# Thrips as unique vectors of tospoviruses

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**KEYWORDS**
**Thripidae, *Tomato spotted wilt virus*, tospoviruses, plant virus transmission, thrips larval ontogeny**

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***Tomato spotted wilt virus*** **(TSWV) has a unique position in plant virology. For decennia this virus was considered to be the only member of a taxonomic virus group. Studies on the biological relations between the vector and the virus were clarified to some extent before the 1980s. In the 1980s, a worldwide expansion of the Western flower thrips, *Frankliniella occidentalis*, was experienced, which was accompanied by a large spread of TSWV diseases in a large variety of agricultural crops, including plant species used in the vegetable and ornamental industry. These developments created a large interest in this virus. New molecular techniques enabled to study the replication of the virus in plant and thrips, and resulted in the discovery of new viruses related to TSWV. These studies also elucidated a specific relationship between these viruses and its thrips vectors. This paper summarizes the most evident features of these relations with emphasis on the transmission of this virus.**

## Introduction

The cuticle and the outer walls of the epidermis cells of leaves and stems form an impenetrable barrier for most plant viruses. This protective barrier can be overcome with the help of vectors, that transport the viruses from infected to healthy plants. Insects are the most important vectors, but some viruses are transmitted by mites, fungi or nematodes. Although mediation of vectors is the commonest way of virus transmission, healthy plants can also become infected by physical contact with infected plants. Viruses are then released via small wounds on leaves, roots and stem(s) and may infect healthy plants. These wounds are, for example, created by gently rubbing the leaf surface by wind, trembling of the plants by animals, or by transplanting seedlings or other farmers' activities. Inoculating plants by rubbing a virus suspension over the leaves of healthy plants after being dusted with carborundum powder is a favorite technique in the laboratory.

Although insect-borne viruses are transmitted in the feeding process, specific relations usually exist between the different vectoring insect species and the various virus species. Some plant viruses are acquired in a few seconds and loose their infectivity in a few hours. Others are acquired in feeding periods of hours rendering the vector infective (viruliferous) for the rest of its life. In this contribution the complex and unique relations between tospoviruses and thrips are reviewed and discussed.

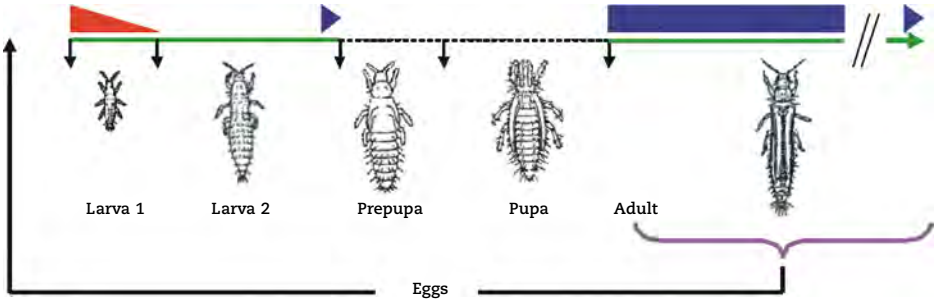
**Abbreviations**

| | |
|---|---|
| TSWV | *Tomato spotted wilt virus* |
| INSV | *Impatience necrotic spot virus* |
| IYSV | *Iris yellow spot virus* |
| Mg1, Mg2, Mg3 | sections of the midgut of thrips |
| EPG | electrical penetration graph |
| L1, L2 | two larval stages of thrips |
| $AAP_{50}$ | median length of the acquisition access period |
| $IAP_{50}$ | median length of the inocculation access period |
| $LP_{50}$ | median length of the latent (incubation) period |

