BARD

FINAL REPORT

PROJECT NO. US-2495-94

**Tomato Spotted Wilt Tospovirus and its Thrips
Vectors: Epidemiology, Insect/Virus Interactions
and Control**

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Antignus, A. Gera**

**הספריה המרכזית
למוציא החקלאות
בית דגן**

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הספריה המרכזית
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Continuation of (Related to) Previous BARD Project:

☐ Yes

☒ No

Number:

Keywords *not* appearing in the title and in order of importance. Avoid abbreviations.

Frankliniella occidentalis, impatiens necrotic spot virus, iris yellow spot virus, tospovirus

Abbreviations used in the report, in alphabetical order: INSV, IYSV, TSWV

Publications & Patents Summary (following page)

Summary of Cooperation (following page)

Budget: IS: \$

US: \$149,800

Total: \$

Appendix GF

630.72
BAR/ULL

Publication Summary (numbers)

	Joint IS/US authorship	US Authors only	Israeli Authors only	Total
Refereed (published, in press, accepted)	0	3	4	7
Submitted, in review, in preparation				
Invited review papers				
Book chapters		1		1
Books				
Master theses		1		1
Ph.D. theses				
Abstracts				
Not refereed (proceedings, reports, etc.)		10	8	18

Patent Summary (numbers)

	Israeli inventor only	US inventor only	Joint IS/US inventors	Total
Submitted				
Issued (allowed)				
Licensed				

Cooperation Summary (numbers)

	From US to Israel	From Israel to US	Together, elsewhere	Total
Visits/Meetings	1	1	1	3
Sabbaticals				
Postdoctorates				

- **Cooperation**, briefly explain whether synergistic, complementary or supportive.

Our cooperation was quite complementary, i.e. sharing of reagents and ideas. The two groups have been supportive of one another and especially synergistic in identification and characterization of a new tospovirus discovered under this BARD funding.

FINAL SCIENTIFIC PROGRESS REPORT
BARD PROPOSAL NO. US-2495-94
TOMATO SPOTTED WILT TOSPOVIRUS AND ITS THRIPS VECTORS:
EPIDEMIOLOGY, INSECT/VIRUS INTERACTIONS AND CONTROL

Investigators: Ullman, Sherwood, German, Raccach, Klein, Antignus and Gera

Institutions: University of California at Davis, University of Georgia (please note, during the course of the grant Sherwood moved to University of Georgia), University of Wisconsin, The Volcani Center, Institute of Plant Protection

I. Overall Summary and Statistics

Abstract

Objectives. The major aim of the proposed research was to study thrips-TSWV relationships and their role in the epidemiology of the virus with the aim of using this knowledge to reduce crop losses occurring due to epidemics. Our specific objectives were:

To determine the major factors involved in virus outbreaks, including: a) identifying the thrips species involved in virus dissemination and their relative role in virus spread; b) determining the virus sources among wild and cultivated plants throughout the season and their role in virus spread, and, c) determining how temperature and molecular variations in isolates impact virus replication in plants and insects and impact the transmission cycle.

Background to the topic. Tospoviruses are among the most important emerging plant viruses that impact production of agricultural and ornamental crops. Evolution of tospoviruses and their relationships with thrips vector species have been of great interest because of crop damage caused world wide and the complete absence of suitable methods of control. Tospoviruses threaten crops in Israel and the United States. By understanding the factors contributing to epidemics and the specific relationships between thrips species and particular tospoviruses we hope that new strategies for control can be developed that will benefit agriculture in both Israel and the United States.

Major conclusions, solutions, achievements. We determined that at least three tospoviruses were involved in epidemics in Israel and the United States, tomato spotted wilt virus (TSWV), impatiens necrotic spot virus (INSV) and iris yellow spot virus (IYSV). We detected and characterized INSV for the first time in Israel and, through our efforts, IYSV was detected and characterized for the first time in both countries. We demonstrated that many thrips species were present in commercial production areas and trap color influenced thrips catch. *Frankliniella occidentalis* was the major vector species of INSV and TSWV and populations varied in transmission efficiency. *Thrips tabaci* is the sole known vector of IYSV and experiments in both countries indicated that *F. occidentalis* is not a vector of this new tospovirus. Alternate plant hosts were identified for each virus. A new monitoring system combining sticky cards and petunia indicator plants was developed to identify sources of infective thrips. This system has been highly successful in the U.S. and was used to demonstrate to growers that removal of plant sources of infective thrips has a dramatic impact on virus incidence. Finally, a putative thrips receptor mediating acquisition of TSWV was discovered.

