Thrips in Relation to Gall-forming and Plant Disease Transmission: A Review[1]

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INTRODUCTION

Thrips are involved in several types of host relationship with plants, besides inflicting mechanical feeding injuries. Gall-forming and plant disease transmission are two such special host relationships. An attempt is made in this paper to summarize all the available information regarding these two topics.

Thrips are one of the well-known gall-forming insects, and the field has been fairly well studied. Most of the contributions have been made in the earlier years and little current work is known; references are briefly reviewed here. Galls are essentially a special type of toxaemia caused by insect toxin, and thus gall-forming is referred to as a phase of insect transmission of plant diseases. Study in the field of plant disease transmission by thrips has made rapid advancement in recent years and quite a large volume of references is available. The field was briefly reviewed about 10 years ago by Bailey (1935) and additional published information was assembled by Sakimura (1937). A large series of new references has been accumulated in the past 10 years and these are all available for the present review to make it as comprehensive as possible. Many old references not cited in the two former reviews, particularly on the subject of negative results of transmission tests, have been freely incorporated in this paper.

SUMMARY

Many thrips galls have been recorded, mainly from the tropic and subtropic regions. The common type of thrips galls is leaf-roll or its modified forms, a simple form, but a few other types, more complicated in structure and more advanced in development, are also known to be produced by thrips.

The available knowledge on toxaemias caused by thrips is far from complete.

Several cases each of bacterial and fungous diseases have been reported to be transmissible by thrips. Knowledge of these groups

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is also incomplete and the spread of many more diseases might be related to thrips. These diseases are rather easily disseminated by thrips.

As many as 41 different viruses have been tested for their vector relation with various species of thrips but none were in a positive relationship except the single case of the spotted wilt virus. There is another case but presentation of the evidence is incomplete. The spotted wilt virus is transmissible by three different species of thrips; some other species might be additional vectors. Thrips are unlikely to be the vectors for the viruses which are transmissible by other groups of insects. Additional thrips-transmissible viruses may possibly be found among a group which are parenchyma or sap-transmissible type but known to be not transmissible by any other group of insects.

Hawaii is subject to possible invasions of the second and third vector thrips of the spotted wilt virus; one of the three vectors has established well in Hawaii. This is a situation calling for protective measures to prevent such invasions which would increase destructiveness of the spotted wilt disease in Hawaii.

Part I: GALL-FORMING

The plant gall consists of deformed tissues produced by plants upon the stimulus induced by feeding of the gall insects. The toxin theory has been advanced for the origin or mechanism of the stimulus induced by insects. In other words, such galls are referred to be a special type of toxaemia caused by toxin secreted and injected by the gall insects at the time of feeding. However, a few of the insect galls appear to be of traumatic origin. Some simple forms of the thrips galls are suspected of belonging to this group. More common gall-formers are gall-mites, gall-midges, and gall-wasps, all of which produce well-defined galls. Thrips are, however, minor and rather primitive gall-formers. The most common types of thrips galls are leaf rolls, leaf folds, and leaf wrinkles. These types are more or less characteristic of the thrips galls. Highly developed galls, as commonly seen among those produced by other gall insects, are very rare among the thrips galls. The few such cases reported are bladder and pouch galls, horn galls, bud galls, and stem galls. No root gall produced by thrips has been reported yet.

The outstanding contributions in the field of thrips galls are the works of Bagnall (1928, 1929), Docters van Leeuwen-Reijnvaan (1926), Karny (1911, 1913), and Karny and Docters van Leeuwen-Reijnvaan (1913, 1914-1916).

The distribution of the thrips galls is more or less limited within the tropic and subtropic regions, particularly the palaeotropic regions. Its abundance is particularly noticeable in the Indo-Malay-Australian regions. A limited number of cases have also been reported from the Mediterranean and North African region and the Oceanic region. The major reference on the Oceanic region is that of Bagnall (1928) which dealt with the Samoan and Tongan thrips.

In Hawaii, the collectors have made some effort but no true gall-forming thrips[8] have yet been discovered. It appears that Hawaii is remote from the outer fringe of the central region where the evolution of gall-forming thrips has been highly developed. Incidentally, even the widely distributed *Ficus* gall thrips, *Gynaikothrips ficorum* (March.) and *G. uzeli* Zimm., are not present in Hawaii. The genus *Ficus* is entirely absent in the Hawaiian native flora, although several common species including *F. retusa* Linn. and *F. Benjamina* Linn. have been introduced in the recent years.

The thysanopterous fauna in the neotropic regions appears poor in gall-forming thrips and only few galls have been known. Several cases reported from North America are doubtful as to whether the thrips recorded are the true gallers or not. A good number of galls caused by the ordinary herbivorous terebrantian species were reported from Europe (Wahlgren, 1945).

The majority of gall-forming thrips belong to the suborder Tubulifera, but a few terebrantian species are also involved in gall-forming. Among Terebrantia, 10 species, which all produce simple forms of gall, belonging to three genera have been recorded from Dutch East Indies (Docters van Leeuwen-Reijnvaan, 1926); 17 species belonging to seven genera have been recorded from Europe (Wahlgren, 1945). Among Tubulifera, taxonomic range of the galler is strictly limited to the Phlaeothripinae, and practically every species belongs to Hoplothripini or Haplothripini. Very few belong to Idolothripini, Histricothripini, and Phlaeothripini, which are all rather primitive or poor gallers. As far as the reviewer is aware, there are about 110 species belonging to 25 genera of Hoplothripini and about 35 species belonging to 13 genera of Haplothripini. The predominating genera are of the *Gynaikothrips-Smerinthothrips* group.

Association of the inquilinous thrips is a very common occurrence in many thrips galls and also in the galls produced by other origins. A differentiation between the true galler and the friendly inquiline or predaceous invader has not always been recorded in the references. Consequently it is difficult to segregate them. However, it appears that a fairly good percentage of the 145 species of Tubulifera aforementioned must be the non-gall-forming species. The available indications suggest that some of the Hoplothripini group and the majority of the Haplothripini group belong to the non-gall-forming species, and the true gallers are more or less limited to the Hoplothripini. Diversity of the host plants on which thrips produce the galls is well noted, and the range includes Pteridophyta, Gym-

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[8] Malformations on foliage or terminals as a result of heavy mechanical injuries caused by the ordinary herbivorous terebrantian species were rarely observed.

nospermae, Dicotyledones, and Monocotyledones. The shape of galls in minute details are usually specific to the host plant on which the galls are produced and also to the thrips by which the galls are produced. In some cases, the same species of thrips produces different shapes of gall on the different species of plant; different species of thrips produce different shapes of gall on the same species of plant.

The most familiar and widely distributed thrips gall of the leaf-roll type is the one on *Ficus*. Ten species of *Gynaikothrips* and two species of *Smerinthothrips* have been recorded as responsible for gall formation on the various species of *Ficus* throughout the world. *G. ficorum* (March.), which more or less specifically feeds on the widely distributed *Ficus retusa*, is the cosmopolitan species (Priesner, 1939) and the rest are more or less regional species, except *G. uzeli* Zimm. which has a little wider range. *Ficus* galls have been reported from Samoa, Tonga, South Australia, Dutch East Indies, Philippines, Formosa, Malay, India, North and South Africa, Italy, Canary Islands, Florida, West Indies, Mexico (Bagnall, 1928) (Priesner, 1939). The inquilinous thrips are very common in the *Ficus* galls and a large number of species has been reported.

Several outstanding galls of the non-leaf-roll type are as follows:

1) *Austrothrips cochinchinensis* Karny produces large elliptical hollow pouch galls in terminal young leaves of *Calycopteris floribunda* Lam. and *Cordia dichotoma* Forst. f. (=*Myxa* Linn.) in India; the size is as large as 2-2.5 inches in diameter (Ramachandra Rao, 1924).

2) *Smerinthothrips heptapleuri* (Karny) produces a mass of pink horn galls, as long as 1.25 inches, on leaves of the various species of *Schefflera* in the Dutch East Indies (Docters van Leeuwen-Reijnvaan, 1926).

3) *Smerinthothrips heptapleuricola* Takahashi produces a mass of greenish, large horn galls on leaves of *Heptapleurum arboricolum* Hay. in Formosa (Takahashi, 1937).

4) *Kladothrips rugosus* Frog., *K. tepperi* (Karny), *K. rodwayi* Hardy and *K. augonsaxxos* Moulton produce large spherical, hollow pouch galls in leaves of the various species of *Acacia* in Australia (Froggatt, 1906) (Karny, 1911) (Hardy, 1916) (Moulton, 1927).

5) *Thaumatothrips froggatti* Karny produces large knob-shaped twig galls, as large as 1.5 inches x 1 inch, on *Casuarina stricta* Aiton in Australia (Karny, 1922).

6) *Onychothrips tepperi* (Uzel) produces small subspherical stem galls on *Acacia aneura* F. Muell. in Australia (Uzel, 1905).