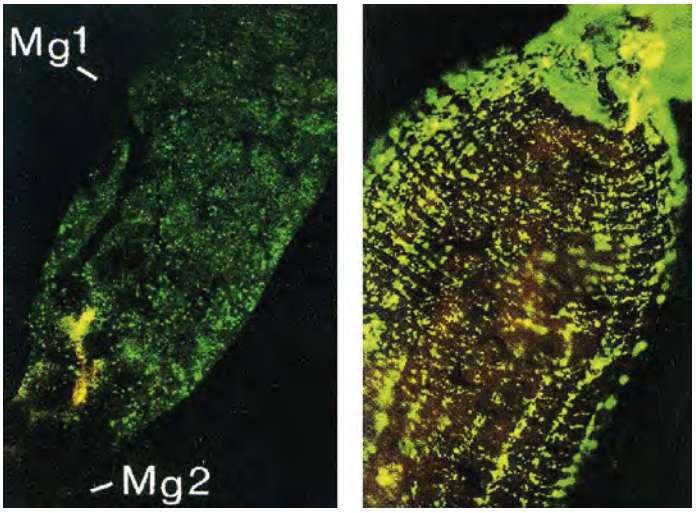
## Tospoviruses

Tomato spotted wilt, a disease caused in tomato by a virus, was for the first time described in Australia in 1919. Twelve years later, Onion thrips, *Thrips tabaci* Lindeman (Thripidae), was discovered as a vector of this virus (Pittman 1927), designated *Tomato spotted wilt virus* (TSWV). This virus, which can be found on all continents, was recorded in The Netherlands in the 1930s. The first studies were mainly focussing on the detection of plant species susceptible to this virus and the identification of thrips species (Best 1968). Until the end of the 1980s, TSWV was considered to be a virus which did not belong to any virus group. At present, almost twenty different species have been distinguished in a newly established group, forming the genus *Tospovirus*, a name derived from Tomato spotted wilt virus. These viruses belong to the family Bunyaviridae, named after Bunyamwera, a village in Uganda (Smithburn *et al.* 1946). This family consists of five genera of which only members of the *Tospovirus* genus infect plants. The tospoviruses are exclusively transmitted by a limited number of thrips species (Thripidae); most of them belonging to the genera *Thrips* and *Frankliniella*.

Of the *Tospovirus* species described thus far only three can be found in The Netherlands. TSWV and *Impatience necrotic spot virus* (INSV) are occasionally encountered in plants of horticultural interest. Both viruses are transmitted by Western flower thrips, *Frankliniella occidentalis* (Pergande). *Thrips tabaci*, which has a great reputation as vector of TSWV, does not play an evident role in the spread of this virus in The Netherlands, but is the main or sole vector of this virus in the tobacco industry on the Balkan and in Greece. *Iris yellow spot virus* (IYSV), transmitted by *T. tabaci*, was discovered in The Netherlands in 1992 in an iris (*Iris hollandica*) crop as a new *Tospovirus* species (Córtes *et al.* 1998) and is found thereafter, or emerged, worldwide in onion crops. In The Netherlands, this virus was occasionally found on some ornamentals and on some onion and leek plants. Recently, evidence is surfacing that the Dutch onion crops are also infected to a great extent with this virus. However, the damage




**1.** The life cycle of thrips illustrating the ingestion of tospovirus from infected plants and replication of the virus in thrips stages (green lines); the acquisition (red triangle) by ingestion of virus in the first larval stage results in transmission by second larval instars and adults (blue triangles and rectangles) the metabolic pupal phase of the thrips (dotted line), and the oviposition period (purple brace). Illustration: Dick Peters.
**1.** De rol van de verschillende tripsenstadia in de overdracht van een tospovirus. De stadia onder de groene lijn nemen het virus op. De opname (verwerving) van het virus door het eerste stadium (rode driehoek) resulteert uiteindelijk in virusoverdracht door laat-tweede-stadium larven en volwassen dieren (blauwe driehoek en balk). De voorpop en pop (stippellijn) nemen geen voedsel op. De paarse accolade duidt op de ovipositieperiode.




**2.** Laser scanning microscope images of *Tomato spotted wilt virus* infected digestive systems of *Frankliniella occidentalis* using FITC-labelled nucleocapsid protein antibodies in the midgut 1 region of a. transmitting adult. The infected muscle cells and their orientation have become clearly visible after sloughing off the mid-gut epithelium during the pupation. Left: midgut region 1 (Mg1), of an infected second-stage larva. Mg2 shows the non-infected anterior part of the midgut region. Right: midgut region 1 of an infected adult. (Nagata & Peters 2004)
**2.** Laser scanning microscopische beeld van een met tomatenbronsvlekkenvirus geïnfecteerde middendarm van een volwassen virusoverbrengende *Frankliniella occidentalis* trips, na kleuring met antilichamen, gelabeld met fluoresceine, tegen het nucleocapside eiwit van het virus De geïnfecteerde spiercellen en hun oriëntatie zijn na de vervelling duidelijk zichtbaar geworden in het eeste gedeelte. Links: eerste deel van de middendarm, Mg1, van een geïnfecteerde tweede-stadium larve. Mg2 laat het voorste deel van een niet-geïnfecteerde middendarm zien. Rechts: eerste deel van de middendarm van een geïnfecteerde adult na de vervelling.

is limited as the virus seems to occur only in small spots around the site where the thrips has actually introduced the virus in the plant, or even infections can be detected in plants with only feeding damage. In contrast to the restricted damage in consumption onion crops, the infection is more serious in seed onions as the flower bearing stem will bend prior to harvesting, by which the seeds are lost.

