INHERITANCE OF SPOTTED WILT RESISTANCE IN THE TOMATO

I. IDENTIFICATION OF STRAINS OF THE VIRUS BY THE RESISTANCE OR SUSCEPTIBILITY OF TOMATO SPECIES

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Summary

Strains of the tomato spotted wilt virus were separated from field-infected material and purified with a range of solanaceous species. These strains were classified into four groups, Tip Blight (TB), Necrotic (N), Ringspot (R), and Mild (M), according to the symptoms developed by susceptible tomato hosts.

Strains within these groups were identified by the resistance or susceptibility of the five tomato types *Lycopersicon peruvianum, L. pimpinellifolium,* and *L. esculentum* var. Rey de los Tempranos, Pearl Harbour, and Manzana. This gave a total of 10 distinct strains.

It is claimed that this method of classifying the strains will facilitate the identification of genes for resistance to spotted wilt, so that their mode of inheritance can be studied.

A possible explanation of the variable resistance of the varieties Rey de los Tempranos, Pearl Harbour, and Manzana is given.

I. INTRODUCTION

The spotted wilt disease of the tomato has been the subject of extensive investigation in Australia and America for many years. Best and Samuel (1936*a*, 1936*b*) and Bald and Samuel (1934) made artificial inoculation a standard technique in the study of this virus when they showed that the infectivity of the virus was considerably prolonged by maintaining the extracted infected plant sap at pH 7.0, and by using a reducing agent, such as sodium sulphite.

Norris (1946) demonstrated the existence of five strains of the virus, which he separated from naturally occurring complexes. He named these strains Tip Blight (TB), Necrotic (N), Ringspot (R), Mild (M), and Very Mild (VM). The variability in the symptoms on tomatoes was shown to be caused mainly by the number and concentration of the individual strains comprising the field complexes.

In the search for tomato varieties with genetic resistance to the tomato spotted wilt (T.S.W.) virus, Dr. D. R. Porter, of the University of California, selected a strain of *L. pimpinellifolium* with high resistance. It was found, however, that a linkage existed between the *L. pimpinellifolium* characters and resistance to T.S.W. In an attempt to break this linkage by back-crossing with

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Porter's strain of *L. pimpinellifolium,* Hutton (1949, 1951) reported the inheritance of resistance as being obscure but likely to be controlled by a polygenic system.

Smith (1944) found that the wild tomato *L. peruvianum* was immune to T.S.W. in the field and by the use of embryo culture he was able to procure crosses with *L. esculentum.* Norris (1946) confirmed the very high resistance of *L. peruvianum,* by inoculating it with his five strains and showing that only the Tip Blight strain was capable of producing even very mild symptoms.

Pearl Harbour, the first commercial variety resistant to T.S.W., was bred by Kikuta, Hendrix, and Grazier (1945) in Hawaii and derived its resistance from Porter's strain of *L. pimpinellifolium.*

Holmes (1948) found that the two Argentinian varieties, Rey de los Tempranos and Manzana, were resistant to T.S.W. in New Jersey, but susceptible in Hawaii and that Pearl Harbour lost much of its resistance when grown in New Jersey. This breakdown of resistance in different localities was assumed to be due to differences in the strain composition of the virus complexes.

Finlay (1951) showed that in Western Australia the varieties Pearl Harbour, Manzana, and Rey de los Tempranos were all susceptible, but that an F_1 hybrid between Pearl Harbour and Rey de los Tempranos had a very high field resistance.

These investigations suggested that there were several genes controlling the inheritance of resistance to T.S.W. and that the presence or absence of some of the strains of the virus in local complexes also had an effect on the resistance or susceptibility of varieties such as Pearl Harbour, Manzana, and Rey de los Tempranos.

The following investigation commenced in 1949, and was based on the hypothesis that there exists a complex of genes for resistance to T.S.W. virus, and that each of these genes controls resistance to one or more individual strains of the virus. To test the validity of this hypothesis it was necessary to separate as many strains of the virus as possible and to ascertain the resistance or susceptibility of tomato varieties and species to these strains.

