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A Literature Review of Tomato Spotted Wilt Virus and Related Viruses and their Vector, Western Flower Thrips, with Reference to the Production of Protected Ornamental Plants

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BACKGROUND: TSWV was first reported in the UK in 1929 on winter cherry *Solanum capicastrum*. Transmitted by it vector, *Thrips tabaci*, it was one of the most important diseases of tomato. Its importance declined and virtually disappeared, a trend which was mirrored in Western Europe. With the recent introduction of a new vector thrips species, the Western flower thrips (WFT) *Frankliniella occidentalis*, a number of serious outbreaks were observed on chrysanthemum. Following the establishment of this new vector, the number of outbreaks of TSWV has increased rapidly particularly on protected ornamental crops.

There are three biological aspects to the pathogenicity of TSWV: the thrips vectors; the virus type and the host plant. The thrips species, combined with multiple TSWV variants, makes the understanding of their ecology more complex than previously recognised. In addition, both the viruses and their thrips vectors have an exceptionally large plant host range.

VIRUS CLASSIFICATION: For 50 years after its discovery, TSWV was regarded as a single virus. TSWV has now been assigned to the recently described genus *Tospovirus*. The distinct isolates are classified on serological and molecular criteria supported by differences in host range and cytopathology. On the basis of this classification seven species of *Tospovirus* have been described, and numerous other isolates have been identified.

TSWV and INSV: The first isolate to be described as a distinct species was INSV, Impatiens necrotic spot virus. It was initially isolated in 1989 from New Guinea impatiens in the USA. It has been found on a wide range of floral crops and has now also spread throughout the glasshouses of western Europe. INSV has been recorded as the predominant *Tospovirus* of ornamental crops in the USA where mixed *Tospovirus* infections were rare.

DIAGNOSIS: The diagnosis of *Tospovirus* species and strains is complicated by the very broad range of host plants and variability in symptom expression. The unique shape of the virus can be identified by electron microscopy. Indicator plants can be used to express distinctive symptoms following mechanical inoculation of specially prepared plant material. Indicator plants, particularly petunia cultivars, have been used to indicate the presence of thrips (white feeding scars) and virus (brown rim to feeding scars and circular lesions).

Serological techniques, using an enzyme-linked immunosorbent assay (ELISA), are now the main means of detection and diagnosis of tospoviruses. Recent diagnostic techniques based on molecular biology offer the advantage of overcoming the high level of background positives (non-specific sap reactions) often found in ELISA.

DIRECT-DAMAGE SYMPTOMS: Direct damage to the plant can result from the feeding and ovipositing activity of thrips. Injury to the plant differs according to the plant species, its development stage and the pest status of the thrips species. Thrips often seek tight, hidden places within rapidly growing buds where damage can remain undetected until some time after the injury is inflicted. The injury can manifest itself as withering or malformation and complete abortion of developing buds, leaves or flowers. Thrips feeding activity on leaves or petals results in many dead and empty plant cells which fill with air. This gives a characteristic silvery appearance to the affected areas which are also marked by dark faecal specks. Thrips feeding on developing and open flowers cause a characteristic scaring damage.

VIRUS-DAMAGE SYMPTOMS: The damage caused by infective thrips can be far more severe than that caused by direct feeding damage alone. A wide range of symptoms are seen on ornamental crops. With a non systemic infection, the symptoms are generally restricted to local lesions often with associated chlorosis and necrosis. With a systemic infection, the list of symptoms is far greater and can vary with plant type and environmental conditions. Typical symptoms include: bronzing, dark ring spots and line patterns which are often necrotic or chlorotic; leaf vein necrosis; chlorotic mottling or blotching; black stem lesions and necrosis; twisted, malformed or stunted leaves or plants; leaf drop; wilting of sections of plant; terminal bud necrosis and terminal dieback. Typical symptoms on flowers include: flower distortion; white ring and line patterns (colour break) and delayed flowering.

The symptoms expressed by plants can vary from mild to severe with different crops, virus strain and temperature. For example, gloxinia and New Guinea impatiens show more severe symptoms in warmer temperatures whereas symptoms are more severe in cyclamen in cool temperatures. Significantly more infection has been recorded in chrysanthemum under cool (21°C Day/16°C Night) rather than warm (24°C Day/18°C Night) conditions.

VECTORS: Since the onion thrips, *T. tabaci*, was first named as a vector of tomato spotted wilt, an increasing number of thrips species have been confirmed as vectors. Eight species are now known as vectors of one or more *Tospovirus* species worldwide. Two primary vector species, onion thrips (*T. tabaci*) and WFT (*F. occidentalis*), are known in Britain. However, there is a risk that other alien vector species, such as melon thrips (*Thrips palmi*), may be introduced with the increasing transport of ornamental plants worldwide.

WFT is an efficient vector of numerous tospoviruses and its worldwide occurrence has led to a general increase in virus incidence and many *Tospovirus* epidemics. Probably its biggest impact has been in the transmission of the TSWV and INSV in protected crops - particularly amongst ornamentals - in the USA, Canada and Europe.