7) *Phrasterothrips conducans* Pr. produces large bud galls on *Myrcia* sp. in Brazil (Costa Lima, 1935).

Part II: PLANT DISEASE TRANSMISSION

Thrips are involved in causing or transmitting four different groups of plant diseases. One group, toxaemias, is caused by toxin injected by the thrips. The other three groups—bacterial, fungous, and virus diseases—are transmitted by thrips. The transmission of the bacterial and fungous diseases, as far as the reported cases are concerned, is of the mechanical type. These pathogens are frequently disseminated by their adhering on the insect body, indicating that their vector relation is not specific. On the other hand, the transmission in the virus diseases is of the biological type and its vector relation is specific. Thrips, as a group, are not commonly vector insects. The plant diseases transmitted by thrips are far less in numbers than those transmitted by other groups of insects.

The first experimental demonstration of insect transmission of a plant disease was reported about 55 years ago, in 1891, by Waite. He concluded that pear blight, a bacterial disease, was transmitted by bees. Then a series of important discoveries followed. The earliest record on thrips in relation to plant disease is that of Whetzel (1904) which stated that thrips injury on onion aids infection of onion blight, a fungous disease. Then Johnson (1911) found that thrips, presumably *Frankliniella tritici* (Fitch), carried rust spores. The first experimentation on vector relation of thrips with virus disease was made by McClintock and Smith (1918), who discovered that cucumber mosaic was not transmitted by *Thrips tabaci* Lind. Then the first positive transmission was reported by Pittman (1927) who was successful in transmitting spotted wilt through *T. tabaci.* The first reference on bacterial disease was delayed until 1927 and 1929 when Caldis and Hansen stated that thrips are probably a vector for the fig spoilage diseases in California and this was followed by Buchanan (1932) on bean bacteriosis transmitted by *Hercinothrips femoralis* (Reuter).

TOXAEMIAS

There are only a few references incriminating thrips as a phytotoxicogenic insect that secretes a toxic substance and injects it into the host plant while feeding. The disease caused by such origin is called toxaemia. Available knowledge on toxaemias related to thrips is still very incomplete. Further observations and experimentations are needed for a thorough understanding of this special host relationship of thrips with the plant life.

Woods (1900) stated that the stigmonose of carnation is caused by the feeding effects of thrips, aphids, and red spider. Leach (1940, p. 124), citing Woods, stated that the carnation stigmonose caused by aphids is a toxaemia, but he did not include thrips as the causal insect. Apparently thrips do not have any relation to the disease.

Curzi (1932) stated that peach plume in Italy is caused by traumatic and toxic effects of the feeding punctures of thrips. Kratochvil and Farsky (1942) stated that a malformation of young shoots of larch in Bohemia and Moravia is due to a toxin injected in the process of feeding by *Taeniothrips laricivorus* K. and F. The reviewer is not aware of the details of their data since the original is not available to him. However, this is the first paper clearly claiming that the toxin secreted by thrips caused the pathogenic conditions of the plants. Reference should be made to the resemblance of the symptoms of this toxaemia with the bud gall produced by thrips.

BACTERIAL DISEASES[4]

Only a few bacterial diseases have been known with which thrips are in vector relation. Such vector relation was experimentally demonstrated, completely or partially, with four diseases and was suspected with two diseases. A negative result of transmission test of a disease was also reported. Of all the cases known, it appears that transmission is of the mechanical type. The pathogen could not be isolated from the internal organs in two cases. Although an association of infection at the sites of feeding injuries was reported in one case, no clear statement was made as to whether actual inoculation or aiding for ingression is provided by thrips. However, it is presumable that inoculation, in the strict sense, may not always take place. On the contrary, aiding ingression, that is the ingression of the pathogen into the tissues through the feeding injuries, may more commonly occur. It is quite probable that thrips may aid dissemination only in certain cases, and in these cases the pathogen may ingress irrespective of any presence of feeding injuries.

In a greenhouse experiment, bean bacteriosis (*Pseudomonas medicaginis* var. *phaseolicola* [Burkh.] Stapp and Kotte) was conclusively demonstrated to be transmissible by *Hercinothrips femoralis* (Reuter) (Buchanan, 1932). The lesions were always associated with the feeding injuries. The observations were not made on the details of transmission mechanism but Leach (1940, p. 206) stated that it appears to be mechanical. Fire blight (*Erwinia amylovora* [Burrill] Winslow *et al.*) of the stone fruit flowers is an historic case of plant disease transmitted by insects (Waite, 1891). Thrips are now considered to be one of the vectors but conclusive experimental demonstration is still lacking. Waite (1894) studied the flower-visiting insects of pears in connection with a search for the vectors but he failed to mention if any thrips were observed. Treherne (1923), 30 years after Waite, stated that *Frankliniella*

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[4] The names of the bacteria are after Weiss and Wood (1943).

tritici (Fitch) has been incriminated as a vector in Canada and Oregon. Thomas and Ark (1934) observed that thrips carry the organism on the body. Bailey (1935) published the supplementary data supporting Thomas and Ark's conclusion; he also stated that the species of thrips involved in one of the tests Thomas and Ark made were *Frankliniella moultoni* Hood and *Taeniothrips inconsequens* (Uzel). Bailey (1935) urged further experimental work on transmission, but evidently nothing had been done by 1944 as Bailey (1944) stated that such tests with *T. inconsequens* were still needed.

The fig spoilage diseases in California are caused by a complex of bacteria, yeasts, and fungi; various species of insects, including thrips, are known to be vectors. The work by Caldis (1927), Hansen (1929), Smith and Hansen (1931), Hansen and Davey (1932), and Davey and Smith (1933) collectively demonstrated that the causal organisms are carried and inoculated by thrips. The several tests made were not conclusive but indications were clear that thrips are of some importance in regard to natural spreading of the diseases. Several species of thrips were involved, and the corrected identification of them given by Bailey (1935) are *Thrips tabaci* Lind., *Frankliniella tritici* (Fitch), *F. moultoni* Hood, *F. occidentalis* (Perg.), *Hercothrips fasciatus* (Perg.), and *Leptothrips mali* (Fitch).

Poos and Elliott (1936) and Elliott and Poos (1940) reported that bacterial wilt of corn (*Bacterium stewarti* E. F. Sm.) was not transmitted by *Hercinothrips femoralis* (Reuter) from corn to corn. *Aeolothrips fasciatus* (Linn.), *Anaphothrips obscurus* (Müll.), and *Frankliniella williamsi* Hood from the infected fields were not carrying the pathogen internally, but *A. obscurus* was carrying it externally. No further transmission test with the last species was made. Ark (1944) experimentally demonstrated that the bacterial canker of tomato (*Corynebacterium michiganensis* [E. F. Sm.] Jensen) was not transmitted by *Thrips tabaci* Lind., and also stated that the pathogen was not isolated from the mouth parts or the internal organs of the thrips. Semenov (1930) stated, without experimental demonstration, that *T. tabaci* was probably responsible for the transmission of a bacteriosis of tobacco (*Bacterium tabaci* [Wolf and Foster] Stapp) in Ukraine.

Pussard-Radulesco (1931) cited a bacteriosis of carnation (*Bacterium dianthi* Arthur and Bolley) transmitted by thrips without giving full reference. Evidently Pussard-Radulesco made an incorrect interpretation of Woods' work (1900), to which he apparently referred. Woods stated that *Bacterium dianthi,* claimed by Arthur and Bolley (1896) to be the pathogen for a carnation disease, is a secondary organism, and the true cause of the disorder, which was renamed by Woods as stigmonose, is the feeding effects of thrips, aphids, and mites.

FUNGOUS DISEASES

Thrips-transmissible fungous diseases are also few in numbers so far as recorded. Four diseases have been known with complete experimental demonstrations, three with incomplete experimental demonstrations, and several others with observational remarks only. The type of vector relation existing in the thrips-transmissible fungous diseases is essentially similar to that of the bacterial disease group. A case of aiding ingression or inoculation played by thrips was reported, but the common occurrence appears to be the aiding of dissemination only. Certain types of fungous spores are readily carried by thrips as commonly as the pollens, and many more fungous diseases than the few cases already recorded might be disseminated by thrips under natural conditions. However, such type of spore would also be wind-borne or rain-borne and so the role played by thrips may be generally insignificant. The above also appears to be true in the cases of bacterial disease.

Howard (1923) demonstrated that *Pestalozzia* sp. on camphor trees was experimentally transmitted by *Liothrips floridensis* (Watson). The spores were carried on the body of the thrips and infection occurred only at the sites of the feeding injuries. Apparently aiding ingression or inoculation was provided by the thrips in addition to dissemination of the pathogen. A rust (*Puccinia graminis* Pers.) was experimentally transmitted by *Hercinothrips femoralis* (Reuter) which previously made contact with urediniospores in the cultures or on the infected plants (Granovsky and Levine, 1932). Many years before the above work was reported, Johnson (1911) observed that rust spores (*Puccinia graminis tritici* Eriks. and Henn. and *P. rubigo-vera tritici* [Eriks.] Carleton) were commonly carried by thrips (presumably *Frankliniella tritici* [Fitch]) on its body, and suspected the thrips to be a disseminator under natural conditions.

