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Major review

Plant viruses transmitted by thrips

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Abstract

All thrips (order Thysanoptera) that are known to be vectors of plant viruses are identified and described. Thrips transmit plant viruses in the *Tospovirus*, *Ilarvirus*, *Carmovirus*, *Sobemovirus* and *Machlomovirus* genera. Tospoviruses are the cause of a number of significant emerging diseases, such as capsicum chlorosis and scape blight of onion. They infect thrips as well as plant hosts and the relationship between pathogen and vector is intimate. Once infected at the larval stage, adult thrips usually transmit tospovirsuses for life. Transmission to plant hosts occurs when thrips feed. Information on the distribution and hosts of all recognised thrips vectors is provided. Fourteen tospovirus species are described with information provided on other tospoviruses that have not yet been designated as species. The history of the research that has led to present knowledge is reviewed in chronological order for each tospovirus. The possible origin of tospoviruses is discussed. Information is presented on viruses, which are thrips-transmitted by mechanical processes, in other genera. Pathways of spread of thrips vectors in relation to the threat of tospoviruses to European agriculture are discussed.

Introduction

Thrips are insects belonging to the order Thysanoptera (Mound, 2005). Some thrips can affect plants by direct feeding, which may leave visible signs of damage, such as leaf silvering (Palmer et al., 1989). A few of these thrips transmit plant viruses. Thrips-transmitted viruses can cause significant diseases of many crop plants and their impact worldwide is immense (Mumford et al., 1996; Ullman et al., 1997). This review provides up-to-date information on the hosts and distribution of individual thrips vectors, and accumulated knowledge on their transmitted viruses, especially tospoviruses, which are emerging as the cause of major new epidemics. The possible evolution of tospoviruses and plant quarantine concerns are discussed. Details of the intimate relationship between thrips and tospovirus and information on the monitoring and control of thrips is beyond the scope of this paper, which complements an earlier review of whitefly-transmitted viruses (Jones, 2003).

Thrips

Thrips are small to minute insects with an adult body size ranging in most species from about 0.5 to 5 mm and adults usually have four slender wings. About 5000 species of thrips have been recognised though this may only represent a little over 60% of the world total. Plant-feeding thrips are believed to have evolved from fungus-feeding, leaf litter-living ancestors. Nine families are currently distinguished with 95% of the known species being in the Thripidae and Phlaeothripidae. The relatively few thrips species that are important plant pests are mainly in the Thripidae (Lewis, 1997). The species that are known vectors of viruses are all members of the Thripidae subfamily

Thripinae. This subfamily has 1400 species in 230 genera (Mound, 1996, 1997).

Species in the *Thrips*, *Frankliniella, Scirtothrips, Microcephalothrips*, and *Ceratothripoides* genera have been shown to transmit plant viruses. *Thrips* is the largest genus in the Thripidae with 275 species currently listed worldwide (Mound and Kibby, 1998; Mound, 2001a) with *Frankliniella* being the second largest genus with about 180 species (Nakahara, 1997). Mound (2001b) believes that the *Thrips* genus-group, which includes *Microcephalothrips* as well as 13 other genera, is a lineage that apparently evolved in the old world while the *Frankliniella* genus-group, which includes nine genera, appears to be much older and may have originated in the ancient supercontinent of Gondwanaland. There are about 100 species in the *Scirtothrips* genus (Hoddle and Mound, 2003). *Microcephalothrips abdominalis* is the only species in the genus *Microcephalothrips* (Mound and Kibby, 1998). *Ceratothripoides* is based on three Old World species, but several neotropical species, which may not be closely related, are also listed for the genus (Mound and Kibby, 1998).

The few thrips species that transmit tospoviruses, which are less than 0.2% of the total, are not closely related to each other (Mound, 2001a, 2005). Only six species of *Frankliniella*, three species of *Thrips* and one species each of *Scirtothrips* and *Ceratothripoides* are known to be vectors.

Thrips that are vectors are among those that lay eggs, which hatch to produce two larval instars that feed. Larval instars are followed by two relatively inactive pupal instars that probably do not feed. In warm conditions, the life cycle usually takes about 20 days from egg to adult. Adults are readily dispersed. Larvae and adults use a similar 'punch and suck' feeding technique. The single mandible punches a hole in the plant surface through which the paired maxillary stylets are then inserted.

Tospoviruses are acquired during the first and early second larval instars when there is a temporary association between mid-gut, visceral muscles and salivary glands (Moritz et al., 2004). They are reintroduced into a plant with the saliva of a feeding adult (Palmer et al., 1989). Between acquisition and inoculation, there is a latent period before the virus can be transmitted during which time the virus multiplies (Sakimura, 1963). Recent research has indicated that the immune system of the thrips is activated after infection (Medeiros et al., 2004).

An adult may remain viruliferous for life, which may be 20–40 days. However, non-viruliferous adult thrips seem not to acquire the virus when feeding on infected plants (de Assis Filho et al., 2004). There is some evidence that thrips may preferentially feed and reproduce on tospovirus-infected plants (Maris et al., 2004). Ullman et al. (1992) and Wijkamp (1995) have discussed the intimate relationship between thrips and *Tomato spotted wilt virus* (TSWV).

The transmission of ilarviruses by thrips is a different mechanism. It involves the physical movement of virus-carrying pollen from one plant to another and its introduction into the plant through feeding wounds. Thrips in the genera *Frankliniella*, *Microcephalothrips* and *Thrips* have been implicated in the spread of ilarviruses though more may be discovered.

There has been one report of transmission of a carmovirus by thrips utilising the same mechanism as for ilarviruses. One sobemovirus can also be transferred with pollen by thrips and plants infected during feeding. This virus can also be carried from one plant to another on the mouthparts of thrips. One machlomovirus is also thought to be thrips-transmitted, but the actual mechanism is not clear.

Thrips vectors of tospovirus species

Ceratothripoides claratris *Schumsher*

Mound and Kibby (1998) report that *C. claratris* is from India and has been recorded on cucurbits, such as watermelon (*Citrullus lanatus*). However, it has also been identified as the predominant thrips species and a serious pest on tomato (*Lycopersicon esculentum*) in central Thailand. It causes damage by infesting leaves, which results in the plants becoming desiccated. Quarantine agencies have been warned of the risks from invasion by *C. claratris* (Murai et al., 2000).

Work on the influence of temperature on the life cycle of *C. claratis* on tomato has been undertaken. This indicates that the optimum temperature for egg to adult development occurs at 32–33 °C. Fecundity was highest at 30 °C. Female longevity was highest at 25 °C and male longevity at 30 °C (Premachandra et al., 2004).

C. claratris has recently been reported as a vector of *Capsicum chlorosis virus* (CaCV) in Thailand (Premachandra et al., 2005).

Frankliniella bispinosa *Morgan*

This thrips species originates in the USA and has also been recorded in the Bahamas, Bermuda (Moritz et al., 2001) and Puerto Rico (Anon., 2002).

Hosts include navel orange (*Citrus sinensis*), strawberry (*Fragaria* x *ananassa*), tobacco (*Nicotiana tabacum*), charlock (*Raphanus raphanistrum*), rose (*Rosa* spp.), rye (*Secale cereale*) and wheat (*Triticum aestivum*) (Anon., 2002). Damage to avocado (*Persea americana*) and citrus blossoms has occurred in Florida (Moritz et al., 2001). The thrips has been intercepted in the UK on asparagus (*Asparagus officinalis*), chrysanthemum (*Chrysanthemum* × *morifolium*) and sweet pepper (*Capsicum annuum*) imported from the USA, but this does not necessarily indicate a host association (D. Collins, CSL, pers. comm.).

F. bispinosa transmits TSWV (Webb et al., 1998).

Frankliniella fusca *Hinds*

The tobacco thrips is native to the eastern USA (Mound, 2001a), but has spread throughout North America. It has been introduced to Martinique, Puerto Rico and the Netherlands. In the Netherlands, it occurs on bulbs of *Hippeastrum* and *Narcissus* (Anon., 2002).

Tobacco (*Nicotinia tabacum*) is an important host of *F. fusca* in eastern North America (Mound and Kibby, 1998). Other primary hosts include tomato, watermelon, sweet pepper, peanut (*Arachis hypogaea*), soybean (*Glycine max*), cotton (*Gossypium* spp.), cowpea (*Vigna unguiculata*) and maize (*Zea mays*). Charlock, crabgrass (*Digitaria sanguinalis*), crownbeard (*Verbesina encelioides*) and wild mustard (*Sinapsis arvensis*) are wild hosts.

Vierbergen (1992) stated that, unlike some other thrips, *F. fusca* had not been reported from interceptions in international trade. However, the species has been found in the UK on *Asparagus* imported from the USA. Again, this does not necessarily imply a host association (D. Collins, CSL, pers. comm.).

F. fusca has long been implicated in the spread of tomato spotted wilt disease (Sakimura, 1963). Although it has been suggested that there was insufficient data to regard it as a vector species (Goldbach and Kuo, 1996), there is now much evidence to suggest it transmits TSWV (Johnston et al., 1995; Groves et al., 2002; de Assis Filho et al., 2004) and *Impatiens necrotic spot virus* (INSV) (Naidu et al., 2001) tospoviruses. It is regarded as an important vector of the former virus in the southern states of the USA with heavy losses suffered in crops, such as tobacco, groundnut and sweet pepper (Mitchell and Smith, 1991; Culbreath et al., 1991; Hobbs et al., 1993; Barbour and Brandenburg, 1994; Johnson et al., 1995).

Frankliniella intonsa *Trybom*

This common, polyphagous, flower-living species is widespread throughout Europe and Asia as far east as Taiwan, where it is a pest of the horticultural industry and responsible for cut chrysanthemum flowers failing quarantine inspection in Japan (Mound, 1996; Mound and Kibby, 1998; Anon., 2002). It normally occurs with other thrips species in flowers and is highly dependent on pollen (Anon., 2002).

Primary hosts of the flower thrips include chrysanthemum, sweet pepper, tomato, peanut, asparagus, soybean, cotton, okra (*Abelmoschus esculentus*), lucerne (*Medicago sativa*), pea (*Pisum sativum*), rice (*Oryza sativa*), common bean (*Phaseolus vulgaris*) and peach (*Prunus persica*). Flowers and fruits/pods are affected. Economic damage has been reported on asparagus, chrysanthemum, okra, tomato and pea. The thrips has also been associated with damage to strawberry and nectarines (*Prunus persica* var. *nectarina*) (Anon., 2002).

F. intonsa transmits *Tomato chlorotic spot virus* (TCSV) and TSWV (Wijkamp et al., 1995).

Frankliniella occidentalis *Pergande*

The western flower thrips is native to the southwestern area of the United States (Mound, 1996). It began to spread out of North America in the 1980s with the ornamental trade and has now been found in temperate countries in all continents. Japan is the only country in Asia

where *F. occidentalis* has been reported. It is very common in Europe (Anon., 1997a), where its introduction and spread has been reviewed (Baker et al., 1993).

F. occidentalis is extremely polyphagous with over 200 plant species from more than 60 families being recorded as hosts. In the USA, it is found outdoors feeding on flowers of many different types of plants, such as pea, tomato, sweet pepper, strawberry, rose, peach, nectarine, apricot (*Prunus armeniaca*), plum (*Prunus domestica*), carnation (*Dianthus caryophyllus*), sweet pea (*Lathyrus odoratus*), cucumber (*Cucumis sativus*), and gladioli (*Gladiolus* spp.). Other hosts include cotton, common bean, beet (*Beta vulgaris*), carrot (*Daucus carota*), grapefruit (*Citrus* × *paradisi*), grape (*Vitis vinifera*), onion (*Allium cepa*), and safflower (*Carthamus tictorius*). In Europe, it has been reported only on a range of glasshouse crops, but predominantly chrysanthemum, gerbera (*Gerbera* spp.) and African violet (*Saintpaulia ionantha*) (Anon., 1997a).

Discoloration of the upper leaf surface with indentations where damage occurs is the major symptom of *F. occidentalis* infestations. 'Halo spotting', silvering, deformity and brown bumps may also be present on leaves of ornamentals. Feeding causes discoloration and scarring of petals. Buds can be deformed if feeding occurs before they begin to open. Direct economic damage is caused to ornamental vegetable and fruit crops (Anon., 1997a).

Second larval instars of *F. occidentalis* can transmit virus when young larvae are given an acquisition period of 24 h (Wijkamp and Peters, 1993).

Western flower thrips is considered to be the most important thrips vector (Goldbach and Peters, 1994). Epidemics of diseases caused by tospoviruses followed its spread, most likely on traded ornamentals, from western USA to other parts of the world in the 1980s. It was the most efficient vector of four tospoviruses in tests reported by Wijkamp et al. (1995).

F. occidentalis transmits *Chrysanthemum stem necrosis virus* (CSNV) (Bezzara et al., 1999), *Groundnut ringspot virus* (GRSV) (Wijkamp et al., 1995), INSV (DeAngelis et al., 1993, 1994; Wijkamp and Peters, 1993), TCSV (Wijkamp et al., 1995) and TSWV (Gardener et al., 1935).

Frankliniella schultzei *Trybom*

The cotton bud thrips or common blossom thrips (Figure 1a) originates from South America (Mound, 1996), but now has a pantropical distribution and is found throughout Africa, Asia, the Caribbean and the Pacific. It is less common in the subtropics and the insect is restricted to heated places, such as glasshouses and storehouses, in temperate regions. *F. schultzei* is commonly found on plants involved in international trade (Vierbergen and Mantel, 1991). Its establishment on Cactaceae flowers in glasshouses in the Netherlands has been reported (Vierbergen and Mantel, 1991) and, more recently, it has been found on other plant species in Dutch glasshouses (Vierbergen, 1995). *F. schultzei* has also been recorded as a glasshouse pest in Belgium and is present in Israel, Egypt, Morocco, Spain (Anon., 1999), Italy and the Canary Islands (Nakahara, 1997). However, the Italian record is now regarded as incorrect (Anon, 1999). A record for the UK (Anon., 1999) is based on a single female found on *Pinus* in Berkshire (Mound, 1968), but the thrips is not regarded as currently present (D. Collins, CSL, pers. comm.).

A dark or typical form and a light form are known to exist. The dark form is common in southern Australia, Africa and South America. The light form is common in parts of India and northern Australia though specimens have been seen from many parts of the tropics. Both forms co-exist in eastern Africa (Mound, 1996; Anon., 2002). The light form transmits fewer viruses than the dark form (Wijkamp et al., 1995) and, in the past, this has led to speculation that the two forms may be different species. The light form has been distinguished by some as *F. sulphurea* (Mound, 1996).

F. schultzei is commonly found on plants involved in international trade. It is a polyphagous species mainly living in the flowering parts of plants. Primary hosts are reported to be tomato, tobacco, peanut, soybean, cotton, pigeon pea (*Cajanus cajan*), lettuce (*Lactuca sativa*), pineapple (*Annas comosus*), lentil (*Lens culinaris* var. *culinaris*), blackgram (*Vigna mungo*), cowpea (*Vigna unguiculata*) and hyacinth (*Hyacinthus orientalis*). Secondary hosts include orchids and cacti (Anon., 2002).