The status of onion thrips as a vector seems to have declined and while it continues to transmit some strains of TSWV it no longer acts as a vector to other TSWV isolates. This shift in the vector-virus relationship over time may reflect either the establishment of different isolates of TSWV (with the spread of WFT), or the coevolution of existing isolates with a new and aggressive vector species (WFT) which has an expanded plant host range.

Melon thrips which occurs naturally in south east Asia has been introduced artificially into many countries. It is not known to transmit TSWV or INSV but is a vector of other tospoviruses, most notably the cucurbit infecting species. TSWV and INSV do not infect the Cucurbitaceae systemically. Melon thrips has become a key pest of cucurbit and solanaceous crops in many temperate and tropical regions but it will also attack a wide range of commercial ornamental crops. It has been imported accidentally on many occasions into several European countries on ornamental and vegetable crops. Recent outbreaks in the Netherlands on *Ficus bejamina*, which were imported from the Guadeloupe, have been eradicated successfully. Melon thrips has long been recognised as a threat to protected crops within the European Community.

VIRUS TRANSMISSION: The cycle of acquiring and transmitting the virus is influenced by the host plant, the distribution of the virus within the plant and the replication of the virus within its thrips vector. The efficiency of viral acquisition relies on the feeding activity of the thrips and the distribution of virus within the plant. Although both adult and larval thrips ingest virus particles when feeding, the adults do not become infective. It is only the larval thrips that become viruliferous and subsequently infective as a late larva or adult. Multiplication of the virus within the thrips vector is probably critical to the subsequent transmission of tospoviruses.

In direct contrast to acquisition, where efficiency increases with increased feeding, transmission of the virus occurs more readily during brief and shallow feeding which may involve little or no ingestion of plant material by thrips. This feeding activity is accompanied by an increased release of virus particles and more living plant cells (required for the initiation of infection) are exposed to virus than during vigorous feeding.

Different host plant suitability may influence not only the feeding pattern but also the activity and dispersal of thrips which may in turn affect the development of a virus epidemic. Invading thrips are likely to stay on a favourable host plant and although infection of that plant may occur, it will not be spread further if the thrips settles and does not disperse. Further virus spread will only occur by secondary dispersion of offspring which have developed on the infected plant. Thrips which land on a less suitable host plant are likely to feed and disperse more readily which will favour the spread of virus. Pesticides and repellents may increase both the shallow feeding activity and thrips dispersion which in turn will aggravate a virus epidemic. However, some products have been investigated for their effect on reducing thrips feeding and reproduction to control viral epidemics.

Other factors such as plant resistance to virus infection may also interact with feeding behaviour to alter transmission efficiency. In several studies on chrysanthemum, resistance to virus was found to be more significant than feeding preference on the spread of the virus.

HOST PLANT RESISTANCE: Early research on breeding cultivars resistant to *Tospovirus* concentrated on resistance to TSWV in tomato where initial efforts were not successful. The limited sources of natural resistance to tospoviruses may be a consequence of their recent evolution as plant viruses. Laboratory cultures of viruses which are maintained by mechanical inoculation can develop into defective forms. Such defective forms have been reported for TSWV and their effect on symptom reduction may provide new ways to protect host plants.

Genetically engineered resistance has been successful in reducing symptom expression and accumulation of the virus in a number of commercial crops including tomato, lettuce and chrysanthemum. This biotechnological approache holds great promise for the future.

BIOLOGICAL CONTROL: The only current practical means of control is to reduce the spread of the disease by controlling thrips populations and to use tested virus free motherstock in vegetatively propagated plants. Attemps to control tospoviruses by means of chemical treatments against the vector have not been entirely successful. The intensive use of insecticides can cause problems with residue and phytotoxicity. Biological methods of pest control may provide a more suitable solution to controlling both the thrips population and virus incidence. In ornamental crops, where little cosmetic damage can be tolerated, a preventative pest control or "Keep-Down" pest strategy needs to be adopted. A number of natural enemies of thrips have been proposed as biological control agents.

A range of pathogenic fungi are known to attack thrips and some products are marketed commercially. The principal drawback to the use of these fungi is their need for high humidity, in excess of 95%, for good control. There is considerable potential to overcome this requirement with alternative formulations, including the use of various classes of adjuvants, combined with different application techniques, such as ULV treatments.

A number of parasites are known from thrips but only two species, *Ceranisus menes* and *C. americensis*, are known to attack WFT and related thrips. Their potential in thrips control is unclear and they need to be evaluated more fully.

The most significant advances in the use of natural enemies in the control of thrips has been through the use of predatory mites and flower bugs which are produced commercially. Phytoseiid mites of the genus *Amblyseius* feed on a wide range of small mites and insects including spider mites, tarsonemid mites (cyclamen mite and broad mite) and thrips. Of those that feed on thrips, only *A. cucumeris* and *A. degenerans* are in commercial production. Only the first larval instar of thrips are attacked by these small mites and control is based on innundative introductions of the mites to the crop. Both species are known to feed and develop on pollen and its presence promotes the successful use of these predatory mites. The extent to which environmental factors or the characteristics of different plants affect the successful use of natural enemies is poorly understood but is of critical importance to the full development of biological and integrated control in ornamental crops.