Weiss and Smith (1940) and Smith and Weiss (1942) reported an experimental transmission of azalea flower spot (*Ovulinia azaleae* Weiss) by *Heterothrips azaleae* Hood. The spores were carried by the insect body but the infection occurred irrespective of the insect abrasions on the flowers; apparently only dissemination was provided by the vector. A transmission test with *Frankliniella tritici* (Fitch) was negative. The causal organisms, including fungi, yeasts, and bacteria, of the fig spoilage diseases of California were transmitted by several species of thrips. The details of this topic have been discussed under the bacterial diseases.

Intimate association of thrips with pathogenic fungi was observed in three cases. These species may quite certainly be capable of disseminating the spores, although no transmission test was made in any of the cases. Ramakrishna Ayyar (1928) observed in India that *Anaphothrips fungivora* Ramakrishna was feeding upon rusts on wheat plants. Bailey (1935) observed *Thrips tabaci* Lind. frequently carrying spores of black mold (*Aspergillus niger* van Tieg.) on bulb onions. Yarwood (1943) observed that *T. tabaci* was feeding upon several species of powdery mildews on vine, rose, strawberry, cantaloupe, clover, and *Oenothera* sp. He also observed in an experimental test that thrips thrived better feeding on the mildewed leaves than feeding on the normal leaves.

Observational notes were made on the following five cases. Whetzel (1904) stated that the infection of *Peronospora schleideniana* de Bary on onion was accentuated where thrips injuries were inflicted. Corbett (1931) suspected a thrips (? *Heliothrips haemorrhoidalis* [Bouché]) of transmitting a pathogen affecting coffee seed in Malay. Laumont and Murat (1934) also suspected a thrips to be a vector of the causal agents, a complex of bacteria and fungi, of the Moucheture disease of grain in Algeria. Russo (1936) stated that *Thrips tabaci* Lind. appeared to facilitate the diffusion of a leaf spot disease of onion in Santo Domingo. Harris (1944) reported an association of *T. tabaci* and a fungus (*Cladosporium* sp.) in pyrethrum flowers in Tanganyika, suspecting a vector relation.

Pussard-Radulesco (1931) cited an *Alternaria* disease on tobacco transmitted by thrips, without giving full reference. The reviewer has not been able to locate the original reference.

VIRUS DISEASES

A considerable knowledge of thrips in their vector relationships with the viruses has been accumulated in recent years. It is far more complete than with the bacterial and fungous diseases. The vector relationships of thrips with the viruses are biological, and are more intimate, specific, or obligatory than those with other groups of pathogens which are mechanically transmitted. Here, thrips acquire the virus internally from the plant tissues infected, process the virus biologically within the body, and inoculate the virus into the plant tissues where the virus can establish itself. Furthermore, the dissemination and inoculation of the viruses are entirely dependent on the insect vectors under field conditions except for a few particular viruses which depend on other means.

The insect-transmissible viruses are divided on the basis of the vector relationships into two groups: persistent and non-persistent types (Watson and Roberts, 1939). The persistent type is characterized by a long retention of the virus by the vector and by a latent period in the vector's body. Only a few viruses belong to this group. The non-persistent type is characterized by a short retention of the virus and the absence of the latent period. Many viruses belong to this type.

The viruses are also divided on the basis of their relation to plant tissues into three groups: phloem, phloem-parenchyma, and parenchyma types (Bennett, 1940). The persistent viruses in most cases are present only in the phloem tissues. Acquisition or inoculation can be made only by the vectors of the phloem feeder type which have a long proboscis that extends deeply into the phloem tissues. This type of virus is not sap-transmissible. The non-persistent viruses in most cases occur in both phloem and parenchyma tissues and acquisition or inoculation can be made through the parenchyma tissues by the vectors which feed chiefly or exclusively on the parenchyma tissues. This type of virus is always sap-transmissible.

The mouth of thrips, both larva and adult, is adapted only to gashing the epidermal and other nearby cells and sucking out the cell content of the parenchyma tissues. The vascular bundle tissues may not be ordinarily reached by the thrips, but such contact may occur under certain conditions. In view of this, thrips could only be vectors for the parenchyma-phloem or parenchyma type of viruses.

Thrips have already been tested for their vector relations with many viruses but only one virus, that of spotted wilt, has been authentically demonstrated to be transmissible by thrips. There is another case, but presentation of the evidence was incomplete. This review includes not only positive cases of transmission but also negative cases and those without experimental proof. For synonyms or affinities in strain relation of viruses, the latest reference by Wiltshire (1946) was consulted principally.

The negative cases of transmission

Cucumber mosaic is the first virus disease with which thrips were tested in regard to the vector relation. McClintock and Smith (1918) noticed *Thrips tabaci* Lind. abundant on diseased spinach plants, the disease being called spinach blight. The result of their transmission test was negative. Doolittle (1920) again demonstrated that *T. tabaci* is not a vector of the virus. Sakimura (1940) could not transmit the commelina mosaic virus, a strain of the cucumber mosaic virus, through *T. tabaci.* Several species of aphids and cucumber beetles are known to be the vectors of the cucumber mosaic virus. Whetzel (1923) suspected *Physothrips eucharii* Morgan (ms.),[5] which was abundant on the diseased plants, to be a possible vector of a mosaic on *Eucharis* lily in Bermuda, probably caused by the lily mosaic virus, which is a strain of the cucumber mosaic virus. Ogilvie (1928a) observed in Bermuda thrips on *Hippeastrum* lily affected with a mosaic, probably caused by the same virus aforementioned; and *Frankliniella insularis* Frank. on lilies affected with the yellow flat virus, a synonym for the lily rosette virus which is distinct from the lily mosaic virus. However, Ogilvie (1928b) and Ogilvie and Guterman (1929) later failed to

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[5] This name was proposed by A. C. Morgan who examined the specimens (Rept. Bd. Dept. Agr. Bermuda 1922: 30, 1923). However, this probably is a manuscript name, since no described species with this name has been recorded.

mention any species of thrips among a list of insects tested for vectors of these two viruses. The latter virus is transmissible by an aphid.

An extensive search was made in the early years for the vector of the sugar cane mosaic virus. Before the authentic discovery was made of the vector relation with *Aphis maidis* Fitch (Brandes, 1920), Smyth (1919) in Puerto Rico made a survey of sugar cane insects and found *Frankliniella* sp. and *Adraneothrips tibialis* (Hood).[6] His small preliminary transmission test with both species suggested a negative indication. Smyth's work was done one year after that of McClintock and Smith (1918), and is the second contribution made in the field of thrips transmission of the viruses. Wolcott (1921) mentioned thrips as a possible vector in Puerto Rico. Bruner (1922) tested a species of thrips, probably *Hercothrips insularis* Hood,[7] in Cuba, but the result was negative. Puttemans (1926) observed *Thrips minutus* var. *puttemansi* Costa Lima[8] abundant on diseased canes in Brazil and suspected its vector relation. Loftin and Christenson (1932) demonstrated that an unidentified thrips did not transmit the virus in Cuba. Ingram and Summers (1936) stated that *Haplothrips graminis* Hood gave negative results in a transmission test conducted in Louisiana. Ingram, Haley and Charpentier (1939) still had the opinion that thrips are a possible vector in Louisiana. The known vectors of the virus are several species of aphids.

Schultz and Folsom (1925) suspected thrips to be a possible vector of the potato mosaic virus complex, based upon their observations of its presence on potato plants in a greenhouse. In the same year, Iddings (1925) reported a negative result of a test with thrips to transmit a potato mosaic which is, he stated, similar to one of the

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[6] For the name of this species, see also Hood, Psyche **32**: 54, 1925.

[7] For the specific name, see Morgan, Proc. Ent. Soc. Wash. **31**: 9, 1929; Hood, Jour. Ent. Soc. S. Africa **3**: 37, 1940; and Bruner, *et al.*, Esta. Exp. Agro. Cuba Bol. **63**: 158, 1945.

[8] *Thrips minutus* van Dev. was briefly described from specimens collected on sugar canes from Java (van Deventer, Handboek Suik.-Cult. Reitsuik.-Fabr. Java **2**: 281, 1906). Its original description is insufficient to recognize the species and no collection of this species has been recorded from any other part of the world. Priesner (Nat. Tijd. Neder.-Indies **94**: 290, 1934) stated that probably *Thrips saccharoni* Moulton (Proc. Haw. Ent. Soc. **7**: 111, 1928), which was described from Hawaii, is a synonym for *T. minutus*. *T. saccharoni* has been collected from New Guinea, New Britain, and Loochoo in the Pacific region. *Thrips minutus* var. *puttemansi* Costa Lima was described from Brazil (Costa Lima, Chacaras Quintaes **34**: 32, 1926). Moulton (Rev. de Ent. **3**: 132, 1933) collected *T. saccharoni* in Sao Paulo, Brazil, but not *T. minutus puttemansi*. He mentioned both species in a treatise on South American thrips (*ibid.*) without giving any statement on the validity of *T. minutus puttemansi*. Because of the fact that some sugar cane insects have been distributed world-wide through the transportation of seedling material, the reviewer is of the opinion that the Javanese, Hawaiian, and Brazilian species may possibly be the same species. In Hawaii, *T. saccharoni* has never been suspected to be the vector of the disease, as Kunkel (1922, 1924) and Hadden (1928) did not specifically mention this species. Present-day workers in Hawaii have seen no field indication for such suspicion.

