Thrips tabaci: an ambiguous vector of TSWV in perspective

E.K. Chatzivassiliou
Aristotle University of Thessaloniki, Faculty of Agriculture, Plant Pathology Laboratory, P.O.Box 269, 540 06 Thessaloniki, Greece.
E-mail: vetta72@yahoo.com

Abstract: The transmission ability of *Thrips tabaci*, one of the first recognized vectors of *Tomato spotted wilt virus* (TSWV), is a matter of much discussion. Although originally considered as an important vector, it failed to transmit TSWV in several laboratory tests. However, destructive outbreaks of TSWV in the tobacco crops of East Europe and the Balkan Peninsula have for long been attributed to *T. tabaci*. Recent results have shown that a large diversity exists in the competence to transmit TSWV or other tospoviruses between the parthenogenetic and sexual populations of this haplodiploid species. Arrhenotokous, sexual, populations, are either poor or very efficient vectors of TSWV. Several populations on leeks were poor vectors of TSWV and did not transmit *Tomato chlorotic spot virus* (TCSV), *Groundnut ring spot virus* (GRSV) or *Impatiens necrotic spot virus* (INSV), while others proved to be very efficient vectors of Iris yellow spot virus (IYSV). Arrhenotokous populations from tobacco were highly effective in transmitting TSWV in laboratory tests as well as in the field. TSWV was acquired by both first and second larval stages of a *T. tabaci* population from tobacco, and most thrips started to transmit after becoming adults. The dynamics of TSWV spread by arrhenotokous *T. tabaci* studied in tobacco fields, showed that primary infections play a major role in the development of epidemics. Large-scale surveys associated this thrips species with TSWV infections in several weed species. Reports by different authors showed that thelotokous, parthenogenetic, populations of *T. tabaci* either do not transmit TSWV, TCSV, GRSV and *Chrysanthemum stem necrosis virus* (CSNV), or transmit TSWV inefficiently. Those populations have also been found to transmit IYSV to onion. The worldwide distribution of *T. tabaci* may have resulted in a large divergence in its competence to transmit TSWV and other tospoviruses. The complex relationships between the viruses and the thrips, as well as the infection mechanisms involved, remain to be investigated.

An historical point of view

Thrips tabaci (Thysanoptera: Thripidae), widely known as the onion thrips, was identified as a vector of *Tomato spotted wilt virus* (TSWV), the type species of the genus Tospovirus (Murphy *et al.,* 1995), shortly after the detection of the virus (Pittman, 1927). Although this thrips species was considered to be an important vector for many decades (Lindorf 1931; 1932; Smith, 1931; Gardner *et al.,* 1935; Sakimura, 1961; 1962; 1963), failures to transmit some TSWV isolates led to questions about its vector ability (Samuel *et al.,* 1930; Jones, 1959; Paliwal, 1974 and 1976). Efficient transmission was reported in Finland (Lemmetty and Lindqvist, 1993), but recent studies obtained only a poor or no transmission of TSWV by several *T. tabaci* populations (Wijkamp *et al.,* 1995), challenging its vector status (Ullman, 1996). Notwithstanding these conflicting results, destructive outbreaks of TSWV in the tobacco crops of East Europe and the Balkan Peninsula have for long been ascribed to *T. tabaci*, the only thrips vector found on tobacco plants in this region (Zawirska, 1978; Jankowski *et al*., 1980; Jenser and Gáborjányi, 1998; Karadjova and Hristova, 1998).

Current status of T. tabaci competence to transmit TSWV

T. tabaci is a haplodiploid species, highly polyphagous and cosmopolitan, but with two forms, one of which is unisexual and parthenogenetic but the other bisexual. Lewis (1973) reported that in East Mediterranean and Iran, speculated as the area of *T. tabaci* origin, the sex ratio is approximately 1:1, while in most areas of the world, males are rare. In contrast, Kendall and Capinera (1990) concluded from published literature that *T. tabaci* males are present in the Western Hemisphere. Though the worldwide distribution of the parthenogenetic and the bisexual form of *T. tabaci*, and the factors determining their presence, are quite ambiguous, recent studies have shown that a large diversity may exist in their competence to transmit TSWV or other tospoviruses.