## Thrips as vector of tospoviruses

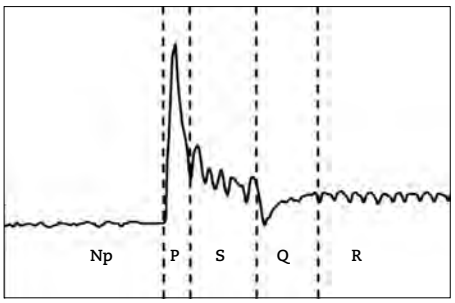
Since the various stages of thrips play a different role in the transmission of tospoviruses, their life cycle will be described briefly (figure 1). The life cycle from egg to adult encompasses two larval, L1 and L2, and two pupal (prepupae and pupae) stages. The larvae and adults are the feeding stages. At 25°C, the first larval instar hatches from the egg after approximately 5 days after oviposition. This instar lasts 30-36 hours and is followed by the second larval instar which becomes prepupa after about 3 days. The prepupa becomes a pupa within 2 days. The pupal instars can be found in litter on the soil surface and upper soil layers. The pupae develop into adults after approximately 3 days. The females, which can live 20 days or longer, produce four to five eggs a day.

Tospoviruses are propagatively transmitted, that is, they have to be replicated in the thrips before they can be transmitted. Both larval stages and the adults will replicate the virus in their mid-gut after ingesting virus from infected plants (figure 2). The virus is transmitted by adults and by the second instar in their last hours just before they prepupate. Surprisingly, these vectors acquired the virus when they were in their first larval stage, and probably very few specimens of the second instars may also become vector when they ingest virus just after becoming second instar. The ability of virus transmission of the adults and also of the old second instars decreases rapidly with the age at which the first instars ingested a virus dose (Van den Wetering *et al.* 1996, figure 1). Most, if not all, second instars and all adults will never become transmitters in spite of a successful ingestion and replication of the virus.

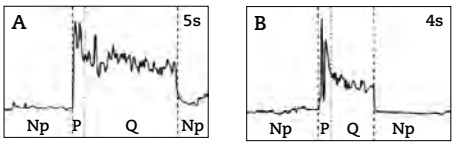
The vectoring second instars will re-introduce the virus into the infected plant, on which they emerged, and will only occasionally inoculate another plant when these larvae are able to migrate to a healthy host via leaf contact or via the ground. Thus, the spread of the tospoviruses is mainly done by the adults, who have a higher mobility. Although males seem to be more effective transmitters than females on a daily base, the female takes the greatest share in the spread because they live considerably longer than the males.

## Replication of tospoviruses in thrips tissues

The first replication of virus after ingestion will take place in the alimentary canal. This canal consists of a foregut, midgut and hindgut. Two loops in the midgut divide it into three regions, designated Mg1, Mg2 and Mg3. Two types of muscle tissue cells surround the midgut. One type lines the midgut in a parallel fashion and the other in a circular fashion. The first virus replication is observed in Mg1, and the infection spreads from Mg1 to Mg2 and then to Mg3. Whether ingested virus infects the Mg1 section, then Mg2 after replication in Mg1, and subsequently Mg3, or the ingested virus infects successively Mg1, Mg2 and Mg3, is an open question. The former suggestion is the most likely, because clear intervals occur between the infection of Mg1, Mg2 and Mg3. The question whether the foregut gets infected is still a matter of controversial results. No clear signs of infection by TSWV have been observed in this organ. Recently, accumulation of the non-structural protein (NSs) encoded on the S RNA