A comparison between the type material of *T. minutus* var. *puttemansi* and *T. saccharoni* was made after this paper had been written. They are identical. A cotype of the former species was made available through the courtesy of Dr. Costa Lima, Instituto Oswaldo Cruz, Rio de Janeiro, Brazil. The material of the latter species compared was a paratype; a series of additional specimens collected on Hawaii and Loochoo was also consulted.

types Schultz and Folsom (*ibid.*) described. Iddings (1925) also stated that the potato leaf roll virus was not transmitted by thrips in a test. Cleveland (1931) reported a negative result with *Thrips tabaci* Lind. in a preliminary transmission test. Again, Cottier (1931) also had a negative result with *T. tabaci* in New Zealand. This virus is transmissible by several species of aphids. Kunkel (1926) stated that *T. tabaci* was not able to transmit the aster yellows virus which is transmissible by a leafhopper.

Böning (1927a) suspected a species of thrips, possibly *Thrips tabaci* Lind., abundant on the affected beets, to be a possible vector of the beet mosaic virus. The virus is transmissible by several species of aphids. Böning (1927b) also conducted a preliminary transmission test of the bean mosaic virus with *Thrips flavus* Schrank which was abundant on the diseased plants. A few positive infections were observed, but he considered the results to be inconclusive. Fajardo (1928, 1930) stated that the bean mosaic virus was not transmitted by *Hercothrips fasciatus* (Perg.). The virus is transmissible by several species of aphids.

Jarrett (1930) demonstrated that *Thrips tabaci* Lind. is not a vector of the tobacco mosaic virus and tomato streak virus; the latter is a strain of the former. Adults as well as larvae were tested. Cleveland (1931) reported that few out of many test plants were infected in a transmission test with *T. tabaci.* The virus was called the tomato mosaic virus. He concluded that *T. tabaci* is probably capable of transmitting the virus to a limited degree. His results are contrary to the conclusive data presented by Jarrett (*ibid.*) and also have not been confirmed since. Presumably, some experimental errors must have been involved in Cleveland's test. This virus is known to be non-insect-borne.

Jarrett (1930) also demonstrated that *Thrips tabaci* Lind. is not the vector of the potato virus X, which has been known in earlier references as potato mosaic. Hamilton (1932) again demonstrated that the virus, which was called *Hyoscyamus* virus IV, was not transmitted by *T. tabaci.* Bawden (1934), studying the potato virus D, a strain of the potato virus X, found that the virus was not transmitted by *T. tabaci.* The potato virus X is known to be non-insect-borne. A presentation of inconclusive data was made by Smith (1937, p. 343) who stated that he has had or appeared to have five positive infections out of 100 tests with various species of flower-infesting thrips. Cockerham (1937), however, presented circumstantial evidence not supporting Smith's data.

Thrips were suspected to be a possible vector for the sandal spike virus in India as early as 1931 (Chatterjee and Dover, 1931). Dover and Appanna (1934) reported a negative result from a preliminary mass transmission test with thrips and other allied insects. Chatterjee (1940) and Rangaswami Iyenger and Griffith (1940) both presented negative results from outdoor transmission tests with many specimens of unidentified thrips. The true vector has not been conclusively determined yet. Hamilton (1932) recorded negative data from transmission tests with *Thrips tabaci* Lind. of the potato virus Y, which was called *Hyoscyamus* virus II, and of the henbane mosaic virus, which was called *Hyoscyamus* virus III. Both viruses are transmissible by the same species of aphid. Hargreaves (1932) stated that a mosaic virus of peanuts, probably the groundnut rosette virus, in Sierra Leone was not transmitted by thrips (unidentified species). The rosette virus is transmissible by an aphid. Hodson (1932) and Hall (1932) suspected *T. tabaci* to be a possible vector of the narcissus mosaic virus. However, the recent experimental demonstrations by Blanton (1939) and Blanton and Haasis (1942) showed that *T. tabaci* and *Frankliniella fusca* (Hinds) did not transmit the virus on a long series of test plants. The virus is transmissible by many species of aphids.

Thrips were once suspected to be a possible vector of the fig mosaic virus in California (Condit and Horne, 1933). No insect vector has been discovered yet. Weimer (1934) stated that the alfalfa mosaic virus was not transmitted by *Frankliniella occidentalis* (Perg.). The vector of the virus is an aphid. The potato yellow dwarf virus was not transmitted by *Thrips tabaci* Lind. in a test conducted by Koch (1934). This virus is transmissible by two species of leafhoppers. Hartzell (1935) demonstrated that the peach yellows virus, of which a leafhopper is the vector, was not transmitted by either the adults or the larvae of *T. tabaci* and *Hercinothrips femoralis* (Reuter). Smith and Bald (1935) also demonstrated with the larval stage that the tobacco necrosis virus was not transmitted by *T. tabaci.* This is one of the non-insect-borne viruses. Chamberlain (1935) reported that *T. tabaci* did not transmit the pea mosaic virus, which was called sore-shin of blue lupines. The virus is transmissible by several species of aphids.

Johnson (1936) stated that the tobacco streak virus was not transmitted by *Thrips tabaci* Lind. and an undetermined species of greenhouse thrips. The vector of this virus has not been discovered. The lucerne witches' broom virus was not transmitted by thrips in a preliminary test conducted by Edwards (1936). Menzies (1946) reported a negative result for the transmission test of the same virus with many sucking insects common on alfalfa, probably including some thrips. This virus is transmissible by a leafhopper. The tomato big bud virus, which was called Stolbur disease, was once considered by Koratshevsky (1936) to be probably transmissible by *Thrips* sp. in Russia. However, Thomas and Krishnaswami (1939) reported the virus, which was called eggplant little leaf, was not transmitted by an undetermined species of thrips, and also Hill (1943) recently stated that *T. tabaci* did not transmit the virus. This virus is transmissible by a leafhopper.

Costa (1937) stated that an unidentified species of thrips present on cotton was suspected of being a possible vector of a cotton mosaic virus in Brazil, distinct from the cotton leaf curl virus. The alfalfa dwarf virus was not transmitted by *Frankliniella occidentalis* (Perg.) in a test conducted by Weimer (1937) and again by thrips in another test conducted by Hewitt *et al.* (1946). This virus is transmissible by several species of leafhoppers. Bennett and Wallace (1938) reported a negative result for *Hercinothrips femoralis* (Reuter) in a transmission test of the beet curly top virus which is transmissible by a leafhopper. Zaumeyer (1938) stated that the pea streak virus in a preliminary test was not transmitted by *Thrips tabaci* Lind. Chamberlain (1939) also stated that *T. tabaci* did not transmit the same virus; the larval stage was used in the test. This virus is transmissible by an aphid. Pea streak mentioned here is distinct from the one known under the same name but caused by the spotted wilt virus and freely transmitted by *T. tabaci* (Linford, 1931b; Whipple, 1936). Goidanich (1938) reported a virus disease of sugar sorghum in Italy without giving its identity. He discussed a possible vector relation of *Limothrips schmutzi* Pr. and *Haplothrips aculeatus* F. which were abundant on the diseased plants. Noble and Noble (1939) stated that five species of thrips, including *Hercinothrips bicinctus* (Bagn.) did not transmit the passion fruit woodiness virus which is transmissible by several species of aphids.

No insect vector has been determined for the *Pelargonium* leaf curl virus, but Pirone (1940) stated that circumstantial evidence suggested that a species of thrips may be one of the possible vectors. Brierley and Smith (1940) and Smith (1940) stated that none of the insects tested, including *Frankliniella tritici* (Fitch), proved to be the vector for the rose mosaic and rose streak viruses. Tate (1940) experimentally demonstrated that *Thrips tabaci* Lind. is not a vector for the onion yellow dwarf virus which is freely transmissible by many species of aphids. Holdaway and Look (1940) stated that none of the insects tested, including *T. tabaci,* transmitted a papaya mosaic in Hawaii. This disease is distinct from papaya ringspot also recently discovered in Hawaii; the latter is transmissible by an aphid (Jensen, 1946). Morrison (1940) was of the opinion that *T. tabaci* and *Frankliniella moultoni* Hood which were abundant on the diseased plants may be possible vectors of the virus-like symptoms observed on hops in the Willamette Valley.