II. Materials and Methods

(*a*) *Strain Separation*

Two complexes of T.S.W. virus, obtained from commercial tomato plants, were used as the original source of strains. The first complex induced typical Tip Blight symptoms on a plant of the variety Wanneroo Late in the field. The second complex, found on a plant of variety King Humbert, had a higher concentration of milder strains as typified by the mild mottling of young leaves followed by a delayed necrosis about 7 days after the appearance of the first symptoms.

(i) *Norris's Method.*—Norris (1946) gave a very full account of his methods of strain separation, using a range of solanaceous plants for their differentiation. These methods were followed in this investigation.

The virus strains were kept in an active state by hand inoculation every 3 weeks onto young tomato plants of the variety Potentate. The plant tissue used as a source of inoculum was selected when the first symptoms were most marked, at which stage they contain a high concentration of virus. The time between inoculation and the appearance of first symptoms, however, varied with the virus strain used.

Infected leaf tissue (1.0 g.) was ground in a mortar with 12.0 ml. of a buffer solution of pH 7.0 made up of 3 parts M/10 Na_2HPO_4 plus 2 parts M/10 NaH_2PO_4 together with 0.2 per cent. sodium sulphite as a reducing agent. Dusting of all plants with fine carborundum powder before inoculating was standard procedure. Inoculation was performed with a ground-glass spatula. All the plant material for the experiments was grown in an insect-proof glass-house.

From the two original complexes in Wanneroo Late and King Humbert four strains of the virus were isolated in a pure or almost pure form. They gave similar reactions to Norris's Tip Blight, Necrotic, Ringspot, and Mild strains. Norris's (1946) Necrotic strain had been isolated from a potato plant and not from tomato.

(ii) *Imported Strains.*—Through the cooperation of Dr. R. J. Best, tomato plants carrying three strains of T.S.W. virus were flown from the Waite Institute, South Australia. These strains Best and Gallus (1947) named A, B, and C in decreasing order of severity of symptoms developed by susceptible tomato plants. When tested these strains were found to produce host reactions similar to those caused by TB, N, and R described by Norris (1946).

(iii) *Possible New Strains.*—During 1951, in a field of 1000 segregating tomato hybrids and parent lines, many of which exhibited resistance to T.S.W., a line of Porter's strain of *L. pimpinellifolium* became badly infected with T.S.W. virus. As Porter's strain of *L. pimpinellifolium* had not previously been reported susceptible in the field, the severe strain of virus was isolated and appeared to be identical to TB strain on susceptible tomato hosts. In Porter's strain of *L. pimpinellifolium* the symptoms were a severe systemic necrosis on the lower leaves, gradually progressing up the stems, and finally killing the plants. This strain was called TB_2.

Several other strains were separated from material in this field, many plants being badly infected, but the strains appeared to be identical with those already isolated. All were maintained, however, for further testing.

(b) Culture and Inoculation of Tomato Species used in Strain Differentiation

The tomato varieties and species selected for differentiating strains of T.S.W. were *L. peruvianum,* Porter's strain of *L. pimpinellifolium,* and the *L. esculentum* varieties, Rey de los Tempranos, Pearl Harbour, and Manzana. All these exhibit resistance to T.S.W. virus in different areas of the world.

Several hundred plants of these varieties were grown in 3-in. pots in an insect-proof glass-house under hot conditions (95-100°F.). This treatment produced hardy plants similar to field-grown ones. When 10-12 in. high these

plants were transferred to a basement room at a temperature of about 85°F., and illuminated by two banks of fluorescent lights (14 40-watt tubes per bank). Commercial "Daylight" and "Soft white" tubes were alternated to give a spectrum range. The banks of lights were lowered to within about 2 in. of the top of the plants, to give a light intensity of about 500 ft.-candles (Plate 1).