Implications, scientific and agricultural. Our findings have contributed to new control measures that will benefit agriculture. Identification of a putative thrips receptor for TSWV and our findings relative to thrips/tospovirus specificity have implications for development of innovative new control strategies.

Achievements

Significance of main scientific achievements or innovations. Our research has resulted in 4 primary achievements: 1) Detection and characterization of three tospoviruses causing serious epidemics in Israel and the United States; 2) Development of new monitoring strategies that allowed determination of the primary thrips species involved in spread of each of the respective tospoviruses and identification of their plant hosts; 3) Development and demonstration of cultural strategies for management of tospovirus spread; 4) Discovery of a putative thrips receptor for TSWV that may mediate virus acquisition and identification of thrips populations with distinct transmission efficiencies.

Knowing the cause of any problem is the first step required in developing a remedy. Our work in detection and virus characterization helped growers identify the causes of several serious problems. Indeed, we were the first to identify INSV in Israel and to find IYSV in Israel and the U.S. With this knowledge, growers could move forward in finding solutions. These findings impact bulb growers (particularly onion producers), ornamental growers and vegetable growers. Dollar figures are not available to measure economic benefits, but suffice it to say, these industries consider thrips transmitted tospoviruses their most intractable management problem. Collaboration was important to progress in this area, i.e. antisera developed in each country was shared and isolates were compared.

In Israel successful monitoring tools for thrips and tospoviruses were developed that enabled detection of important species. In the U.S. a new monitoring system that used sticky traps, petunia indicator plants and an immunoblotting detection method was developed. This system was demonstrated in a commercial cut flower and bulb production area. We demonstrated that we could pinpoint sources of infective thrips and more importantly showed that removal of these sources dramatically reduced virus incidence. The demonstration area was 74% infected at the onset of our studies. Using our monitoring strategies and cultural control measures, the grower reduced the virus incidence in his fields to less than 1% in year 1, 8% in year 2 and less than 1% in year 3. This was particularly impressive to other growers because, tospoviruses were especially serious in this time period in all the surrounding production areas. The monitoring system has received considerable grower attention, with articles published in Grower Talks and GM Pro, both important U.S. trade journals. A University of California IPM brochure describing the system is under preparation and the research effort has been expanded to greenhouse settings and to vegetable crops with funds from other agencies. We do not have data on the economic benefit in terms of dollars, but we did document an impressive increase in bulb size and yield. This research will have the greatest benefit in ornamental production, but should be applicable to any crop situation.

Perhaps the most exciting findings emerging from our collaborations was the discovery of thrips populations with varying transmission efficiencies and identification of a putative thrips receptor for TSWV. These studies provided the foundation for continuing research to clone the receptor and determine whether receptor mediation governs acquisition of the virus and efficiency of vector populations. If, as we suspect,

this proves to be the case, this knowledge can be used to design new management strategies and as a tool to assess vector populations.

II. Body of Report

Background, scientific and agricultural relevance of the project

Tospoviruses are among the most important emerging plant viruses that impact production of agricultural and ornamental crops. Evolution of tospoviruses and their relationships with thrips vector species have been of great interest because of the damage caused world wide and the complete absence of suitable methods of control. The major aim of the proposed research was to study thrips-TSWV relationships and their role in the epidemiology of the virus with the aim of using this knowledge to reduce crop losses occurring due to epidemics. As the proposed research progressed, new tospoviruses were identified in Israel and the United States necessitating some expansion of the original objectives. This report provides a final summary of our progress.

Methodologies, materials and results

Research efforts in Israel centered on:

1. Partial analysis of the spatial and temporal distribution of the virus in the field in Israel.
2. Identification of thrips species in epidemic areas.
3. Determination of the relative transmission efficiency (using three populations of WFT).
4. Partial characterization of two tospoviruses that are new in Israel.