Zazhurilo and Sitnikova (1941) demonstrated that the winter wheat mosaic virus in Russia which is transmissible by a leafhopper was not transmitted by *Haplothrips tritici* Kurdjumov. *Selenothrips rubrocinctus* (Giard) was tested with a negative result for transmitting the cacao swollen shoot virus in Gold Coast (Posnette, 1941). The vector has not been conclusively determined yet. *Heliothrips haemorrhoidalis* (Bouché) and an unidentified thrips found on the infected plants were listed among possible vectors of the tea phloem necrosis virus; the true vector has not been determined (King, 1941). Cardamon mosaic of India was once suspected to be transmissible by *Taeniothrips cardamomi* Ramakrishna (Anonymous, 1941), but Uppal, Verma and Capoor (1945) reported that the disease was not transmitted by *T. cardamomi* but by an aphid. Costa (1941) suspected thrips to be a possible vector for a peanut ringspot virus in Brazil which, he stated, resembles somewhat the groundnut rosette and spotted wilt viruses.

A tomato ringspot virus which symptomatologically resembles the spotted wilt virus was not transmitted by *Thrips tabaci* Lind.; no other insect has been tested for vector yet (Samson and Imle, 1942). Jones (1942) reported that an eggplant yellows, which has not been identified with any other known virus, was not transmitted by all the insects tested, including *T. tabaci.* A zonate chlorosis of citrus in Brazil was suggested to be of virus origin and thrips were suspected to be a possible vector (Reiniger 1942). Smith (1943) demonstrated that the belladonna mosaic virus is not transmissible by *T. tabaci.* This virus is sap-transmissible but has been thought to be non-insect-borne. Jones (1944) stated that the cineraria mosaic virus which is transmissible by an aphid was not transmitted by *T. tabaci.* Jones (1945) also stated that the carnation mosaic and carnation streak viruses were not transmitted by *T. tabaci.* The vector for the former virus has not been determined yet but the latter virus is transmissible by an aphid. Orlando and Silberschmidt (1945) stated that two species of thrips are not vectors of infectious chlorosis of *Sida* spp. in Brazil, which is probably caused by the abutilon variegation virus. The *Sida* virus is transmissible by an aleyrodid. One of the thrips tested was *Sericothrips sidae* Crawford,[9] but the identity of the second species has not been published yet.

The foregoing references on the negative data from the transmission experiments are summarized in Table 1. Thrips were mentioned in connection with 48 viruses. Thirty-nine viruses out of the 48 were experimentally demonstrated for their negative transmission through the species of thrips tested, and 9 viruses were suspected for their possible vector relation but remained without any experimental proof. However, the number of viruses tested is only about one-fifth of all the known viruses and many more remain to be tested. Most of the principal viruses are more or less included among those already tested.

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[9] For the name of the species, see also Crawford, Proc. Ent. Soc. Wash. 46: 200, 1944.

Table 1. Summary of Negative Data from Transmission Experiments of Viruses by Thrips

Virus	Thrips	Reference
Cucumber mosaic	*Thrips tabaci* Lind.	McClintock & Smith (1918) ; Doolittle (1920) ; Sakimura (1940)*.
Sugar cane mosaic	*Frankliniella* sp. *Adraneothrips tibialis* (Hood) ? *Hercothrips insularis* Hood A thrips *Haplothrips graminis* Hood	Smyth (1919) ; Bruner (1922) ; Loftin & Christenson (1932) ; Ingram & Summers (1936).
Potato leaf roll	Thrips *Thrips tabaci* Lind.	Iddings (1925) ; Cleveland (1931) ; Cottier (1931).
Aster yellows	*Thrips tabaci* Lind.	Kunkel (1926).
Beet mosaic	? *Thrips tabaci* Lind.	Böning (1927a).
Bean mosaic	*Thrips flavus* Schrank *Hercothrips fasciatus* (Perg.)	Böning (1927b) ; Fajardo (1928, 1930).
Tobacco mosaic	*Thrips tabaci* Lind.	Jarrett (1930) ; Cleveland (1931)*.
Potato virus X	*Thrips tabaci* Lind.	Jarrett (1930) ; Hamilton (1932) ; Bawden (1934)*.
Sandal spike	Thrips	Dover & Appanna (1934) ; Chatterjee (1940) ; Rangaswami Iyenger & Griffith (1940).
Potato virus Y	*Thrips tabaci* Lind.	Hamilton (1932).
Henbane mosaic	*Thrips tabaci* Lind.	Hamilton (1932).
Groundnut rosette	A thrips	Hargreaves (1932).
Narcissus mosaic	*Thrips tabaci* Lind. *Frankliniella fusca* (Hinds)	Blanton (1939) ; Blanton & Haasis (1942).
Alfalfa mosaic	*Frankliniella occidentalis* (Perg.)	Weimer (1934).
Potato yellow dwarf	*Thrips tabaci* Lind.	Koch (1934).
Peach yellows	*Thrips tabaci* Lind. *Hercinothrips femoralis* (Reuter)	Hartzell (1935).
Tobacco necrosis	*Thrips tabaci* Lind.	Smith & Bald (1935).
Pea mosaic	*Thrips tabaci* Lind.	Chamberlain (1935).
Tobacco streak	*Thrips tabaci* Lind. A greenhouse thrips	Johnson (1936).
Lucerne witches' broom	Thrips	Edwards (1936).
Tomato big bud	A thrips *Thrips tabaci* Lind.	Thomas & Krishnaswami (1939) ; Hill (1943).

Table 1—Continued

Virus	Thrips	Reference
Alfalfa dwarf	*Frankliniella occidentalis* (Perg.) Thrips	Weimer (1937); Hewitt *et al.* (1946).
Beet curly top	*Hercinothrips femoralis* (Reuter)	Bennett & Wallace (1938).
Pea streak	*Thrips tabaci* Lind.	Zaumeyer (1938); Chamberlain (1939).
Passion fruit woodiness	*Hercinothrips bicinctus* (Bagn.) Four other species	Noble & Noble (1939).
Rose streak	*Frankliniella tritici* (Fitch)	Brierley & Smith (1940); Smith (1940).
Rose mosaic	*Frankliniella tritici* (Fitch)	Brierley & Smith (1940); Smith (1940).
Onion yellow dwarf	*Thrips tabaci* Lind.	Tate (1940).
Papaya mosaic	*Thrips tabaci* Lind.	Holdaway & Look (1940).
Winter wheat mosaic	*Haplothrips tritici* Kurdjumov	Zazhurilo & Sitnikova (1941).
Cacao swollen shoot	*Selenothrips rubrocinctus* (Giard)	Posnette (1941).
Cardamon mosaic	*Taeniothrips cardamomi* Ramakrishna	Uppal, Verma, & Capoor (1945).
Tomato ringspot	*Thrips tabaci* Lind.	Samson & Imle (1942).
Eggplant yellows	*Thrips tabaci* Lind.	Jones (1942).
Belladonna mosaic	*Thrips tabaci* Lind.	Smith (1943).
Cineraria mosaic	*Thrips tabaci* Lind.	Jones (1944).
Carnation streak	*Thrips tabaci* Lind.	Jones (1945).
Carnation mosaic	*Thrips tabaci* Lind.	Jones (1945).
Sida infectious chlorosis	*Sericothrips sidae* Crawford A thrips	Orlando & Silberschmidt (1945).

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* References dealing with separate strains are also included.

There is an obvious shortcoming in evaluating such type of data on the negative results of transmission tests. Many of the tests reported were parts of exploratory work for search of the vectors which were conducted before the discovery of the true vectors. Naturally, design of these tests were generally not very elaborate and adequate repetitions were not made. Generally speaking, any experimental demonstration for proving the negative relationship requires a reasonable number of repetitions of test to provide sufficient evidence for the final conclusion. This general principle should be true in the present cases and the indications seen in some of the tests which are apparently of a preliminary nature are technically not conclusive. However, some of the transmission tests, although few in numbers, are apparently conclusive because of design of the tests and number of the replicates tested. Another type of conclusive demonstration is the case where the same species of thrips is tested with a virus more than once under different circumstances. Regardless of whether the experiments were conclusive or not, almost all of the negative results are convincing because of supporting circumstantial evidence.

Negative acquisition of the virus by the adult stage of thrips was well demonstrated in the case of the spotted wilt virus. It is entirely a matter of speculation to foresee whether or not this special feature in the mode of transmission may be commonly true with other potential thrips-transmissible viruses. If this be true, some of the data may not be valid because the tests made might not have included the larval insects at the time of acquisition. In fact, clear statements were rarely made in the references on the stages of insect used in the test. However, the larval stage was used in some of the tests, as it was so stated or the procedure of the tests so suggested.