Due to the difficulties in controlling WFT with phytoseiid mites, recent attention has been focused on the use of predatory flower bugs of the genus *Orius*. They are larger and attack a broader range of insects including all the life stages of thrips. A number of species have been reported as thrips predators on vegetable and ornamental crops. Substantial opportunities still exist to determine the full potential of these predators, which have only recently been produced commercially, for the biological control of thrips on ornamental crops.

Summary

Tomato spotted wilt virus (TSWV) belongs to the recently described genus *Tospovirus*, of which it is the type member within the family Bunyaviridae (de Haan *et al.* 1989; Elliott 1990; Franki *et al.* 1991). The Bunyaviridae are a recognised group of, mainly arthropod transmitted, animal viruses some of which cause widespread epidemics of serious and fatal illnesses in both human and domestic animals (Elliott, 1990). The genus *Tospovirus* is consequently unusual among plant viruses. It has a unique mode of transmission and is distinctive in both particle morphology and genome structure (Peters *et al.*, 1991).

The virus was first described from tomato in Australia in 1915 (Brittlebank, 1919) and was later shown to have a viral etiology (Samuel *et al.*, 1930). For the following 50 years it was considered as the only member of the monotypic tomato spotted wilt virus group of plant viruses (Ie, 1970 & Matthews, 1982). This unique position in the taxonomy of plant viruses was recently questioned (Milne & Franki, 1984) and strongly challenged (Law & Moyer, 1990; Law *et al.* 1991a,b; Moyer *et al.*, 1991; Reddy *et al.*, 1991). Recent research has revealed the presence of several distinct viruses: Tomato spotted wilt virus (TSWV); Tomato chlorotic spot virus (TCSV); Groundnut ringspot virus (GRSV); Impatiens necrotic spot virus (INSV); Watermelon silver mottle virus (WSMV); Groundnut bud necrosis virus (GBNV) and Melon spotted wilt virus (MSWV). In addition there are as many as ten or more other isolates which could be distinct species of tospoviruses (Mumford *et al.*, in press).

A very wide range of plants are infected by tospoviruses. Sixty three plant families with recorded host species are listed on page 23. In addition, pages 24-38 list records of host plant compiled from the literature which show that there are at least 249 plant genera with in excess of 520 species, and a further 160 or more cultivars and varieties (670^+ taxa), which act as host to tospoviruses.

All species of *Tospovirus* are transmitted only by thrips of which there are eight vector species known worldwide (German *et al.*, 1992; Goldbach & Peters, 1994). Western flower thrips (WFT), *Frankliniella occidentalis*, is generally considered to be the most important vector of tospoviruses. The geographic spread of WFT has lead to a general increase in the incidence of tospoviruses and resulted in many epidemics in a variety of crops worldwide. This has been particularly true for protected ornamental crops in the USA, Canada and Europe (Hausbeck *et al.*, 1992; Matteoni & Allen, 1989; Vaira *et al.*, 1993; Marchoux *et al.*, 1991).

The underlying relationships of the thrips-virus interactions are as yet poorly known and an improved understanding of this complex relationship will provide a strong foundation for the future management of both thrips and virus (Ullman *et al.*, 1995a). Transmission of the virus is primarily carried out by adult thrips and more rarely by larvae (Sakimura, 1963). However, adult thrips can not acquire the virus and it is only the first larval stage which acquires the virus from feeding on infected plants (Sakimura, 1963). The infection cycle occurs when adult female thrips lay their eggs in the leaves of plants that are already infected with *Tospovirus* on which the young thrips develop and acquire the virus (Ullman *et al*, 1992). Once acquired by the larvae the virus persists within the thrips which then remain viruliferous for the rest of their lives (Sakimura, 1962b). Infection of host plants can be very rapid with as little as 5 minutes exposure time being sufficient for inoculation of the virus (Sakimura, 1963). Persistence of the virus within infected thrips, which is assured by viral replication within the cells of a variety of internal organs, results in thrips that are infective for the duration of their life. Viruliferous thrips which disperse widely or are transported on plant material may harbour the virus over long periods of time even without further access to tospovirus infected plants. Adult thrips can live for between 30-60 days and lay anything between 150-300 eggs (Lublinkhof & Foster, 1977; Robb *et al.*, 1988a; Robb 1989, 1992). Thus, a single viruliferous thrips can potentially infect many different plants in its lifetime (Mau *et al.,* 1991; Ullman *et al.,* 1992a).

Introduction

Spotted wilt was first described from Australia in 1915 as a disease of tomato (Brittlebank, 1919). The earliest report of the condition as tomato spotted wilt virus (TSWV) dates from 1930 (Samuel *et al.,* 1930). TSWV, along with a number of what are now known to be distinct but similar viruses, have been the cause of serious damage in a wide range of crops worldwide (Franki & Hatta, 1981). In addition, they have caused many significant disease epidemics in tropical, subtropical and temperate regions of the Americas, Europe, Asia and Australia (Cho *et al.,* 1984, 1987b; Greenough *et al.,* 1985; Allen & Broadbent, 1988; Brown *et al.,* 1991; Jones & Baker, 1991; Mitchell & Smith, 1991; Stobbs *et al.,* 1992; Yeh *et al.,* 1992).

