Epidemiology of Tomato Spotted Wilt Virus Disease on Crisphead Lettuce in Hawaii

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ABSTRACT

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Tomato spotted wilt virus (TSWV) causes a devastating disease of lettuce in Hawaii. TSWV disease and thrips species surveys were conducted on Maui during 1981–1984. TSWV disease incidence and thrips numbers were greatest at a low elevation (366 m) farm compared with higher elevation farms. Three known insect vector species of TSWV were found on Maui: *Frankliniella occidentalis, F. schultzei,* and *Thrips tabaci. F. occidentalis* was the predominant species at both low (366 m) and middle (643 m) elevation farms. *T. tabaci* was the predominant species at the highest farm, located at 701 m. Twenty-three other thrips species were found in Kula. Three are new records for Hawaii: *Neohydatothrips gracilipes, Baileyothrips limbatus,* and *Scirtothrips inermis.* A lettuce isolate of TSWV was transmitted to *Emilia sonchifolia* plants by *F. occidentalis.* There were significant correlations between mean number of thrips trapped per week for each month sampling was done and tomato spotted wilt disease incidence in lettuce, total monthly rainfall, mean monthly temperature, minimum monthly temperature, and (at $P \leq 10\%$) maximum monthly temperature.

Tomato spotted wilt virus (TSWV) disease was first observed in Hawaii in 1926 (12) on pineapple and is presently found on all major islands where susceptible crops are cultivated.

During the late 1960s, this virus disease seriously affected tomato production on the island of Oahu and resulted in cessation of tomato production in leeward Oahu. Leaf lettuce was also affected by TSWV during this period; however, disease losses were tolerated because they were high only during summer months. Unfortunately, the problem has increased and has resulted in losses of 50–90% during all seasons of the year.

In recent years, TSWV has severely affected production of crisphead (*Lactuca sativa* L.), cos (*L. sativa* var. *longifolia* Lam.), and leaf (*L. sativa*) lettuce, tomato (*Lycopersicon esculentum* Mill.), and green pepper (*Capsicum annuum* L.) in major vegetable production areas including Waianae on Oahu, Kula on Maui, and Waimea on the island of Hawaii, where TSWV incidence is increasing.

Pittman, in 1927 (16), was the first to establish that TSWV could be transmitted by onion thrips. Six thrips species listed currently as TSWV vectors are: the tobacco thrips, *Frankliniella fusca* (Hinds); the western flower thrips, *F. occidentalis* (Pergande); *F. schultzei* Trybom; *Thrips setosus* Moulton; the onion thrips, *T. tabaci* Lindeman; and *Scirtothrips dorsalis* Hood (1,4,8,14, 19,21). *T. tabaci* (13), *F. occidentalis* (15), and *F. schultzei* (20) have been reported in Hawaii.

Surveys were initiated in Kula to better understand the biology and epidemiology of TSWV and its insect vectors. A thorough understanding of interrelationships between the crop, the pathogen, and its insect vector is necessary for developing pest management strategies to reduce crop losses.

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MATERIALS AND METHODS

TSWV disease and thrips species surveys were conducted at four lettuce farms in Kula, Maui, from November 1981 to December 1982. Farm sites were selected at three elevations in Kula: 366 m for farm 1, 643 m for farms 2 and 3, and 701 m for farm 4. Further surveys were conducted on farm 1 until December 1984. For disease surveys, three replicate plots were established at each farm site. Each plot consisted of five beds 14 m long and contained about 300 transplanted lettuce plants (cultivar Mesa 659) on double rows. Plants were spaced about 36 cm apart within rows on raised beds that were 51 cm wide with 102-cm centers. Plots were surveyed biweekly from 1 wk after transplanting until crop maturity or until >90% TSWV disease incidence had occurred. Estimation of TSWV disease incidence was based on the average number of plants infected at the end of each crop survey period. New survey plots were initiated about 1 wk after the end of each survey period. Plants were considered infected on the basis of the appearance of typical symptoms characterized by marginal wilting, yellowing, and brown spotting of leaves and midribs.

