Tospoviruses and Thrips-is There an Evolutionary Relationship?

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ABSTRACT

Evidence from evolutionary relationships among Thysanoptera suggest that the associations between a few unrelated species of these insects with the Bunyaviridae. Tospoviruses does not have a long evolutionary history. Since tospoviruses are fully dependent for their existence on the few vector thrips species, the implication is that tospoviruses are a recent evolutionary phenomenon. The suggestion is made that variation in vector ability might be a more useful avenue for research than plant breeding to control these essentially vertebrate viruses.

Keywords: tospoviruses, *Frankliniella*, *Thrips*, vector ability, inheritance

INTRODUCTION

The infection of a plant with a Tospovirus leads to necrosis of the plant tissues, distortion of fruits, serious yield reduction in some crops, and sometimes death of entire plants. The 800 or more species of plants that have been recorded as being infected by tospoviruses include many crops, such as tomatoes, capsicums, watermelons, lettuce, and groundnuts, as well as flower crops such as chrysanthemums, irises, and impatiens. Tosposviruses occur in every major agricultural area around the world, and they rank among the ten most detrimental plant viruses worldwide. That is, for anyone involved in horticultural crop production, tospoviruses are important.

However, tospoviruses cannot exist in nature on their own. They are neither seed transmitted nor root transmitted, and thus they cannot move from plant to plant, whether across a single field, or within a field from one season to the next. Under field conditions tospoviruses are transmitted from one plant to another only by particular species of thrips. Moreover, this association is highly specific, in that for an adult to be able to transmit a tospovirus, it must have obtained that virus during its development at the second instar larval stage [(4)]. Adult thrips cannot acquire and then transmit a

tospovirus. As a result of this association, Tospoviruses do not have an independent existence-they are fully dependent on just a few particular species of thrips for their continued existence in nature. In the laboratory, plant pathologists transmit tospoviruses by rubbing sap from an infected leaf into an uninfected leaf, but this does not happen in nature. The other essential fact to be considered is that Tospoviruses are members of the Bunyaviridae-a family of viruses that are associated with animals and are not plant viruses.

Thus we have a remarkable situation. How did one or more virus in an animal come to be associated with, and dependent on, a few species of insects that feed on plants, and how have these animal viruses come to cause serious damage to plant cells. Accepting that nothing makes sense in biology except in the light of evolution, the essential question thus becomes-what was the origin of the associations between thrips and tospoviruses? Did one plant-feeding thrips acquire from some unknown animal a particular bunyavirid species, and was this then modified within the thrips and inserted into a plant? Such a route seems unlikely, but the alternative is even less likely. This would involve an animal infected with a bunyavirid browsing on and infecting a plant with that virus. The bunyavirid would then need to have been modified within the plant, and subsequently ingested by a thrips that then transmitted the disease to another plant. Considering the second of these two scenarios, there is a good probability that many animals infested with bunyavirids will browse on plants, but the rest of this transformation route seems too tortuous for serious consideration. In contrast, some of the thrips species that are tospovirus vectors are predatory on other arthropods, and adults of several species of thrips probe the skin of vertebrates, including man. Moreover, the typical thigmotactic behaviour of adult thrips commonly results in these insects being found in dark places, including the nests of birds and mammals. A potential pathway thus exists for a bunyavirid from a vertebrate directly into a thrips-but this is still a bunyavirid, not a tospovirus.

Leaving such conjectures concerning the origin of tospoviruses for consideration by future molecular biologists, the next important question concerning the thrips association with tospoviruses becomes – did the association evolve once only, or did it evolve several times? That is, did the genus *Tospovirus* evolve from Bunyaviridae just once and subsequently diversify into a series of species, progressively acquiring the diverse thrips vectors that are now recognised? Or did the association between thrips and these viruses arise several times, possibly even from different Bunyaviridae, and in

association with different thrips species? This second possibility involves the genus *Tospovirus* being polyphyletic, with several virus species having evolved independently in association with different thrips species, possibly even on different continents.

Tospovirus specialists will consider the molecular evidence relevant to such questions, but the present discussion is concerned with the evidence from thrips. First, only a few thrips species are tospovirus vectors, and these species are not all closely related. Thus only five of the 160 species of *Frankliniella*, and only 3 of the 280 species of *Thrips* genus, are known to be tospovirus vectors (Table 1). These two large genera are not sister genera, and are not considered to be particularly closely related within the subfamily Thripinae of the Thripidae [(1)]. The genus *Franklliniella* is essentially New World, whereas *Thrips* is primarily Old World with some species in North America but no species native to South America. The two genera thus possibly evolved around the time that the Atlantic Ocean was developing between these two land masses. Was the association between thrips and tospoviruses in existence at that time, such that the ancestors of *Frankliniella* and *Thrips* were already vectors? If so, then either there must be many species in these two genera that are unrecognised vectors of unrecognised tospoviruses, or else most species in these genera have lost the ability to be vectors. There is no evidence to support either of these scenarios, and neither of them seems likely. Moreover, if this discussion is extended to consider the three unrelated vector thrips in the genera *Ceratothripoides*, *Dictyothrips*, and *Scirtothrips*, the situation becomes even more complex. This would then involve an assumption that the ancestor of the family Thripidae was a tospovirus vector, and that more than one thousand species in this family have lost the vector ability.