The plants were given 24 hours dark treatment before inoculation and from then on a 12-hour day until the trial was completed. These lighting and temperature treatments were given to standardize environmental conditions within reasonably close limits because different reactions had been noted under varying environmental conditions. Four leaves just below the growing tip were inoculated on each plant.

This experimental procedure was adopted in order to simulate as nearly as possible field conditions as experienced in Western Australia, because it was hoped that the knowledge gained from these experiments might be applied directly to practical breeding for resistance to the T.S.W. virus disease. The environmental conditions imposed on the experimental plants just prior to and following inoculation tended to favour the virus.

Because of space limitation under the banks of fluorescent lights, a series of trials were conducted over a period of about 12 months, under environmental conditions as nearly identical as possible.

A 9 by 9 latin square layout was employed, made up of three varieties inoculated with three strains and replicated nine times. The trials were conducted so that tomato types *L. peruvianum,* Porter's strain of *L. pimpinellifolium,* and Rey de los Tempranos were inoculated by three virus strains in a latin square design, and placed under one bank of fluorescent tubes. Tomato types Rey de los Tempranos, Pearl Harbour, and Manzana were inoculated with the same three strains and placed under the other bank of fluorescent tubes.

At the end of each trial (usually 30-40 days) further plants were inoculated with two of the strains used in the previous trial plus one new strain. This procedure was continued until each variety had been inoculated at three different intervals of time, by the same virus strain, i.e. 27 plants of each variety had been inoculated with each strain, except variety Rey de los Tempranos, which was inoculated with each strain 54 times, being duplicated under each set of fluorescent lights (Table 1).

The necessity of conducting a series of trials with relatively small numbers of plants has tended to reduce the statistical precision of this experiment. By maintaining constant environmental conditions, plus employing standardized inoculum and inoculating technique, the error has been reduced to a minimum.

Although a fully susceptible variety of tomato was not included in the trials, the symptoms of all virus material were checked before and after the experiments on the fully susceptible tomato variety Potentate.

The reactions of the tomato varieties and species were classified into three categories:

Immune—plants that showed no reaction to the virus, even after two inoculations.

Resistant—plants exhibiting symptoms, but able to overcome the effect of the virus and continue growth free of the virus.

Susceptible—plants exhibiting symptoms, but unable to overcome the effect of the virus.

TABLE 1

NUMBERS OF IMMUNE (I), RESISTANT (R), AND SUSCEPTIBLE (S) PLANTS OF FIVE TOMATO SPECIES AND VARIETIES WHEN INOCULATED WITH 10 STRAINS OF T.S.W. VIRUS.

Tomato variety		*L. peruvianum*			*L. pimpinellifolium*			Rey de los Tempranos			Pearl Harbour			Manzana		
No. plants inoculated		27			27			54			27			27		
Plant reaction		I	R	S	I	R	S	I	R	S	I	R	S	I	R	S
Strains of T.S.W. virus	TB_1	1	26			26	1		54 (3)*				27			27
	TB_2	27					27		54				27		27	
	TB_3	27				27 (3)				54		27 (27)				27
	N_1	27				27 (3)				54		27 (2)				27
	N_2	27				27			54							27
	R_1	27			27					54			27			27
	R_2	27			27				54			27 (27)			27 (2)	
	R_3	27			27			53	1				27 27		27 (1)	
	M_1	27			27			53	1		27					27
	M_2	27			27			54			27				27 (27)	

* The figures in parentheses indicate the number of resistant plants with systemic infection in addition to local lesions on inoculated leaves.

III. RESULTS

By using the method of strain differentiation outlined, 10 distinct strains of the T.S.W. virus were identified. The strains were named TB_1, TB_2, TB_3, N_1, N_2, R_1, R_2, R_3, M_1, and M_2. Table 2 classifies the resistance or susceptibility of the five tomato types to these strains.

(*a*) *Strain* TB_1

This is Best's strain A, which gives a typical tip blight reaction on susceptible tomato varieties.