Research efforts in the United States focused on:

- Assessing the abundance and diversity of thrips species in commercial ornamental production areas.
- Developing a monitoring system that combined use of sticky cards to assess thrips population abundance and movement, indicator or bait plants to assess virus spread and serological testing for virus incidence.
- Implementing management strategies based on information obtained through monitoring.
- Analyzing interactions between tospovirus glycoproteins and potential thrips receptor proteins.

Research regarding trapping, monitoring, detection and virus incidence: In the U.S. collaborative arrangements were forged with Karen Robb, Cooperative Extension (CE) Farm Advisor in San Diego County, Julie Newman CE Farm Advisor in Ventura County and growers in both regions. Thrips were trapped using yellow sticky cards and a technique for lifting thrips off sticky traps using citrus oil has been developed that is compatible with methods for mounting and identifying species. A complete collection of keys to the Thysanoptera of North America was made. We collaborated with Dr. Laurence Mound (Specialist in Thysanoptera Taxonomy and Systematics) who traveled to California, provided identifications of our thrips collections and produced a key to thrips vectors of TSWV. At least 8 thrips species were identified from sticky cards, only two of which are known vector species. We have shown that *F. occidentalis* is the

predominant species in California agricultural and ornamental production areas, followed by *T. tabaci*. In Israel, *T. tabaci* and *F. occidentalis* were found with the latter being the most common vector species outside of onions. Transmission efficiencies of several *F. occidentalis* populations were characterized. One of these populations was highly efficient (greater than 80%) in virus transmission and one was identified that did not transmit TSWV.

Israeli efforts on thrips trapping and monitoring focused on use of blue sticky traps combined with bait plants. Efforts by the U.S. investigators focused on combining directional traps with use of indicator or bait plants as a monitoring system that can assist growers in identifying sources of infective thrips and directing control measures accordingly. In addition, a rapid direct blotting technique for detecting the TSWV NSs protein (an indicator of replication and vector competency) in plants, was developed in the Ullman laboratory. This assay will replace the use of enzyme-linked immunosorbent assay (ELISA). Its advantages are that it is rapid (requiring a few hours rather than 2 days) and requires no sophisticated equipment. Ultimately we hope to collaborate with companies marketing detection tools for agricultural production to develop this technique into a format easily used by growers.

The first occurrence of TSWV in Israel was in nurseries. The major danger from the virus is natural spread, by vector transmission in fields and through vegetatively propagated crops in nurseries. For this reason, it was of particular importance for Israeli agriculture to establish the existence of natural spread and the spatial and temporal parameters of the spread. Research was done in peppers and lettuce in several locations. It was determined that bait plants and blue sticky traps were successful tools for studying virus spread. Like many other studies of epidemiology, it was clear in these fields that numbers of thrips are not correlated to virus incidence. The most important determining factor is apparently transmission efficiency of the population and the incidence of infective thrips, the latter being better indicated by bait plants.

In the U.S. our specific objective was to: 1) determine whether infectious thrips and virus spread can be efficiently detected using petunia indicator plants, 2) evaluate directional traps for monitoring thrips movements in combination with petunia indicators to identify sources of infective thrips, and, determine the abundance of thrips species in ornamental production areas. We demonstrated that petunias are excellent indicator plants for detection of thrips carrying TSWV, INSV and IYSV. Directional sticky traps gave an excellent indication of the direction from which thrips entered the crop production area, but as in the Israeli study, thrips numbers did not correlate with virus incidence. We compared various numbers of petunias and sticky traps, as well as different patterns of trap/bait plant distribution in the field. Our findings show that bait/indicator plants distributed across a production area provide an excellent way to identify sources of infective thrips. We used this information to remove plants that were sources of infective thrips and found this cultural management strategy had a profound impact on virus incidence, reducing virus incidence in our study area from 74% to less than 1%. Sticky traps were less useful, but still important in monitoring thrips population levels and determining whether thrips treatments are warranted and/or effective. Our findings show sticky traps could be used at approximately one directional trap/10,000 sq. ft, while at least 5 petunia indicator plants were required for a similar area.