Ten infected lettuce plants showing typical TSWV disease symptoms were randomly selected from each of four survey farm sites in Kula. Mechanical transmission and detection of TSWV by ELISA were performed for each plant. For sap inoculations, leaf tissues from separate plants showing necrotic brown spots were triturated with a mortar and pestle in 0.1 M potassium phosphate buffer, pH 7.0, containing 0.01 M sodium sulfite and inoculated by rubbing leaves of two 1.5-mo-old cos lettuce plants previously dusted with 600-mesh Carborundum. ELISA was determined by the direct (double-antibody sandwich) method as described previously (6). The antiserum was produced from a TSWV strain obtained from an infected lettuce plant on the island of Maui (9). Buffer controls consisted of six wells that contained ELISA extraction buffer. ELISA reactions were measured spectrophotometrically at 405 nm with an EL307B EIA reader (Bio-Tek Instruments). Samples were considered TSWV-positive if the A_{405nm} reading was greater than twice the average buffer and/or healthy lettuce control readings, whichever was higher.

Two TSWV isolates obtained from infected lettuce in Kula were maintained in the greenhouse in *Nicotiana benthamiana* Domin. plants for further studies. The homogeneity of each isolate was ensured by five single local lesion transfers in *N. benthamiana.* In host range studies, six plants (three per isolate) of each species were inoculated. Six uninoculated plants of each species served as controls. All plants were observed for symptom development 7–14 days after inoculation. All plants were assayed for TSWV infection via ELISA.

Thrips populations were monitored with sticky traps made with 270-ml yellow plastic cups (Solo, Urbana, IL) coated with Tack Trap (Animal

Repellants, Inc., Griffin, GA) that were mounted upside-down on a 15-cm-long piece of 1.3-cm-diameter PVC pipe fitted with a 6.5-cm piece of foam rubber (17). Six to nine traps per field, two or three per plot, were placed in the center of each plot about 12–15 m apart and mounted on galvanized iron pipes 79 cm above ground level. Traps were collected, replaced weekly, and brought back to the laboratory, and insects were counted under a dissecting microscope.

Identifications of thrips species were made from samples collected during November and December 1981 from farms 1, 2, 3, and 4 and again from June to September 1983 from farm 1. Each week, 10 thrips were randomly selected from six to nine traps per farm site, removed with a small camel's-hair brush, placed in a glass jar containing 25 ml of petroleum distillate solvent, then transferred into glass vials containing 70% ethanol for subsequent identifications by K. Sakimura.

F. occidentalis, the major thrips species found in Kula, was tested for its ability to transmit TSWV. Adult thrips were collected from diseased lettuce plants, immobilized under carbon dioxide anesthesia, and identified under 100X with a Wild M-8 stereomicroscope. Nine groups of five *F. occidentalis* were placed on separate *Emilia sonchifolia* (L.) DC. plants and confined on a single leaf by a modified microsandwich cage (18). Thrips were allowed to feed for 6 days on two separate leaves of a single plant. The plants were placed in a greenhouse and treated with abamectin (Avid 0.15EC) at 12 μg a.i./ml after removal of thrips and again 10 days later to eliminate the development of larvae from eggs oviposited by thrips. Plants were kept for 30 days and observed for TSWV symptom development. Ten *E. sonchifolia* plants not exposed to thrips served as controls. TSWV infection was confirmed by ELISA and sap inoculations on 1.5-mo-old cos lettuce seedlings.

Remote microcomputer weather station monitors (CR21 Micrologger, Campbell Scientific, Inc., Logan, UT) located at each farm site collected temperature, rainfall, relative humidity, solar radiation, wind speed, wind direction, and leaf wetness information from lettuce plots. Each microcomputer analyzed the microclimate information and recorded data summaries on audiocassette tapes, which were collected and replaced bimonthly. A computer facilitated further weather data summaries and analyses.