(i) L. peruvianum.—The development of numerous small, necrotic lesions was evident on 26 plants of this species. One plant showed no reaction to the virus even after reinoculation. The lesions did not enlarge or become systemic. This species was, therefore, rated as resistant to strain TB_1.

(ii) L. pimpinellifolium.—This developed necrotic local lesions with a gradual systemic spreading of the disease, but under the environmental conditions imposed by the experiment, 26 of the 27 plants outgrew the infection and appeared healthy after 35-40 days. One plant died. They were rated as resistant. It was noted that when this species was grown at lower temperatures and the plants were much "softer" they were quite susceptible.

(iii) *Rey de los Tempranos.*—This variety gave a reaction typically the same as *L. pimpinellifolium* with the disease spreading gradually up the stems. The plants appeared, however, to be able to localize the disease eventually and grow away quite normally. This strain had no effect on the setting or quality of fruit even in the diseased portion of the plant, and the variety was rated as resistant.

(iv) *Pearl Harbour and Manzana.*—These appeared to be quite susceptible, the inoculated leaves exhibiting necrotic local lesions after 6-7 days, followed by a rapid systemic spreading to the upper portion of the plant, causing darkened stems that collapsed and died rapidly. The plants were all dead within 21 days. Both of these varieties were rated as susceptible.

TABLE 2

REACTION OF FIVE TOMATO TYPES TO 10 STRAINS OF SPOTTED WILT

Tomato Differentials	T.S.W. Virus Strains									
	Tip Blight Group			Necrotic Group		Ringspot Group			Mild Group	
	TB_1	TB_2	TB_3	N_1	N_2	R_1	R_2	R_3	M_1	M_2
L. peruvianum	R	I	I	I	I	I	I	I	I	I
L. pimpinellifolium	R	S	R	R	R	I	I	I	I	I
Rey de los Tempranos	R	R	S	S	R	S	R	I	I	I
Pearl Harbour	S	S	R	R	S	R	S	S	I	I
Manzana	S	R	S	S	S	S	R	R	S	R

I = immune; R = resistant; S = susceptible.

(*b*) *Strain* TB_2

This strain was isolated from plants of Porter's strain of *L. pimpinellifolium* infected in the field.

(i) L. peruvianum.—This appeared to be quite immune to this strain, showing no lesions on inoculated leaves, and it was rated as immune.

(ii) L. pimpinellifolium.—Definite yellow, local lesions appeared after 7-8 days but they rapidly became necrotic on inoculated leaves. After about 14 days the systemic spread of the disease was evident, causing a diffuse mottling on the younger leaves, which later developed into an interveinal necrosis and finally either shrivelled or abscissed. After an average of about 35 days the virus had progressed up the stems and killed the whole plant. Rated as susceptible.

(iii) *Rey de los Tempranos and Manzana.*—These were similar to *L. pimpinellifolium* in reaction to this strain, but the symptoms were less severe, only odd leaflets exhibiting a necrosis developing from the diffuse mottling. All the plants grew away and apparently completely recovered after about 35-40 days. These varieties were rated as resistant.

(iv) *Pearl Harbour.*—The reaction was typical of normal Tip Blight, the plants being killed in 14-16 days after inoculation; rated as susceptible.

Owing to the typical Tip Blight reaction of this strain on susceptible plants and Pearl Harbour it must be classed in the TB group, even though its reaction to *L. pimpinellifolium* is atypical.

(*c*) *Strain* TB_3

The strain was isolated from a plant of the variety Wanneroo Late growing in the field.

(i) L. peruvianum.—This gave no reaction on any of the 27 plants inoculated and was rated immune.

(ii) L. pimpinellifolium.—After 7-8 days necrotic local lesions appeared on 25 of the 27 plants that were inoculated and after 14-16 days these were followed, in three plants, by a mild chlorotic systemic infection on three to five leaves above those inoculated. No spread of the disease was evident up to 30 days after inoculation. After 10 days the other two plants were reinoculated and produced substantially the same symptoms as the other 25, indicating a "miss" in inoculation. This variety was rated as resistant.