For 50 years after its discovery TSWV was considered as the only member of the monotypic tomato spotted wilt group of plant viruses (Ie, 1970; Matthews, 1982). As recent worldwide interest in the virus has increased its unique position in the taxonomy of plant viruses was questioned first by Milne & Franki (1984) and later strongly challenged (Law & Moyer, 1990; Law *et al.* 1991a,b; Moyer *et al.*, 1991; Reddy *et al.*, 1991). TSWV has now been classified as belonging to the recently described genus *Tospovirus,* of which it is the type member within the family Bunyaviridae (de Haan *et al.* 1989a; Elliott, 1990; Franki *et al.*, 1991). The Bunyaviridae are a recognised group of, mainly arthropod transmitted, animal viruses some of which cause widespread epidemics of serious and fatal illnesses in both humans and domestic animals (Elliott, 1990).

The genus *Tospovirus* is consequently unusual among plant viruses. It has a unique mode of transmission and is distinctive among plant viruses in both particle morphology and genome structure (Peters *et al.*, 1991). In addition, a number of other *Tospovirus* species have been described as distinct from TSWV. Initially, two distinctive isolates, previously designated as separate strains (TSWV-L, lettuce strain and TSWV-I, impatiens strain), were described as different species called TSWV and Impatiens necrotic spot virus (INSV) (Law *et al.,* 1991a). Other characterised species include tomato chlorotic spot virus (TCSV), Groundnut ringspot virus (GRSV), Watermelon silver mottle virus (WSMV), Groundnut bud necrosis virus (GBNV) and Melon spotted wilt virus (MSWV) (de Avila *et al.,* 1993a). There are as many as ten, and perhaps more, other isolates or strains which could be distinct species of tospoviruses (Mumford *et al.*, in press).

Tospoviruses have a worldwide distribution, with one or more species recorded from over 50 different countries in the Americas, Europe, Asia and Australia (Franki & Hatta, 1981; Smith *et al.,* 1992). Tospoviruses are known from a very wide range of host plants including many ornamental, fruit and vegetable crops (Cho *et al.,* 1986, 1987a; Goldbach & Peters, 1994; Peters *et al.,* 1991; Sether & DeAngelis, 1992; Zitter *et al.,* 1989). TSWV is considered a serious pathogen of field crops (Chamberlin *et al.,* 1992) and damage to commercial crops can be severe with extremely high infection rates commonly leading to 80-90% losses (Cho *et al.,* 1987b; Ghanekar *et al.,* 1979). Protected crops are affected by tospoviruses in both the ornamental and edible sectors with TSWV and INSV posing a major threat to protected horticultural crops in North America and Western Europe (Allen & Matteoni, 1988; Jones & Baker, 1991; Marchoux *et al.,* 1991; Hausbeck *et al.,* 1992; Goldbach & Peters, 1994).

Tospovirus species cause a very wide range of stem, leaf, flower and fruit symptoms in infected plants. These symptoms include: necrosis; chlorosis; ring and line patterns; mottling; bronzing; silvering; stunting; and a range of local lesions (German *et al.,* 1992; Franki & Hatta, 1981). Symptoms vary according to the host-virus combination, seasonality and environmental conditions (Allen *et al.,* 1991).

The possibility of seed transmission of tospoviruses has often been raised. There are reports of seed transmission in *Cineraria* and tomato (Jones, 1944). Levels of 1% infection via seed transmission have been reported for tomato where the virus was detected in the seed coat and not the embryo (Crowley, 1957). Most viruses that can be detected in the seed coat are not transmitted to the next generation (van Blockland, 1991). More recently the virus has been detected in both the seed coat and the embryo giving a 5% transmission of TSWV in tomato seed (van Blockland, 1991). Positive tests for the virus have been observed in pepper, pea, *Nicotiana rustica, Stellaria sp., Symphyta officinale* and *Galinsoga parviflora* but the virus itself was neither observed nor transmitted to the progeny (Mertelík *et al.,* 1995). However, other authors consider seed transmission to be unlikely or at least of minor importance (Reddy & Wightman, 1988; Goldbach & Peters, 1994).

Once infected, tospoviruses are widespread among the cells of their plant and insect hosts (Urban *et al.,* 1991; Ullman *et al.,* 1992b, 1995a). Only larval thrips can acquire tospoviruses but it is the adult, and more rarely the larval, thrips which transmit the virus in a persistent fashion (Sakimura, 1963). Recent evidence shows that tospoviruses replicate in their thrips hosts and that viral replication may contribute to the infectivity of viruliferous thrips (German *et al.*, 1991; Ullman *et al.*, 1992a, 1993, 1995a; Wijkamp *et al.*, 1993b, 1995b). There are widely different values reported in the literature for the biological determinants of viral transmission including virus acquisition and inoculation thresholds and their latent periods (German *et al.*, 1992; Wijkamp & Peters, 1993; Wijkamp *et al.*, 1995a). The underlying relationships of the thrips-virus interactions are as yet poorly known and an improved understanding of this complex relationship will provide a strong foundation for the future management of both thrips and virus (Ullman *et al.*, 1995a).