Transmission of TSWV by arrhenotokous populations

Arrhenotokous populations, the bisexual form of *T. tabaci*, are either poor or very efficient vectors of TSWV. Recent laboratory studies showed that several arrhenotokous populations of *T. tabaci* on leeks transmitted TSWV inefficiently with rates varying from 0.7 to 11.7 % (Wijkamp *et al.,* 1995; Chatzivassiliou *et al.,* 1999a), when tests were performed with single thrips or up to 16.6% (Karadjova and Hristova, 1998) or 36% (Tsuda and Fujisava, 2001) when using more than one individual. Different TSWV isolates were also transmitted at different rates (Chatzivassiliou *et al.,* 1999a). Incompatibility of thrips and virus isolates of different origin has been proposed as a reason for the inefficient transmission of TSWV by *T. tabaci* (Paliwal, 1974), however transmission was still inefficient when *T. tabaci* and TSWV isolates from the same area were tested (Chatzivassiliou *et al.,* 1999a). Host effects were recorded on virus acquisition and transmission by arrhenotokous populations on leek; TSWV was more efficiently acquired on *Datura stramonium* than on *Emilia sonchifolia* infected leaf material, while the later species was found more susceptible (Chatzivassiliou *et al.,* 1999a). These effects on tospovirus acquisition can be attributed to host suitability for feeding (Lewis, 1973), virus distribution and titer in the plant, and the number cells infected that determine the amount of virus acquired, the rate at which it is acquired and the number of thrips transmitting (German *et al*., 1992). Differences in the transmission efficiency among host plants have been attributed to the susceptibility of the species and the feeding activity of thrips. Shallow feeding on non-preferred hosts usually seems to favor transmission (German *et al.,* 1992; Van de Wetering *et al*., 1998).

On the other hand arrhenotokous populations from tobacco were highly effective in transmitting TSWV in laboratory tests as well as in the field. *T. tabaci* adults, collected on naturally infected tobacco plants from different areas in Greece, transmitted TSWV with rates varying from 16.7 to 48.5% and remained efficient transmitters when kept on tobacco in the laboratory with transmission rates of 66.7% (Chatzivassiliou *et al.,* 1999b).

Both males and females of the arrhenotokous tobacco populations transmitted TSWV with high efficiency (Chatzivassiliou *et al.,* 1999b), although males of the leek populations tested were more efficient transmitters than females (19 out of 176 vs 5 out of 494) (Chatzivassiliou *et al.,* 1999a). Those differences are possibly due to the degree by which the epithelium midgut of *T. tabaci* male and females becomes infected (Nagata *et al*., 1999b).

Transmission of TSWV by thelotokous populations

Thelotokous populations of *T. tabaci* from Japan and The Netherlands did not transmit the Brazilian isolate BR-01 (Wijkamp *et al.,* 1995) or a Greek isolate (Chatzivassiliou *et al.,* 1999b). However an Italian thelotokous population could transmit, although inefficiently, an Italian isolate (16.7%) as well as the BR-01 (2.0%) (Tedeschi *et al.,* 2001). A Japanese population could also transmit the virus in a rate up to 10% (Ihoue *et al.,* 2001).

Kinetics of TSWV transmission by T. tabaci

Transmission of TSWV after its ingestion by *T. tabaci* larvae of different age: Lindorf (1931 and 1932) and Sakimura (1962) have shown that TSWV can be acquired after ingestion only by larvae of *T. tabaci*. Recent studies showed that both first and second instar larvae of a *T. tabaci* population from tobacco can successfully acquire the virus from tobacco, but this ability decreases with the age of larva that acquired the virus. 61% of male and 51% of female larvae can acquire the virus when newly hatched, whereas some *T. tabaci* larvae can still acquire the virus when 4 to 5 day old, when 0-24 h old larvae were used (Chatzivassiliou *et al.,* 2000).

The median acquisition access period (AAP_{50}) in which *T. tabaci* acquires TSWV: The feeding threshold for TSWV acquisition by *T. tabaci* was in the past estimated either one day (Lindorf, 1932), 30 min from *Nicotiana rustica* (Razvyankina, 1953) or 15 min (Sakimura, 1962). Recent studies showed that a tobacco population can acquire TSWV in feeding times as short as 5 min, similar to those of other tospoviruses and thrips vectors (Wijkamp *et al.,* 1997).