Comparisons were made between mean thrips numbers per trap per week for each month of the year with total TSWV disease incidence at crop maturity, total monthly rainfall, and monthly means, maxima, and minima for temperature and relative humidity values.

RESULTS

All cos lettuce plants sap-inoculated with suspected TSWV-infected lettuce became infected. Plants showed disease symptoms identical to those observed in the field. Initial symptoms started as necrotic leaf spots 4–7 days after inoculation. The infection became systemic 12–14 days after inoculation and extended to the heart leaves, resulting in cessation of development and causing the plant to twist to one side. Leaves showing discoloration were malformed and chlorotic.

Host range studies were conducted with two TSWV isolates obtained from initial inoculations. All inoculated plants became infected and showed disease symptoms 7–14 days after inoculations. None of the controls became infected. TSWV infection was confirmed by ELISA in all cases. Local and systemic symptoms were produced in *N. benthamiana, L. esculentum,* and *C. annuum*. Only local lesions were produced on *Petunia hybrida* Vilm. cv. Purple Plum and *Cucumis sativus* L. cotyledons. Only systemic symptoms were observed on *Tropaeolum majus* L. Local lesions were chlorotic or necrotic. Systemic symptoms consisted of chlorotic mottling, mosaic, veinclearing, veinal necrosis, malformation, stunting, necrotic spots and ringspots, wilting, and killing of the plant.

TSWV was detected by ELISA from all lettuce plants showing typical TSWV symptoms collected from four Kula farm sites and from greenhouse-inoculated lettuce plants. A_{405nm} values for all infected samples were > 1.9. Mean A_{405nm} values for buffer and healthy controls were 0.12 and 0.11, respectively.

In transmission studies, typical TSWV symptoms were observed on three of nine *E. sonchifolia* plants 5 days after *F. occidentalis* adult thrips were removed. None of the six remaining plants became diseased after 30 days. None of the 10 uninoculated plants became infected in these studies. All cos lettuce plants sap-inoculated with suspected TSWV-infected *E. sonchifolia* plants became infected and produced typical TSWV symptoms. TSWV infection was detected by ELISA from all plants showing TSWV symptoms. A_{405nm} values for all infected samples were 1.7. Mean A_{405nm} values for buffer and healthy controls were 0.144 and 0.138, respectively.

Disease incidence and thrips numbers were generally higher on farm 1 than on farms at higher elevations (Table 1). Spotted wilt incidence ranged from about 6 to 32% on farm 1 compared with highs of 17, 10, and 1% for farms 2, 3, and 4, respectively. Average weekly thrips numbers per month ranged from about 26 to 121 on farm 1, from 2 to 159 on farm 2, from 3 to 139 on farm 3, and from 5 to 60 on farm 4.

Three species known from the literature to be TSWV vectors constituted the major portion of thrips trapped in 1981 from four farm sites (Table 2): *F. occidentalis, F. schultzei,* and *T. tabaci*. *F. occidentalis* was the predominant species at both the low (366 m) and middle (643 m) elevation farms; however, at the middle elevation, the ratio of this species to the other two species sharply decreased. On the other hand, *T. tabaci* was predominant at the higher elevation farm, located at 701 m. Twenty-three other thrips species were trapped: suborder Terebrantia—*Baileyothrips limbatus* (Hood), *Bregmaothrips venustus* Hood, *Ceratothrips frici* (Uzel),

Table 1. Incidence of tomato spotted wilt on lettuce and average thrips numbers associated with four lettuce farms located in Kula, Maui, from November 1981 to December 1982