The most commonly tested species is *Thrips tabaci* Lind., because of its common occurrence in greenhouses where tests were made, and also because of the earlier discovery of its positive vector relationship with the spotted wilt virus. Twenty-four other viruses have been tested for their transmission through this species and none was transmitted. *Frankliniella occidentalis* (Perg.), another known vector of the spotted wilt virus, was tested on two different viruses. The other species tested on more than one virus are *Frankliniella tritici* (Fitch) and *Hercinothrips femoralis* (Reuter). The species tested on one virus only are *Hercothrips fasciatus* (Perg.), *H. insularis* Hood, *Hercinothrips bicinctus* (Bagn.), *Selenothrips rubrocinctus* (Giard), *Sericothrips sidae* Crawford, *Frankliniella fusca* (Hinds), *Taeniothrips cardamomi* Ramakrishna, *Thrips flavus* Schrank, *Adraneothrips tibialis* (Hood), *Haplothrips graminis* Hood, and *H. tritici* Kurdjumov. More than 13 species tested remained undetermined.

Among 39 viruses tested, ten or more belong to the persistent type. The viruses of this type are usually not available in the parenchyma tissues, on which the thrips feed. Any virus of this type may not be thrips-transmissible. About 25 or less of the viruses tested, at least most of them, belong to the non-persistent type. The viruses of this type are usually available in the parenchyma tissues and may be ingested by thrips. In these cases, the negative transmissions are probably due to some internal barrier or a negative specificity within the insects. A few of the non-persistent type viruses are transmitted with extreme ease by many vectors belonging to a single order or even to different orders of insects. Some workers consider that this group is transmitted mechanically by insects, and others disagree with this concept. The cucumber mosaic virus and the onion yellow dwarf virus are known to belong to this group and yet the thrips tested failed to transmit them. Four viruses tested are known to belong to the non-insect-borne type.

The vector relation of insects with the viruses are specific. The specificity, however, varies in degree with the different viruses, but at least group specificity always occurs except in the few cases aforementioned. No virus is known to have co-vectors belonging to different orders of insects. This generalized fact suggests that the thrips are unlikely to be additional vectors of the viruses known to be transmissible by insects other than thrips. In other words, all the known insect-transmissible viruses except the spotted wilt virus may not be thrips-transmissible. The possibility of finding additional thrips-transmissible viruses appears to be small. However, the aforementioned generalized fact suggests that the potential ones will be those of the parenchyma or sap-transmissible type but known to be not transmissible by any other group of insects.

Thrips injuries once confused as of virus origin

There are several cases of pathological disorder once attributed to virus origin but since discovered to be caused by thrips injuries. Uppal (1929, 1930) reported a mosaic disease of chillies in Bombay Presidency which he then thought was experimentally transmitted by *Thrips* sp. In his recent correspondence with the reviewer, he stated that the disease has been found to be caused by the feeding of thrips and that a paper on the subject is expected shortly. Park and Fernando (1938) and Johnpulle (1939) stated that chilli leaf curl in Ceylon, probably allied with chilli mosaic (*ibid.*), is not an insect-borne virus disease but direct injuries of thrips. Subsequently, *Scirtothrips dorsalis* Hood was found to be responsible for the disorder (Anonymous, 1942). Curzi (1932) concluded that peach plume in Italy is not of virus origin but is caused by the feedings of thrips. Kratochvil and Farsky (1942) also concluded that a malformation of young shoots of larch is not a virus disease but a toxaemia caused by *Taeniothrips larvicivorus* K. & F.

The positive cases of transmission

In contrast to a long series of references reviewed on the negative cases of transmission there are only two viruses with the positive vector relationship. One is the spotted wilt virus which has been extensively tested, and the details will be discussed in the next chapter. The other is a pistachio rosette in USSR which was stated to be transmissible by *Liothrips pistaciae* Kreutzberg. In 1940, Kreutzberg published a brief preliminary note on a new virus disease of pistachio trees found in Tulkoman, Uzbekistan, and Tadjikistan. He presented a brief summary on the result of his transmission test but never mentioned any description or procedure of the test and the original data. He stated simply, "*L. pistaciae* was tested and found able to transmit the disease." He also stated that the disease was transmitted by seeds and occasionally by grafting, but not by pollen and juice inoculation. There appears to be a slight discrepancy in these characteristics mentioned from the general type of thrips-transmissible virus. The reviewer is not aware of any other paper published on the same subject. Because of the incomplete presentation of the data, the reviewer will ignore this reference in the general discussion of the subject. There is another case of positive transmission of *Lycopersicum* virus 7. This virus, however, is suspected to be a strain of the spotted wilt virus and will be discussed in the next chapter.

SPOTTED WILT

The vectors

Spotted wilt is the only plant virus disease authentically demonstrated to be transmissible by thrips. The disease was recorded as early as 1906 by Lounsbury in the Union of South Africa and in 1919 by Brittlebank in Australia. However, critical studies of the disease particularly in respect to its insect vector were not started until the late 1920s, when three groups of workers initiated their studies independently in widely separated districts. The Australian workers started their project in 1926 (Dickson, 1929), the Hawaiian workers in 1927 (Illingworth, 1931), and the South African workers in 1929 (Moore, 1933).

Pittman (1927) from Australia first reported a successful transmission by *Thrips tabaci* Lind. He tested several insects found on diseased tomato plants but transmission was made only by thrips, probably *T. tabaci* but other species might also have been mixed. This is the first reference of thrips transmission of plant virus disease. Further results of tests conducted in Australia were reported by Samuel, Bald and Pittman (1930) who stated that the virus was freely transmitted by *Frankliniella insularis* Frank. Again, Samuel and Bald (1931) reported transmissions by *T. tabaci* and *F. insularis* confirming the previous results. Further work on *F. insularis* was reported by Bald and Samuel (1931). The results of the Hawaiian workers were first published in 1931. Linford (1931a) briefly reported the vector relationship of *T. tabaci* with the yellow spot virus, which is now known to be identical with the spotted wilt virus with perhaps a different strain composition. Illingworth (1931) also presented data on his exploratory work. The discovery by the Hawaiian workers was made independently of the Australian workers. Discovery of egg punctures of thrips near the local lesions on pineapple plants led to the effort to test *T. tabaci* which was common on a weed, *Emilia sonchifolia* (L.) DC., that was infected by the virus, unidentified at that time.

Smith (1931b) who identified the spotted wilt virus at Cardiff, Wales, demonstrated that *Thrips tabaci* Lind. is the vector there.

A preliminary work on the vector of this virus was also reported in his previous paper (Smith, 1931a). It is interesting to note that Samuel and Bald (1931), Linford (1931a), and Smith (1931b), all reporting positive transmissions by *T. tabaci,* were published at about the same time from March to September of the same year. Both Linford (1932) and Smith (1932) gave the full reports on the data which were briefly reported previously (Linford, 1931a) (Smith, 1931b). Moore in South Africa published a brief note in 1932 and a full report in 1933 (Moore, 1932; 1933). She stated that *Frankliniella* sp. transmitted the Kromnek virus which is now accepted as identical with, or as a strain of, the spotted wilt virus. The specific name of the vector was later given as *Frankliniella schultzei* (Tryb.) (Moore and Anderssen, 1939). Gardner and Whipple (1934) and Gardner, Tompkins, and Whipple (1935), who identified the spotted wilt virus in California, stated that the virus was transmitted by *T. tabaci* and *Frankliniella* sp. Bailey (1935), who examined the specimens tested by the above workers, identified *Frankliniella moultoni* Hood; but his species concept was such that another allied species, *occidentalis* (Perg.), is also included (see Sakimura, 1940, p. 282). Whipple (1936) reported an experimental transmission of the spotted wilt virus by *T. tabaci* to garden pea in Wisconsin.

Taylor and Chamberlain (1937) and Chamberlain and Taylor (1938) demonstrated that the spotted wilt virus was transmitted by *Thrips tabaci* Lind. in New Zealand. They stated that *Frankliniella insularis* Frank. was not found there. Bonnemaison (1939) stated that transmission of the spotted wilt virus was made by *T. tabaci* in France. Moore and Anderssen (1939) of South Africa reported further tests with *Frankliniella schultzei* (Tryb.), and also reported an experimental demonstration of transmission by *T. tabaci,* and the probable identity of the Kromneck with the spotted wilt virus. McWhorter and Milbrath (1938) and Milbrath (1939) discovered in Oregon a new virus, tomato tip blight, which was stated to be closely related but distinct from the spotted wilt virus. Thrips transmission tests were made with mixed lots of several species, including *T. tabaci, Frankliniella moultoni* Hood, and *F. occidentalis* (Perg.). They concluded that *T. tabaci* is the chief vector but other species of thrips may also be vectors. Holmes (1939, p. 138) in his classification system of the viruses placed this virus as a strain of the spotted wilt virus. Norris (1943) presented the evidence that the tip blight virus is one of the component strains of the spotted wilt virus which is a compound entity.