(iii) *Rey de los Tempranos.*—This reacted to TB_3 in a manner similar to its behaviour with strains TB_1 and TB_2 but instead of the plants gradually overcoming the virus, the systemic spread gradually built up, producing a chlorotic mottle followed rapidly by severe interveinal necrosis and some necrotic spotting on the very young leaves. The plants died after 25-30 days and were rated as susceptible.

(iv) *Pearl Harbour.*—After 6-7 days local necrotic lesions appeared and these were followed by systemic necrotic spotting and stunting of the growing tip. New growth completely free of disease formed 28-32 days later. No virus infection could be produced on *Nicotiana glutinosa* from sap extracted from the new, healthy shoots and the plants were rated as resistant.

(v) *Manzana.*—Local lesions formed after 5-6 days with systemic necrosis in the stems and leaves above and sometimes below inoculated leaves. After 16-18 days the plants were dead and were classed as susceptible.

(*d*) *Strain* N_1

This strain was obtained from a plant of the variety King Humbert grown in the field.

(i) L. peruvianum.—No symptoms were evident on any of the inoculated plants, which were rated as immune.

(ii) L. pimpinellifolium.—After 12-14 days indefinite yellow spots appeared surrounded sometimes by fine concentric yellow rings. With three plants these spread and after about 28 days the systemic infection had caused slight vein clearing and curling down of the young leaves, eventually stunting the growth. New growth on these three plants developed without symptoms and as the other 24 plants showed no systemic spread the variety was rated as resistant.

(iii) *Rey de los Tempranos.*—Indefinite chlorotic spotting, which later became necrotic, appeared after 10-12 days on all the plants. Systemic vein clearing was also evident in all plants with curling down of leaves and stunting of the growing tip whilst necrosis was later evident in the systemically affected areas. New growth developed with similar symptoms and produced a few fruit, which were small and showed a distinct yellow ring pattern, causing the variety to be classed as susceptible.

(iv) *Pearl Harbour.*—Very mild, indefinite, yellow spotting developed, which spread slowly to form a diffuse mottling and an occasional sharply defined green "island." Only two plants showed signs of systemic infection, and then only on two or three leaves above those inoculated. The growing tip and new growth developed without symptoms and the variety was rated as resistant.

(v) *Manzana.*—This gave substantially the same reaction as Rey de los Tempranos except that the systemic spread was generally more rapid and severe, much more necrosis being evident on young leaves. The rating was susceptible.

(*e*) *Strain* N_2

This strain gives the same reaction and is identical with Best's strain B.

(i) L. peruvianum.—No symptoms were evident on any plants, which were rated as immune.

(ii) L. pimpinellifolium.—Yellow ringspot lesions appeared on inoculated leaves after 7-8 days and these gradually enlarged, becoming necrotic around the circumference. There was no systemic spread of the disease, giving a resistant rating.

(iii) *Rey de los Tempranos.*—Indefinite, yellow mottling and ringspot lesions on inoculated leaves after 7-8 days, a necrotic pattern becoming evident on the outer edges of the chlorotic areas after about 20 days. There was no systemic spread of the disease, which rated the variety as resistant.

(iv) *Pearl Harbour and Manzana.*—These two varieties reacted similarly to this strain, local chlorotic lesions appearing after 7-8 days, which later became necrotic at the circumference of the lesions to produce a necrotic pattern, which caused leaves to shrivel and die. Sixteen to 20 days after inoculation bronze spot-

ting became evident on the young leaves and also a chlorotic mottling with some necrosis on some of the leaves below those inoculated. The upper leaves wilted and shrivelled slowly.

After about 40 days, weak new growth appeared on five plants of Pearl Harbour and four plants of Manzana, but even this exhibited a stunting and diffuse mottle on the leaves. Two young shoots also had some bronze spotting and the varieties were rated as susceptible.

(*f*) *Strain* R_1

The strain is equivalent to Best's strain C.