Tospoviruses are amongst the most important plant pathogens in the world at present. Their status has resulted from the recent global expansion in the distribution of their thrips vectors combined with the large, overlapping host ranges of tospoviruses and their vectors. A number of different thrips species act as vectors (German *et al.*, 1992) and an excess of 650 plants are thought to act as hosts for one or more *Tospovirus* species (Goldbach & Peters, 1994). This report lists at least 249 plant genera with in excess of 520 species, and a further 160 or more cultivars and varieties (670^+ taxa), as host to tospoviruses (pages 24-38). Thrips are a large and diverse group of insects with many polyphagous species which are often regarded as serious crop pests in their own right (Lewis, 1973). The most important thrips vector of tospoviruses is considered to be Western flower thrips, *Frankliniella occidentalis* Pergande (German *et al.*, 1992; Goldbach & Peters, 1994). Control of this pest and the tospoviruses it can transmit is one of the greatest global challenges to the protected ornamental industries today.

Classification of Tospoviruses

The classification of tospoviruses has advanced rapidly in the last few years. Initially TSWV was considered to be the sole member of the monotypic tomato spotted wilt virus group of plant viruses (Ie, 1970; Matthews, 1982). However, a number of significant similarities were noted with a well established group of animal viruses in the family Bunyaviridae (Milne & Franki, 1984). Subsequent molecular studies confirmed that TSWV was closely related to Bunyaviridae viruses (de Haan *et al*, 1989a; Elliot, 1990). TSWV has now been classified as belonging to the recently described genus, *Tospovirus*, of which it is the type member within the family Bunyaviridae (Franki *et al.*, 1991).

For 50 years after its discovery TSWV was regarded as a single virus that was unique among plant viruses. More recently a number of distinct isolates were identified (Law & Moyer, 1990; de Avila *et al.*, 1990, 1992; Law *et al.* 1991a,b; Moyer *et al.*, 1991; Reddy *et al.*, 1991). A classification system for the increasing list of distinct isolates was constructed primarily on serological and molecular grounds but also incorporated differences in host range and cytopathology (de Avila *et al.*, 1990, 1992; 1993a,b). A number of TSWV-like strains have now been characterised as sufficiently distinct from TSWV to be designated as separate virus species of the genus *Tospovirus*. A virus is designated as a *Tospovirus* on the basis of its particle morphology, genome organisation and thrips transmission, and is assigned to one of four serogroups. Distinct species are recognised within a serogroup on the basis of molecular criteria. On the basis of this classification a list of characterised *Tospovirus* species are given in Table 1. Numerous other isolates have been identified as distinct but not yet fully described as different species of *Tospovirus* (Resende *et al.*, 1995; Hall *et al.*, 1993; Chen & Chiu, 1995; Singh & Krishnareddy, 1995; Yeh *et al.*, 1995).

The first isolates to be described as a distinct species was INSV, Impatiens necrotic spot virus (Law *et al.*, 1991a). It was initially isolated from New Guinea Impatiens in the USA (Law & Moyer, 1989) where it is now found on a wide range of floral crops (Hausbeck *et al.*, 1992). This species has also now spread throughout the glasshouses of western Europe, with reports from the Netherlands (de Avila *et al.*, 1992), France (Marchoux *et al.*, 1991), Italy (Vaira *et al.*, 1992, 1993) and Spain (Lavina & Batlle, 1994). It is distinct from TSWV with little or no serological cross-reactivity of the two viruses when using either polyclonal or monoclonal antibodies (Davis *et al.*, 1991). In addition, although both species have broad host ranges, INSV does not infect solanaceous plants (German *et al.*, 1992) and despite being the most predominant *Tospovirus* in glasshouse crops in the USA (Hausbeck *et al.*, 1992) it only rarely infects field crops where TSWV is dominant (Chamberlin *et al.*, 1992). INSV has been recorded as the predominant *Tospovirus* of ornamental crops (82% of positive tospovirus samples) in the USA where, in addition, mixed *Tospovirus* infections were found to be rare (1.5% of positive samples) (Davis *et al.*, 1991).

A number of *Tospovirus* species other than TSWV and INSV have now been described (Table 1). TCSV and GRSV are closely related to TSWV and the three viruses exhibit a degree of cross-reactivity (de Avila *et al.*, 1990). There is little available information on TCSV and GRSV and their economic importance is unclear (Goldbach & Peters, 1994). Other distinct tospoviruses include: GBNV (Adam *et al.*, 1993) on groundnut in India; WSMV (Yeh & Chang, 1995) on cucurbit crops in Japan (Iwaki *et al.*, 1984), Taiwan (Yeh *et al.*, 1992) and Brazil (Boiteux *et al.*, 1993a) and MSWV also infecting cucurbits but not solanaceous plants (Kato, 1995). The latter two *Tospovirus* species are notable in view of the fact that TSWV and INSV do not systemically infect members of the Cucurbitaceae (Yeh *et al.*, 1992). There is probably a much greater diversity of *Tospovirus* species awaiting detailed characterisation (Adam *et al.*, 1995)

Table 1. Characterised species of the genus *Tospovirus*.