With regard to detection of tospoviruses, several were shown to play a role in epidemics in Israel and the U.S. In the U.S., INSV and TSWV commonly occur together in epidemic situations. The prevalence of the viruses varies over time in given location

and it is not uncommon to find mixed infections. The Israeli investigators were the first to detect INSV in Israeli crops. The following is a description of their findings:

In January 1999, leaves of *Anemone coronaria* L., imported from Europe, and grown in open fields, near Jerusalem in Israel, showed ringspots and foliar necrosis. Within few weeks of the first appearance of symptoms, further plants in the surrounding were affected and seriously damaged. The damage was initially attributed to bacterial or fungal pathogen, but neither was isolated. Impatiens necrotic spot tospovirus (INSV) was detected in affected plants by enzyme-linked immunosorbent assay (ELISA) (anti-INSV monoclonal antibodies were provided by H.T. Hsu, USDA, Beltsville, USA and a polyclonal antibody to INSV purchased from Loewe, Germany). Crude sap from symptomatic tissue was mechanically transmitted to several test plants. Inoculated *Emilia* spp, *Petunia hybrida*, *Nicotian glutinosa*, *N. benthamiana* and *N. rustica* plants developed symptoms characteristic for INSV infection. ELISA tests of leaf sap extracted from *Anemone* and mechanically inoculated plants, gave a clear and strong positive reaction, verifying it as INSV. Leaf samples of *Anemone* were analyzed by transmission electron microscopy (EM) of leaf dip preparations. Typical tospovirus-like particles were observed only with samples taken from symptomatic plants. EM studies with ultrathin sections of infected *Anemone* and *Emilia* leaves revealed the presence of tospovirus-like particles.

This first report of INSV interception in Israel, brings the count of the *Tospovirus* members in Israel to three, including TSWV, which was found in the past to infect *Anemone* and other ornamental crops, and the IYSV infecting onion (see later report). INSV is known to occur in Europe and in the USA, mostly in flowers grown in greenhouses. The virus is transmitted by the Western Flower Thrips (WFT) (*Frankliniella occidentalis*, Pergande). Although, all infected plants were destroyed, precautions to prevent further introduction of the virus, must be made. INSV might spread by the WFT, which is abundant in most areas of the country, year round, and might also infect other greenhouse or field crops.

The Israeli and U.S. investigators were involved in the first discovery of a new tospovirus, IYSV, in each of our respective countries. The virus was characterized in each country by standard virological methods. Antisera were made by investigators in Israel and the U.S. and shared so that isolates from each country could be compared. Details of the Israeli protocols and findings are summarized in the following. Similar methods were applied in the U.S. with strikingly similar results and thus, are not repeated here.

Purification of IYSV and production of diagnostic antibodies to plant viruses, utilizing denatured coat proteins and booster immunization with partially purified virus

Finding a new *Tospovirus* in onions [Gera et al., (1998). Plant Disease 82:127]:

Iris Yellow Spot Tospovirus Detected in Onion (*Allium cepa*) in Israel. During March 1997; 20 to 30% of field-grown onion (*Allium cepa*), observed in Bet Shean Valley, Israel, had unusual viral symptoms of straw-colored ringspots on leaves and flower stalks; leaf samples were analyzed by transmission electron microscopy (EM) of leaf dip preparations; typical tospovirus-like particles were observed only with samples taken from symptomatic plants. Crude sap from symptomatic tissue was mechanically transmitted to *Nicotiana benthamiana*, *Chenopodium quinoa*, and *Gomphrena globosa*.

On inoculated plants of *N. benthamiana*, chlorotic spots developed on inoculated leaves, followed by systemic necrosis, 4 and 7 days post inoculation (DPI), respectively. On inoculated plants of *C. quinoa* and *G. globosa*, necrotic local lesions developed by 4 to 5 DPI. EM studies with ultrathin sections of infected onion, and *N. benthamiana*, leaves revealed the presence of tospovirus-like particles.