	Farm 1		Farm 2		Farm 3		Farm 4	
Date	Disease incidence[a] (%)	Av. no. thrips[b] (±SD)[c]	Disease incidence (%)	Av. no. thrips (±SD)	Disease incidence (%)	Av. no. thrips (±SD)	Disease incidence (%)	Av. no. thrips (±SD)
Nov. 1981	18	121 ± 21	12	32 ± 8	1.0	63 ± 44	0.1	11 ± 7
Dec. 1981	32	75 ± 49	Cab.[d]	30 ± 5	5.0	21 ± 25	1.0	5 ± 3
Feb. 1982	6	26 ± 18	Cab.	2 ± 2	3.0	3 ± 2	1.0	7 ± 4
May 1982	8	86 ± 13	1	67 ± 25	10.0	6 ± 2	0.3	5 ± 1
Jul. 1982	18	100 ± 53	17	159 ± 107	4.0	139 ± 107	ND[e]	60 ± 11
Dec. 1982	ND	51 ± 14	4	24 ± 178	0.2	10 ± 3	0.2	8 ± 2

[a] Disease incidence based on mean total infected at crop maturity for each month.
[b] Average number of thrips based on mean number of thrips trapped per week for each month.
[c] Standard deviation.
[d] Only cabbage planted.
[e] No data taken.

Chirothrips mexicanus Crawford, *Dorcadothrips cyperaceace* (Bianchi), *Frankliniella invasor* Sakimura, *F. minuta* (Moulton), *Kurtomathrips morrilli* Moulton, *Leucothrips piercei* (Morgan), *Merothrips morgani* Hood, *Microcephalothrips abdominalis* (Crawford), *Neohydatothrips gracilipes* (Hood), *Plesiothrips perplexus* (Beach), *Rhamphothrips pandens* Sakimura, *Scirtothrips inermis* Priesner, *Scolothrips pallidus* (Beach), *S. priesneri* Sakimura, *Stenchaetothrips minutus* (van Deventer), *Thrips australis* (Bagnall), and *T. hawaiiensis* (Morgan); suborder Tubulifera—*Haplothrips gowdeyi* (Franklin), *Haplothrips robustus* Bagnall, and *Karnyothrips melaleuca* (Bagnall). Three thrips species are new records for Hawaii: *Neohydatothrips gracilipes* (comb. nov. by K. Sakimura), *Baileyothrips limbatus*, and *Scirtothrips inermis*. Further identifications of thrips trapped from farm 1 during 1983 showed that *F. occidentalis* was the predominant thrips species at 99.3%, *T. tabaci* at 0.4%, and other species at 0.3% of the total population identified.

Average weekly thrips numbers trapped per month fluctuated during 1982–1984 (Fig. 1). Numbers were highest during the warm, dry summer months and lowest during the cooler months.

Comparisons between disease incidence, thrips trapped, and environmental factors were made from the information collected from farm 1 during November in 1981–1984 (Table 3). These comparisons showed a significant correlation ($P \leqslant 0.05, r = 0.555$, df = 17) between disease incidence and mean weekly thrips numbers per month. Significant correlations also occurred between thrips numbers and the mean and minimum monthly temperatures in 1983. There was a significant negative correlation between thrips catches and total monthly rainfall in 1982, when high rainfall occurred. Correlation values between thrips catches and maximum monthly temperature were significant at $P = 0.1$ in 1982 and 1983. No significant correlations occurred in 1984, when thrips populations were low.

DISCUSSION

We concluded that the disease of lettuce was caused by TSWV on the basis of host range, serological reaction, and thrips transmission data of the virus. These properties are similar to those reported by Ie (11). For example, typical disease symptoms were observed on inoculated diagnostic plant species and on lettuce, TSWV infections were confirmed by ELISA, and our tests demonstrated successful transmission of TSWV by *F. occidentalis*.

TSWV disease of lettuce has caused serious losses in crisphead lettuce production in the Kula vegetable region

Table 2. Percentage occurrence of various thrips species trapped on lettuce farms at three elevations in Kula, Maui, during November and December 1981

Farm[a]	Elevation (m)	Total thrips trapped (no.)	*Frankliniella occidentalis* (%)	*F. schultzei* (%)	*Thrips tabaci* (%)	Other (%)
1	366	1,305	77	5	13	5
2 and 3	643	1,790	40	27	21	12
4	701	810	15	8	68	9

[a] See Materials and Methods for description of farm sites.