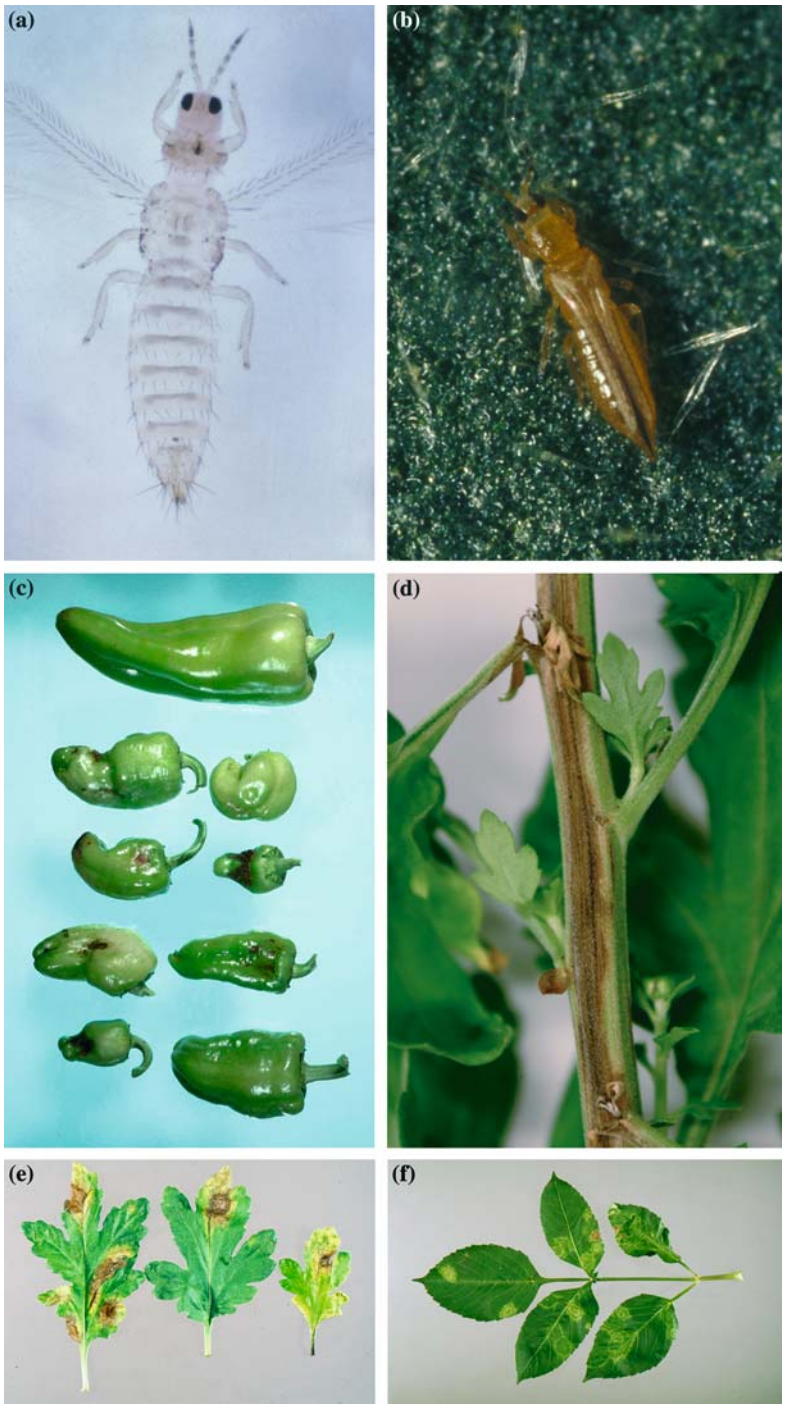

Figure 1. (a) *Frankliniella schultzei*, the cotton bud or common blossom thrips (Crown copyright courtesy of CSL). (b) *Thrips palmi*, the melon thrips (Crown copyright courtesy of CSL). (c) Fruit of sweet chilli pepper with distortions plus necrotic streak and spot symptoms caused by *Capsicum chlorosis virus*. The fruit at the top of the picture is uninfected (published previously by McMichael et al., 2002). (d) Chrysanthemum stem with a necrotic lesion caused by *Chrysanthemum stem necrosis virus* (Crown copyright courtesy of CSL). (e) Chrysanthemum leaves with necrotic lesions caused by *Impatiens necrotic spot virus* (Crown copyright courtesy of CSL). (f) Dahlia leaves with concentric ring patterns and chlorosis caused by *Tomato spotted wilt virus* (Crown copyright courtesy of CSL).

On cotton, *F. schultzei* causes deformation and destruction of young plants and seedlings. Injury to cotton flowers and withered spots on the boll pericarp have been attributed to infestations in southern Iran (Anon., 2002). Hyacinth bulb propagation has been affected in the Netherlands (Viebergen and Mantel, 1991).

F. schultzei transmits CSNV (Bezzara et al., 1999), GRSV (Wijkamp et al., 1995), TCSV (Wijkamp et al., 1995) and TSWV (Samuel et al., 1930; Wijkamp et al., 1995). *Groundnut bud necrosis virus* (GBNV) has also been recorded as being transmitted by *F. schultzei*, but at a very low frequency and only in the laboratory (Lakshmi et al., 1995).

Frankliniella zucchini *Nakahara and Monteiro*

Frankliniella zucchini originates in São Paulo State in Brazil (Nakahara and Monteiro, 1999). It has not been identified outside this area, but the disease caused by the virus it transmits has now been seen in central Brazil (Bezerra et al., 1999) and, therefore, it may have a wider range than current records suggest. This thrips has been described from zucchini squash (*Cucurbita pepo*) (Nakahara and Monteiro, 1999), but it presumably also feeds on watermelon and cucumber, which are natural hosts of the virus it transmits.

F. zucchini transmits *Zucchini lethal chlorosis virus* (ZLCV) in Brazil (Nakahara and Monteiro, 1999).

Scirtothrips dorsalis *Hood*

Scirtothrips dorsalis, the chilli thrips, is found in Asia from Pakistan through Malaysia and Indonesia to Taiwan and Japan. It also occurs in some Pacific locations, such as Papua New Guinea, Solomon Islands and Australia. A record also exists for South Africa (Gilbert, 1986). The species appears to be currently expanding its range in Africa as it has been reported from Côte d'Ivoire (Bournier, 1999) and intercepted in the UK on plants imported from Ghana (D. Collins, CSL, pers. comm.). More recently, it has become established in Israel (Anon., 2004c).

Citrus, cotton, peanut, tobacco, tomato, onion, cashew nut (*Anacardium occidentale*), castor bean (*Ricinus communis*), chilli pepper (*Capsicum annuum*), mango (*Mangifera indica*) and tea (*Camellia sinensis*) are the primary crop hosts of this polyphagous thrips. Heavily infested plants turn brown to black and can be defoliated. The main wild host plants are probably *Acacia* species (Anon., 2002; Reyes, 1994).

S. dorsalis has been reported to transmit GBNV (Amin et al., 1981), but there is some doubt now as to the validity of this record (Palmer et al., 1990). *S. dorsalis* has been found to transmit *Groundnut chlorotic fan-spot virus* (GCFV) (Chen et al., 1996; Chen and Chiu, 1996) and *Groundnut yellow spot virus* (GYSV) (Reddy et al., 1991).

Thrips flavus *Schrank*

This thrips has been recorded as the vector of *Watermelon bud necrosis virus* (WBNV) in India (Singh and Krishnareddy, 1995). However, there is a strong possibility that the thrips in question may have been *T. palmi*, which is very close morphologically to *T. flavus* (Mound, 1996). The matter needs resolving. For this reason, no further details of *T. flavus* are given in this review.

Thrips palmi *Karny*

The melon thrips (Figure 1b) is believed to be from Southeast Asia (Mound, 1996). It was first described from Sumatra and Java in Indonesia in 1925, but a few years later it was found as far west as Sudan and as far north as Taiwan. Extensive outbreaks have been reported in Japan since 1978 (Murai, 2001) and it has been spreading in the Caribbean region since 1985. It has now been reported in many countries in South and Southeast Asia, Australia and a number of islands in the Pacific region including Hawaii, many islands in the Caribbean plus Florida in the USA, and northeastern South America (Anon., 1997b). In Europe, there have been several limited occurrences in glasshouses in the Netherlands since 1988 and one in the UK in 2000. All these outbreaks were eradicated. However, in 2004, *T. palmi* was reported on an outdoor crop in northwest Portugal (Anon., 2004b).

T. palmi is a polyphagous pest, especially of species in the Cucurbitaceae and Solanaceae, such as sweet pepper, tobacco, cucumber, watermelon, melon (*Cucumis melo*), squash and pumpkin (*Cucurbita* spp.), aubergine (*Solanum melongena*) and potato (*Solanum tuberosum*). However, other

crops, such as cotton cowpea, pea, common bean, soybean, sunflower (*Helianthus annus*) and sesame (*Sesamum indicum*) are also hosts. *T. palmi* can also infest flowers, such as those of citrus in Florida and mango in India, and weeds including those in glasshouses. In Portugal, it was detected on flowers of Kiwi fruit (*Actinidea chinensis*) (Anon., 2004b). Ornamentals under glass are also at risk (Anon., 1997b). The outbreak in the UK was on glasshouse-grown chrysanthemum.

T. palmi cannot overwinter outdoors beyond a northern limit, such as a small part of southern Japan. However, it can survive further north in Japan in glasshouses. *T. palmi* may only be capable of limited survival outdoors in the UK during the winter and overwintering would be limited to protected environments (McDonald et al., 2000). At 25 °C, the life cycle from egg to adult lasts 17.5 days. The adults emerge from pupae in the soil and migrate to leaves and flowers of host plants, where they can be found in pockets, cracks or crevices. Eggs are laid on the host. The second stage larva goes into the soil, where it develops and pupates, thus completing the life cycle (Anon., 1997b).

T. palmi has only moderate dispersal potential by itself, but is liable to be carried on fruit or plants for planting, or in packing material (Anon., 1997b).

T. palmi transmits GBNV (Palmer et al., 1990; Vijayalakshmi, 1994; Lakshmi et al., 1995), *Melon yellow spot virus* (MYSV) (Kato et al., 2000) and *Watermelon silver mottle virus* (WSMoV) (Yeh et al., 1992). It may also transmit WBNV whose vector in India has been reported as *T. flavus* (Singh and Krishnareddy, 1995), which can easily be confused with *T. palmi*. *T. palmi* has also been implicated in the transmission of TSWV (Fujisawa et al., 1988; Persley et al., 2005) and CaCV (Persley et al., 2005).

Thrips setosus *Moulton*

This species has only been recorded in Japan (Mound, 1996). Its host plants include aubergene, common bean, chrysanthemum, citrus, cucumber, tobacco, tomato, dahlia (*Dahlia* sp.), fig (*Ficus carica*), grape (*Vitis vinifera*), impatiens, lettuce, melon, soybean, sesame, strawberry, sweet pepper, pea, tea, mint (*Mentha arvensis*) pumpkin (*Cucurbita moschata*) and white clover (*Trifolium repens*) (Miyazuke and Kudo, 1988).

T. setosus transmits TSWV (Fujisawa et al., 1988).

Thrips tabaci *Lindeman*

The onion thrips is thought to have originated in the eastern Mediterranean and in countries bordering the Black and Caspian Seas. It is now almost cosmopolitan, although rare in the humid tropics and subtropics. In Europe, it is common in both field and protected crops (Anon., 2002).

T. tabaci is particularly abundant in warm, dry sites especially where onion, its preferred host, is grown. Other primary hosts include cotton, cucumber, tobacco, garlic (*Allium sativum*), leek (*Allium ampeloprasum var. porrum*), cabbage (*Brassica oleracea* var. *capitata*), and black pepper (*Piper nigrum*). Secondary hosts include potato, melon, tomato, sugarbeet (*Beta vulgaris* var. *saccharifera*), pigeonpea (*Cajanus cajan*) and cassava (*Manihot esculenta*) (Anon., 2002). More recently in Japan, *T. tabaci* has been reported for the first time on Satsuma manderin (*Citrus unshiu*) and persimmon (*Diospyrus kaki*). Resistance of *T. tabaci* to insecticides used on glasshouse-grown asparagus is also casing concern (Murai, 2004).

T. tabaci has caused serious damage to onion, especially seed crops, in the USA. On broadleaved plants, such as tobacco, *T. tabaci* shelters along veins under the leaf. Damage can be severe in strips following leaf venation. On cotton, the thrips causes proliferation and branching with early damage reducing yields and seed. Discolouration, necrosis of leaves, malformation of plant parts and even death of the entire crop are other symptoms of attack (Anon., 2002).

T. tabaci is a major pest of glasshouse crops, such as cucumber, sweet pepper, chrysanthemum and many bedding plants (Anon., 2002).

T. tabaci is known to transmit TSWV (Pittman, 1927). However, its status as a major global vector of TSWV was questioned after studies showed that it seems incapable of transmitting some isolates (Cho et al., 1988). Later, it was shown that populations of *T. tabaci* that consisted of males and females (arrhenotokous populations) transmitted TSWV at a low rate, but that populations of only females (thelotokonous populations) did not transmit at all (Wijkamp et al., 1995). This difference in transmission ability between male and female has been attributed to different feeding habits

of the sexes and to physiological differences. In one study, the efficiency of transmission of a Greek isolate of TSWV by adults from six arrhenotokous populations of *T. tabaci* varied from 0.7% to 11.6%, whereas transmission by *F. occidentalis* was 34.8%. The transmission rate also varied between two isolates of TSWV. The host plant used as a source of TSWV also affected transmission efficiency. This phenomenon may be related to the suitability of the source plant species for feeding (Chatzivassiliou et al., 1999). The subject has been reviewed by Chatzivassiliou (2001).

IYSV is another tospovirus transmitted by *T. tabaci* (Cortês et al., 1998).

Thrips vectors of virus species in other genera

F. occidentalis, described under 'Thrips vectors of tospovirus species' above, has been found to transmit *Pelargonium flower break virus* (PFBV) (Krczal et al., 1995), a carmovirus. This thrips may transmit *Tobacco streak virus* (TSV), an ilarvirus (Kaiser et al., 1982).

F. schultzei, also described above, transmits TSV.

T. tabaci, another thrips described above, can transmit TSV (Sdoodee and Teakle, 1987) and *Prunus necrotic ringspot virus* (PNRSV) (Greber et al., 1991) ilarviruses. It is also a vector of *Maize chlorotic mottle virus* (MCMV) (Ullman et al., 1992), a machlomovirus, and *Sowbane mosaic virus* (SoMV) (Hardy and Teakle, 1992), a sobemovirus.

Microcephalothrips abdominalis *Crawford*

There are records for *M. abominalis* for Bangladesh, China, India, Indonesia, Japan, Korea, Taiwan, Thailand and the Philippines in Asia. It has also been found in Australia, Fiji, Guam, Hawaii, Palau, and Solomon Islands in the Pacific. Other records are for Canada, Mexico, USA, Cuba, Puerto Rico, Argentina and Peru in the Americas, Canary Islands and Italy in Europe and Egypt, Israel and Turkey in the Middle East (Anon., 2002; Reyes, 1994; G. Vierbergen, PPS, pers. comm.). It has been suggested that it is a New World species, which has been transported elsewhere by man (Stannard, 1968).

Some of the main crop hosts of *M. abdominalis* are reported as citrus, tomato, rice orchids, cucumber, sunflower (*Helianthus annus*) and chenopodium (*Chenopodium giganteum*) (Anon., 2002; G. Vierbergen, PPS, pers. comm.). Many ornamental species in the family Compositae, such as chrysanthemum, African marigold (*Tagetes erecta*), blue billygoatweed (*Ageratum houstonianum*) cosmos (*Bidens formosa*), pyrethrum (*Tanacetum coccineum*) and zinnia (*Zinnia elegans*) are also susceptible. Heavy infestations damage the corolla, stamens and developing seed. Petals lose pigmentation and drop prematurely (Anon., 2002; Baker, 1994).