Serogroup	Virus	
I	Tomato spotted wilt virus	(TSWV)
II	Tomato chlorotic spot virus	(TCSV)
	Groundnut ringspot virus	(GRSV)
III	Impatiens necrotic spot virus	(INSV)
IV	Watermelon silver mottle virus	(WSMV)
	Groundnut bud necrosis virus	(GBNV)
	Melon spotted wilt virus	(MSWV)

Detection and Diagnosis of Tospoviruses

TSWV was first reported in the UK in 1929 on winter cherry *Solanum capicastrum* (Smith, 1932). Transmitted by it vector *Thrips tabaci* (Smith, 1931a) it was responsible for the incidence of disease in a number of crops including tomato (Smith, 1933), dahlia (Smith, 1931a) and potato (Smith, 1931b). Initially it was one of the most important diseases of tomato in the UK (Smith, 1933) but its importance declined and virtually disappeared (Anon, 1959), a trend which was also mirrored in Western Europe (Smith *et al.*, 1992). With the introduction of a new vector thrips species, the Western flower thrips (WFT) *Frankliniella occidentalis* (Pergande), a number of serious outbreaks were observed on AYR chrysanthemum in the UK (Barker, 1989). Due to the subsequent establishment of this new vector the number of outbreaks of TSWV has increased rapidly particularly on protected ornamental crops (Barker, 1989; Fletcher, 1990; Spence, 1993).

Biological variants of tospoviruses have long been recognised (Best & Gallus, 1953) and seem to arise because the virus naturally tends to generate isolates with altered host ranges and symptoms (Norris, 1946). Historically, these variants have been described either as strains or as defective isolates (German *et al.*, 1992). Strains were distinguished on the basis of host range, symptom severity and serological tests. Defective isolates have an altered phenotype, expressed for example as a weakened symptomatology, explained by deletions in parts of the genome (Verkleij & Peters, 1983; Resende *et al.*, 1991a,b). With the recognition of the biological diversity of the tomato spotted wilt group of viruses a number of strains have been described as distinct viruses or species within a recently described genus, *Tospovirus* (German *et al.*, 1992).

The diagnosis of *Tospovirus* species and strains is complicated by the very broad range of host plants (670^{+} taxa, see pages 24-38) and variability in symptom expression. Members of the genus can be identified directly by electron microscopy as they are the only spherical, membrane bound (enveloped) plant viruses (Black *et al.*, 1963). Indicator plants can be used to express distinctive symptoms with a mechanical inoculation of specially prepared infected plant material (Ie, 1970; Franki & Hatta, 1981; Brown *et al.*, 1991). Indicator plants, particularly Petunia cultivars, have also been suggested for use within nurseries to indicate the presence of both thrips, by feeding marks (white scarring), and virus (brown rim to feeding scars and circular lesions) (Allen & Matteoni, 1991; Pundt, 1993). There are particular drawbacks to the use of either electron microscopy or indicator plants (Mumford *et al.* in press) and tospoviruses detection and diagnosis is now based primarily on serological techniques (Feldman & Boninsega, 1968). The production of high quality *Tospovirus*-specific antisera used in conjunction with an enzyme-linked immunosorbent assay (ELISA) (Gonsalves & Trujill, 1986) is now the main means of detection and diagnosis of tospoviruses. ELISA has also been adapted to permit the detection of tospoviruses within individual thrips (Cho, *et al.*,1988, 1991; Bandla, *et al.*,1994). The use of ELISA with a panel of polyclonal and monoclonal antibodies has indicated four distinct serogroups (based on capsid proteins) and a number of serotypes (based on glycoproteins) (Sherwood *et al.*, 1989; Huguenot *et al.*, 1990; Wang & Gonsalves, 1990; Adam, *et al.*,1991). However, a number of tospovirus isolates are known worldwide that will escape detection by ELISA with the currently available antibodies (Adam *et al.*, 1995).

In addition to symptomatology and serological methods, techniques based on molecular biology have been used for diagnostic purposes (German *et al.*, 1992). Their advantage lies in overcoming the high level of background positives (non-specific sap reactions) often found in ELISA but their use is restricted by high costs and the requirement for specialised facilities for using radioisotopes (Rice, *et al.*,1990; German, *et al.*,1992). More recently, tests based on the polymerase chain reaction (PCR) have been developed (Mumford, *et al.*, 1994). This procedure involves the enzymatic amplification of genetic material and the detection of specific DNA products by gel electrophoresis. It is possible to distinguish between TSWV and INSV (Mumford *et al.*, 1994) or to detect all tospoviruses (Wood *et al.*, 1995) using these tests. In addition, they are more specific than ELISA and overcome the problem of non-specific sap reactions encountered with ELISA (Mumford *et al.*, 1994).