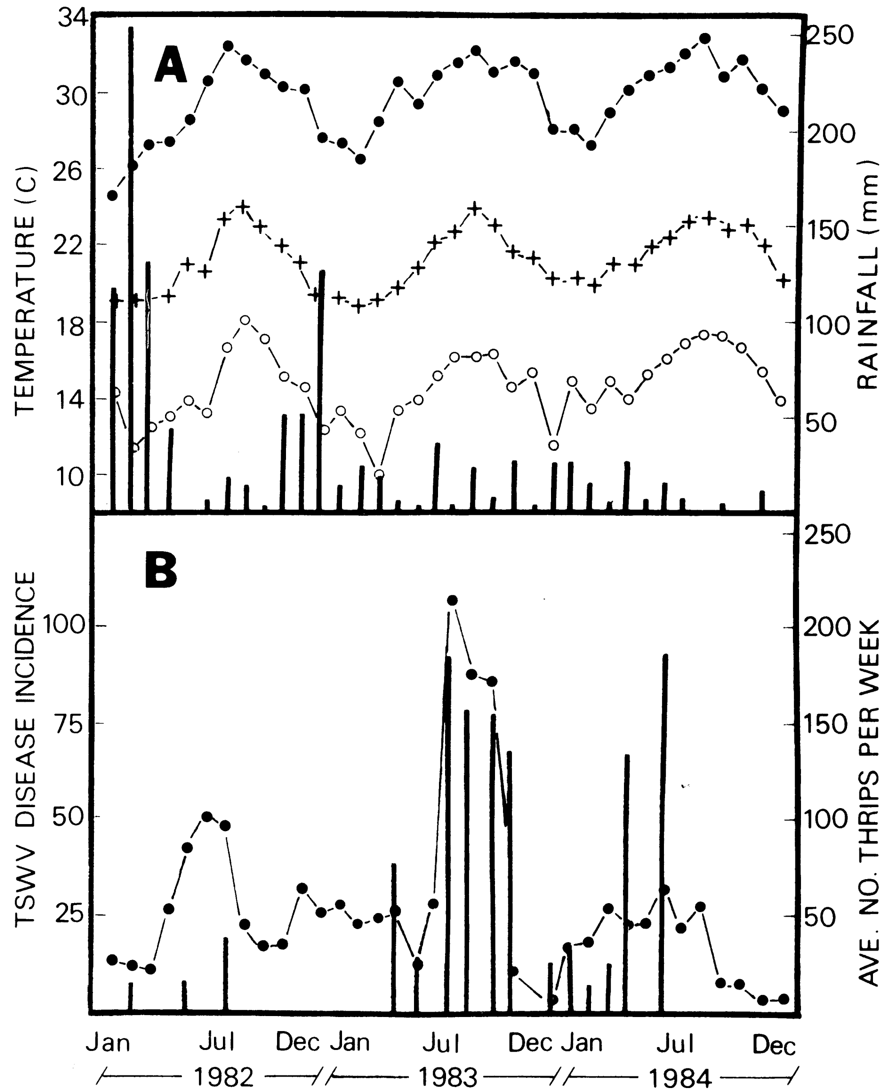

Fig. 1. Monthly summaries from farm 1, Kula, HI (elevation 366 m), during 1982–1984. **(A)** Comparison of monthly maximum (•), mean (+), and minimum (o) temperatures and total monthly rainfall (bar graph). **(B)** Comparison of tomato spotted wilt virus disease incidence (bar graph) and average number of thrips captured per week for each month (•).