The South American workers brought out a number of reports in 1937 and 1938. The disease had been known for some time under several different names, Corcova, Vira-cabeca, Necrose do topo, and Peste negra. This virus is now accepted as identical with, or a separate strain of, the spotted wilt virus. Bennett *et al.* (1946, p. 26) who observed the disease at Tucuman, Argentina, stated recently, "it may be a strain, perhaps different from any yet described from other parts of the world." Fawcett (1938) of Tucuman reported an experimental transmission of the virus by *Frankliniella paucispinosa* Moulton, and a detailed description of his test was published later (Fawcett, 1940). At about the same time, the Brazilian workers also discovered that the disease is transmissible by *Frankliniella* sp. A series of their papers published are Forster and Costa (1938), Costa and Kiehl (1938) and Costa and Forster (1938). The species of *Frankliniella* involved was subsequently believed by the Brazilian workers to be *paucispinosa* (see Sakimura, 1940, p. 282). The earliest reference of thrips transmission in South America is that of Silberschmidt (1937) who simply cited the data collected by Costa and his co-workers before the originals had been published. Costa and Forster (1941) stated that *Thrips tabaci* which is very common in Brazil has not been studied in any experimental transmission test there.

In Hawaii, Parris (1940) and Sakimura (1940) presented the evidence for the co-identity of the Hawaiian yellow spot virus and the spotted wilt virus. The latter used the vector, *Thrips tabaci* Lind., throughout his experiments. McWhorter, who studied the tomato tip blight virus, expressed his opinion in correspondence with the reviewer in 1940 that symptomatologically the Hawaiian yellow spot virus more closely resembles the tip blight virus than the spotted wilt virus. Norris (1943) presented a new basis for the better understanding of the strain relationship existing between the allied viruses of the spotted wilt virus group. He separated several strains from the spotted wilt virus recovered from field-infected plants in Australia. One of the strains was identical with tip blight from Oregon. He stated that neither one of these strains has been found separately under natural conditions in Australia, and that the spotted wilt virus is not a single entity but a complex of closely related strains. He also stated that the variation in the symptoms of the spotted wilt virus can be simply explained by a variation in the ratio of the strains mixed.

In cooperation with Norris, the reviewer made a preliminary trial on the strain-splitting of the Hawaiian yellow spot virus. Norris wrote to the reviewer upon examining the data and photographs that the evidence is clear for the presence of the ringspot strain and necrotic strains, either necrotic or tip blight. He also stated that the tip blight strain is suspected to be suppressed to a very low concentration in the *Emilia* host commonly growing in the Hawaiian pineapple fields, but increasing of the concentration may possibly be made by a series of sap inoculations through a particular host sequence. The reviewer is now of the opinion that the yellow spot virus is not the tip blight virus, as McWhorter suggested, but is the spotted wilt virus possibly different in strain composition from that of the typical one in Australia.

Khuduina (1941) reported a successful transmission by *Thrips tabaci* Lind. of a tobacco virus in Russia which he stated to be probably identical with the spotted wilt virus. Jones (1944) studied cineraria streak which was found to be caused by a strain of the spotted wilt virus and to be transmissible by *T. tabaci.*

Schussnig (1943) reported the *Lycopersicum* virus 7 from south Moravia and Czechoslovakia which was experimentally transmitted by *Thrips tabaci* Lind. He stated that the virus has analogies with, but is distinct from, the tip blight virus. Although further affinity was not mentioned by Schussnig, the virus, in the reviewer's opinion, is suspected to be another strain of the spotted wilt virus. This virus, which was called a mosaic, was first recorded by Baudye (1933). Frimmel and Lauche (1940) stated that a flower-infesting thrips is the vector of a tomato mosaic in Moravia. The tomato mosaic dealt with by Frimmel and Lauche may be the one referred to by Baudye, and also may be the same disease as the one subsequently demonstrated by Schussnig to be transmissible by *T. tabaci.*

There is one reference reporting a doubtful case of the spotted wilt virus. Serrano (1935) stated that yellow spot disease of pineapple identical with that reported from Hawaii was present in the Philippines; that the disease was transmitted by *Thrips tabaci* Lind. Carter (1939) who made observations in the Philippines concluded that the disease dealt with by Serrano is not yellow spot but another disease. Another reference on the related subject is that of Cook (1936) who seems to be confused in recognizing yellow spot on pineapple plants growing in Puerto Rico.

There are at least five different species of thrips mentioned in the references as the vectors of this virus. These should be re-examined under the new synonym established by the taxonomist. The reviewer was informed by Mr. Dudley Moulton of a synonym to be presented in his forthcoming monograph of the genus *Frankliniella.* According to him, the Australian *nigripes* (Girault) (=*lycopersici* Andrewartha; *insularis* Morison, nec Franklin) and the South American *paucispinosa* Moulton are synonyms for the South African *schultzei* (Tryb.). For the old synonyms of the Australian species, see Jensen (1946, p. 592). This new synonym is very significant because this offers a basis for a new interpretation of the facts. It indicates that a single species of *Frankliniella* transmits the separate strains of the virus, as claimed by workers, in the different districts throughout the world. In addition to a common vector in the southern hemisphere, *Frankliniella moultoni* Hood is a regional vector restricted in its distribution to the Pacific coast of North America. *F. occidentalis* (Perg.) is a color phase of *F. moultoni. Thrips tabaci* Lind. is a cosmopolitan vector throughout the world but no confusion has been noted in the references of virus transmission.

In conclusion, there are three different species known to transmit the spotted wilt virus and its strains.

The non-vectors

Non-vectors of the spotted wilt virus may be considered in two general classes: thrips and insects other than thrips.

Experimenting with insects other than thrips, Hamblin (1921) and Noble (1928) in Australia found that the virus was not transmitted by a pentatomid bug (*Nezara viridula* L.) and a mirid bug, and an aphid, ? *Myzus persicae* (Sulz.) or *Macrosiphum solanifolii* (Ashmead) (=*M. gei* [Koch]). Then Pittman (1927) and Samuel, Bald and Pittman (1930) also reported negative results from a large number of test plants on which six species of insect were tested: 2 species of jassid leafhoppers; aphids, probably *Myzus persicae* and *Macrosiphum solanifolii;* a white fly (*Trialeurodes vaporariorum* [Westw.]); a red spider (*Tetranychus telarius* Linn.); and a mite (*Phyllocoptes lycopersici* Tryon). Illingworth (1931) of Hawaii stated that several preliminary tests with various species of insects and mites were made, but his tests consisted of mass transfers of field specimens.

Smith (1931a) in England tested two species of aphids, *Myzus persicae* and *Macrosiphum solanifolii.* He had negative results in most of the cases, but also had occasional positive cases with *M. persicae.* Later in another paper (Smith, 1932), he stated that his previous tests needed confirmation before being regarded as conclusive. However, his data were not confirmed by the ones previously reported by Samuel, Bald and Pittman (1930). Moore (1933) in South Africa did not make any tests along this line. Forster and Costa (1938) of South America recorded a mirid bug (*Dicyphus* sp.) and an aphid (probably *Aphis gossypii* Glov.) with negative results from a small preliminary test. Fawcett (1940) of South America reported negative results from preliminary tests with a mirid bug (*Eugylatus notatus* Distant), jassids (*Agalliana ensigera* Oman[10], *Empoasca* sp., and *Eutettix* sp.), aphids (*Myzus persicae* Sulz. and *Aphis rumicis* Linn.), and coleopterons (*Epitrix* spp. and *Diabrotica punctata*[11]).

These tests made by the various workers include mites, white fly, aphids, leafhoppers, and plant bugs which well represent all the known groups of insects related to the plant virus transmission. It is quite certain that some of these tests were strictly preliminary in nature but the others were not, particularly so with the aphid group. Although the available data are not extensive and conclusive, they are strongly suggestive that insects other than thrips may have no

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[10] For the name of this species, see also Oman, Rev. de Ent. 4: 336, 1934.

[11] The validity of this name is doubtful. (See Blackwelder, U. S. Nat. Mus. Bull. **185**: 679-686, 1946.) There is a South American species infesting tomato with an allied name of *D. limitata* (Sahlberg) (= *quindecimpunctata* Germ.).

vector relation with the spotted wilt virus. A fact that supports the above deduction is that there is no virus known, except the few cases aforementioned, to be transmissible by insects which belong to more than one group. This is particularly true with the persistent type of virus which has a highly developed specificity between the vector and the virus, and the spotted wilt virus belongs to this group.

So far as thrips are concerned, very little work has been done on species other than the three known vectors. Samuel, Bald and Pittman (1930) attempted to test several species which died before the tests were complete; they are *Thrips* sp., *Thrips nigropilosus* Uzel, *Haplothrips* sp., and *Taeniothrips simplex* (Morison). However, these workers tested a large number of *Othinanaphothrips tersus* (Morison)[12] in adult and larval stages which conclusively gave negative results. Bonnemaison (1937) stated that *Frankliniella intonsa* (Tryb.) which was tested in France appeared not to transmit the virus. McWhorter and Milbrath (1938) stated that *Anaphothrips obscurus* (Müll.) was present in the thrips lots tested but nothing was known about the ability of the species.