Microcephalothrips abdominalis is known to transmit TSV (Greber et al., 1991).

Thrips parvispinus *Karny*

This thrips has been identified in Indonesia, Malaysia, Philippines, Thailand and Taiwan in Asia. It has also been recorded in Australia, Papua New Guinea and the Solomon Islands in Australasia (Anon., 2002; Reyes, 1994).

Primary crop hosts are reported to be watermelon and papaw (*Carica papaya*) (Anon., 2002). Other plant associations noted include potato, sweet pepper, tobacco, blackjack (*Bidens pliosa*), coffee (*Coffea* sp.) and impatiens (*Impatiens balsamina*), (Anon., 2002; Reyes, 1994).

T. parvispinus caused damage to gardenia (*Gardenia* sp.) in a commercial galsshouse in Greece in 1998. This outbreak in Europe was eradicated (Mound and Collins, 2000).

T. parvispinus is known to transmit TSV (Klose et al., 1996).

Tospoviruses transmitted by thrips

Tospoviruses are a group of plant pathogens naturally transmitted by thrips. They belong to the *Bunyaviridae*, which is large family of viruses that usually infect vertebrates and are largely transmitted by mosquitoes, ticks, phlebotomine flies and other arthropods (Elliot et al., 2000). Tospoviruses cause necrosis, chlorosis, ring patterns, mottling, silvering, stunting and local lesions in plant hosts. Symptoms vary according to the virus, host, cultivar, time of year and environment (German et al., 1992).

Table 1. Classification of the tospoviruses

Tospovirus	Serogroup[a]	Group[b]	Nucleotide identities compared to TSWV[c]	Derived amino acid identities compared to TSWV[c]
Tomato spotted wilt virus (TSWV)	I	TSW	100.0	100.0
Groundnut ringspot virus (GRSV)	II	TSW	76.7	78.3
Tomato chlorotic spot virus (TCSV)	II	TSW	75.8	76.7
Impatiens necrotic spot virus (INSV)	III	–	57.0	55.3
Groundnut bud necrosis virus (GBNV)	IV	WSMo	46.2	32.8
Watermelon bud necrosis virus (WBNV)	IV	WSMo	43.3	32.3
Watermelon silver mottle virus (WSMoV)	IV	WSMo	44.4	33.7
Groundnut yellow spot virus (GYSV)	V	–	41.9	24.1
Iris yellow spot virus (IYSV)	VI	–	47.1	37.3
Melon yellow spot virus (MYSV) = Physalis severe mottle virus (PhySMV)	VII	–	46.1	30.8
Chrysanthemum stem necrosis virus (CSNV)	VIII	TSW	74.0	76.0
Zucchini lethal chlorotic virus (ZLCV)	IX	TSW	72.7	72.9
Groundnut chlorotic fan-spot virus (GCFV)	X	–	43.6	24.4

Key: [a]Serogroups I, II, III and IV are established in the literature and accepted by most virologists. The allocation of tospviruses to Serogroups V to X varies in the literature - the designations above follow van der Wettering (1999); [b]Classification based on Moyer (1999) and Chu et al. (2001), TSW, Tomato spotted wilt group; WSMo, Watermelon silver mottle group; [c]Percentage nucleotide identities for the N gene and derived amino acid identities of the N protein compared to those of *Tomato spotted wilt virus*, the type species for the *Tospovirus* genus, from Chu et al. (2001).

Tospoviruses have quasi-spherical, enveloped particles with diameters of 80–100 nm and a tripartite single stranded (ss) RNA genome. The three RNA segments are designated L (large), M (medium) and S (small). The L RNA is of negative polarity and the M and S RNA have an ambisense coding strategy. Virions contain at least four structural proteins, denoted L (the putative RNA polynerase), G1/G2 (membrane glycoproteins) and N (nucleocapsid) that are encoded by L, M and S RNAs respectively (Chu et al., 2001).

By definition, members of the genus *Tospovirus* are transmitted by thrips in a persistant, propagative manner (German et al., 1992; Ullman et al., 1993). The vectors of some tospoviruses have not yet been identified, but the viruses are included in this review as thrips transmission is almost certain. The G1 and G2 glycoproteins of tospoviruses are involved in virus-vector relationships. These are encoded in the complimentary sense RNA of the M genome segment (Elliot et al., 2000).

For many years, TSWV was thought to be the sole representative tospovirus. Strains of TSWV had been identified on the basis of reaction with indicator plants (Best and Gallus, 1955), but it was not until the advance of serological testing that other tospoviruses could be distinguished. As a consequence, many early records attributed to TSWV could have been caused by other tospoviruses.

Vector specificity, host range and the nucleotide sequence homology of the nucleocapsid (N) gene have been important criteria for designation of tospoviruses to species level (Goldbach and Kuo, 1966). The genus *Tospovirus* has been subdivided in the past into serogroups (Table 1), which were originally based on the serological cross reactivity of the coat protein of virus particles formed by the N gene (N protein) and their antisera. Viruses in the same serogroup were related serologically. This method of classification dates from the time when isolates of TSWV were first being identified as distinct species. This system worked well when there were few recognised tospoviruses. However, in recent years, with an increase in the number of tospoviruses, especially those that belong to monotypic serogroups, the numerical classification of serogroups has become confusing and conflicting. In addition, cross-reactions of the N protein can occur between different tospovirus species, such as between TSWV and GRSV (Chu et al., 2001).

Moyer (1999) and Chu et al. (2001) have called for the numerical serogroup system to be abandoned and replaced with a type species in the group. It has been proposed that any tospoviruses with an amino acid sequence of the N protein showing more than 90% identity should be considered as strains of the same virus species. Those

with 80–90% sequence homology are classified as strains or as distinct viruses depending on additional criteria. Those with less than 80% homology to all other known tospovirsuses are classified as distinct species. In this system, all viruses serologically related with 80–90% sequence homology to TSWV should be placed in the TSWV group and those serologically related to WSMoV placed in the WSMoV group (Table 1). Other virus species are monotypic and, as such, are not yet classified as groups.

The International Committee on Taxonomy of Viruses has recognised eight tospoviruses as species and five as tentative species (Elliot et al., 2000), but this classification is now in urgent need of review. There is much evidence to suggest that at least 14 tospovirus species are distinct and qualify as species. Information on these tospoviruses and those that are still regarded as tentative species is presented below.

Tospovirus species

Capsicum chlorosis virus *(CaCV)*

CaCV was first identified in symptomatic sweet pepper, chilli pepper and tomato in the Bundaberg area and soon afterwards in the Ayr/Bowen area of Queensland, Australia in 1999 (McMichael et al., 2002). CaCV is now widespread occurring in all major sweet pepper production areas of Queensland, often at a higher incidence than TSWV (M. Sharman, CRCTPP, pers. comm.). In 2004, CaCV was detected in capsicum plants near Kununurra in the Kimberly region of Western Australia and in tomato at Coffs Harbour on the north coast of New South Wales (Persley et al., 2005).

Young leaves of infected capsicum plants show marginal and interveinal chlorosis and often become narrow and curled. Older leaves are chlorotic and may develop ringspot and line pattern symptoms. Infected plants are often stunted with small, distorted fruit that develop necrotic lesions and scarring (Figure 1c) (McMichel et al., 2002, Persley et al., 2005). The incidence of affected plants is commonly 1–10%, but has exceeded 60% (Persley et al., 2005). A source of resistance has been identified in *Capsicum* germplasm and this is being incorporated into a breeding programme (Persley et al., 2003, 2005).

Symptoms on tomato are more similar to those caused by TSWV with plants being stunted and necrotic flecks and spots developing on leaves and petioles, Chlorosis, mottling and purple ringspots are often other leaf symptoms (McMicheal et al., 2002).

CaCV has also been found in peanut in the Bundaberg area of Queensland and has the potential of becoming a significant problem in this crop. Symptoms in peanut are similar to those caused by GBNV. Leaves of infected peanut develop chlorotic spots, blotches and ringspots. New leaves become smaller and internodes reduced in length. Wilting and necrosis may occur in terminal shoots and leaves. An archived peanut sample collected on the Atherton Tableland of Queensland in 1992 has tested positive for CaCV, which shows the tospovirus was present in Australia before its discovery in 1999 (Persley et al., 2005).

Another natural host of CaCV is the Australian native plant *Hoya australis* found infected in Brisbane. Ringspots, line patterns, chlorotic blotches and necrotic etching have been reported as symptoms (Persley et al., 2005).

In inoculation studies, no systemic symptoms were observed on watermelon or squash, which are important cucurbit hosts of WSMoV (McMichael et al., 2002).

CaCV has reacted with antiserum to tospovirus Serogroup IV. Isolates from Bundaberg in Southeast Queensland and Ayr in northern Queensland were 97% identical in their N gene nucleotide sequences and 98% identical at the N protein amino acid level. They both shared 80–85% N gene sequence identity with WSMoV. Outside Serogroup IV, they were most closely related to MYSV and IYSV with respective sequence identitities of 57% and 40% at the N protein amino acid level (McMichael et al., 2002).

The thrips vector that transmits CaCV in the field in Queensland has not yet been identified unequivocally. *T. palmi* has been shown to be a vector in laboratory tests, but CaCV was present on the Atherton Tableland eight years before *T. palmi* was first found in the area (Persley et al., 2005). *F. schultzei* is the dominant thrips in the Bundaberg area, but this species failed to transmit CACV in tests as did *F. occidentalis* (Persley et al., 2005).

A tospovirus with 97% N gene nucleotide sequence homology with an Australian isolate of

CaCV has been detected on tomato and peanut in Thailand (P. Chiemsombat, Kasetsart University, pers. comm.). *C. claratris* has been shown to transmit CaCV in Thailand (Premachandra et al., 2005). These findings may indicate a Southeast Asian origin for CaCV.

Chrysanthemum stem necrosis virus *(CSNV)*

The virus later known as CSNV was first recognised on chrysanthemum in Atibaia in São Paulo State in Brazil during a survey in the mid-1990s (Nagata et al., 1994). It was originally described as either belonging to a new serogroup of TSWV or a possible novel tospovirus and was tentatively designated Chr 1 or Chry 1. Symptoms caused by the virus were described as necrotic lesions surrounded by yellow areas on leaves followed by necrosis on stems, peduncles and floral receptacles (Duarte et al., 1995). A lesion on the stem of chrysanthemum caused by an outbreak of CSNV in the UK is shown in Figure 1d.

Later, the same virus was found to be closely related to an isolate from tomato designated BR-11t (Duarte et al., 1995; Resende et al., 1996). Stem necrosis with necrotic spots and rings on leaves were the symptoms in tomato (Nagata et al., 1998).

The virus was found in four nurseries in the Netherlands during 1994–1995 on chrysanthemum cuttings imported from Brazil (Verhoeven et al., 1996). Symptoms on chrysanthemum were described as being similar to those caused by TSWV. These were mild and severe necrotic streaks on the stem, wilting of leaves and stems and chlorotic and/or necrotic spots and rings on some leaves. However, symptoms of CSNV were observed to be more severe than those caused by TSWV and could result in complete necrosis of the stem resulting in wilting of sections of plants (Verhoeven et al., 1996). It was concluded that the new virus, which they tentatively designated Ch-1, was a distinct tospovirus.

On inoculated tomato, systemic symptoms were described as chlorotic and necrotic lesions, chlorosis, rugosity and severe growth reduction, although not all inoculated plants developed symptoms. On comparing the reaction of the test tomato cultivars to those caused by TSWV, it was considered that tomato might be less susceptible to Ch-1 than to TSWV (Verhoeven et al., 1996). In other inoculation experiments, sweet pepper, squash, pea, common bean and cowpea have been systemically infected, but not watermelon (Bezarra et al., 1999; Verhoeven et al., 1996).

The virus did not react in DAS-ELISA tests with antisera of TSWV, INSV, IYSV and Tospo-To, a strain of WSMoV from tomato in Taiwan, in tests undertaken in the Netherlands. An antiserum to CSNV was produced against Ch-1 (Verhoeven et al., 1996).

F. occidentalis was implicated in the spread of Ch-1 in glasshouses in the Netherlands (Verhoeven et al., 1996). The disease caused by the virus was considered serious enough to warrant eradication. It has not been found in the Netherlands since 1996 when an eradication campaign was initiated (Verhoeven and Roenhorst, 1998).

Nagata et al. (1998) used the name chrysanthemum stem necrosis tospovirus when describing an occurrence of the virus on tomato (*L. esculentum*) in Minas Gerais State in Brazil. However, Bezerra et al. (1999) made the first formal recognition of a new virus species when serological studies and an analysis of nucleotide sequences of the N gene showed that the deduced N protein of virus was distinct from GBNV, GRSV, GYSV, IYSV, TCSV, TSWV, WSMoV, WBNV and ZLCV. ZLCV was the most similar with 80% identity. Western immunoblot analyses also demonstrated that Chry 1 was different from other tospoviruses, although a slight cross-reaction with antibodies against TSWV, TCSV and GRSV was observed. Bezarra et al. (1999) proposed that Chry 1 be designated CSNV.

Bezarra et al. (1999) demonstrated that *F. occidentalis* and *F. schultzei* could experimentally transmit CSNV, the latter being proposed as an important vector of CSNV in Brazil. *T. tabaci* was not found to be a vector in these experiments. These results have been confirmed in more recent studies where CSNV was efficiently transmitted by *F. occidentalis* (65.1%) and *F. schultzei* (78.1%), but not at all by *T. tabaci* (0.0%) (Nagata and de Ávila, 2000).

CSNV is growing in economic importance in Brazil having spread to new geographic areas since 1997. It is expected to become widespread and important (Bezerra et al., 1999). In 2002, there was an outbreak of the virus in a UK nursery that had imported chrysanthemum cuttings from Brazil (Mumford et al., 2003). CSNV was detected in

F. occidentalis (R. Mumford, CSL, pers. comm.), which infested plants in the glasshouse with the disease. CSNV was declared eradicated in the UK in 2003. In Slovenia, CSNV was recorded on chrysanthemum in 2001 Infected plants were destroyed and CSNV was not found in Slovenia in 2003 (Ravnikar et al., 2003, 2004). However, there has been a report of CSNV in gerbera in Slovenia in 2004 (A. Roy, EPPO, pers. comm.).

Groundnut bud necrosis virus *(GBNV)*

Reddy et al. (1968) first described a disease causing necrosis of the terminal buds of peanut and found that the causal agent was graft-transmissible. A virus was suggested as the pathogen and the name 'bud necrosis' given to the disease. The incidence of 'bud necrosis' in some fields of a recently introduced African peanut cultivar in Andra Pradesh, India was observed to be as high as 50%. Since then, peanut losses of up to 80% have been recorded in India (Ghanekar et al., 1979).

S. dorsalis and *F. schultzei*, which were prevalent on peanuts in Hyderabad, have been reported as vectors. *S. dorsalis* was reported as the least efficient vector. *T. tabaci* was found not to be a vector (Amin et al., 1981). However, *S. dorsalis* was found later not to be a vector and *F. schultzei* only transmitted the virus at a very low frequency (2%) in the laboratory (Lakshmi et al., 1995). The principal vector is now believed to be *T. palmi* (Palmer et al., 1990; Vijayalakshmi, 1994; Lakshmi et al., 1995).