**3.** A characteristic EPG (Electrical Penetration Graph) waveform of the Western flower thrips with all possible waveforms on a sweet pepper leaf. Np = non-penetration, P = penetration with the mandible, S = repetitive head nodding to protrude and insert the mandible downward and upward, Q = insertion of the maxillary stylets, and R = ingestion of cell contents. The y-axis is the amplitude and the x-axis represents an interval of exactly 5 seconds. (Kindt *et al.* 2003)
**3.** Een karakteristiek EPG (Electrisch penetratie diagram) beeld van een golfvorm van *Frankliniella occidentalis* met de meest voorkomende signalen op een paprikablad. Np = geen penetratie, P = penetratie vam de mandible, S = op- en neerwaardse beweging van de mandible veroorzaakt door het knikken van de kop, Q = inbrengen van de maxillaire stiletten in een cel, en R = opnemen van celinhoud. De y-as geeft de amplitude weer en de x-as is precies 5 seconden. De onderbroken lijnen geven de veronderstelde grenzen tussen de fasen aan.




**4.** Two single probes (A and B) produced by infected thrips (*Frankliniella occidentalis*) that resulted in a successful transmission of *Tomato spotted wilt virus* with the waveforms P and Q. The waveforms S and R are missing. s = seconds, for other abbreviations see figure 3. (Kindt 2004)
**4.** Twee penetraties (A en B) door een Californische trips, die resulteerden in een geslaagde overdracht van het tomatenbrons-vlekkenvirus. In deze golfvormen, die respectievelijk 5 en 4 s duurden, komen alleen de P- en de Q-fase voor (de S- en de R-fase ontbreken). s = seconden, zie figuur 3 voor de andere afkortingen.

segment has been found in the foregut of *T. tabaci* infected with IYSV. This protein is an indicator for virus replication, as it does not form a constitutional protein of the virus particle. During pupation the midgut epithelium is sloughed off, by which the infection in the muscle cells in the parallel and circular orientation becomes convincingly visible in the adults (figure 2).

Insect-borne mammal-infecting viruses, as well as most plant-infecting viruses, will be translocated from the alimentary canal to the hemocoel and subsequently to the salivary glands, where the virus, after replication, will be added to the saliva. In the feeding process the virus is then introduced with saliva into a new host. Contrary to expectation, no evidence has been found for the presence of tospovirus particles in the hemocoel to date. Infections in blood cells have not been detected and electron microscopic studies did not reveal any budding of virus particles from the midgut cells into the hemocoel. Even injection of TSWV in the hemocoel did not result in virus transmission. Absence of virus particles in the hemocoel might demonstrate that dissemination from the midgut into the hemocoel is blocked; hence it is likely that a midgut escape barrier exists.

How then do the salivary glands become infected? The answer has probably to be found in a study on the ontogeny of larvae made by Moritz *et al.* (2004). In the first instars the cibarial muscles in the head capsule are in a process of strong development and consequentially displace the supra-oesophageal ganglion into the thorax. This displacement forces the salivary glands further into the thorax, where they will make contact with the Mg1 region of the midgut. Now the virus may be translocated from the visceral cells into the salivary glands. In the course of further metamorphotic development, the wing muscles develop such that the brain is retracted back in the thorax in the direction of the head capsule. Hereby, the salivary glands loose their contact with the midgut. Probably, infection of the salivary glands will no longer occur once this contact is broken. The rapid decrease of the ability of the first-phase larvae to become virus vectors can be explained by a retraction of the salivary glands before sufficient levels of virus have been replicated in the midgut.

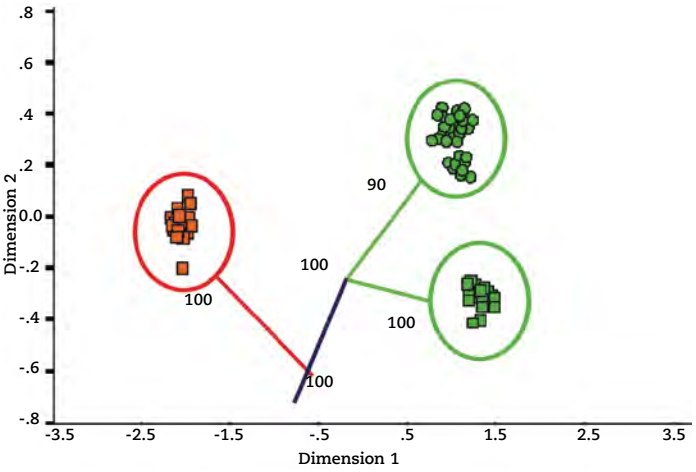
The infection is not always evenly distributed over the salivary glands. Occasionally, signals for infection have been observed in one gland, while no virus could be detected in the other (Nagata *et al.* 1999). This observation may indicate that contact of the glands with the midgut is not necessarily a symmetrical process and that this contact is physiologically not an essential requirement in the development of a thrips.