(i) L. peruvianum.—No symptoms were evident up to 30 days after inoculation, giving an immune rating.

(ii) L. pimpinellifolium.—No symptoms appeared up to 30 days. Rated immune.

(iii) *Rey de los Tempranos.*—A chlorotic mottle appeared after about 20 days, varied slightly from plant to plant, but it was either in the form of a fine, concentric, yellow line pattern, or a diffuse mottling with a few sharply defined green "islands."

No necrosis was evident on any of the plants at any stage of infection. The younger leaves were stunted and rugose, having a tendency to curl downwards. Rated as susceptible.

(iv) *Pearl Harbour.*—Vein clearing and downward curling of the inoculated leaves was followed by the appearance of a diffuse mild mottle on two or three leaves above those inoculated. In no plants did the disease become fully systemic, the plants growing on quite normally after a slight reduction in the growth rate for between 10 and 30 days. Rated resistant.

(v) *Manzana.*—Symptoms similar to those produced in Rey de los Tempranos (iii) except that five plants exhibited a marked interveinal necrosis on some young leaves, which subsequently shrivelled and died. Rated susceptible.

(*g*) *Strain* R_2

This strain was isolated from a tomato plant of the variety King Humbert.

(i) L. peruvianum.—No symptoms evident after inoculation. Rated immune.

(ii) L. pimpinellifolium.—No symptoms. Rated immune.

(iii) *Rey de los Tempranos.*—Vein clearing and curling down of inoculated leaves occurred after 8-9 days and these leaves yellowed and fell off. On only two plants did systemic infection manifest itself as a slight vein clearing on some of the younger leaves. Rated resistant.

(iv) *Pearl Harbour.*—Vein clearing and curling down of inoculated leaves occurred after 7-8 days. The plants became dwarfed with chlorotic, rugose,

and distorted leaves. Some younger leaves developed a bronze pattern and others a definite concentric line ring pattern. New growth exhibited a strong mottle and distortion with sharply defined, raised, green "islands." Rated susceptible.

(v) *Manzana.*—This variety reacted in a similar manner to strain R_2 as did Rey de los Tempranos. Rated resistant.

(*h*) *Strain* R_3

This strain was isolated from a complex infecting a hybrid tomato plant of genetic constitution resulting from a tetraploid hybrid Pearl Harbour × Rey de los Tempranos crossed with a diploid Manzana.

(i) L. peruvianum, L. pimpinellifolium, *and Rey de los Tempranos.*—No symptoms appeared on any of these plants after inoculation, except local lesions on inoculated leaves of one plant of Rey de los Tempranos. Rated immune.

(ii) *Pearl Harbour.*—A diffuse mottle appeared after 8-9 days on inoculated leaves. The systemic symptoms comprised a vein clearing with down-curling of the young leaves, stunting of the plants, and the appearance of sharply defined mottling with some interveinal necrosis and rugosity of the leaves. The new growth was mottled and rugose. Rated susceptible.

(iii) *Manzana.*—A vein clearing and down-curling of inoculated leaves was evident after about 7-8 days and this was followed by a slight mottling of the young leaves, but this gradually disappeared, leaving apparently healthy plants after about 28-30 days. Rated resistant.

(*i*) *Strain* M_1

This strain was obtained from plants of *L. esculentum* var. King Humbert infected with a mild complex in the field and also from *L. pimpinellifolium.*

(i) L. peruvianum, L. pimpinellifolium, *Rey de los Tempranos, and Pearl Harbour.*—Symptoms were only evident on inoculated leaves of one plant of Rey de los Tempranos. Rated immune.

(ii) *Manzana.*—Slight vein clearing on the inoculated leaves became evident after about 12 days. A systemic mild mottling of young leaves with slight rugosity appeared after 21-25 days. No effect on the vigour of the plants was noticed, but slight traces of the mottle were evident for a considerable time. On six of the plants the fruit showed faint yellow ring markings. Rated susceptible.