Purification protocol used for the Israeli IYSV:

The Israeli IYSV isolated from onion was raised on *N. benthamiana* plants. The purification protocol was based on that of Shinya et al., (1991) with minor modifications:

N. benthamiana infected leaves were homogenized in 3 volumes of 0.1M Phosphate buffer, pH 7.1 containing 0.01M Na_2SO_3 (extraction buffer). The slurry was clarified by low speed centrifugation for 15 min. The supernate was filtered through a cloth and placed on top of a 5ml of 25% sucrose cushion in purified and 0.02M Phosphate buffer, pH 7.0, containing 0.01M $(\text{Na})_2\text{EDTA}$ and 0.1% (w/v) L-cysteine. The filtrate was centrifuged at 120000g for 90 min. The pellet was collected and resuspended in 30 ml extraction buffer. The resuspended pellet was clarified by low speed centrifugation and the supernate was placed again on top of 15 ml 15% sucrose cushion in 0.02M Phosphate buffer, pH 7.0, containing 0.01M $(2\text{Na})\text{EDTA}$ and 0.1% (w/v) L-cysteine. The solution was then centrifuged at 60000g for 45 min. The fraction containing the virus particles was further purified on a sucrose gradient (40-60% sucrose in 0.02M Phosphate buffer, pH 7.0, containing 0.01M $(2\text{Na})\text{EDTA}$ and 0.1% (w/v) L-cysteine, and centrifuged at 60000g for 16hrs. The virus layer was retrieved by a fraction collector. The virus purity was ascertained spectrophotometrically and by electron microscopy. Finally, virus purity was confirmed by SDS polyacryl amid electrophoresis (PAGE) followed by western blots using antibodies against viral proteins.

Shinya, T., Natsuki, K. T., and Keiichi, T. 1991. Purification of tomato spotted wilt virus isolated from tobacco plants in Morioka, Japan. *Ann. Phytopathological Society of Japan*. 57:239-246.

Preparation of antisera against the Israeli IYSV:

Partially purified virus (ppV) suspensions of IYSV (about 0.1 mg/ml) were emulsified with an equal volume of Freund's incomplete adjuvant and injected intramuscularly (IM) into both hip muscles of 6-wk-old female New Zealand white rabbits. Four IM injections were given at weekly intervals. Two wk after the last injection a booster intravenous (IV) injection with ppV was given. Such antisera (designated ppV/ppV) were collected 12 days after boosting. Alternatively, the proteins from purified virus preparations were denatured with SDS and separated by SDS-PAGE. Stained protein bands (SDS-PB) were excised from the gel, washed, crushed in 1 ml of 0.01 M phosphate buffer, pH 7, and emulsified with Freund's complete or incomplete adjuvant for the first and subsequent injections, respectively. Rabbits were given four IM injections at weekly intervals. Two wk after the last injection, a booster injection with ppV or SDS-PB was given. Antisera were again collected 12 days after boosting. These antisera are designated SDS-PB/ppV and SDS-PB/SDS-PB, respectively. All antisera were tested using Western blotting and ELISA.

Polyacryl amide electrophoresis, Western blotting and ELISA

Purified IYSV proteins, when denatured with SDS and analyzed by PAGE, gave three sharp bands, which by analogy with TSWV, were G1 (78 kDa), G2 (58 kDa) and

the nucleocapsid protein (NC) (31 kDa), respectively. Immunoblots with SDS-PB/ppV and ppV/ppV of IYSV, gave a clear and strong reaction with the polypeptides corresponding to NC protein as identified by their molecular weight. Although both IYSV antisera reacted with the NC protein, the reactivity and specificity of the SDS-PB/ppV antisera were higher.

ELISA titres (OD/405 nm) were considerably higher with the SDS-PB/ppV antisera than with ppV/ppV antisera. The reaction of ppV/ppV antisera against IYSV with *N. benthamiana*-infected tissue in DAS-ELISA was weak and gave a high unspecific background with healthy plant extracts. These antibodies evinced a nonspecific reaction with healthy tissue. Our results indicate the considerable advantage of using primary injection and boosting with gel separated and native antigens, respectively, to obtain higher titer antisera suitable for ELISA.

Interactions between TSWV Membrane Glycoproteins (GPs) and the putative receptor proteins in *Frankliniella occidentalis*.