Sakimura (1962) reported an increase in transmission of TSWV by *T. tabaci* from 4% in 15 min, via 33% in 1 hour and 59% in 1 day, to 77% in 4 days. The transmission efficiency of TSWV for both males and females studied recently increases with the AAP, although not in linear fashion, and optimum values were reached in only 21 h as when it is transmitted by *F. occidentalis* (Wijkamp *et al.,* 1997).

Fifty percent of *T. tabaci* larvae (0-24 h old) were able to acquire an effective dose of the virus from infected tobacco in 41 min (AAP_{50}). These values were 65 min and 35 min for males and females, respectively (Chatzivassiliou *et al.*, 2000).

The median latent period (LP_{50}) of TSWV in *T. tabaci*: Preliminary studies have shown that TSWV can be transmitted by *T. tabaci* reporting a minimum latent period of either 3 (Razvyazkina, 1953), 4 (Sakimura, 1963), 5 (Smith, 1931), or 10 days (Lindorf, 1932).

Latest results using a tobacco population showed that *T. tabaci* larvae can transmit the virus, however when using 0-24 h old larvae for virus acquisition on tobacco the majority of *T. tabaci* individuals made the first transmission as adult. Larvae kept at 20 °C transmitted the virus at a rate of 25%, whereas a rate of only 8% or 7% was found when they were kept at 25 or 27 °C, respectively. After becoming adults 54, 64 and 67% transmitted TSWV respectively at the temperatures used (Chatzivassiliou *et al.,* 2000). The LP_{50}, defined as the period between the start of the AAP and the end of that IAP in which 50% of the vectors make cumulatively a first transmission, recorded for *T. tabaci* adults was approximately 10 days at 27°C, 13 at 25°C and 16 days at 20°C (Chatzivassiliou *et al.,* 2000) lower than those of *F. occidentalis* that were calculated for the larval and not for the adult stage (Wijkamp and Peters, 1993).

The time required for larval development, the number of larvae transmitting TSWV as well as LP values decreased with increasing temperatures, as observed for *F. occidentalis* (Wijkamp and Peters, 1993). However, increased transmission efficiency by adults was possibly due to a higher virus replication rate (Duffus, 1963).

The median inoculation access period (IAP_{50}) of *T. tabaci*: After the end of the latent period, viruliferous *T. tabaci* are able to transmit the virus to healthy *N. rustica* (Razvyazkina, 1953) as well as on tobacco or petunia (Chatzivassiliou *et al.,* 2000) in short probes of 5 min. In general, short feeding periods are expected for the successful inoculation of TSWV, as transmission requires intact cells. However it has been confirmed that for a more effective transmission increasing times are necessary (Sakimura, 1962 and 1963; Wijkamp *et al.,* 1997). The IAP_{50} (the feeding period at which 50% of the viruliferous thrips transmit) estimated was 246 min to tobacco and 365 min to petunia for males and 96 and 345 min for females, respectively (Chatzivassiliou *et al.,* 2000).

Involvement of T. tabaci in destructive epidemics of TSWV

TSWV in tobacco crops: Sakimura, since 1962, pointed out that TSWV spread and its vector status in tobacco crops consists an interesting epidemiological case with strong host specificities. *T. tabaci* is the only vector species colonizing tobacco and is associated with epidemics of the virus in South East Europe and South Russia (Zawirska, 1978; Jankowski *et al.*, 1980; Jenser, and Gáborjányi, 1998; Karadjova and Hristova, 1998; Chatzivassiliou *et al.,* 1999c). However, *F. fusca* (Hinds) is the most abundant (McPherson *et al.,* 1992 and 1999) and the most effective (Eckel *et al.,* 1996) vector of TSWV in the tobacco in USA and although *T. tabaci* is present in North America and the South Hemisphere it does not infest tobacco.

These differences are possibly associated with the preference that the different populations of *T. tabaci* show for tobacco. Preliminary laboratory tests showed that some arrhenotokous populations collected from bean or leek thrive poorly on tobacco and only a few individuals seem to survive on tobacco after the introduction of large numbers on the plants, while some thelotokous leek populations tested do not live at all (Chatzivassiliou *et al.,* 1998).