Although the virus was thought to be a strain of TSWV (Ghanekar et al., 1979), antisera of TSWV did not react with the Indian peanut virus (Sreenivasulu et al., 1991). The virus was purified and antisera produced. Experiments showed that it was serologically distinct from TSWV and INSV. It was named 'bud necrosis virus' (Reddy et al., 1992).

The 'bud necrosis' peanut virus from India was compared serologically to tospovirus isolates from watermelon in Taiwan (Tospo-W), tomato in Taiwan (Tospo-To) and also TSWV and INSV using polyclonal and monoclonal antibodies in ELISA and electroblot immunoassays. The peanut isolate from India and the watermelon and tomato isolates from Taiwan did not react to antibodies to TSWV or INSV. These three isolates were found to have N protein components with the same weight of 32 kDa compared to 29 kDa for the N protein of TSWV and INSV. The name groundnut bud necrosis virus was proposed for all three isolates sharing similar size and properties of the N protein that differentiate them from TSWV and INSV. However, it was realised that there were differences in host reaction and serology between these three isolates (Adam et al., 1993).

The tospoviruses from watermelon and tomato in Taiwan were later identified as two strains of WSMoV and the name groundnut bud necrosis virus (GBNV) was retained only for the distinct peanut isolate from India (Yeh et al., 1996).

Amino acid sequence analysis of the N protein of GBNV, as peanut bud necrosis virus, showed a close relationship with WSMoV, but a more distant relationship with tospoviruses in Serogroups I, II and III. The work suggested that GBNV was a distinct tospovirus within Serogroup IV (Satyanarayana et al., 1996a).

GBNV has been reported to cause substantial yield losses in Nepal. Complete pod loss could result from infection during an early stage of plant development (Sharma, 1996). A peanut disease caused by GBNV has also been recorded in Vietnam (Thuan and Trung, 1996) and Thailand (Wongkaew and Chuapong, 1997).

A disease of mungbean (*Vigan radiata*) near Bangalore in Karnataka state is caused by a strain of GBNV. Symptoms include necrosis of leaves, stems, petioles buds, pods and growing points. Incidence was reported as up to 70% (Thien et al., 2003). It remains to be seen whether tospovirus diseases of blackgram, cowpea and soybean in India are caused by GBNV (Bhat et al., 2001). The weeds *Ageratum conyzoides* and *Cassia tora*, which are common in peanut fields, have been implicated as both hosts of *T. palmi* and GBNV. They and other weeds are likely reservoirs of inoculum (Reddy et al., 1983; Lakshmi et al., 1995).

Groundnut chlorotic fan-spot virus *(GCFV)*

A disease of peanut characterised by large chlorotic, fan-shaped spots with conspicuous concentric rings that often occurred in succession along the main veins of the leaflets was first noticed in October 1992 in central Taiwan. Affected areas of leaves later turned bright yellow and finally brown and necrotic (Chen and Chiu, 1996; Chen et al., 1996).

The virus was initially denoted as Tospo-P (Yeh et al., 1998). In mechanical inoculation tests, a yellow mottle resulting from a systemic infection was noticed on the upper leaves of cowpea. The infection in *Nicotinia benthamiana* was also systemic with necrotic lesions occasionally being observed on upper leaves. Chlorotic and necrotic lesions were formed on the inoculated leaves of a range of other tests plants (Chen et al., 1996).

In screenhouse tests, *S. dorsalis* transmited the virus in a persistent manner. *F. williamsi* and *T. palmi* were not found to be vectors. Thin sections of diseased tissue revealed particles typical of those of other tospoviruses. The virus was tentatively named peanut chlorotic fan-leaf virus (Chen et al., 1996).

The virus was found not to be serologically related to TSWV, GRSV, WSMoV or INSV. Nucleotide sequencing also indicated that it was a distinct member of the genus *Tospovirus* (Chen and Chiu, 1996; Yeh et al., 1998).

The virus was named GCFV, a tentative tospovirus species, by Elliot et al. (2000). Further analysis, which included sequencing of the viral S RNA and comparisons of nucleotide identies in the N gene and amino acid identities of the N protein with those of 13 other tospoviruses including GYSV from India, led to the conclusion that GCFV was a new tospovirus species (Chu et al., 2001).

Groundnut ringspot virus *(GRSV)*

In 1990, 20 isolates of 'TSWV' from various hosts and countries were serologically differentiated (de Ávila et al., 1990). Sixteen isolates were of the same serotype and typical of TSWV. These were placed in Serogroup I. Four different isolates belonging to two distinct serotypes were placed in Serogroup II. Two of these isolates of one serotype were isolated from tomato in Brazil and were later designated as TCSV. The isolates of the other serotype came from tomato in Brazil (isolate B8) and peanut in South Africa (isolate A5). The nucleotide sequence of the N gene of SA-05 (formerly designated A5) was used to help differentiate species of tospovirus in Brazil. The name GRSV was proposed for isolate SA-05 (de Ávila et al. 1993).

In experiments in the Netherlands, *F. occidentalis* and the dark form of *F. schultzei* transmitted GRSV. GRSV was not transmitted by the light form of *F. schultzei*, *F. intonsa* and *T. tabaci* (Wijkamp et al., 1995).

In Brazil, a virus in coriander (*Coriandum sativum*) with disease symptoms in Pernambuco state was later identified as GRSV (Lima et al., 1999). In São Paulo state, three samples of lisianthus (*Eustoma grandiflorum*) and two of aster (*Callistephus* sp.) with virus symptoms were also shown to contain GRSV. While one sample of aster was infected with GRSV alone, all other samples were infected with a combination of other tospoviruses (Alexandre et al., 1999).

Lettuce with typical tospovirus symptoms was found infected with GRSV in São Jose dos Campos state (Chaves et al., 2001). GRSV was also detected in stunted sweet pepper plants with foliar mosaics, foliar necrosis and ringspots in fruit in São Paulo state (Colariccio et al., 2001b). In 2002, GRSV was identified in cubiu (*Solanum sessiliflorum*) with mosaic symptoms growing in the state of Rio de Janeiro (Boari et al., 2002).

The first report of GRSV in Argentina was on tomato (Dewey et al., 1995). Tomato in northwest and central Argentina affected by 'peste negra' disease was found to contain GRSV. The same disease in the northeast was caused by TCSV and in the Rio Negro Valley in the south by TSWV. It was speculated that the spread of *F. schultzei* may have been responsible for the wider distribution of GRSV (Williams et al., 2001). When potato with necrotic spots on leaves and necrotic streaks along the petioles and stems ending in 'top necrosis' from Mendoza province in Argentina was analysed for tospovirus infection, 38% of plants had GRSV, 23% had TSWV, 4% had TCSV (Granval de Millan et al., 1998). A later survey detected GRSV in the weed *Datura ferox* in addition to tomato and lettuce (Gracia et al., 1999).

Soybean with leaf mottle symptoms growing in the Northwest Province and KwaZulu-Natal in South Africa has been found to be a host of GRSV (Pietersen and Staples, 1996; Pietersen and Morris, 2002).

Groundnut yellow spot virus *(GYSV)*

Peanut yellow spot disease was first reported in peanut in India in 1979 (Anon., 1980). Symptoms begin with chlorotic/yellow leaf spots, which later coalesce and become necrotic. The incidence of the

disease in farmer's fields reached 90%. However, yield losses have not been determined (Satyanarayana et al., 1996b). A similar disease was also reported later in Thailand (Wongkaew and Sae-Wien, 1985).

Reddy et al. (1991) reported that the disease was caused by a distinct tospovirus based on particle morphology, host range and serology tests with TSWV and GBNV antisera. This virus became systemic in pea, mungbean and cowpea at temperatures between 20 and 30 °C. (Reddy et al., 1991).

Preliminary transmission studies suggested that the virus in India was transmitted by *S. dorsalis* (Reddy et al., 1991). However, the vector is still regarded officially as undetermined (Elliot et al., 2000).

In ELISA and immuno-blot analysis, the virus did not react with antisera of TSWV, INSV and GBNV. Other tests and a lack of nucleotide homology between the three other tospoviruses suggested that the new virus, known as peanut yellow spot virus, should be considered a distinct species of tospovirus under a new serogroup, putatively designated Serogroup V (Satyanarayana et al., 1996b). Later work showed that the N protein had 24–28% amino acid sequence identity and 44–51% sequence similarity with members of other serogroups. This and other research confirmed the authors' belief that GYSV belonged to a new serogroup (Satyanarayana et al., 1998).

It had been noted that the virus had some similarities, such as the same vector, with GCFV in Taiwan (Satyanarayana et al., 1996b). However, it has since been shown that GCFV, although similar, is a distinct tospovirus species (Chu et al., 2001).

Impatiens necrotic spot virus *(INSV)*

In the late 1980s, a serologically distinct member of the TSWV group was isolated from New Guinea impatiens (*Impatiens* sp.) in the USA. This isolate, which was termed TSWV-I, had been frequently detected in flower crops such as antherium, begonia, exacum, gloxinia as well as New Guinea impatiens. TSWV-I did not infect cucurbits. It was considered to be a distinct tospovirus in a new serogroup as comparisons of structural proteins by serology and hybridisation analysis of the small and middle RNAs revealed clear differences between TSWV-I and TSWV (Law and Moyer, 1990). Analaysis of nucleotide sequences in the N gene showed 59% identity between TSWV-I and TSWV and an analysis of amino acid sequences of the N protein showed 67% identity. The name impatiens necrotic spot virus (INSV) was proposed (Law et al., 1991a, b, c).

INSV, originally isolated as NL-07 or H7, was also found in Europe following new outbreaks of diseases caused by TSWV-like pathogens that occurred after the near-global spread of *F. occidentalis* in the 1980s (de Ávila et al., 1992; Marchoux et al., 1991). Characterisation research by de Ávila et al. (1992) confirmed the findings of Law and Moyer (1991) that a new, distinct tospovirus had been identified. The nucleotide sequence of the S RNA of INSV was determined by de Haan et al. (1992).

Anemone, *Bowardia*, *Ranunculus*, *Antirrhinum*, *Fatsia* and *Limonium* were soon afterwards found infected by INSV in Italy (Vaira et al., 1993). Reports from Portugal showed that INSV has been found in *Aphelandra*, *Chrysanthemum*, *Gazania*, *Gerbera*, *Gladiolus*, *Helichrysum*, *Hydrangea*, *Penstemon*, *Ruscus* and *Sinningia* (Louro, 1996). More than 40 plant species grown indoors were found with INSV in the Netherlands in genera that included *Aeschynanthus*, *Alstroemeria*, *Anthurium*, *Arabidopsis*, *Ardsia*, *Bromelia*, *Cardamine*, *Curcuma*, *Eustoma*, *Gentiana*, *Hippeastrum*, *Iris*, *Kalanchoe*, *Lobelia*, *Nemesia*, *Phalaenopsis*, *Primula*, *Saxifraga*, *Schizanthus*, *Senecio* and *Zantedeschia*. Symptoms were said to be similar to those of TSWV on many species (e.g. *Anemone*, *Begonia* and *Ficus*), but different on others (e.g. *Bouvardia* and *Cyclamen*) (Verhoeven and Roenhorst, 1998). Symptoms caused by INSV in *Chrysanthemum* in the UK are illustrated in Figure 1e. INSV was first found in the UK in *Cineraria* growing as a protected crop (Weekes et al., 1998). Many more ornamental species are now listed as hosts in various publications (e.g. Daughtrey et al., 1997; Volvas and Potere, 1997; Gotta et al., 1999; Roggero et al., 1999; Mertelik et al., 2002). A variety of symptoms caused by INSV on a range of glasshouse ornamentals, including *Agrostemma*, *Capsicum*, *Pericallis*, *Browallia*, *Calceolaria*, *Callistephus*, *Dahlia*, *Diascia*, *Eustoma*, *Osteospermum*, *Pelargonium*, *Petunia*, *Platycodon*, *Portulaca*, *Primula*, *Schizanthus*, *Solenostemon*, *Stephanotis* have been described (Daughtrey, 1996). Mixed

infections with TSWV were detected in some hosts. INSV has also been detected in an *Oncidium* orchid (Koike and Maghew, 2001), prickly pear cactus (*Opuntia microdasys* var. *albata*) (Blockley and Mumford, 2001) and more recently in various ornamentals in Iran (Shahraeen et al., 2002).

In addition to ornamentals, INSV has been found in the Netherlands in pepino (*Solanum muricatum*), spinach (*Sinacia oleracea*) and sweet pepper (Verhoeven and Roenhorst, 1998). In Italy, field lettuce, glasshouse cucumber and nursery sweet pepper has been found infected (Vicchi et al., 1999).

In Georgia in the USA, where INSV has been detected in sweet pepper (Naidu et al., 2005), peanut and tobacco, the virus has also been found in symptomless yellow nutsedge (*Cyperus esculentus*) and purple nutsedge (*C. rotundas*). Both cause serious weed problems in southeastern USA and are now thought to also act as reservoirs of infection (Martínez-Ochoa et al., 2004).

For many years *F. occidentalis* was considered to be the only vector of INSV (DeAngelis et al., 1993, 1994; Wijkamp and Peters, 1993). Wijkamp et al. (1995) reported that INSV was not transmitted by *F. intonsa*, *T. tabaci* or the light or dark forms of *F. schultzei*. However, *F. intonsa* has since been reported to transmit INSV, albeit at a low efficiency compared to *F. occidentalis*, and by only one third of those insects that tested positive for the virus by ELISA (Sakurai et al. (2004). *Thrips setosa* and *T. palmi* have been shown not to be vectors (Sakurai et al., 2004). *Frankliniella fusca* was reported as a vector by Naidu et al. (2001).

INSV has a distinct host range affecting mainly ornamental hosts. It does not usually affect solanaceous crops as does TSWV. Studies with an isolate of INSV that was recently found naturally infecting glasshouse-grown potatoes indicated that, although systemic, it was not efficiently maintained in potato or transmitted to progeny tubers. These attributes could explain why INSV is not a problem in field potatoes (Perry et al., 2005).

The known host range of INSV is second only to TSWV among the tospoviruses (Peters, 1998). INSV is still increasing its distribution and host range. In 1999, INSV was first found in Israel in *Anemone coronaria* imported from Europe (Gera et al., 1999). In 2003, it was found for the first time in New Zealand on freesia (*Freesia* × *hybrida*), a new host. The New Zealand isolate shared 96–98% nucleotide identity with isolates from the USA, Japan and the Netherlands (Lebas et al., 2004).

INSV from *Impatiens* was recognised as different from TSWV simultaneously in North America and Europe, but was soon found in many other locations. Relationship analysis suggests that INSV is more akin to tospoviruses in the TSWV subgroup, which are found in South America, than to tospoviruses in other subgroups (Figure 2) (Chu et al., 2001; Silva et al., 2001). However, the two known thrip vectors of INSV are of North American origin. The wide distribution and host range of INSV, second only to TSWV, may indicate that it has been in existence for some considerable time.