(*j*) *Strain* M_2

This strain was obtained from plants of several different tomato varieties. All the isolates gave the same reaction, so that all except that from one line were discarded.

(i) L. peruvianum, L. pimpinellifolium, *Rey de los Tempranos, and Pearl Harbour.*—No symptoms became evident after inoculation; the varieties were rated immune.

(ii) *Manzana.*—A slight mottling appeared on the young leaves of all plants but this quickly disappeared. It had no effect on the vigour of the plants, which were rated as resistant.

IV. Discussion

The reaction of genetically different tomato hosts to individual strains of the spotted wilt virus has enabled the number of known strains to be increased to 10. Norris (1946) was able to isolate a very mild strain, which has not as yet been accomplished in this project. It is reasonable then to assume that there is at least one more strain in existence, apart from the 10 described in this paper.

It is proposed to classify these strains by grouping them firstly according to the symptoms they produce on susceptible tomato hosts, e.g. Tip Blight (TB), Necrotic (N), Ringspot (R), and Mild (M). The strains within any one group are further differentiated by the resistance or susceptibility of the five selected tomato types to them, and are numbered as identified, e.g. TB_1, TB_2, etc. This method of classification is simple and will accommodate further strains as they appear.

A possible explanation of the results gained by Holmes (1948) and Kikuta, Hendrix, and Grazier (1945) is offered by this work. It is suggested that the Hawaiian T.S.W. complex consists of all or some of the strains TB_3, N_1, R_1, M_1, and M_2, accounting for the high resistance of Pearl Harbour in that locality. The New Jersey complex, however, may consist of any number of the strains TB_1, TB_2, N_2, R_2, R_3, M_1, and M_2. This would account for the apparent resistance of Rey de los Tempranos and Manzana, and could also explain the apparent higher resistance of Rey de los Tempranos as compared with Manzana. The latter variety is susceptible to strains TB_1 and N_2, which may occur only occasionally in the complexes, causing the resistance of Manzana but not of Rey de los Tempranos to break down.

It is not known whether the strains of the spotted wilt virus present in other countries are identical with those found in Australia but judging by the susceptibility of tomato varieties found to be resistant in other parts of the world it appears likely that a greater range is present in this country.

Although specific resistance or susceptibility reactions are obtained by genetically different tomato plants, these cannot be used in strain purification. Norris (1951) obtained evidence of synergism of strains of spotted wilt, by showing that although Mild and Very Mild strains are present with Ringspot strains in the naturally occurring virus complexes found in potatoes, the former are unable to invade the potato in their pure form. Further evidence of a synergism appeared during the experiments described in this paper, when *L. pimpinellifolium* became infected with T.S.W. in the field. A virulent strain

TB_2, which apparently accounted for the breakdown of resistance, was isolated from this complex, but strains R_2 and M_1 were also obtained from this plant. *L. pimpinellifolium* is immune to the pure forms of strains R_2 and M_1.

The strain reactions given in Table 2 demonstrate the benefits to be gained by perseverence with hybrids involving *L. peruvianum* as a source of resistance. *L. pimpinellifolium,* however, is susceptible to strain TB_2. It is therefore inadvisable to use this species in breeding work, at least in Western Australia, where other strains are able to infect the plants if they are present in a complex with strain TB_2.

Finlay (1951) noted that the F_1 hybrid Pearl Harbour × Rey de los Tempranos had a very high resistance to T.S.W. complexes in the field, even though the two parent varieties were susceptible. The resistance possessed by each of the parents to some of the individual strains of the virus, as shown in Table 2, was transferred to the F_1 hybrid additively, producing resistance to a wide range of strains as may be found in field complexes.

It is proposed to use the methods described in this paper in an attempt to elucidate the number and mode of inheritance of the genes controlling resistance to T.S.W. The F_1 and F_2 populations of crosses in all combinations of Porter's strain of *L. pimpinellifolium,* Rey de los Tempranos, Pearl Harbour, and Manzana are being tested with the 10 strains so far identified. This work will be published later as Part II of this study.