Table 3. Correlation between average weekly number of thrips captured per month in lettuce field traps with tomato spotted wilt virus (TSWV) disease incidence in that field, total monthly rainfall, monthly mean temperature, monthly minimum temperature and monthly maximum temperature from farm 1, Kula, Maui, from November 1981 to December 1984

Thrips numbers with:	df	Correlation coefficient[a]		
TSWV disease incidence	17	0.555**		
		Correlation coefficient for year		
		1982	1983	1984
Total rainfall	12	−0.605**	−0.319	0.185
Mean temperature	12	0.339	0.635**	0.130
Minimum temperature	12	0.116	0.594**	0.057
Maximum temperature	12	0.515*	0.497*	0.234

[a] * = Significant at $P \leqslant 0.1$ and ** = significant at $P \leqslant 0.05$.

on the island of Maui. Highest losses have been observed to occur with the production of susceptible crops at lower elevation farms located between 328 and 630 m compared with farms of higher elevation. Several factors may account for this phenomenon; for example, consistently higher thrips populations were associated with the low elevation farm 1 than on higher farms. The higher percentage of potential vector species, which are known from this study and the literature, observed at farm 1 than at higher farms suggests that population composition may be important.

Variable virus transmission efficiency by vector species has been demonstrated; for example, *F. schultzei* was more efficient in transmitting TSWV than *S. dorsalis* (1). No difference in transmission rates was observed between *F. fusca* and *T. tabaci* (19); however, Sakimura (20) suggested that the pale color form *F. schultzei* found in Hawaii may not transmit TSWV. The western flower thrips was the predominant vector species found at the lower elevation farm compared with higher farms and may be a more efficient vector than the other vector species. Therefore, it may be difficult to interpret the significance of our data, which showed a significant correlation between thrips numbers and TSWV disease incidence with only transmission data for *F. occidentalis*. Studies are being conducted to compare the efficiency of TSWV transmission of the three vector species found in Hawaii.

Duffus (7) emphasized that wild plants (weeds and native and naturalized flora) and cultivated plants may play an integral part in the occurrence and spread of plant virus diseases. Samuel et al (21) indicated that TSWV-infected weed hosts were major sources for infection within tomato fields. In Hawaii, *E. sonchifolia* was shown to be a primary TSWV reservoir weed source in the epidemiology of pineapple yellow spot disease transmitted by *T. tabaci* (12,13). Several weeds found within Hawaii's vegetable-growing regions were found to serve as reservoirs for TSWV (5,6) and the western flower thrips (22). The percentage of these weeds found infected with TSWV was previously shown to be higher at low elevation farms than at higher farms in Kula (6).

Continual planting of a susceptible crop appears to influence TSWV incidence. During our surveys, only lettuce was cropped at farm 1, where TSWV incidence was highest. On the other hand, the planting of nonsusceptible crops in alternation or between fields planted with lettuce appeared to reduce the incidence of TSWV. For example, TSWV disease incidence was only 1% in May 1982 at farm 2 (Table 1), where cabbage was grown previously. Furthermore, disease incidence was lowest on farm 4, where both cabbage and lettuce were cultivated. On farm 4, cabbage and lettuce plantings are grown in rotation in two 1.2-ha fields that are separated by a 9-m road. Disease incidence on farm 3 is atypical because this farm is isolated from the major farming area.

Knowledge of migration into the field, dispersal within the field, and subsequent movement on the plant by vector thrips is essential for understanding the epidemiology of TSWV. Population dynamics of thrips are influenced by environmental factors. Bailey (2) recorded an increase in thrips in a fruit orchard when reduced rainfall and higher temperatures accelerated drying of a nonirrigated reservoir host. Bald (3) noted that temperatures higher than 23.8 C were most favorable for dispersal of *F. schultzei* and *T. tabaci* and that lower temperatures reduced adult activity and lengthened development time. Lower thrips populations observed during winter in Kula may be related to lower temperatures and higher rainfall associated with that period. Harding (10) observed that thrips movement was reduced by heavy rains and low temperatures. Similarly, cyclical changes that coincide with changes in temperature and rainfall have been observed in thrips populations and TSWV disease incidence at Kula.

Further studies have been initiated to better understand the epidemiology of this disease in order to develop feasible control recommendations. Distribution of reservoir plant hosts for the virus and insect vectors, the efficiency of transmission from these hosts to economically important crops, the importance of other environmental factors in determining disease outbreaks, and the importance of other thrips species found in Kula as possible new vectors are currently being assessed.

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