Sakimura (1940, 1946) made efforts in testing the other thrips for their possible vector relationship. He adapted a new scheme of test which had never been attempted by the other workers. A mixed colony of the known vector species and the species to be tested is established on the diseased plants, and insects of each species are separately transferred to the test plants. With this procedure, the evidence for availability of virus within the source plants is readily provided by the results of the known vector species. When the test is repeated with adequate numbers of test plants and test insects, the results of such tests, in the reviewer's opinion, are conclusive. It will be desirable to repeat the tests on more than one species of the test plants. He has already tested *Thrips nigropilosus* Uzel and *Frankliniella sulphurea* Schmutz, which are both widely distributed general feeders, and *Hercinothrips femoralis* (Reuter) and *Anaphothrips* (*Chaetanaphothrips*) *orchidii* (Moulton), which are both common greenhouse species throughout the world; all were proved to be non-vectors.

Although the negative vector relation has been demonstrated with five or six different species of thrips, the fact that there are three vector species still strongly suggests a possible presence of other vector species of thrips. Thrips, irrespective of the vector or the non-vector species, may equally be able to ingest the virus, but a specific permeability of the gut wall which allows the virus to penetrate, might determine the vector species. The number of thrips species associated with plants is very large; a few particular species should have permeability similar to that common in the three known

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[12] For the name of this species, see also Morison, Bull. Ent. Res. **21**: 9, 1930; Crawford, Proc. Ent. Soc. Wash. **45**: 151, 1943.

vectors. Suspicion is particularly placed on the members of the two genera, *Frankliniella* and *Thrips,* to which the known vectors belong. Further studies along this line are highly desirable.

The mode of transmission

The spotted wilt virus is acquired by the vector in its larval stage only, and the adults emerged from such larvae remain infective for a long period although no longer able to acquire further virus. This is a pronounced peculiarity and no analogous case has been seen among the insect vectors of the plant viruses, except an allied case of *Perkinsiella saccharicida* Kirk. with Fiji disease. This fact was demonstrated with *Thrips tabaci* Lind. by Smith (1932) in England, and Linford (1932) in Hawaii; as well as with *Frankliniella schultzei* (Tryb.) by Bald and Samuel (1931) in Australia, and Moore (1933) in South Africa; and also with *Frankliniella moultoni* Hood by Whipple as cited by Bailey (1935) in California.

Several different hypotheses have been advanced for the mechanism of the negative acquisition by adult thrips, but none has been experimentally demonstrated. Linford (1932) advanced the digestion theory; that is, digestion may destroy the virus ingested during the adult stage. Smith (1932; 1933, p. 152) and Bailey (1935) suggested morphological differences as the reason. Points which can be ruled out are the feeding mechanism and the plant tissues to be fed because they are practically the same in both larval and adult stages. Lately, Bawden (1939, p. 71) expressed another view, the permeability theory, based on new data. He stated that the virus may not be destroyed by digestion when ingested during the adult stage, but may be unable to penetrate through the gut wall. Bawden's view is particularly based on the findings of Bennett and Wallace (1938) on the presence of the virus in the alimentary tract of the non-vector insects; also of Storey (1933) who punctured the gut wall of inactive insects (a strain unable to acquire the virus) and rendered them active. It would be highly interesting to make a test to determine whether or not such puncturing will enable the adult thrips to acquire the virus.

The length of the retaining period of the virus by the vector thrips has been studied by several workers. The length of the period is usually erratic; the infective adults sometimes remain viruliferous throughout their life, or lose their infectivity before their natural death. The maxima in days tested so far are more than 24 days with *Frankliniella schultzei* (Samuel, Bald and Pittman, 1930; Bald and Samuel, 1931); 30 days both with *Thrips tabaci* (Carter as cited by Bailey, 1935) and with *Frankliniella moultoni* (Whipple as cited by Bailey, 1935).

The latent period in the vector body, the delay between the time when the vectors acquire the virus and when they are able to transmit, was also studied by the various workers. The minima in days reported are five days (Smith, 1932) and about 10 days (Linford, 1932) with *Thrips tabaci;* five days with *Frankliniella schultzei* (Bald and Samuel, 1931); and about 10 days with *Frankliniella moultoni* (Whipple as cited by Bailey, 1935). Moore and Anderssen (1939) observed an occurrence of such a period with *F. schultzei* but did not determine its length. The similarity seen among the three vectors in regard to the negative acquisition by the adult insects, the retaining period and the latent period are notable. The specificity, if any, between three vector species appears to be insignificant. A slight divergence seen in the latent period was possibly caused by different designs of the tests.

In view of the fact that the vectors have a long retaining period and a definite latent period, the spotted wilt virus is a persistent type of virus. However, the virus is, as suggested by the type of symptoms, doubtless a parenchyma-phloem type in the tissue relation. Thrips which are parenchyma feeders readily acquire the virus from the parenchyma tissues. This fact indicates that the spotted wilt virus, on the other hand, also has characteristics common to the non-persistent type. Furthermore, sap-transmissibility of the virus supports the above conclusion. The sap-transmission is readily made in all the strains of the virus except the tip blight virus which was reported by Milbrath (1939) to be difficult to transmit. The yellow spot virus was once reported by Carter (1935) to be difficult to transmit on pineapple plants, but Parris (1940) stated that it is not so on several solanaceous plants.

In conclusion, the spotted wilt virus belongs to the persistent type of viruses, but has definite affinity to the non-persistent type in aspects of mouth-structure of the vectors, and tissue relation and sap-transmissibility of the virus. It is apparently an intermediate type between both categories and no analogous case has been known.

A local problem

Attention should be called to the fact that the problem of insect vectors of the spotted wilt virus is directly of local interest. This virus disease has been known here in Hawaii for about 20 years. At the time of its first discovery, the disease was once gravely feared as a major disease of pineapple plants. However, with the exception of some minor localized outbreaks here and there, this disease has rarely proved to be serious in Hawaii. The status of the disease on the tomato crop is different from that on pineapple. The tomato crop in the past several years has suffered extensively in several different districts.

Severeness of the virus diseases is largely governed by the factors involving the insect vectors which spread the diseases. There is in Hawaii at present only one species of the three known vectors, that is, *Thrips tabaci* Lind. It is quite natural that the situation would be drastically changed if additional vectors were introduced into

Hawaii. The host preference, reproductive potential, and resistance to ecological factors would vary with different species of vector and other vector species could be more destructive than the one we already have here. It is quite certain that pineapple, tomato and other crops would suffer more than ever from such an invasion of additional vectors.

The second vector, *Frankliniella moultoni* Hood, is a common species in the Pacific coast region. It is a constant menace due to the possibility of invasion. Fortunately no evidence has been found indicating that this species has become established in Hawaii. The third vector, *Frankliniella schultzei* (Tryb.), is known to be distributed as near to Hawaii as in New Guinea.[13] This is another menace. There is one recent instance of thrips invasion from the south; that is *Frankliniella sulphurea* Schmutz. The nearest locality of its distribution known before its invasion into Hawaii was also New Guinea.[13] Consequently, we must recognize the very real possibility of a similar invasion by *F. schultzei.*

As was discussed previously there is a good reason to believe a possible presence of additional vectors, particularly among the members of the genera *Frankliniella* and *Thrips*. Therefore any species of these two genera which has no known status for the vector relationship with the spotted wilt virus will be a dangerous addition to the local fauna, if and when it should be introduced here. As was cited a few lines before, *Frankliniella sulphurea* is a good example. This species is extremely polyphagous in host range and abundant in number; that would qualify this species to be a possible dangerous vector. In view of this fact, when this species was first discovered in 1942, prompt attention was paid to testing its vector relationship with the spotted wilt virus. Fortunately the test revealed that the species is not a vector (Sakimura, 1946).

There is another case of a new introduction of *Frankliniella fusca* (Hinds) (Sakimura, 1947) which was discovered on imported narcissus plants at Hilo, Hawaii, in late 1945. So far, no evidence has been found of its spreading from the original site of the discovery or its firm establishment in the vicinity. This species, which is also a general feeder, should be tested for its possible vector relationship. *Frankliniella formosae* Moulton and *F. tenuicornis* (Uzel) as well as several native species of the genus *Thrips,* none of which have been tested for their vector relation, are common species in Japan and China. They are also potential invaders because of their geographical nearness to Hawaii.

In conclusion, Hawaii should be well protected from possible invasion by other species of tiny thrips which may accentuate the seriousness of the destructive spotted wilt disease in Hawaii.

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[13] Moulton notified the reviewer that *Frankliniella clitoriae* Moulton and *F. pembertoni* Moulton, both reported from New Guinea, are synonyms for *F. schultzei* (Tryb.) and *F. sulphurea* Schmutz, respectively.

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ADDENDUM

Dickson, R. C. and Johnson, M. M. (Insect investigations in relation to quick decline. Calif. Citrograph **32**: 159-162. 1947) stated that four species of thrips were tested for vector relation with citrus quick decline which was believed of virus origin. This paper is a progress report and the final result of the test was not given.

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