This research was published in Bandla, M.D., Campbell, L.R., Ullman, D.E. and J.L. Sherwood. 1998. Interaction of tomato spotted wilt virus (TSWV) glycoproteins with a thrips midgut protein, a potential cellular receptor for TSWV. *Phytopathology* 88:98-104.

Gel overlay assays and immunolabeling were used to investigate the putative role of TSWV GPs as viral attachment proteins and determine whether a corresponding cellular receptor may be present in *F. occidentalis*. A single band in the 50 kDa region was detected with murine monoclonal antibodies (Mabs) to the TSWV-GPs when isolated TSWV or TSWV GPs were used to overlay separated thrips proteins. This band was not detected when blots were probed with antibody to the nonstructural protein encoded by the small RNA of TSWV or the TSWV nucleocapsid protein, nor were proteins from non-vector insects labeled. Anti-idiotypic antibodies were prepared to murine MAb against GP1 or GP2. As anti-idiotypes, these mimic the glycoproteins. It was compelling that both anti-idiotypes specifically labeled a single band at 50 kDa in Western blots and the plasmalemma of larval thrips midguts. These results support the putative role of the TSWV GPs as viral attachment proteins and identified potential cellular receptor(s) in thrips. During the last year of this grant efforts to make thrips protein expression library to ultimately identify and clone the receptor protein were successful. Screening of the library will be a future goal for the German and Ullman laboratories.

Discussion and scientific implications

Our findings indicate:

- Epidemics in Israel and the U.S. (and likely elsewhere in the world) are frequently caused by a mixture of tospoviruses. In the U.S. TSWV and INSV were frequently present together in epidemic proportions. INSV was detected for the first time in Israel and was not thought to be established. A newly emerged tospovirus, IYSV, was detected for the first time in Israel and the U.S. Collaboration between the Israeli and U.S. investigators led to characterization of the new virus.
- *F. occidentalis* is the predominant vector of TSWV and INSV in both countries, although populations can vary dramatically in their efficiency of transmission. This finding suggests that the competence of the vector population is key in determining

whether epidemics occur. This research provides a foundation and potential model for identifying the factors mediating acquisition and transmission efficiency.

- *T. tabaci* is the vector of IYSV in both countries. *F. occidentalis* is not a vector of IYSV. This is a fascinating finding, because *F. occidentalis* has been shown to transmit most of the known tospoviruses. These results strongly indicate that vector specificity occurs that is comparable to that identified for aphid-transmitted viruses (i.e. the luteoviruses). Furthermore, the two thrips species and their relationships with IYSV and TSWV provide an excellent model for study of vector specificity.
- Systems for monitoring for infective thrips were developed in both countries. The petunia indicator system developed in the U.S. has received wide acceptance in the ornamentals industry in California. This method of monitoring led to growers making sound cultural decisions that resulted in dramatic reductions in tospovirus incidence. Continued use of the petunia indicator monitoring system in making management decisions allowed participating growers to maintain extremely low virus incidence. This research has provided an excellent demonstration of how cultural management practices can influence tospovirus epidemics.
- Our research on the interaction between TSWV GPs and a 50 kDa thrips midgut protein provided strong evidence that the TSWV GPs serve as viral attachment proteins. The evidence from immunolabeling and Western blotting with anti-idiotypes shows the specificity of the interaction and strongly indicates that a 50 kDa protein acts as a receptor for TSWV at the thrips midgut. This is the first putative insect receptor that has been identified for a plant virus and provides a foundation for the research necessary to characterize and clone the receptor protein.

Potential impact on agriculture, industry, environment, policy, legislation

Thrips transmission of tospoviruses is of global importance. Our research impacted vegetable and ornamental crops in Israel and the U.S. by identifying the causal agents for important diseases and helping to direct control strategies. The monitoring systems developed will help growers in decision making. Furthermore, the significance of cultural methods for control were well demonstrated. This type of control is environmentally sound and its success certainly reduced unnecessary pesticide spraying against thrips populations. The foundation was laid for understanding vector specificity. If we are successful in identifying the basis for specificity, there is no doubt that a plethora of new, novel control measures will emerge.

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