Symptomatology

Direct damage to the plant can result from the feeding and ovipositing activity of thrips (Robb, 1992). Injury to the plant differs according to the plant species, its development stage and the pest status of the thrips species (Childers & Achor, 1995). Thrips often seek tight, hidden places within rapidly growing buds where damage can remain undetected until some time after the injury is inflicted. The injury can manifest itself as withering or malformation, or in some circumstances, complete abortion of developing buds, leaves or flowers. In fruiting crops the fruit can become distorted or develop blemishes in response to thrips feeding or oviposition activity. Thrips feeding activity on fully expanded leaves or petals results in many dead and empty plant cells which fill with air to cause the leaves to take on a characteristic silvery appearance. There will also be dark faecal specks in the area of thrips activity. Thrips feeding on developing and open flowers cause a characteristic scaring damage with faecal spotting. On dark petals this shows up as a white scarring but on light coloured petals the scarring can be a brown colour (Robb *et al.*, 1988a; Robb, 1992).

The damage caused by thrips carrying *Tospovirus* can be far more severe than that caused by direct feeding damage alone (Jones & Baker, 1987; Robb *et al.*, 1988; Gebre-Selassie *et al.*, 1989; Nameth *et al.*, 1988, 1989; Powell, 1990; Robb, 1992; Hill 1994). A very wide range of symptoms have been reported and described in the literature for particular ornamental crops (Ie, 1970; Jones & Baker, 1987, 1991; Ascerno, 1988, 1989; Nameth *et al.*, 1988, 1989; Robb *et al.*, 1988; Baker & Jones, 1990; Allen *et al.*, 1991; Robb, 1992). On non systemic hosts the symptoms are generally restricted to local lesions with chlorosis and necrosis developing in some instances. On Systemic hosts the list of symptoms is far greater and these can vary from plant to plant and with environmental conditions. Typical symptoms include:

> bronzing, dark ring spots and line patterns which are often necrotic or chlorotic; leaf vein necrosis; chlorotic mottling or blotching; black stem lesions and necrosis; twisted, malformed or stunted leaves or plants; leaf drop; wilting of sections of plant; terminal bud necrosis and terminal dieback;

and on flowers typical symptoms include:

> flower distortion; white ring and line patterns (colour break) in coloured flowers and delayed flowering.

The symptoms expressed by plant hosts can vary from mild to severe with different crops, virus strain and temperature (Allen *et al.*, 1991; Jones & Baker, 1991). For example, gloxinia and New Guinea impatiens show more severe symptoms in warmer temperature whereas symptoms are more severe in cyclamen in cool temperatures (Jones & Baker, 1991). Significantly more infection has been recorded in chrysanthemum under cool (21°C Day/16°C Night) rather than warm (24°C Day/18°C Night) conditions (Allen *et al.*, 1991).

Thrips Vectors

There are three biological determinants of the pathogenicity of tospoviruses: the thrips vectors; the *Tospovirus* variant (species or serological type) and the host plant of both thrips and virus (German, *et al.*, 1992). The species of thrips vectors combined with the need to consider multiple tospovirus variants makes the understanding of their ecology more complex than previously recognised. In addition, there is an exceptionally large and overlapping plant host range of both the *Tospovirus* species complex and their thrips vectors.

Since the onion thrips, *Thrips tabaci*, was first named as a vector of tomato spotted wilt (Pittman, 1927), an increasing number of thrips species have been confirmed as vectors (German, *et al.*, 1992; Goldbach & Peters, 1994). Eight species are now known as vectors of one or more *Tospovirus* species worldwide (Table 2).

Table 2. Confirmed thrips vector species of tospoviruses worldwide.

Thrips tabaci Lindeman*	Onion thrips	(Pittman, 1927)
Thrips palmi Karny	Melon thrips	(Yeh *et al.*, 1992)
Thrips setosus Moulton		(Kobatake *et al.*, 1984)
Frankliniella occidentalis (Pergande)*	Western flower thrips	(Sakimura, 1962a)
Frankliniella schultzei Trybom	Common blossom thrips	(Sakimura, 1969)
Frankliniella fusca (Hinds)	Tobacco thrips	(Sakimura, 1963)
Frankliniella intonsa Trybom*		(Wijkamp *et al.*, 1993a)
Scirtothrips dorsalis Hood	Chilli thrips	(Amin *et al.*, 1981)

* species known from Britain.

The transmission of particular tospoviruses is restricted to specific thrips vector species. A summary of the current knowledge on confirmed tospovirus-vector relationships is given in Table 3. Testing the ability of different thrips vector species to transmit the range of tospoviruses is by no means exhaustive and has in reality only just begun (German *et al.*, 1992). It is difficult to predict how the virus-vector interaction will manifest itself with the artificial spread of a range of thrips species into previously uninhabited geographic regions and their consequent contact with different viral variants.