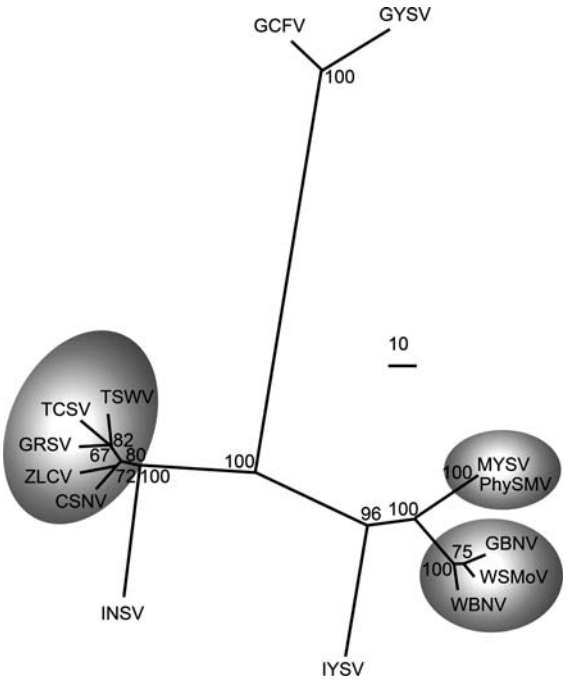

Figure 2. Phylogenetic relationships derived from the sequence of amino acids of the N proteins of tospoviruses. The scale for genetic distances is indicated in the middle right quadrant. Viruses with potential serological relationships are shadowed in the same cluster (from Chu et al., 2001). Key: CSNV, *Chrysanthemum stem necrosis virus*; GBNV, *Groundnut bud necrosis virus*; GCFV, *Groundnut chlorotic fan-spot virus*; GRSV, *Groundnut ringspot virus*; GYSV, *Groundnut yellow spot virus*; INSV, *Impatiens necrotic spot virus*; IYSV, *Iris yellow spot virus*; MYSV, *Melon yellow spot virus*; PhySMV, Physalis severe mottle virus; TCSV, *Tomato chlorotic spot virus*; TSWV, *Tomato spotted wilt virus*; WBNV, *Watermelon bud necrosis virus*; WSMoV, *Watermelon silver mottle virus;* ZLCV, *Zucchini lethal chlorosis virus*.

Iris yellow spot virus *(IYSV)*

In 1992, iris (*Iris hollandica*) grown in the field in the Netherlands for cut flowers was noticed to have yellow and sometimes necrotic spots on leaves. The disease was also recognised in glasshouse-grown iris at two other locations. Affected plants were infected with a putative tospovirus that did not react with antisera of INSV or TSWV. Leek or onions grown for seed in the vicinity of the infected iris were heavily infested with thrips. The main species was suspected to be *T. tabaci* (Derks and Lemmers, 1996). At one outbreak location, leek had been seen with virus-like symptoms, but plants were removed by the grower before tests could be undertaken (Verhoeven and Roenhorst, 1998; J. Verhoeven, PPS, pers. comm.).

In the spring of 1997, the same tospovirus was detected in the Netherlands in leek grown in a glasshouse for seed. Symptoms were described as chlorotic, elongated, eye-spots over veins that eventually become necrotic (Anon., 1998).

Molecular and serological classification work undertaken with the original isolate at this time showed that the virus was a new and distinct tospovirus species belonging to none of the then recognised Serogroups I, II, III and IV. An analysis of the amino acids in the N protein of the virus showed only 30–44% sequence identity with those of other tospoviruses identified so far. The highest homology was found with the Asian tospoviruses GBNV and WSMoV, which are both in Serogroup IV. *T. tabaci* was confirmed as the vector. *F. occidentalis* and *F. schultzei* were not found to be vectors (Nagata et al., 1999). The virus was named IYSV (Cortês et al., 1998).

An unknown tospovirus, associated with a disease of onion called 'sapeca', was found in Brazil during a survey in the mid-1990s. An isolate was designated BR-10o and serological studies indicated that it belonged to a new serogroup (Pozzer et al., 1994b; Resende et al., 1996). Comparing the nucleotide sequences of the Brazilian isolate from onion with the Netherlands isolate from iris, Pozzer et al. (1999) found 90.5% homology. The authors proposed that the Brazilian isolate should be considered a strain of IYSV. The Brazilian strain was designated $IYSV_{BR}$ and the Netherlands strain as $IYSV_{NL}$. As was found by Cortês et al. (1998, 1999), Pozzer et al. (1999) showed that $IYSV_{BR}$ was more closely related to GBNV and WSMoV than other tospoviruses.

In 1996, IYSV was reported in plants of amaryllis (*Hippeastrum hybridum*) with chlorotic sports and rings growing in the Jordan Valley and Besor area of Israel (Gera et al., 1998b; Kritzman et al., 2001).

In 1997, the virus was detected in onion in Israel (Gera et al., 1998a, b). Symptoms of this 'straw bleaching' disease (Kritzman et al., 2001) were reported as straw-coloured ringspots on leaves and flower stalks (Gera et al., 1998a, b). IYSV was soon afterwards reported in onion in India (Kumar and Rawal, 1999).

A 'scape blight' of onion first reported in the USA in 1993 (Hall et al., 1993) is also now known to be caused by IYSV (Mohan and Moyer, 2002; Schwartz et al., 2002; du Toit et al., 2003; Creamer et al., 2004; Gent et al., 2004). IYSV has also been detected in onion in Slovenia (Mavric and Ravnikar, 2001), Australia (Coutts et al., 2003) and Japan (Zen et al., 2003).

IYSV has been found in leek and garlic chive (*Allium tuberosum*) in the USA (Mohan and Moyer, 2002). There are some publications that list garlic (*Allium sativum*) and chive (*A. schoenoprasum*) as hosts of IYSV (e.g. Coutts et al., 2003), but this has not been confirmed and seems to have arisen erroneously from the report that garlic chive is a host (S. Mohan, University of Idaho, pers. comm.). Leek is also a host in Slovenia (Mavric and Ravnikar, 2001) and Australia (Coutts et al., 2003).

IYSV was first detected in astroemeria (*Alstroemeria* sp.) in Japan (Murai, 2004: Okuda and Hanada, 2001; Okuda et al., 2003). Lisianthus is a host of IYSV in Israel (Kritzman et al., 2000, 2001) and Japan (Doi et al., 2003; Murai, 2004). IYSV has since been detected in *Clivia minata* and *Bessera elegans* in Japan at one location where astroemeria was infected (M. Okuda, NARC for Kyushu Okinawa, pers. comm.). An ornamental *Portulaca* is a host in the Veneto area of Italy (Cosmi et al., 2003). A *Cycas* sp., *Pelargonium* × *horturum*, a *Rosa* sp. and a *Scindapsis* sp. have been recorded as hosts in Iran (Shahraeen and Ghotbi, 2003; N. Shahraeen, PPDRI, pers. comm.). The natural host range and distribution of IYSV is steadily increasing.

The IYSV isolated from lisianthus in Israel was designated $IYSV_{IL}$. $IYSV_{IL}$ was found to have

96% homology with $IYSV_{NL}$ and 91% homology with $IYSV_{BR}$. $IYSV_{IL}$ was reported to have 99% homology with the Israeli onion strain (Kritzman et al., 2000, 2001). The onion and amaryllis strain of IYSV in Israel have been reported to be serologically identical (Kritzman et al., 2001). IYSV isolated from leeks in Slovenia in 1999 differed in its reaction on test plants from the reactions of both $IYSV_{NL}$ and $IYSV_{BR}$ (Mavric and Ravnikar, 2001).

A genetic diversity study of isolates of IYSV in the USA using RT-PCR with specific primers to amplify the N gene showed two distinct groups. Isolates from onion in Idaho grouped with IYSV from the Netherlands ($IYSV_{NL}$) and Israel ($IYSV_{IL}$) whereas onion isolates from Utah grouped with IYSV from Brazil ($IYSV_{BR}$). Chive isolates from Idaho, although grouped with the Brazilian sub-clade, formed a distinct subgroup and exhibited the least similarity (81% amino acid level) when compared to the IYSV type strain ($IYSV_{NL}$), suggesting it may be a different virus species (Abad et al., 2003).

In Australia, one isolate of IYSV from onion in New South Wales and two from onion in Victoria were described as being 91–96% identical at the nucleotide level to $IYSV_{NL}$ and $IYSV_{IL}$ (Coutts et al., 2003).

IYSV would seem to be causing the most serious economic problems on onion. Spring onion crops have been abandoned because of IYSV in Australia (Coutts et al., 2003). In the USA, IYSV is described as causing an emerging and potentially devastating disease of onion (Gent et al., 2004). However, despite attempts, it has not been demonstrated that IYSV is carried through to the next generation in the bulbs of its hosts (Derks and Lemmers, 1996; Kritzman et al., 2001). Volunteer onion plants have been seen with symptoms in the USA, but it is not known if they emerged from the ground infected or became infected soon after emergence by viruliferous thrips (Gent et al., 2004).

IYSV, although first identified in Europe in an ornamental, was quickly found at various locations around the world. Information from molecular characterisation studies with IYSV (Cortês et al., 1998; Pozzer et al., 1999) shows it is more closely related to Asian tospoviruses than those from elsewhere. The phylogenetic analyses of Chu et al. (2001) and Silva et al. (2001) also shows IYSV to be more related to Asian tospoviruses than to the South American tospoviruses (Figure 1). Cortês et al. (1998) suggested that IYSV may have its most important niche in Asia.

Melon yellow spot virus *(MYSV)*

In 1992, there was an outbreak of a serious disease in netted melon (*Cucumis melo*) grown glasshouses in Shizuoka prefecture in Japan. Vein clearing and chlorotic spots developed on newly developed leaves. These leaves showed yellowing and necrotic spots as they aged. If infection occurred early, mosaic symptoms formed on fruit. Infection had a deleterious effect on the visual appeal and the taste of fruit. The disease quickly spread and resulted in considerable crop losses (Kato et al., 1999).

A tospovirus-like virus was isolated from diseased melon that had a unique host range and was strongly virulent on members of the Cucurbitaceae. Electron microscopy revealed tospovirus-like particles. The virus was not serologically related in ELISA tests to TSWV and WSMoV previously reported in Japan. *Thrips palmi* was found to be a vector (Kato et al., 1999).

Comparisons of amino acid sequences of the N protein revealed that the virus was most closely related to three tospoviruses in Serogroup IV, but identities to GBNV, WSMoV and WBNV were only 58–60%. It was proposed as a distinct species with the name *Melon yellow spot virus* (MYSV) (Kato et al., 2000). MYSV also infects cucumber in Japan (Okuda et al., 2004).

A tospovirus serologically distinct from established tospovirus species was found in Thailand on *Physalis minima*. The N-protein is the largest known for any tospovirus. Sequence comparisons revealed the closest relationship with WBNV (58% identity), WSMoV (57% identity) and a distant relationship to GYSV (23% identity) and GCFV (22% identity) (Cortêz et al., 2001). This virus was called Physalis severe mottle virus (PhySMV).

Comparisons between PhySMV (see Table 1) and MYSV (see Table 1) have shown that their N proteins share 99.6% amino acid identity and have no apparent nucleotide sequence distance (Chu et al., 2001). The two viruses are now regarded as strains of the same species. It is uncertain which name takes precedent, but this will undoubtedly be decided in the near future.

The nucleotide sequence of the open reading frame (ORF) or the L RNA segment has been shown to have 71.0% identity with GBNV and 70.6% identity to WSMV (Okuda et al., 2004).

Tomoto chlorotic spot virus *(TCSV)*

In 1990, four tospovirus isolates recovered from tomato in Brazil were serologically differentiated from sixteen other isolates of 'TSWV' from various hosts in different countries. The four different isolates were placed in a new Serogroup II to distinguish them from true TSWV in Serogroup I. The four isolates comprised two distinct serotypes. Isolates B3 and B6 were placed in one serotype as they reacted similarly to antibodies raised against the nucleocapsid and glycoproteins of TSWV (de Ávila et al., 1990). The nucleotide sequence of the N gene was used to establish phylogenetic parameters to delineate other Brazilian species of tospovirus. The name tomato chlorotic ringspot virus (TCRV) was proposed for isolate BR-03 (formerly designated B3) of this serotype (de Ávila et al., 1993).

In addition to tomato, TCSV was found affecting sweet pepper mainly in Santa Catarina state (Boiteux et al., 1993). In a survey of tospoviruses in Brazil in 1995, 36% were identified as TCSV. These came predominantly from tomato specimens collected in São Paulo state, but some also came from tomato in the states of Minas Gerais, Rio Grande do Sul and Paraná, and potato in São Paulo state.

Transmission studies have shown that TCSV is transmitted effectively by *F. occidentalis* and the dark form of *F. schultzei*. *F. intonsa* and the light form of *F. schultzei* were poor transmitters. TCSV was not transmitted by *T. tabaci* (Wijkamp et al., 1995).

Serious outbreaks of a disease of lettuce caused by tospoviruses began in Brazil in the mid 1980s. Today, infection occurs most frequently in summer leading to losses of 30–100%. Both TCSV and GRSV have been implicated in lettuce disease in São Paulo state. TCSV has been found in hydroponically grown lettuce (Colariccio et al., 2001c).

TCSV has been detected in endive (*Cichorium endiva*) with mosaics, necrosis, chlorotic and necrotic ringspots and a reduction in leaf size in São Paulo state (Colariccio et al., 2001a).

In 2002, TCSV was isolated from gilo (*Solanum gilo*) showing mosaic, blistering and stunting symptoms in the state of São Paulo (Eiras et al., 2002). Incidence was reported as high (Rabelo et al., 2002).

In Argentina, TCSV has been detected in celery, lettuce, lisianthus, potato, sweet pepper, tomato as well as the weeds *Amaranthus* sp., *Datura ferox* and *Coronopus didymus* and the ornamental *Portulaca oleracea* (Dal Bio et al., 2001; Gracia et al., 1999; Granval de Millan et al., 1998).

Tomato spotted wilt virus *(TSWV)*

'Spotted wilt' disease of tomato was first recognised in Victoria in Australia in 1915 (Brittlebank, 1919). Later, it was demonstrated that the disease was transmitted by *T. tabaci* (Pittman, 1927). In 1930, 'spotted wilt' was found to have a viral etiology and *Frankliniella schultzei* implicated as another vector (Samuel et al., 1930). The virus became known as tomato spotted wilt virus (TSWV). Leaf symptoms on tomato included bronzing, curling necrotic streaks and spots. Plants became stunted and ripe fruit showed a paler red or yellow skin colours. Sometimes, only fruit symptoms were seen. At other times, necrotic symptoms could be so severe that the plant was killed.

TSWV was subsequently reported as the cause of many other plant diseases. In addition to tomato, some of the main crop hosts of TSWV are aubergine, cabbage, cowpea, cucumber, common bean, lettuce, papaya, pea, peanut, pineapple, potato, soybean, spinach, sweet pepper, tobacco, broad bean, celery (*Apium graveolens* var *dulce*) and cauliflower (*Brassica oleracea*) (Anon., 2002; Mumford, 1994).

By the mid-1930s, it was considered that diseases of some ornamental species were caused by TSWV (Smith, 1932; Gardener et al., 1935), though in hindsight some of these infections could have been caused by INSV. In 1935, a *Frankliniella* sp., later shown to be *F. occidentalis*, was reported as a vector of TSWV in the USA (Gardener et al., 1935).

TSWV had been identified in many countries by the 1940s, but had virtually disappeared soon afterwards as the cause of serious disease. This decline has been attributed to new and effective measures in controlling *T. tabaci* that appeared at

this time. However, in countries in Eastern Europe, where these control measures were not implemented, no decline in disease caused by TSWV occurred and *T. tabaci* remained a major vector. There have also been reports that certain populations of *T. tabaci* transmit TSWV at different efficiencies (Chitzivassiliou, 2000; see also under *Thrips tabaci* above).