## Kinetics of tospovirus transmission

Transmission of plant viruses by insects can be defined by three parameters: (1) the acquisition access period (AAP), that is the period in which the dose of virus can be acquired that converts an insect into a transmitter; (2) the inoculation access period (IAP), that is the period that a viruliferous insect needs to infect a host; and (3) the latent (incubation) period (LP), that is the period between the start of the acquisition and the first successful transmission of the virus. To avoid discussions on how these periods have to be measured, their median lengths are commonly used, and expressed as $AAP_{50}$, $IAP_{50}$ and $LP_{50}$ (Sylvester 1965).

The values for $AAP_{50}$ and $IAP_{50}$ for TSWV vary between one to two hours (Wijkamp *et al.* 1996). These periods are short compared to the $AAP_{50}$'s and $IAP_{50}$'s of one or more days usually required for acquisition and transmission of other circulativily or propagativily transmitted plant viruses (Van den Broek & Gill 1980). The difference has to be explained by the source tissue (parenchyma cells) from which virus has to be acquired and the target tissue (parenchyma cells) that will be inoculated. The propagatively transmitted plant viruses are usually acquired from the sieve tubes of the phloem and have to be inoculated to the phloem parenchyma and companion cells. The sieve tube elements will not support the replication of virus as they basically lack the cellular instruments to replicate virus.

The suitability of the host as food source, the position of the cells on the leaf, and probably also the quality of the cells from which food will be ingested by the thrips are determined by probes with their sucking mouth organ. This organ consists of one mandible and a pair of maxillary stylets. The feeding behaviour can be analysed using an electrical penetration graph (EPG) monitoring system (Tjallingii 2006) when an electric current is established between the plant and the penetrating stylets. Several waveforms, elucidating various phases with different amplitudes in the process of penetration, probing and ingesting, can be distinguished in diagrams (figure 3). The leaf tissue is penetrated and punctured by the mandible during the P-phase. In the next phase, the S-phase, the thrips move the mandible up and down by nodding its head, meanwhile piercing several cells. The cell contents are then probed in the Q-phase, probably mixed with some saliva, and ingested by the maxillary stylets in the R-phase. The virus is ingested along with the contents of damaged cells (Kindt *et al.* 2003), which are left behind more or less empty. Clusters of these empty cells are filled with air and are recognisable by the characteristic silvery scars on the leaves. These scars are often used as a quantitative measure to estimate preference for a host.




**5.** Results of genetic analysis of the mitochondrial cytochrome oxidase I (COI) gene, indicating three distinct lineages or sub(species) in *Thrips tabaci* populations consistent with a tobacco group and two groups preferring other hosts. Red squares = Greek arrhenotokous tobacco populations, green squares = Greek arrhenotokous leek populations, green dots = Greek thelytokous leek populations. Diagram supplied by Dr. P.C. Brunner.
**5.** Resultaten van een genetische analyse van het mitochondriale cytochroom oxidase I (COI) gen, dat weergeeft dat er drie lijnen of binnen *Thrips tabaci* populaties te onderscheiden zijn, waarvan er een een voorkeur heeft voor tabak en twee voor andere plantensoorten. Rode vierkanten = Griekse arrhenotoke tabakspopulaties, groene vierkanten = Griekse arrhenotoke preipopulaties, groene rondjes = Griekse thelytoke preipopulaties.

These damaged and emptied cells do not form a suitable substrate for virus replication. EPG waveforms demonstrated that the virus was successfully transmitted in short penetrations missing the S- and R-phase (figure 4, Kindt 2004). Inoculation of plants during these short punctures seems contradictory to the $IAP_{50}$'s of 1-2 hour required to infect half of the offered plants in tests. This discrepancy might be explained by a low number of penetrations leaving the cells viable, or by the absence of virus in the samples of saliva produced in the exploring penetrations and punctures.