Field experiments in tobacco crops in Greece showed that TSWV spread is associated with the cumulative number of *T. tabaci individuals of an arrhenotokous population caught in blue sticky traps.* Analysis of spatial and temporal TSWV suggests that it depends on primary infections, while secondary spread is rather limited (Chatzivassiliou *et al.,* 1999c). Sources of TSWV for primary infections in tobacco fields can be found among several weed hosts of TSWV such as *Solanum nigrum*, *Plantago major, Datura stramonium*, *Artemisia vulgaris*, *Ballota nigra*, *P. lanceolata*, *Capsella bursa–pastoris*, *Sonchus* sp. and *Cichorium intybus* that are associated with *T. tabaci* (Chatzivassiliou *et al.,* 2001).

TSWV seems to be an emerging problem in potato crops. In 1998 virus infections were observed for the first time in Iran coinciding with high population of *T. tabaci* (Pourrahim *et al.,* 2001). In Australia especially in the island state of Tasmania *T. tabaci* is the only thrips-vector implicated with epidemics of TSWV in potato (Horne and Wilson, 2000) and some vegetable crops (Wilson, 1995). The spread of the virus does not show obvious aggregation patterns that suggest, as in tobacco crops, that virus sources originated from neighboring weeds (Wilson, 1998). Although informations for the potato *T. tabaci* populations in Iran are not available, those in Australia consist of both males and females (Dr Alan Clift, personal communication).

T. tabaci as a vector of other tospoviruses except TSWV

The ability of *T. tabaci* to transmit other tospoviruses except TSWV is not completely studied. Several arrhenotokous leek populations of *T. tabaci* were tested in the laboratory and failed to transmit *Tomato chlorotic spot virus* (TCSV), *Groundnut ring spot virus* (GRSV) and *Impatiens necrotic spot virus* (INSV) (Wijkamp *et al.,* 1995). However, studies conducted in Israel, where the incidence of *Iris yellow spot virus* (IYSV) often reaches 50-60%, resulting in heavy losses of onion-bulb production (Gera *et al.,* 1998), showed that this spread is strongly associated with arrhenotokous populations of *T. tabaci* infesting the crop. Those populations were consisted of a large number of viruliferus individuals (33-50%), when collected from infected onion fields and transmitted efficiently the virus in laboratory tests as well (Kritzman *et al.,* 2000). The Israeli arrhenotokous onion populations of *T. tabaci* were also found responsible for IYSV spread from onion to *Lisianthus* (Kritzman *et al.,* 2001).

The arrhenotokous tobacco populations, that are very efficient vectors of TSWV (Chatzivassiliou *et al.,* 2000) have not been tested yet for their ability to transmit any other tospovirus except TSWV. No thelotokous populations of *T. tabaci,* have been found capable of transmitting INSV, TCSV, GRSV (Wijkamp *et al.,* 1995; Tedeschi *et al.,* 2001) or *Chrysanthemum stem necrosis virus* (CSNV) (Nagata and de Ávila, 2000). However a Brazilian thelotokous population of *T. tabaci* has recently been demonstrated as the most important vector species of IYSV in onion, transmitting the virus in a rate of 45.8% (Nagata *et al.,* 1999a).

Conclusions

Reviewing the vector status of *T. tabaci* has revealed distinct level of specificity in tospovirus transmission. Some populations of *T. tabaci* are still very competent to transmit TSWV, however the biological relationship of this thrips species with TSWV or other tospoviruses seems to be more complicated than previously believed.

Zawirska (1976) concluded that *T. tabaci* forms a complex of two biotypes or even subspecies, one, denoted *T. tabaci* spp. *tabaci* that consists of males and females and the other one, *T. tabaci* spp. *communis,* that comprise populations with only females, and she attributed the spread of TSWV to only the first one that solely infests tobacco. Genetic analysis is also needed to explore inter-population variation in TSWV transmission as biotypic variation.

Ullman (1996) pointed the altered status of *T. tabaci* and suggested that possibly both or each of insect and virus evolved such that the complex events leading to acquisition and transmission of tospoviruses can or cannot occur. The worldwide distribution of the *T. tabaci* populations in an extensive range of hosts may have generated specific associations with the tospoviruses that had an impact in their transmission.