Table 1. Generic relationships of tospovirus vector species

Genera of Thripinae	Species described in genus	Species recorded as vectors
Ceratothripoides	5	1
Dictyothrips	1	1
Frankliniella	230	5
Scirtothrips	100	1
Thrips	280	3

Inoue and Sakurai [(2)] examined the phylogenetic relationships between a series of tospovirus species and a series of thrips species. They concluded that there was

considerable congruence between the phylogeny of thrips and that of tospoviruses, and they were able to recognise three different clades among tospoviruses (Fig. 1). One of these was associated with species of genus *Thrips* as vectors, and these viruses are found primarily in plants of the Cucurbitaceae and Liliaceae. A second clade of tospoviruses was associated with species of *Frankliniella* as vectors, and these viruses are found mainly in Solanaceae and Asteraceae. A third clade was associated with *Scirtothrips* as vector, and these viruses are found on Fabaceae. This study suggests the possibility that the associations between groups of tospoviruses and different genera of thrips vectors have originated independently. Unfortunately, this type of investigation is complicated by the fact that several pest thrips, and many crop plants and their viruses, have been disseminated widely around the world by human trade. *Thrips tabaci* probably evolved in the eastern Mediterranean in association with the genus *Allium*. But the Romans took onions and garlic across Europe to Britain, and Alexander's army presumably did the same across Asia to India. Later, the Spanish took onions and their thrips to South America, the Portuguese to India, the Dutch to Indonesia, and the British to Australia. The areas of origin of the tospoviruses are thus likely to be more difficult to predict than the areas of origin of the known vector species. This translocation of vectors and of viruses between continents has presumably facilitated the ability of a widespread species such as *Thrips tabaci* to vector relatively unrelated tospovirus species.

Table 2. Geographical areas of origin of tospovirus vector species

Vector species	American continent	Asia	Eurasia
Frankliniella bispinosa	+		
Frankliniella fusca	+		
Frankliniella occidentalis	+		
Frankliniella schultzei	+		
Frankliniella zucchini	+		
Ceratothripoides claratris		+	
Scirtothrips dorsalis		+	
Thrips palmi		+	
Thrips setosus		+	
Dictyothrips betae			+
Frankliniella intonsa			+
Thrips tabaci			+

Five of the vector species originated unequivocally on the American continent, whereas four of the vectors are equally clearly Asian in origin, and three vector species seem to be of European or Eurasian origin (Table 2). However, these three areas of origin of the vector species need not reflect the areas where a particular thrips species became associated with one or more tospoviruses. Moreover, since some vector species transmit more than one tospovirus, it is possible that for such species the ability to transmit one virus might have facilitated the acquisition, and ability to transmit, other tospoviruses. Two parts of the world are noticeably absent from this discussion, Australia and tropical Africa. Studies on the insects and viruses of Africa are not extensive, but the thrips fauna of Australia has been intensively studied in recent years, and there is no evidence that any Australian native thrips species is a tospovirus vector. Moreover, despite many plant species that have been introduced to Australia suffering from tospovirus infections, where the viruses are vectored only by non-native thrips species, there is no evidence that any native Australian plant is infected by a tospovirus when growing in its natural habitat.

Because tospoviruses affect plants, much of the research on these organisms is carried out by plant pathologists and plant breeders. As a result the major research target is on producing tospovirus resistance in plants. In contrast, much of the success in controlling human diseases has been, not through breeding disease resistant humans, but though reducing the rates of disease transmission. In this way, the population of a pathogen is reduced below a critical level for continued transmission. Crop entomologists emulate this strategy by insecticide spraying, with the hope of reducing thrips populations and hence virus transmission. However, a more effective long-term solution might be to exploit the known variation in vector ability among populations of thrips species [(5)]. Such variation investigated by Jacobson & Kennedy [(3)] suggests that thrips might carry genes that are involved in limiting the efficiency with which individuals of some populations act as vectors. Breeding from thrips individuals with reduced vector capacity, and releasing such populations under controlled conditions, might well drive down the rate of transmission and thus hold the possibility of eliminating locally a targeted tospovirus. However, biological approaches such as this, involving critical studies on the behaviour and genetics of the insect vectors, are at present less likely to attract research funding than molecular studies on viruses.