The $LP_{50}$ of TSWV and also that of INSV is approximately 4 days (Wijkamp *et al.* 1993). The $LP_{50}$ value for tospoviruses in thrips compares well with the $LP_{50}$'s for other propagatively transmitted plant viruses before they are transmitted. This period reflects the period necessary for the virus to infect the midgut epithelial cells, to replicate in these cells, to infect the visceral muscle cells, and to be translocated to salivary glands in which new rounds of replication will occur. The virus will then finally be added to the saliva and inoculated to the plant.

## Specificity of the ability to transmit

Among the twelve thrips species that transmit one or more tospoviruses (Nagata & Peters 2001), most studies on the ability to transmit tospovirus are mainly restricted to TSWV and its main vectors *F. occidentalis* and *T. tabaci*. The ability to transmit TSWV varies considerably among different *F. occidentalis* populations. Variation can also be found when one population is allowed to transmit different TSWV isolates. Interestingly, the efficiency of *T. tabaci* vectoring TSWV is shown to be strongly related to their preferred host plant (Zawirska 1976). Zawirska recognised two biotypes in this species: the 'tabaci type', associated with the spread of TSWV in tobacco and is an excellent transmitter, and the 'communis type', infesting a variety of host plants, but has no preference for tobacco and is a poor transmitter.
Zawirska claimed also that the second-phase larvae (but not the other instars) of the two types could be distinguished morphologically. Three groups of *T. tabaci* populations differing in the competence to transmit TSWV were distinguished by Wijkamp *et al.* (1995) and Chatzivassiliou *et al.* (2002): efficient transmitters, poor transmitters and non-transmitters. The first two groups consisted of populations with males and females (arrhenotokous populations) and the last group of only females (thelotokous populations). Existence of three groups was confirmed by analysing the nucleotide sequence of the mitochondrial cytochrome oxidase I (COI) gene; hence the genetic findings are congruent with the difference in morphology, host range preference and vector competence (figure 5, Brunner *et al.* 2004).

TSWV causes tremendous damage in the tobacco industry at the Balkan, in Greece and in the southern states of the USA. However, *T. tabaci* is the only or the main vector on tobacco in Europe, while this species does not seem to play a role in the spread of TSWV in the USA. *Thrips tabaci* populations in the USA probably prefer other hosts than tobacco and males are rarely found in the USA populations. *Frankliniella fusca* (Hinds) is considered to be the main vector of TSWV in tobacco crops in the USA. *Frankliniella occidentalis*, an efficient transmitter of TSWV, is rarely encountered on tobacco and will consequently play no role in the spread of TSWV on tobacco.

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## Samenvatting

**Tripsen als unieke vectoren van tospovirussen**

Een tiental tripssoorten brengt tospovirussen van geïnfecteerde naar gezonde planten over, waaronder het zeer schadelijke tomatenbrons-vlekkenvirus (TSWV). De relatie tussen de tripsen als virusoverbrenger en deze virussen is uniek. Het virus wordt door tripslarven en -adulten uit geïnfecteerde planten opgenomen en komt in deze stadia tot vermeerdering. Het virus kan echter alleen overgebracht worden door tweede-stadium larven vlak voor hun verpopping en door adulten, die afstammen van larven die het virus tijdens het eerste stadium opgenomen hebben. De verspreiding van de tospovirussen in het veld komt daardoor nagenoeg geheel op het conto van de adulten, omdat larven zich amper verplaatsen. Het vermogen van de eerste larvale stadia om virusoverbrengende afstammelingen te produceren daalt heel snel en is aan het einde van dit stadium nagenoeg geheel verloren gegaan. Het vermogen van eerste-stadium larven kan geweten worden aan een tijdelijk contact van de speekselklieren met het voorste (eerste) gedeelte van de middendarm waar het virus zich vermeerdert; tijdens dit contact gaat het virus waarschijnlijk over. Het snelle dalen van het vermogen van dit stadium om virus over te gaan brengen moet verklaard worden door de trage opbouw van de virusconcentratie in de middendarm. In tegenstelling tot andere plantenvirussen, die in hun vectoren moeten vermeerderen om overgedragen te kunnen worden, kunnen tripsen in korte voedingsperioden de tospovirussen opnemen en afgeven. Deze andere plantenvirussen worden door hun vectoren uit het floëem opgenomen en worden afgegeven aan cellen rond het floëem, terwijl tripsen vlak onder de epidermis het virus kunnen opnemen en afgeven aan de parenchymcellen.

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