Transmission of TSWV by *F. occidentalis* was confirmed by Sakimura (1962). *F. fusca* was also later found to be a vector (Sakimura, 1963). *T. palmi and T. setosus* have also been reported to transmit TSWV (Fujisawa et al., 1988).

The similarities between TSWV and animal viruses in the *Bunyaviridae* was recognised by Milne and Francki (1984). This led to the inclusion of the *Tospovirsus* genus into the *Bunyaviridae*.

There was a resurgence of disease caused by TSWV in North America and Western Europe in both protected and outdoor crops beginning in the late 1980s. The new epidemics and a general increase in incidence of diseases caused by TSWV have been attributed to the spread of *F. occidentalis* from its origin in the western part of the USA to eastern USA, Europe and other areas of the world (Marchoux et al., 1991). Some country/location examples of first occurrences and then re-emergence of diseases caused by TSWV are given below.

In the Hawaiian Islands, yellow spot disease of pineapple, which was first reported on Oahu in 1926, was later recognised as being caused by TSWV. *T. tabaci* was identified as the vector and the weed *Emilia sonchifolia* as an important reservoir of infection. Managing the weed reduced the incidence of the disease. TSWV became a limiting factor in tomato production on Oahu in the 1940s with plant losses of 75–100%. Resistance bred into tomatoes was overcome by the introduction of new strains. In 1955, *F. occidentalis* was discovered in the Hawaiian Islands and in the late 1960s epidemics of TSWV began to occur in lettuce, tomato and other vegetable crops on the sheltered side of Oahu in the summer months. Although tolerated initially, TSWV increasingly forced some growers to stop production or to produce alternative crops. In 1989, TSWV caused 50–90% losses in lettuce during any season of the year. A similar pattern of TSWV build-up occurred on Maui and Hawaii. In the early to mid 1980s, TSWV started to cause economic losses in lettuce. By 1989, major losses were also occurring in tomato and sweet pepper. At this time, *T. tabaci* was no longer regarded as the most significant vector of TSWV in Hawaii. Likewise, *F. schultzei*, which was rarely collected on lettuce, tomato and sweet pepper, was deemed relatively unimportant. The predominant vector was believed to have been *F. occidentalis*, which was implicated in TSWV epidemics on lettuce, sweet pepper, tomato and chrysanthemum (Cho et al., 1989).

TSWV was first reported in Greece in 1972 in tobacco crops and was associated with infestations of *T. tabaci*. After 1989, TSWV occurred mainly in tomato and sweet pepper crops in northern Greece. This was associated with the spread of *F. occidentalis*. Sweet pepper crops were severely affected and crop failures were frequent in glasshouses. Since then, TSWV has been found in lettuce, peanut, endive and ornamentals including *Anemone*, *Callendula*, *Callistephus*, *Cineria*, *Dahlia, Chrysanthemum*, *Dieffenbachia*, *Gazania*, *Gerbera, Impatiens*, *Ranunculus*, *Salvia*, and *Zinnia* (Chatzivassiliou et al., 1996). In a more recent survey, very high levels of infection were found in *Gazania*, *Dahlia*, *Chrysanthemum* and *Tropaeolum* with *Antirrhinum*, *Aster*, *Beloperone*, *Catharanthus*, *Cellosia*, *Coleus*, *Dianthus, Fuchsia Saintpaulia*, *Tagetes* and *Zantedeschia* (Chatzivassiliou et al., 2000). The symptoms caused by TSWV in *Dahlia* in the UK are illustrated in Figure 1f.

TSWV was first reported in Portugal in 1990 in association with imported ornamental plants. As a quarantine precaution, all these plants were destroyed. However, several glasshouse crops infested with *F. occidentalis*, which was probably introduced into Portugal in 1989, were found to be infected with TSWV in 1991. In 1996, TSWV was reported in 30 different species including vegetables, ornamentals and weeds. Lettuce, sweet pepper and tomatoes were among crops most seriously affected, but others susceptible were broad bean, common bean, potato, aubergine, onion and chicory (*Cichorium intybus*). Ornamentals with TSWV included *Antherium*, *Convolvulus*, *Conyza*, *Dracaena*, *Fuchsia*, *Gladiolus*, *Hydrangea*, *Jasminum*, *Nerium*, *Pelargonium*, *Penstemon* and *Sinningia* (Louro, 1996).

The first report of TSWV in the UK was in 1929 on ornamental winter cherry (*Solanum capsicastrum*) with concentric ring symptoms on leaves. Host range studies showed that many species in

the Solanaceae were susceptible as well as some ornamentals in other plant families (Smith, 1932). A little later, natural infections were reported on tomato, potato and dahlia, and *T. tabaci* was found to be the vector. TSWV became one of the most important diseases of tomato in the 1930s, but its significance diminished after the mid-1940s and it virtually disappeared. However, a number of serious outbreaks were reported in 1987, beginning mostly on chrysanthmum. In 1989, cineraria, cyclamen and tomato were affected followed in 1990 by begonia, impatiens, lettuce, pelargonium and primula. The reappearance of diseases caused by TSWV occurred soon after the arrival of *F. occidentalis* in the UK in 1986. Measures aimed at excluding *F. occidentalis* were in place until 1989, but by then the pest was widespread and controls were lifted (Baker et al., 1993; Mumford, 1994).

The documented host range of TSWV was expanded in the 1980s as the use of more sophisticated diagnostic techniques, such as DAS-ELISA using polyclonal antibodies to the whole virion (Gonsalves and Trujillo, 1986), became possible. Antisera developed against TSWV from lettuce were used to detect the virus in individual infected thrips (Cho et al., 1988). When TSWV-specific monoclonal antibodies were developed and antisera raised against different parts of the virus, such as the N protein, virus isolates formerly designated as 'strains', could be compared (Sherwood et al., 1989; de Ávila et al., 1990; Law and Moyer, 1990; Wang and Gonsalves, 1990; Adam et al., 1991). This led to the identification of an impatiens strain of TSWV (Law and Moyer, 1990; Law et al., 1991a, b, c), which became known as INSV. Since 1991, various other TSWV-like viruses have been reported to be serologically distinct and different species.

In 1995, *F. schultzei* was confirmed as a vector and *F. intonsa* found to be an additional vector (Wijkamp et al., 1995). *F. bispinosa* was shown to transmit TSWV in 1998 (Webb et al., 1998). In 2004, *F. intonsa*, *F. occidentalis*, *T. tabaci* and *T. setosus* were confirmed as vectors, but not *T. palmi*. The *Frankliniella* species were more efficient vectors than the *Thrips* species. *T. hawaiiensis* was found not to transmit TSWV (Inoue et al., 2004). The transmission of Australian isolates of TSWV by *T. palmi* and *F. shultzei* has recently been reported (Persley et al., 2005).

TSWV has now been detected on a very wide range of hosts (1090 plant species in 15 families of monocotyledonous plants, 69 families of dicotyledonous plants and one family of Pteridophytes) (Parrella et al. (2003).

New crop hosts in new locations are regularly being found. Habanero pepper and Tabasco pepper were recorded as hosts for the first time in Florida in 2000 (Momol et al., 2000). TSWV has been recorded in many countries in North and South America, Africa, Europe, Asia and Australasia (Anon., 2002). TSWV is prevalent because there are many weed hosts that harbour the pathogen (Hobbs, 1996; Chatzivassiliou et al., 1998; Cho and Mau. 1998; Mertelik et al., 1998; Wilson, 1998; Mertilik and Mokrá, 1999) and its main vector *F. occidentalis* is difficult to control.

TSWV was first detected in Australia, but it was subsequently found on all continents in a short period of time. TSWV may have been the first tospovirus to spread and hence become recognised because (1) it was the first to infect a variety of ornamentals that were traded internationally and (2) its vector *T. tabaci* was the first thrips to attain a world-wide distribution. TSWV is related to others in the 'American' groups of Chu et al. (2001) and Silva et al. (2001) and one could hypothesise an American origin. However, this is by no means certain.

TSWV is the type species of the *Tospovirus* genus (Elliot et al., 2000).

Watermelon bud necrosis virus *(WBNV)*

A virus serologically related to the TSWV-W isolates from Taiwan and Japan has been reported causing a disease of watermelon near Bangalore in Karnataka state, India (Singh and Krishnareddy, 1996). Incidence of the disease caused by the virus was reported as 39–100% with an estimated yield loss of 60–100%.

The virus caused symptoms on watermelon that were characterised by leaf mottling, yellowing and necrotic streaks on veins, shortened internodes, and necrosis and dieback of buds (Jain et al., 1998b).

The vector of this virus was identified as *T. flavus* (Singh and Krishnareddy, 1995), but this species can easily be mistaken for *T. palmi* (Mound, 1996). A similar disease of watermelon

was reported in the states of Andra Pradesh and Maharshtra (Singh and Krishnareddy, 1995). The virus was named WBNV.

Sequence analysis of the N protein showed that the virus was most closely related to that of WSMoV from Taiwan (84% identity) and GBNV (82% identity) from India in Serogroup IV. It was concluded from this and the results of host range studies that WBNV was a distinct tospovirus (Jain et al., 1998a, b). WBNV was not recognised as a virus species by Elliot et al. (2000), but Chu et al. (2001) considered it to be a distinct species.

Recently, a strain of WBNV has been identified in ridge gourd (*Luffa acutangula*) with yellowing leaves near Coimbature in Tamil Nadu state in India (Mandal et al., 2003).

Watermelon silver mottle virus *(WSMoV)*

In 1982, a 'strain of TSWV' was first found infecting watermelon in Japan. The symptoms caused by this virus were described as a silver mottle on leaves and a chlorotic mottle on fruit, which were malformed. The disease was different from other known diseases of watermelon and caused considerable reductions in yield and quality of fruit from infected plants (Iwaki et al., 1984).

Mechanical inoculation experiments showed that the virus was systemic in a range of economically important plants including melon, cucumber, sweet pepper, tomato, tobacco and squash (*Cucurbita pepo, C. maxima*) (Iwaki et al., 1984).

The watermelon strain of TSWV in Japan was later reported to be serologically distinct from TSWV and it was named TSWV-W (Kameya-Iwaki et al., 1988).

In 1988, novel disease symptoms were seen on watermelon in Taiwan. Affected plants were stunted with shortened internodes. Younger branches grew upright and tip necrosis and dieback were observed. Leaves were mottled and crinkled with a reduced leaf lamina and yellow spots. Fruit was small and malformed with necrotic spots or a silver mottle. Fruit set was reduced. A virus isolated from diseased plants appeared to be a tospovirus from particle morphology, serology and host reactions, and because it was transmitted by *T. palmi*. It was different in serological reactions from isolates of TSWV, but related to the virus isolated from watermelon in Japan. The isolate was also designated TSWV-W. The same virus was causing a damaging epidemic on melon in Taiwan (Yeh et al., 1992).

The watermelon isolates from Japan and Taiwan (both designated TSWV-W), a peanut isolate from India (designated GBNV) and a tomato isolate from Taiwan (designated Topso-To) were all shown to possess larger N proteins than other tospoviruses. GBNV was suggested as the virus name for all these isolates (Adam et al., 1993). However, the N gene of a Taiwanese isolate of the virus from watermelon designated Tospo-W was later found to have a distinct nucleotide sequence and the name watermelon silver mottle virus (WSMoV) was proposed (Yeh and Chang, 1995). It was later revealed that Tospo-To was a strain of WSMoV with 98.7% S RNA sequence homology (Heinze et al., 1995; Yeh et al., 1996). Satyanarayana et al. (1996) also concluded that this virus, designated PBNV-To, was a strain of WSMoV from 99% amino acid sequence identity of their N proteins.

A strain of WSMoV, which was determined by serological tests and transmission by *T. palmi*, was isolated from wax gourd (*Beincasa hispida*), a cucurbit growing in Taiwan (Chen et al., 1995). WSMoV has become a major limiting factor for growing watermelon and other cucurbits in Taiwan (Yeh and Chu, 1999).

More recently, WSMoV has been detected in glasshouse tomato in the western part of Thailand where symptoms were described as leaf, bud and stem necrosis (P. Chiemsombat, Kasetsart University, pers. comm.).

Zucchini lethal chlorosis virus *(ZLCV)*

Although previously sporadic in occurrence, many plants of zucchini (*Cucumis pepo*) were seen with symptoms of a disease that is now known to be caused by ZLCV in Campinas County in São Paulo state in Brazil in 1991 (Nakahar and Monteiro, 1999). Severe mosaic, leaf distortion, stunting and often death are symptoms on zucchini. At the time, *Watermelon mosaic virus* was suspected as the causal agent (Bezerra et al., 1999). However, a tospovirus isolated from zucchini in 1993 was thought to be a possible new species in a new serogroup (Pozzer et al., 1994a).

Field-grown melon was observed with concentric ringspots on leaves and fruit, fruit malformation

and stunting in 1991. At the time, it was suggested that these symptoms may have been caused by the strain of TSWV responsible for watermelon silver mottle disease in Japan. Using an antibody to TSWV, the causal virus was found to be related to, but serologically distinct from TSWV (Boiteux et al., 1994).

Since 1991, disease symptoms on zucchini in São Paulo state were observed with more frequency (Nakahar and Monteiro, 1999). In the late 1990s, large areas of zucchini were found diseased with accompanying high yield losses of marketable fruit (Bezerra et al., 1999).

During a survey in six states in Brazil in the mid 1990s, 15 isolates of tospovirus from a range of plants failed to react in DAS-ELISA tests with antisera of the TSWV, TCSV, GRSV and INSV, which were recognised as present in the country at that time. Four candidates for new tospovirus species were discovered. One isolated from chrysanthemum and designated Chryl 1 and another isolated from tomato and designated Br11t were both later found to be CSNV. A third isolated from onion and designated Br10o was later found to be a strain of IYSV. A fourth designated as Br-09z was isolated from zucchini in São Paulo state. Serological relationship studies using polyclonal antibodies against the N-protein and Western blot analysis indicated that the isolates were representatives of three new serogroups within the genus Tospovirus (Resende et al., 1996).

Br-09z had a narrow artificial host range infecting only a few species in the Amaranthaceae, Cucurbitaceae and Solanaceae. After a few mechanical passages through hosts, Br-09z hardly infected cucurbit hosts. Fresh isolates that strongly reacted with Br-09z antiserum were able to systemically infect new hosts, such as *Capsicum annuum* and *Datura stramonium*. This suggested to the authors that host range studies are not stable parameters to classify tospoviruses because many isolates may drastically reduce their virulence after a few mechanical passages (Resende et al., 1996).

In 1996, the name 'zucchini lethal chlorotic virus' was proposed for the new virus (Pozzer et al., 1996) and information was later given on its incidence, biological and serological characteristics (Resende et al., 1997).

During the survey in the mid 1990s when isolate Br-09z was collected from zucchini, an unknown tospovirus was also found in cucumber (*Cucumis sativus*) in the Federal district of Brazil. These isolates were now found to react strongly with the antibody to 'zucchini lethal chlorosis tospovirus', and not with antibodies to TSWV, TCSV, GRSV, CSNV or IYSV, which were the other tospoviruses identified in Brazil by this time (Nagata et al., 1998). This indicated that both zucchini and cucumber were natural hosts of the new virus, which now also occurred at a location outside São Paulo state.