Histological tools can provide an exceptional opportunity to fully investigate the vector specificity of the *T. tabaci* populations. Differences in the present of midgut receptors, or midgut properties or salivary glands properties affecting replication rate of tospoviruses and their translocation in thrips (Nagata *et al.,* 1999b), may explain the differences in the ability of *T. tabaci* population to transmit tospoviruses.

The complicated relationship between tospoviruses and *T. tabaci* as well as the infection mechanisms involved in this pathosystem remains to be unsolved. Understanding the factors determining the vector competence of *T. tabaci* populations may provide useful knowledge to manage tospovirus epidemics.

References

Chatzivassiliou EK, Katis NI and Peters D. 1998. Transmission of tomato spotted wilt virus (TSWV) by *Thrips tabaci* grown on tobacco or non-tobacco crops. Pages 59-62 in: Recent Progress in tospovirus and thrips research. Peters, D. and Goldbach, R.W. (eds), *Proceedings of the Fourth International Symposium on Tospovirus and thrips in floral and vegetable crops*, Wageningen, The Netherlands.

Chatzivassiliou EK, Nagata T, Peters D and Katis NI. 1999a. The transmission of tomato spotted wilt tospovirus (TSWV) by *Thrips tabaci* Lind. (Thysanoptera: Thripidae) populations originating from leek. *Plant Pathol*. **48**, 700-706.

Chatzivassiliou EK, Katis NI and Peters D. 1999b. Transmission of tomato spotted wilt virus (TSWV) by *Thrips tabaci* populations and determination of the median latent period. *VII^th^ Intern. Virus Epidemiol. Symp. Plant Virus Epidemiology: Current status and future prospects*, Aguadulce, Spain, Abstr. p 42-43.

Chatzivassiliou EK, Zintzaras I, Jenser G and Katis NI. 1999c. Temporal and spatial spread of tomato spotted wilt tospovirus (TSWV) in relation to thrips populations in tobacco crops in Northern Greece. *VII^th^ Intern. Virus Epidemiol. Symp. Plant Virus Epidemiology: Current status and future prospects*, Aguadulce, Spain, Abstr. p 106-107.

Chatzivassiliou EK, Peters D and Katis NI. 2000. Transmission of tomato spotted wilt tospovirus (TSWV) by *Thrips tabaci* Lindeman populations and determination of transmission parameters. *EMBO Workshop: Plant Virus Invasion and Host Defense.* Kolimbari Creta. Abstr. p 69.

Chatzivassiliou EK, Mpoumpourakas I, Drossos E, Eleftherohorinos I, Jenser G, Peters D and Katis NI. 2001. Differential *Tomato spotted wilt virus* infection and vector species infestation of weeds in greenhouses and tobacco fields. *Plant Dis*. **85**, 40-46.

Duffus JE. 1963. Possible multiplication in the aphid vector of sowthistle yellow vein virus, a virus with an extremely long insect latent period. *Virology* **21**, 194-202.

Eckel SC, Kijong C, Walgenbach JF, Kennedy G and Moyer W. 1996. Variation in thrips species composition in field crops and implications for the tomato spotted wilt epidemiology in North Carolina. *Entomol. Exp. Appl*. **78**, 19-29.

Gardner MW, Tomkins CM and Whipple OC. 1935. Spotted wilt of truck crops and ornamental plants. *Phytopathology* **25**, 17.

Gera A, Cohen J, Salomon R and Raccah B. 1998. Iris Yellow Spot Tospovirus detected in Onion (*Allium cepa*) in Israel. *Plant Dis*. **82**, 127.

German TL, Ullman DE and Moyer JW. 1992. Tospoviruses: diagnosis, molecular biology, phylogeny, and vector relationships. *Ann. Rev. Phytopathol*. **30**, 315-48.

Horne P and Wilson C. 2000. Thrips and tomato spotted wilt virus. p. 103-106, in Williams C.M. and Walters, L.J. (eds). *Australian potato research, development and technology*. Transfer Conf, Adelaide, S. Australia.

