in the ex typical had ceased growth in the majority of terminals and showed the typical mottle accompanied by marked translucent areas and vein clearing in the terminals. The yellow spot mottle was present on the older leaves and a bunching, twisting and marginal waving of the young leaves occurred. Foliage



Fig. 17. Difference in Symptoms Produced in Secateur Transmission Test. Left, ex 88 (fern leaf). Right, ex 89 (typical).

colour generally was a light-green. It would appear that the "typical" isolate produced a crippling disease, whereas the "fern leaf" isolate had a significantly milder effect.

The one remaining infected plant in the ex typical produced two fern leaves and a yellow spot mottle on the older leaves.

Nine days after the conclusion of the secateur transmission trial, detailed observations were made on six plants of the ex 88 and five of the ex 89. A summary of these is contained in Table 8.

Table 8.

Ac Nun	cn. iber.	Total Numbér Leaves.	Number Fern Leaves.	Number with Typical Mottle.	Number with Yellow Spot Mottle	Number with Ring Spot.	Terminal Vein Clearing.
			Fron	n 88 (ex fern	leaf).		
1		25	8	i — .			+
2		5	1	-		·	+
3		12	4	-	-		+
4		32	4	_	1		+
5		31	6	1	_		+
6		29	1	2	6	2	4-
			Fre	om 89 (ex typ	vical).		
1		13		3	2	_	+
2	••	18	1	7	1		+
3		22		6	1	_	+
4	••	16	—	8	5		+
5	••	32	? 1	5	8	—	+
		Súmmo	ury :		Total Number Leaves.	Percentage Fern Leaves.	Percentage Typical Mottle
	\mathbf{Fr}	om 88 (ex Fer	n leaf)		. 134	18	2
	\mathbf{Fr}	om 89 (ex Typ	oical)		. 101	2	29

SYMPTOM EXPRESSION FOLLOWING INOCULATION WITH FERN LEAF AND TYPICAL STRAINS OF THE WOODINESS VIRUS.



Fig. 18. Fern Leaf Transmitted Mechanically and Uncontaminated with the Typical Mottle. T. MCKNIGHT.



Fig. 19.

Grafting Transmission Tests. Left-hand Pair, 57 days after grafting. Right-hand Pair, same pair 154 days after grafting. Note persistence of grafted leaves. The plant at the left in each case was inoculated with fern leaf and shows no terminal reaction; that on the right was inoculated with typical mottle and a terminal reaction is shown.

It was found that while other symptoms of the virus (yellow spot mottle, terminal vein clearing) remained present in the two sources of the virus used in this test, it was possible to obtain a number of plants (1-4 from ex 88) which produced fern leaves uncontaminated with the typical mottle (Fig. 18), and three plants (1, 3 and 4 in the ex 89) which produced the typical mottle uncontaminated with the fern leaf.

It was then shown, by taking fern leaves from the ex 88 plants and by taking typical mottle leaves from the ex 89 plants and leaf grafting to healthy passion vine seedlings, that the typical mottle component is responsible for the terminal bending and twisting symptoms, while the fern leaf component is unable to produce the terminal reaction (Fig. 19). For 46 days after leaf grafting with fern leaves the seedlings remained normal and exhibited no terminal reaction or mottle. Fifteen days after leaf grafting with the typical mottle, the seedlings showed the usual marked terminal reaction. Forty-six days after inoculation the plants had ceased to grow and showed bunching of the terminals and yellow spot mottle.

STRAIN COMPLEX HYPOTHESIS

Nattrass (1940, 1944) referred to a form of the woodiness virus which produced little or no effect on the foliage but which produced woody fruit, and also to three other distinct types present in parts of Kenya. Unfortunately, no description of these three types was given. The form producing little or no foliage effect but producing woody fruit has not been encountered in Queensland.

Hitherto, the woodiness virus as it occurs in Australia has been regarded as a single entity. However, during the course of greenhouse experiments and field observations, evidence has consistently appeared to support the view that this virus exists as a complex of strains. This evidence is summarised below.

During greenhouse transmissions it was found that when leaves infected with typical mottle were inoculated into healthy seedlings the whole series of symptoms characteristic of the virus were produced. From such infected seedlings selections were made of the fern leaf, yellow spot mottle, ring spot mottle and typical mottle components and by leaf-grafting and by mechanical transmissions in a new series of plants the majority of such transmissions were found to reproduce again the whole series of symptoms of the virus. From a number of transmissions, however,—

(1) It was found possible to exclude the typical leaf mottle from the range of symptoms by selecting fern leaves for leaf grafts which were contaminated by the yellow spot mottle only. Such fern leaf grafts were shown to be unable to produce the terminal reaction, while grafts of the typical mottled leaves carried out at the same time did produce this reaction.

No acceleration in time in producing fern leaves occurred by selecting fern leaves for grafts as compared with selecting typical mottle for grafting; neither was there any difference in time in the production of fern leaves by employing typical or fern leaf material for mechanical transmissions.

It was shown that simultaneous leaf grafting to separate leaders of the one plant of the typical mottle and the fern leaf component results in a positive terminal reaction on the leader grafted with the typical mottle, and a negative reaction on the leader grafted with the fern leaf.

(2) It was determined that inoculation from the fern leaf component segregated from the typical mottle, and contaminated only by the yellow spot mottle, produces reasonably good growth.

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- (3) It was found that inoculation from the typical mottle uncontaminated with the fern leaf produces a severe and crippling disease.
- (4) While the normal type of isolate of the woodiness virus may be carried on seedlings in the greenhouse for two years without producing death, it is possible to obtain a virulent strain which may cause chlorosis of *Passiflora edulis* followed by tip blight within nine weeks.
- (5) It was found that selections made from leaves of greenhouse plants showing exceptionally pronounced vein clearing may produce large areas of clearing in inoculated plants (involving half of the leaf blade) which is followed by leaf chlorosis and death.

These, and other experiments, have demonstrated that it is possible, in the greenhouse, by selective mechanical and leaf-graft transmissions to alter the relative concentrations of different symptom components.

In the field, different components of the virus may vary markedly in symptom expression. It is possible to select plants showing these differences which, when inoculated to healthy seedlings, will produce reactions of varying intensities. It has also been shown that seasonal fluctuations occur in the expression of the different components.

Assuming that the virus exists in nature as various combinations of strains, it is considered probable that the ring spot of the foliage is associated with the ring spot of the fruit and that the typical foliage mottle is associated with the malformed woody fruit and the terminal bunchiness. The yellow spot foliage mottle is relatively a much milder foliage symptom than the typical foliage mottle and it may be associated with the stippled fruit condition. Except for the alteration in leaf shape with the fern leaf condition, this component does not markedly affect the vigour of the plant.

It is suggested that a mild strain-immunity from the fruit-destroying form of this virus might be sought.

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