LITERATURE CITED

1. Buckman, R. S., Mound, L. A., and Whiting, M. F. 2013. Phylogeny of thrips (Insecta: Thysanoptera) based on five molecular loci. Systematic Entomology 38:123-133.

2. Inoue, T., and Sakurai, T. 2007. The phylogeny of thrips (Thysanoptera: Thripidae) based on partial sequences of citochrome oxidase I, 28S ribosomal DNA and elongation factor-1å and the association with vector competence of tospoviruses. Applied Entomology and Zoology 42(1):71-81.
3. Jacobson, A. L., and Kennedy, G. G. 2013. Specific insect-virus interactions are responsible for variation in competency of different *Thrips tabaci* isolines to transmit different *Tomato Spotted Wilt Virus* isolates. PLOS One 8:1-7.
4. Moritz, G., Kumm, S., and Mound, L. A. 2004. Tospovirus transmission depends on thrips ontogeny. Virus Research 100:143-149.
5. Okuda, S., Okuda, M., Matsuura, S., Okazaki, S., and Iwai, H. 2013. Competence of *Frankliniella occidentalis* and *Frankliniella intonsa* strains as vectors for Chrysanthemum stem necrosis virus. European Journal of Plant Pathology 136:355-362.

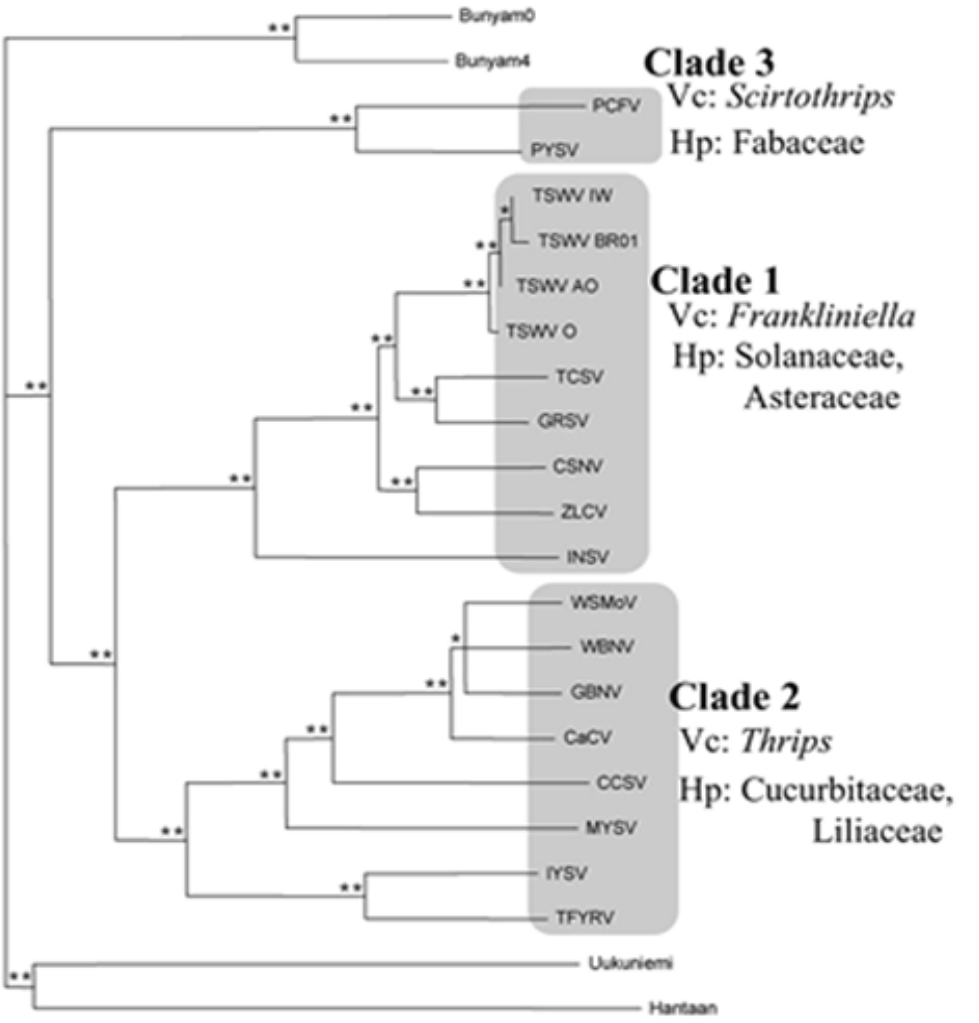


Fig. 1. Phylogenetic relationships between tospoviruses and thrips - after Inoue and Sakurai [(2)].