Ihoue T, SakuraiT, Murai T and Maeda T. 2001. Intraspecific variation in transmission of TSWV by thrips have relations to virus multiplication during developmental stage: distinct pattern between two Thripinae genera, *Frankliniella* and *Thrips*. *Thrips and tospoviruses. Proceedings of the seventh International Symposium on Thysanoptera*, Reggio Calabria

Jankowski F, Slawinski FA, Mazur M, Micinski B and Wegorek W. 1980. The economic importance of the TSWV in tobacco growing and the results of control of the vector of this disease the tobacco thrips *Thrips tabaci* Lind. Page 279, in: *Proc. XIX Conf. Scient. Inst. Plant Protect.*, 1979: Materialy XIX Sesji Naukowej Instytutu Ochrony, Roslin.

Jenser G and Gáborjányi R. 1998. Ecological aspects of tomato spotted wilt epidemy in Hungary. Pages 81-82 in: Recent Progress in tospovirus and thrips research. Peters, D. and Goldbach, R.W. (eds), *Proc. Fourth Intern. Symp. Tospovirus and thrips in floral and vegetable crops*, Wageningen, The Netherlands.

Jones JP. 1959. Failure of thrips to transmit an isolate of tomato spotted wilt virus. *Phytopathology* **49,** 452-453.

Karadjova O and Hristova D. 1998. Transmission of tomato spotted wilt virus by bulgarian population of *Frankliniella occidentalis* Perg. and *Thrips tabaci* Lind. Pages 95-96 in: Recent Progress in tospovirus and thrips research. Peters, D. and Goldbach, R.W. (eds), *Proc. Fourth Intern. Symp. Tospovirus and thrips in floral and vegetable crops*, Wageningen, The Netherlands.

Kendall DM and Capinera JL. 1990. Geographic and temporal variation in the sex ratio of onion thrips. *South. Entomol*. **15**, 80-88.

Kritzman A, Beckelman H, Alexandrov S, Cohen J, Lampel M, Zeidan M, Raccah B and Gera A. 2000. Lisianthus leaf necrosis a new disease of lisianthus caused by iris yellow spot virus. *Plant Dis*. **84**, 1185-1189.

Kritzman A, Raccah B and Gera A. 2001. Distribution and Transmission of Iris Yellow Spot Virus. *Plant Dis*. In press.

Lemmetty A and Lindqvist I. 1993. *Thrips tabaci (Lind.) (Thysanoptera: Thripidae), another vector for tomato spotted wilt virus in Finland. Agric. Sci. Finland* **2, 189-194.**

Lewis T. 1973. *Thrips-their biology, ecology and economic importance.* New York Academic Press, London.

Lindorf MB. 1931. Further studies of the transmission of the pineaple yellow spot virus by *Thrips tabaci. Phytopathology* **21**, 999.

Lindorf MB. 1932. Transmission of the pineaple yellow-spot virus by *Thrips tabaci*. *Phytopathology* **22**, 301-324.

McPherson RM, Pappu HR and Jones DC. 1999. Occurrence of five thrips species on flue-cured tobacco and impact on spotted wilt disease incidence in Georgia. *Plant Dis*. **83**, 765-767.

Murphy FA, Fauquet GM, Bishop DHL, Ghabrial SA, Jarvis AW, Martelli GP, Mayo MA and Summers MD. 1995. Virus Taxonomy. *Sixth Rpt. Int. Comm. Taxonomy of Viruses. Arch. Virol.* Suppl. **10**, 1-586.

Nagata T, Almedia AL, de Resende R and de Avila C. 1999a. The identification of the vector species of iris yellow spot tospovirus occurring in onion in Brazil. *Plant Dis*. **83**, 399.

Nagata T, Inoue-Nagata AK, Smid H, Goldbach R and Peters D. 1999b. Tissue tropism related to vector competence of *Frankliniella occidentalis* for tomato spotted wilt virus. *J. Gen. Virol*. **80**, 507-515.

Nagata T and de Ávila AC. 2000. Transmission of chrysanthemum stem necrosis virus, a recently discovered tospovirus, by two thrips species. *J. Phytopathol*. **148**, 123-125.

Paliwal YC. 1974. Some properties and thrips transmission of tomato spotted wilt virus in Canada. *Can. J. Bot*. **52**, 1177-1182.

Paliwal YC. 1976. Some characteristics of the thrips vector relationship of tomato spotted wilt virus in Canada. *Can. J. Bot*. **54**, 402-405.