Published host range studies showed that the virus, as Br-09, became systemic in watermelon cucumber, melon and zucchini. Infected zucchini plants showed symptoms identical to those observed in the field. In vector studies, *F. occidentalis*, *F. schultzei* and *T. tabaci* failed to transmit the virus (Bezerra et al., 1999). *Frankliniella zucchini* has been identified as a vector of the virus (Nakahara and Monteiro, 1999), though this was not officially ratified by Elliot et al. (2000).

The nucleotide sequence of the N gene of the virus displayed some similarities with previously described tospovirus species ranging from 20 to 75%, but was more closely related to CSNV at 80% homology. A new tospovirus species was proposed with the name 'zucchini lethal chlorosis virus' (Bezerra et al., 1999). It has now been officially recognised as a new species and has been designated as ZLCV (Elliot et al., 2000).

ZLCV can be said to have a high incidence on zucchini in Brazil and to occur sporadically on melon, watermelon and cucumber. A virus found in chayote (*Sechium edule*) reported by Silveira et al. (1985) as TSWV may also have been ZLCV, but the isolate is no longer available for study (A. de Ávila, EMPRAPA, and J. Rezende, University of São Paulo, pers. comm.).

Tentative tospovirus species

Calla lily chlorotic spot virus (CCSV)

During a survey of calla lilies (*Zantedeschia* spp.) in nurseries in Taiwan in 2001, chlorotic spots and a few yellow spots about 2 mm in diameter were seen radiating from the midrib of middle leaves of some plants. A virus, which had the characteristics of a tospovirus, was isolated from symptomatic plants (Chen et al., 2005).

In mechanical inoculation studies, the virus systemically invaded calla lily, watermelon, melon,

cucumber, pumpkin, wax gourd (*Benicasa hispida*), and other species. Symptoms were mostly light green spots on leaves. Further work showed that the virus was transmitted by *T. palmi* (Chen et al., 2005).

The virus reacted weakly, but positively, to WSMoV antiserum in ELISA tests and in immunoblot analysis, but not with antisera to TSWV, INSV or PCFV. A DNA fragment was amplified by RT-PCR from total RNAs extracted from virus-infected plants using degenerate primer pairs designed from the conserved regions of L genes of tospoviruses. The amplified DNA product was cloned and the sequence compared with the conserved region of the L proteins of WSMoV, TSWV, INSV, GBNV, MYSV and tomato yellow fruit ring virus (TYFRV). The results showed that the virus, named calla lily chlorotic spot virus (CCSV), was closest in this analysis to WSMoV and furthest from INSV.

CCSV has been tentatively proposed as a new tospovirus species (Chen et al., 2005).

Cineraria tospovirus

A tospovirus has been isolated from cineraria (*Senecio* sp.) growing in a glasshouse of a commercial nursery in Shiraz in Iran. Symptoms include leaf ring spots and chlorotic/necrotic areas on leaves, and wilting. Three populations of *T. tabaci* have transmitted the virus (K. Izadpanah, Shiraz University, pers. comm.).

Polyclonal antisera have been developed against the nucleocapsid and whole particles. Using the antisera, the virus has been detected in several crops including tomato, sweet pepper and aubergine (K. Izadpanah, Shiraz University, pers. comm.).

The L protein-like gene of this tospovirus isolated from *Cineraria* in Iran has been partially sequenced and details lodged with the National Center for Biotechnological Information (Anon., 2004a). Sequences seem closer to GBNV and INSV than to TSWV, although symptoms are more similar to those caused by TSWV (K. Izadpanah, Shiraz University, pers. comm.).

Gloxinia-HT virus (GHTV)

This virus was discovered during studies into defective forms of tospoviruses. Defective forms of TSWV and INSV that fail to produce virions after repeated mechanical transmission have been identified in the past (Ie, 1982; Verkleji and Peters, 1983; Urban et al., 1991). In experiments involving the serial passage of an isolate of INSV from gloxinia (*Sinningia speciosa*) through *Nicotinia benthamiana*, changes in cytopathology and serological reactions were observed in plants grown at high temperature (Lawson et al., 1992, 1993, 1994, 1996). One of the high temperature variants designated HT-1 that was recovered from the INSV-infected plant produced a heterogenous mixture of viral structure and modified host membranes (Lawson et al., 1993, 1994). In addition, the HT-1 isolate did not react with polyclonal antisera produced against the N protein of INSV (Hsu and Liu, 1996).

It was initially thought that the HT-1 isolate was derived from the defective isolate of INSV (Lawson et al., 1996). However, the defective INSV virus and the HT-1 virus showed very distinct cytopathological and serological properties (Hsu and Liu, 1996; Lawson et al., 1992, 1993, 1994, 1996).

In later investigations, HT-1 was shown to be serologically related to WSMoV, but not to INSV or TSWV. The conclusion was that the HT-1 was unlikely to have been derived from INSV. The HT-1 virus shares high N gene nucleotide (76–81%) and derived N protein amino acid (85–92%) similarities with WSMoV and GBNV. The virus was proposed as a distinct species in Serogroup IV. This was the first time that a tospovirus similar to those found in Asia had been identified in the USA (Hsu et al., 2000).

Phalaenopsis chlorotic ringspot virus (PCRV)

This tospovirus was isolated from a *Phalaenopsis* orchid showing chlorotic ringspots collected in southern Taiwan. After purification, polyclonal and monoclonal antibodies were produced against the N protein. Serological tests showed that the virus was unrelated to TSWV, GRSV, INSV, WSMoV and GCFLV, which are serologically distinct (Table 1). The same virus was also isolated from tomato in the field (Chen et al., 1998).

The virus has a strong serological reaction to WSMoV. The S RNA sequence indicates that it is closely related to Gloxinia HT-1 virus and it may be a strain of CaCV. By mechanical inoculation, most *Phalaenopsis* spp. cultivated in Taiwan are reported to be susceptible (S.D. Yeh, National Chung Hsing University, pers. comm).

Potato stem necrosis virus (PSNV)

Since 1982, a disease of early potato crops characterised by extensive stem and petiole necrosis, leaf spotting and deformation plus stunting have been seen in the states of Madhya Pradesh and Rajasthan in India. Incidence has been reported as up to 80% causing losses of up to 40%. A tospovirus, which reacted strongly with antiserum raised against GBNV and moderately to antisera raised against WSMoV and WBNV, was detected in diseased tissue. These tests indicated that the virus belonged to Serogroup IV (WSMoV group) (Khurana et al., 1998; Jain et al., 2000).

The same potato cultivars as those found infected were inoculated with GBNV. This resulted in a few small necrotic spots on leaves, but petiole and stem necrosis, dwarfing and chlorosis of plants were not observed (Khurana et al., 1998).

Transmission of the virus was demonstrated using *T. palmi* and *S. dorsalis*, which have been reported as vectors for GBNV (Khurana et al., 1998).

Further characterisation of the tospovirus is required to determine relationships with GBNV and other known species.

Pterostylis blotch virus (PtBV)

Several plants of *Pterostylis curta*, *P. hispidula*, *P. plumosa*, *P. reflexa*, *P. revoluta* and *P. aff. parviflora* from five locations in the Australian Capital Territory, New South Wales and Victoria in Australia were found with chlorotic blotch symptoms. The virus has gene sequences that are related to, but distinct from, those of other tospovirus and its virions react only weakly with antisera against TSWV and INSV. It was concluded that the wild orchids were infected with a previously undescribed tospovirus and the name Pteroslytis blotch virus was proposed (Gibbs et al., 2000).

The identity of the thrips vector is not known. The relationship of this virus with Phalaenopsis chlorotic ringspot virus from Taiwan has not been investigated.

Sunflower necrosis virus (SuNV)

Sunflower in Bangalore, Dharward and Hyderabad in India was seen with a disease causing necrosis of leaves, petioles, stems and the floral calyx. A virus isolated from an affected plant showed a positive serological relationship with GBNV and WSMoV in ELISA tests using polyclonal antisera directed against the N protein (Jain et al., 2000a).

In a separate report, a tospovirus was found in sunflower with severe mosaic and systemic necrosis along the stem and floral heads, leaf distortion and leaf ringspots symptoms in and around Tirupati in India. In ELISA tests, the purified virus reacted with antiserum to GBNV, but not with antisera to IYSV, TSWV and INSV. From the results of this and other research, it was considered possible that the virus may be a distinct isolate in Serogroup IV (Subbaiah et al., 2000). However, the exact identity of the virus remains to be determined (Jain et al., 2000a).

Tomato necrosis virus (ToNV)

A tospovirus isolated from field-grown tomato and sweet pepper in northeastern Thailand has been given the name Thailand tomato virus. Symptoms caused by this virus included chlorotic/necrotic ringspots on fruit and leaves (P. Chiemsombat, Kasetsart University, pers.comm.). Nucleotide sequences of the N gene have been lodged with the National Center for Biotechnology Information (Anon., 2004a).

The nucleotide sequences of this virus were found to have 98% homology with another tospovirus from tomato in central Thailand that was given the name tomato necrosis virus. Symptoms caused by this strain included severe necrosis of leaves and chlorotic ringspots on fruit (P. Chiemsombat, Kasetsart University, pers. comm.). Nucleotide sequence information on the N gene of this strain is also available from the website of the National Center for Biotechnology Information. The virus is reported to be in Serogroup IV (WSMoV group) (Anon., 2004a).

Tomato TSWV-B

A tospovirus isolate from tomato in Brazil (Wang and Gonsalves, 1990) was found to infect a transgenic tobacco plant, which displayed a broad spectrum of resistance to various other isolates of TSWV (Pang et al., 1992). The isolate caused a systemic mottle and crinkle in leaves of infected tobacco and *Nicotinia benthamiana*, but did not infect squash or cucumber. ELISA (enzyme-linked

immunosorbent assay) with polyclonal antibodies against the N protein of TSWV and INSV showed that the N protein of the isolate was not serologically related to either TSWV or INSV (Pang et al., 1992).

In later work, the isolate, which was designated as TSWV-B, was found to systemically infect *Petunia hybrida*, which was a local lesion host of TSWV. Nucleotide sequence analysis of the S RNA indicated that TSWV-B was related more to other TSWV isolates than to INSV. However, TSWV-B appeared to be a distinct tospovirus (Pang et al., 1993).

Analysis of the intergenic region sequences of the S RNA of TSWV-B showed it to be different from TSWV, INSV, GBNV, WSMoV, IYSV, GYSV and GCFSV (Pappu et al., 2000).

Tomato yellow fuit ring virus (TYFRV)

TYFRV, as tomato Varamin virus (ToVV), was first isolated from tomato in the Varamin area of Iran, which is about 35 km to the southeast of Tehran. Symptoms were very similar to those caused by TSWV. An isolate was lodged with Deutsche Sammlung von Mikroorganismen und Zellkulturen in Braunschweig (DSMZ) in Germany (N. Shahraeen, PPDRI, pers. comm.).

Antiserum produced by DSMZ detected TYFRV as well as TSWV in symptomatic field samples of tomato, soybean and potato in Iran (Sharaeen and Ghotobi, 2003). The incidenece of TYFRV in crops suggests that it is of considerable economic importance (Ghotobi et al., 2005).

TYFRV has also been found in ornamentals in the genera *Alstroemeria, Althea*, *Calandula*, *Cheiranthus*, *Cineraria*, *Cycas*, *Cyclamen*, *Dendranthema*, *Ficus*, *Helianthus*, *Pelargonium*, *Rosa* and *Saintpaullia* in Tehran province In the Mahallet area of Markazi province, additional ornamental genera found infected with TYFRV include *Anthirrhinum*, *Bougainvillea*, *Dahlia*, *Dianthus*, *Gazania*, *Gomphrena*, *Jasminum*, Linda, *Lonicera*, *Magnolia*, *Tagetes*, *Tropaeolum* and *Verbena*. Mixed infections with TSWV, INSV or IYSV were reported. One *Gazania* had TYFRV plus TSWV and INSV in a mixed infection of three tospoviruses. Weeds in the genera *Amaranthus*, *Chenopodium*, *Cuscuta*, *Euphorbia*, *Portulaca* and *Rosmarinus* were found with TYFRV. In addition, *Lactuca aculeata* has been recorded as TYFRV positive in infected chrysanthemum fields (Shahraeen and Ghotbi, 2003; Ghotobi et al., 2005; N. Shahraeen, PPDRI, pers. comm.).

TYFRV has been partially sequenced at DSMZ. Sequence information, serology and other characteristics indicate that is a distinct tospovirus. It is more related to IYSV (72–75% identity) than to any other tospovirus (S. Winter, DSMZ, pers. comm.).

The thrips vector of TYFRV has not been absolutely determined, but the virus has been consistently detected in *T. tabaci* from ornamentals. *F. occidentalis* has not yet been found infesting ornamentals in Tehran and Markazi provinces (Ghotobi et al., 2005).

Verbesina mosaic virus (VMV)

Mosaic symptoms were observed in yellow ironweed (*Verbesina alternifolia*) in Arkansas in the USA and the inoculation of sap to *Chenopodium quinoa* and *Nicotinia rustica* resulted in local necrotic lesions. Ultastructural studies of the local lesion hosts revealed virus particles similar to TSWV, but unlike TSWV they were individually enclosed in a second outer membrane. In addition, cytoplasmic inclusions were not typical of those induced by TSWV. ELISA tests showed no serological relationship between the virus and common isolates of TSWV or an isolate of INSV (Hayati et al., 1990). No further reports of this virus have been published.

Origin of the tospoviruses

The origin of tospoviruses has not been satisfactorily determined. Although the first record of TSWV, which was the first tospovirus to be identified, was from Australia, it most likely did not originate from this continent (Best, 1968). Tospoviruses present in Australia have been predominantly recorded in non-native plant species and are vectored by non-native thrips species so they are most likely introductions. Also, it cannot be assumed that a tospovirus originates in an area where its thrips vectors originate. The virus may have acquired an association after the thrips vectors had been disseminated from their centre of origin (Mound, 2001a).

The evolution of the tospoviruses can only be speculated. Genetic mutation, genome segment

reassortment and perhaps the occasional recombination event has undoubtedly led to the production and spread of those tospovirus genomes that can take advantage of new thrips vectors and new host species. Recent work on molecular population genetics of tospoviruses has identified positive selection pressure favouring divergence between species (Tsompana et al., 2005).

Thrips transfer tospoviruses at different efficiencies. The fitness and adaptability of the thrips is another important factor in determining tospovirus incidence. Some thrips that are vectors of tospoviruses have increased their distribution dramatically in the last few decades. The movement of *F. occidentalis*, a moderate to efficient tospovirus vector with a very large number of hosts, to new environments around the world has resulted in a worldwide increase in diseases caused by those tospoviruses that can utilise this insect and infect its hosts.

An early attempt to classify tospoviruses was based on nucleotide sequences of the N gene. This showed a putative phylogenetic tree for TSWV, GRSV, TCSV and INSV, which spanned three serogroups (de Ávila et al., 1993). Pappu et al. (2000) conducted phylogenetic studies based on intergenic region sequences of S and M RNAs. This work found that percent identity of S RNA between distinct tospovirus species varied from 42 to 57%, whereas it was 79 to 99% among isolates of the same species. Between M RNAs, identity between isolates of the species was 84–98% compared to 46–59% between different species. Phylogenetic trees derived from S RNA and M RNA analysis were produced that showed relationships between GYSV and GCFSV, and GBNV and WSMoV. IYSV was more related to GYSV and GCFSV than GBNV and WSMoV. INSV was more akin to TSWV than others. A later phylogenic study of tospoviruses based on N and NS_M proteins placed TSWV, TCSV, GRSV, ZLCV, CSNV, and INSV together as in an 'American' group and WSMoV, WBNV, GBNV, and IYSV in a 'Eurasian' group. These designations were believed to reflect the most probable region of virus origin (Silva et al., 2001).