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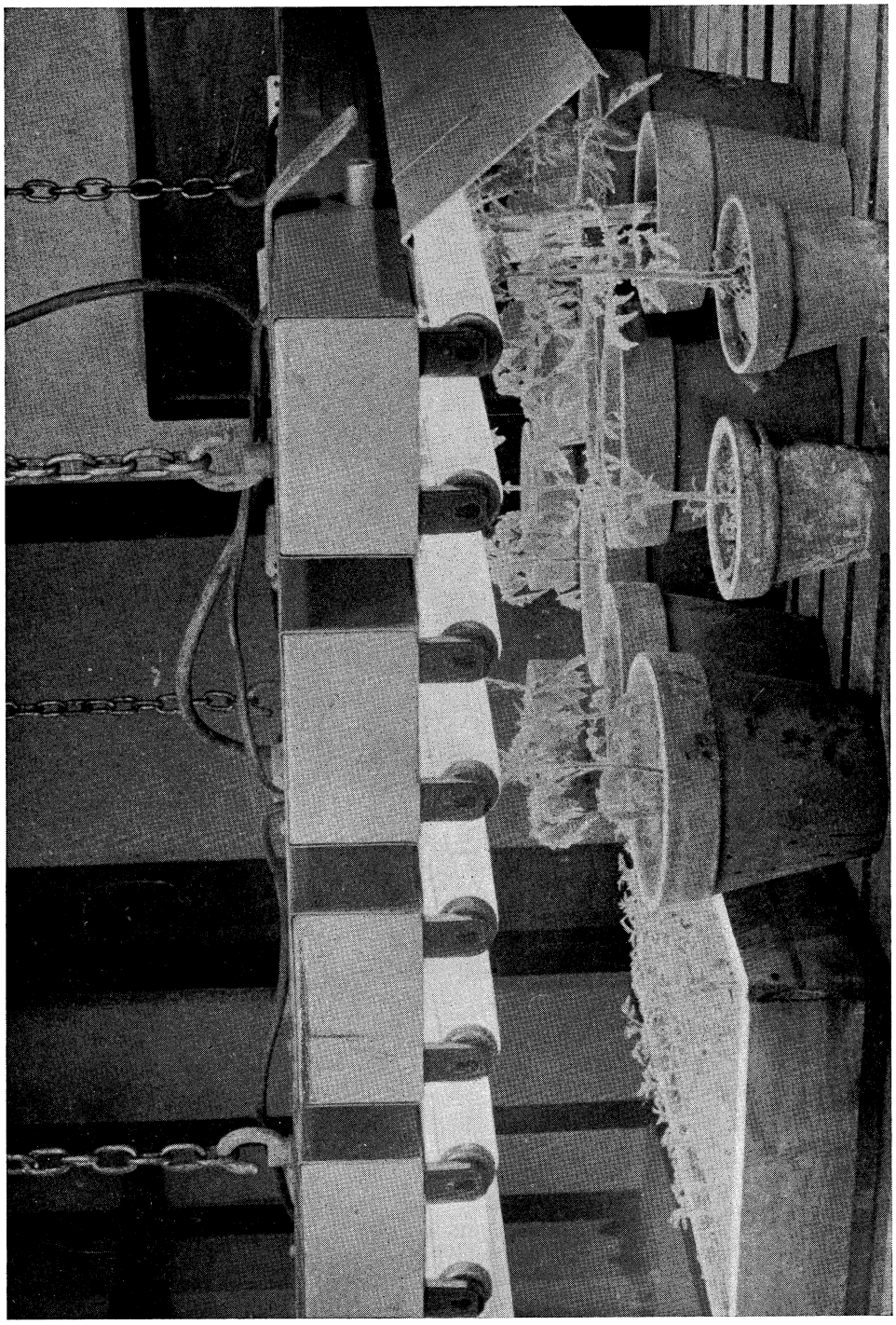

Fluorescent lights used to control the light intensity and length of day on experimental plants after inoculation.