Pittman HA. 1927. Spotted wilt of tomatoes. *J. Austr. Council Sci. Ind. Res*. **1**, 74-77.

Pourrahim R, Farzadfar Sh, Moini AA and Shahraeen N. 2001. First report of Tomato spotted wilt virus in potatoes in Iran. *Plant Dis*. **85**, 442.

Razvyaskina GM. 1953. The importance of the tobacco thrips in the development of outbreaks of tip chlorosis of Makhorka (In Russian). Doklady Vsesyuz. Akad. Sel'skokhoz. Nauk. Im. V.I. Lenica **18**, 27-31. (Abstr. In *Rev. Appl. Entomol*. A**42**, 146).

Sakimura K. 1961. Field observations on the thrips vector species of the tomato spotted wilt virus in the Sao Paolo area, California. *Plant Dis. Rept*. **45**, 772-776

Sakimura K. 1962. The present status of thrips-borne viruses. Pages 33-40, in: *Biological transmission of disease agents*, K. Maramorosch ed., Academic Press, New York.

Sakimura K. 1963. *Frankliniella fusca*, an additional vector for the tomato spotted wilt virus, with notes on *Thrips tabaci,* another vector. *Phytopathology* 53, 412-415.

Samuel G, Bald JG and Pittman HA. 1930. Investigations on 'spotted wilt' of tomatoes. *Austr. Counc. Sci. Ind. Res. Bull*. **44**, 64 p.

Smith KM. 1931. *Thrips tabaci* as a vector of plant virus disease. *Nature* **127**, 852-853.

Tedeschi R, Ciuffo M, Mason G, Roggero P and Tavella L. 2001. Transmissibility of four tospoviruses by a thelytokous population of *Thrips tabaci* from Liguria, Northwestern Italy. *Phytoparasitica* **29**, 37-45.

Tsakiridis J P and Gooding GV. Jr. 1972. Tomato spotted wilt virus in Greece. *Phytopathol. Mediter*. **11**, 42-47.

Tsuda S and Fujisava I. 2001. Will *Thrips palmi* become a vector of Tomato spotted wilt virus? *Thrips and tospoviruses. Proceedings of the seventh International Symposium on Thysanoptera*, Reggio Calabria.

Ullman DE. 1996. Thrips and Tospoviruses: advances and future directions. *Acta Hort*. **431**, 310-324.

Van de Wetering F, Hulshof J, Posthuma K, Harrewijn P, Goldbach R and Peters D. 1998. Distinct feeding behaviour between sexes of *Frankliniella occidentalis* results in higher scar production and lower tospovirus transmission by females. *Entomol. Exp. Appl*. **88**, 9-15.

Wijkamp I, Alarza N, Goldbach R and Peters D. 1995. Distinct levels of specificity in thrips transmission of Tospoviruses. *Phytopathology* **85**, 1069-1074.

Wijkamp I and Peters D. 1993. Determination of the median latent period of two tospoviruses in *Frankliniella occidentalis,* using a novel leaf disk assay. *Phytopathology* **82**, 986-991.

Wijkamp I, van de Wetering F, Goldbach R and Peters D. 1997. Transmission of tomato spotted wilt virus by *Frankliniella occidentalis; median acquisition and inoculation access period. Ann. Appl. Biol.* **129,** 303-313.

Wilson CR. 1995. Tomato spotted wilt virus-a serious threat to Tasmanian horticulture? *Proc. 1995 Austr. & N.Z. Thrips Workshop*. p 31-32.

Wilson CR. 1998. Incidence of weed reservoirs and vectors of tomato spotted witl tospovirus on southern Tasmanian lettuce farms. *Plant Path*. **47**, 171-176.

Zawirska I. 1976. Untersuchungen über zwei biologische Typen von *Thrips tabaci* Lind. (Thysanoptera, Thripidae) in der VR Polen. *Archives für Phytopathologie und. Pflanzenschutz* **12**, 411-22.

Zawirska I. 1980. Studies on the tobacco thrips (*Thrips tabaci* Lind.) and it role in the transmission of tomato spotted wilt virus (TSWV) on tobacco. Pages 267-278, in: *Proc. XIX Conf. Scient. Inst. Plant Protect*., 1979: Materialy XIX Sesji Naukowej Instytutu Ochrony, Roslin:279.