Chu et al. (2001) produced a phylogram showing relationships between 13 tospovirus species based on amino acid sequences of the nucleocapsid protein (Figure 2). TSWV, TCSV, GRSV, ZLCV and CSNV cluster in a 'South America' group with INSV having a close affinity. GBNV, WSMoV and WBNV form another cluster in a 'South and East Asia' group that has affinities to MYSV (=PhysMV) and IYSV. GCFV and GYSV are remote from both the 'South America' and 'South and East Asia' groups. Both of these have been detected only in South Asia and have been reported to have *S. dorsalis* as their vector.

If one origin of the tospoviruses is accepted and not two as has been suggested by Silva et al. (2001), it is likely that this tospovirus precursor may have arisen in South or East Asia. These are the regions where 10 of the 14 tospovirus species are found and the only locations where six of these have been recorded (Table 2). These six tospoviruses fall into four of the seven recognised tospovirus subdivisions (Table 2). Centres of greatest genetic diversity of a pathogen group are usually centres of origin.

Ilarviruses transmitted by thrips

There have been a number of reports of the transmission of viruses in the *Ilarvirus* genus by thrips. Transmission involves the physical movement of virus-carrying pollen from one plant to another by the thrips vector.

Transmission of TSV by a *Frankliniella* species was first recorded in Brazil (Costa and da Costa Lima Neto, 1976). Later, transmission by a mixture of *T. tabaci* and *F. occidentalis* was described in Washington State in the USA (Kaiser et al., 1982). Further work showed that transmission involved the physical movement of virus-carrying pollen to a recipient host. Infection was presumed to have occurred as a result of the virus-carrying pollen becoming intimately associated with wounds caused by feeding thrips. *T. tabaci and Microcephalothrips abdominalis* were found to be vectors (Sdoodee and Teakle, 1987; Greber et al., 1991b). In an additional study, the thrips species *F. schultzei* and *T. parvispinus* were also shown to transmit TSV with virus-carrying pollen. The efficiency of transmission varied considerably with factors associated with the virus-affected pollen (Klose et al., 1996). The spread of TSV in tomato plants in southern France may be due to thrips (Marchoux et al., 1999).

TSV causes a serious disease of peanut and sunflower in India. Pollen from sunflowers infected with TSV was dusted onto cowpea leaves and

Table 2. The distribution of tospovirus species and a list of their vectors – most viruses within horizontal lines are related at the amino acid sequence level of the N gene (Chu et al., 2001)

Tospovirus	Continent of distribution	Vector(s)
TSWV	North America, South America, Africa, Europe, Asia (West, South and East) and Australia	*Frankliniella bispinosa, F. fusca. F. intonsa, F. occidentalis, F. schultzei, Thrips. palmi, T. setosus, T. tabaci*
TCSV	South America, Asia (West)	*Frankliniella intonsa, F. occidentalis, F. schultzei.*
GRSV	South America, Africa	*Frankliniella occidentalis, F. schultzei*
CSNV	South America, Europe	*Frankliniella occidentalis, F. schultzei*
ZLCV	South America	*Frankliniella zucchini*
WSMoV	Asia (East)	*Thrips palmi*
WBNV	Asia (South)	*Thrips palmi?*
GBNV	Asia (South)	*Frankliniella shultzei*[b], *Thrips palmi*
CaCV[a]	Asia (East), Australia	*Ceratothripoides claratris, Thrips palmi*
INSV	North America, South America, Africa, Europe, Asia (West, South and East), Australia	*Frankliniella fusca, F. intonsa, F. occidentalis*
MYSV (=PhySMV)	Asia (East)	*Thrips palmi*
IYSV	South America, Europe, Asia (West, South and East), Australia	*Thrips tabaci*
GYSV	Asia (South)	*Scirtothrips dorsalis*
GCFV	Asia (South)	*Scirtothrips dorsalis*

Key: [a]Included with WSMoV group because of <85% nucleotide and amino acid sequence identity with recognised members of Serogroup IV (McMichel et al., 2002); [b]transmits GBNV at a very low frequency (Lakshmi et al., 1995); CaCV, *Capsicum chlorois virus*; CCSV, Calla lily chlorotic spot virus; CSNV, *Chrysanthemum stem necrosis virus*; GBNV, *Groundnut bud necrosis virus*; GCFV, *Groundnut chlorotic fan-spot virus*; GRSV, *Groundnut ringspot virus*; GYSV, *Groundnut yellow spot virus*; INSV, *Impatiens necrotic spot virus*; IYSV, *Iris yellow spot virus*; MYSV, *Melon yellow spot virus*; PhySMV, Physalis severe mottle virus; TCSV, *Tomato chlorotic spot virus*; TSWV, *Tomato spotted wilt virus*; WBNV, *Watermelon bud necrosis virus*; WSMoV, *Watermelon silver mottle virus*; ZLCV, *Zucchini lethal chlorosis virus*. Asia (South) is defined as the Indian subcontinent, Asia (West) as Iran and environs, Asia (East) as China, Japan and Southeast Asia. The abbreviation of the type representative of the two tospovirus groups identified is in bold font.

F. schultzei allowed to feed. The cowpeas became systemically infected with TSV. It was suggested that damage caused by the feeding thrips allowed infection to occur (Reddy et al., 2002).

The transmission of PNRSV to cucumber in infected plum pollen dusted on to *T. tabaci* has been reported (Greber et al., 1991a). Other thrips species are likely to transmit pollen-borne ilarviruses in a similar manner.

Other viruses transmitted by thrips

PFBV, which is a carmovirus, has been shown in experiments to be transmitted from infected to healthy pelargonium plants by *F. occidentalis* (Krczal et al., 1995). The thrips is implicated in moving pollen carrying the virus, which infects through feeding wounds, in much the same way as described for TSV above.

Chenopodium spp. became infected with SoMV, a sobemovirus, when *Thrips tabaci* were allowed to feed on leaves dusted with pollen from an infected *C. amaranticolor* plant. Transmission also occurred when *T. tabaci* was dusted with virus-carrying pollen and then transferred to leaves of *C. quinoa*. Tests showed that most virus was carried superficially on the pollen surface (Hardy and Teakle, 1992).

Transmission of SoMV by *T. tabaci* also occurred between infected and non-infected non-flowering *Chenopodium* seedlings in the absence of virus-carrying pollen. This indicated that the virus was acquired by the thrips during feeding. SoMV is unusual in that it is transmitted by insects belonging to several different orders (Bennett and Costa, 1961). The high stability of SoMV and its high concentration in plants is believed to contribute to its survival on the mouthparts of its insect vectors (Hardy and Teakle, 1992).

MCMV, a machlomovirus, has been listed as thrips-transmissible by Ullman et al. (1992). Although the method of transmission is unknown, it has been suggested that it may be non-circulative (Jiang et al. unpublished data reported in Ullman et al., 1992). An outbreak of MCMV in Hawaii may have been associated with thrips (Jiang et al., 1990).

Discussion

Thrips can transmit viruses as (1) a mechanical accident of feeding on leaves covered with virus-carrying pollen, (2) by transferring virus-carrying pollen and then infecting by mechanical accident through feeding and (3) as the result of a more sophisticated relationship in which the virus is ingested and multiplies within the body of the insect. The third mechanism, which is restricted to viruses in the *Tospovirus* genus, has resulted in the most serious threat to world agriculture.

The incidence of some tospoviruses in many ornamentals indicates that the global floriculture industry has helped harbour and spread these pathogens. TSWV and INSV in particular are known to have a wide ornamental host range and the number of ornamental hosts of IYSV is increasing. A recent analysis of the amino acid sequences of proteins encoded by genes of TSWV isolates from a number of countries suggests that an isolate from the Netherlands may have been introduced to North Carolina in the USA, possibly in imported dahlia (Tsompana et al., 2005).

It may be that the ability to infect many hosts is inherent in tospoviruses. If this assumption proves to correct, then polyphagous thrips that are also vectors would be expected to spread the tospoviruses they transmit efficiently to many species in nurseries.

Thrips, some of which are virus vectors, have been detected hitch-hiking on ornamentals moving in international trade. The cut flower trade in particular has been implicated in this movement. Notifications of interceptions provided by EU Member States since 1995 suggest that thrips are regularly found on cut orchid flowers originating in Thailand. Thrips have also been found on occasions on orchid flowers from Malaysia and Singapore. Cut flowers of *Chrysanthemum*, *Dianthus*, *Eryngium*, *Gypsophila, Gladiolus, Iris*, *Liatris*, *Ranunculus*, *Ornithogalum*, *Magnoliophyta* and *Proteus* from South Africa have also been found to harbour exotic thrips as well as *Bupleurum, Dianthus, Gypsophila, Eustoma* and *Veronica* from Kenya. Exotic thrips have also been detected on cut flowers of *Amaranthus*, *Campanula*, *Chrysanthemum, Dianthus*, *Gypsophila*, *Iris* and *Limonium* from the Netherlands, which is a major floral import–export centre. Interceptions have also been recorded on *Dianthus* from Ecuador and Colombia, *Helianthus* from French Guiana, *Rosa* from Brazil and *Cynara* from Spain (A. MacLeod, CSL, pers. comm.).

Other types of plant produce can also carry thrips. Thrips have been intercepted on aubergine (*Solanum melongena*) from Ghana and the Dominican Republic; sodom apple (*S. aculeatissimum*) from the Dominican Republic; balsam apple and balsam pear (*Momordica* spp.) from Kenya, the Dominican Republic, Indonesia and Bangladesh; basil (*Ocmimum basilicum*) from Thailand; *Brassica oleracea* from Spain (A. MacLeod, CSL, pers. comm.).

Although all the thrips reported to the EU were of plant health concern, the available records do not indicate the proportion of these that were virus vectors. However, some diagnostic results from the UK highlight the risks. Between 1995 and 2001, *T. palmi* was identified on many occasions on orchids and *Momordica* from Thailand, *F. schultzei* was intercepted many times on material from the Netherlands and Kenya, and *S. dorsalis* found on *Dendrobium* from Thailand and cashew from Ghana (D. Collins, CSL, pers. comm.). This and similar interception information pertaining to other quarantine pests has led to the plant inspection service in the UK targeting certain imports perceived to be of a high risk (A. MacLeod, CSL, pers.comm.).

Between 2001 and 2004, *F. schultzei* was intercepted in the UK on 10 occasions on *Veronica* imported from Kenya. During the same period, *F. schultzei* was also intercepted on *Veronica*, *Limonium* and *Aphelandra* from the Netherlands and *Trachelium* from Israel. Imports of *Gypsophila* and *Eryngium* of unknown origin were also found with *F. schultzei*. *Thrips palmi* was detected on *Dendrobium* from Thailand and a *Momordica* sp. from the Dominican Republic. *T. palmi* has been recognised as a pest that should be prevented from establishing in the UK because of potential damage to crops (MacLeod and Baker, 1998; MacLeod et al., 2004).

Table 3. Distribution of known thrips vectors of tospoviruses in Europe

Thrips vector	Tospovirus implicated as being transmitted by thrips in nature	Distribution of vector in Europe
Ceratothripoides claratris	CaCV	Not established
Frankliniella bispinosa	TSWV	Not established
Frankliniella fusca	TSWV; INSV	Netherlands only
Frankliniella intonsa	TCSV; TSWV	Widespread
Frankliniella occidentalis	CSNV; GRSV; INSV; TCSV; TSWV	Widespread
Frankliniella schultzei	CSNV; GRSV; TCSV; TSWV	Netherlands, Belgium, Spain including the Canary Islands
Frankliniella zucchini	ZLCV	Not established
Scirothrips dorsalis	GBNV; GYSV	Not established
Thrips palmi	CaCV, CCSV; GBNV; MYSV; WSMoV; TSWV	Portugal only; eradicated from protected environments in the Netherlands and UK
Thrips setosus	TSWV	Not established
Thrips tabaci	IYSV; TSWV	Widespread

Key: CCSV, Calla lily chlorotic spot virus; CSNV, *Chrysanthemum stem necrosis virus*; GBNV, *Groundnut bud necrosis virus*; GCFV, *Groundnut chlorotic fan-spot virus*; GRSV, *Groundnut ringspot virus*; GYSV, *Groundnut yellow spot virus*; INSV, *Impatiens necrotic spot virus*; IYSV, *Iris yellow spot virus*; MYSV, *Melon yellow spot virus*; TCSV, *Tomato chlorotic spot virus*; TSWV, *Tomato spotted wilt virus*; WBNV, *Watermelon bud necrosis virus*; WSMoV, *Watermelon silver mottle virus*; ZLCV, *Zucchini lethal chlorosis virus*.

The status of thrips vectors in Europe and the viruses they transmit are summarised in Table 3. *F. schultzei*, *S. dorsalis* and *T. palmi*, which are being intercepted in the UK, have not yet established. Exporting countries are endeavouring to improve control of quarantine pests at source. However, with increasing global trade in ornamentals and tropical plant produce plus global warming effects, it may only be a question of time before more thrips that are virus vectors enter and establish in the UK and in other locations in the EU.

Following the introduction of thrips vectors, movement of tospoviruses from ornamentals to crop plants may occur outdoors in countries with warm climates and in glasshouses in countries with cooler environments. Experience has shown that virus diseases usually follow the establishment of vectors. Indeed, exotic tospoviruses may already be present at a low level in ornamentals and await the opportunity to spread that would be afforded by the arrival of vectors. Multiple infections of tospoviruses in ornamentals are also not uncommon events (e.g. Daughtrey, 1996; Alexandre et al., 1999). One sample of lisiathius in Brazil has been reported to have been infected with CSNV, TCSV, GRSV and TSWV (Alexandre et al., 1999). Although recombination has not yet been shown to occur between tospoviruses, multiple infections means that there is potential for this to happen, although it may be an extremely rare event (J. Moyer, NCSU, pers. comm.). New tospovirus genomes may be being produced in ornamental hosts at a very low frequency. Therefore, there is scope for the creation and dissemination of new tospoviruses in ornamentals. Industry propagators should be encouraged to test stock plants for tospovirus. This is especially important given the location of major supplies of ornamentals in the Americas and more recently Asia where tospoviruses predominate.

It is difficult to predict what crops in which countries will succumb next to new tospoviruses. Virus epidemics usually follow from the introduction and establishment of an efficient vector just as the incidence of TSWV increased after the spread of *F. occidentalis*. *F. schultzei* is now established in some parts of Europe and this thrips is a known vector of four tospoviruses (Table 3). Outbreaks of *T. palmi* have already been reported in glasshouses in the Netherlands and the UK. These outbreaks have been eradicated, but *T. palmi* is still being intercepted on plant imports. *T. palmi* has also recently been found on an outdoor crop in Portugal and this raises concerns for the future. The host ranges of *T. palmi*-transmitted viruses may be much larger than is known at the moment. Crops, such as tomato, cucurbits and sweet pepper, are threatened. If these tospovirus vectors spread across

Europe, then there is a strong possibility that tospoviruses transmitted by this thrips will become important on the continent. The thrips ability to overwinter and breed, and the availability of virus reservoirs, would impinge on the importance of the virus diseases.

It may only be a matter of time before outbreaks and the failure of subsequent eradication programmes leads to the establishment of exotic thrips that are tospovirus vectors in Eurpoean nurseries. Dissemination of tospovirus diseases within nursery industries may be expected to occur after vector establishment.

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