Table 3. Reported associations between *Tospovirus* species and thrips vector species.

Thrips tabaci	Onion thrips	TSWV
Thrips palmi	Melon thrips	WSMV, GBNV, MSWV
Thrips setosus		TSWV
Frankliniella occidentalis	Western flower thrips	TSWV, INSV, GRSV, TCSV
Frankliniella schultzei	Common blossom thrips	TSWV, TCSV, GRSV
Frankliniella fusca	Tobacco thrips	TSWV, INSV
Frankliniella intonsa		TSWV, TCSV
Scirtothrips dorsalis	Chilli thrips	GBNV

See Table 1 (page 8) for abbreviations used.

Of the thrips vectors listed in Tables 2 & 3, only two species, Onion thrips (*Thrips tabaci*) and WFT (*Frankliniella occidentalis*), are currently known to occur in Britain.

However, there is a risk that other alien vector species, such as occurred in the Netherlands with *Thrips palmi* (Baker *et al.*, 1993), may be introduced with the increasing transport of ornamental plants worldwide (Vierbergen, 1995).

Western flower thrips is considered to be the most important vector of *Tospovirus* (Goldbach & Peters, 1994). It is an efficient vector of numerous tospoviruses (Table 3) and the expansion from its original range in the western states of the USA (Reddy & Wrightman, 1988) into the rest of North America (Broadbent *et al.*, 1987) and later Europe (Bournier & Bournier, 1987; Anon, 1989b; Marchoux *et al.*, 1991) has led to many *Tospovirus* epidemics and a general increase in virus incidence. Probably the biggest impact of WFT has been in the transmission of the TSWV and INSV species of *Tospovirus* in protected crops - particularly amongst ornamentals - in the USA, Canada and Europe (Matteoni & Allen, 1989; Marchoux *et al.*, 1991; Hausbeck *et al.*, 1992; Vaira *et al.*, 1992, 1993).

T. tabaci was once considered to be the principal vector of TSWV worldwide (Anon, 1959; Cho *et al.*, 1989; Smith *et al.*, 1992). Its status as a vector seems to have declined and while it continues to transmit some strains of TSWV (Fujisawa *et al.*, 1988; Lemmetty & Lindqvist, 1993; Goldbach & Peters, 1994) it no longer acts as a vector to other TSWV isolates (Paliwal, 1974, 1976; Cho *et al.*, 1988, 1989, 1991; Mau *et al.*, 1991). This shift in the vector-virus relationship over time may reflect either the establishment of different isolates of TSWV with the spread of WFT, or the coevolution of existing isolates with a new and aggressive vector species (WFT) which has an expanded plant host range (German *et al.*, 1992).

Thrips palmi (Melon thrips) is an important pest of outdoor vegetable crops were its high reproductive potential and broad spectrum of resistance to insecticides makes it a difficult pest to control (Anon, 1989a). It is not known to transmit TSWV or INSV but acts as a vector of other tospoviruses, most notably the cucurbit infecting species (Table 3). TSWV and INSV do not infect members of the Cucurbitaceae systemically (Yeh *et al.*, 1992). Occurring naturally in South east Asia, *T. palmi* has been introduced artificially into many other countries including Japan, Hawaii, Australia, Central America, the Caribbean and Florida (Tommasini & Maini, 1995). It has become a key pest of cucurbit and solanaceous crops in many temperate and tropical regions but it will also attack a wide range of commercial ornamental, lettuce, bean and citrus crops (Tommasini & Maini, 1995). It has been accidentally imported on many occasions into several European countries on ornamental and vegetable crops (Anon, 1989a; Baker *et al.*, 1993; Schliephake, 1990; Vierbergen, 1995). Recent outbreaks in the Netherlands on *Ficus bejamina*, which were imported from the Guadeloupe, have been eradicated successfully (Baker *et al.*, 1993). *T. palmi* has long been recognised as a threat to protected crops within the European Community (Anon, 1989a).

Another vector species, *F. schultzei* (Common blossom thrips) has been recorded in the Netherlands on a wide range of imported crops from North and South America, Africa and Israel (Vierbergen, 1995). It has also been recorded in Britain as an introduced species (Mound *et al.*, 1976)

Vector Biology

There are more than 5,000 species of thrips known worldwide. Several hundred species are recorded as economic pests worldwide (Lewis, 1973) but only a small number, about 20, are considered to be major pests of commercial crops (Mound & Teulon, 1995; Tommasini & Maini, 1995). Eight of these are known to be harmful by acting as vectors of different *Tospovirus* species in addition to causing direct damage resulting from their plant feeding and egg laying activities.

The thrips vector species are all small insects, less than 2 mm in length, that are cryptic, living between the folded leaflets, the vegetative and floral buds as well as the flowers and leaves of their host plants. The pest species of thrips have a large well developed external ovipositor which consists of two serrated blades. These blades are worked alternatively to saw into the plant tissue and hollow out a cavity beneath the epidermis into which a single egg is deposited (Childers & Achor, 1995). There are two nymphal stages that are active feeding forms, followed by two more nymphal stages termed the pre-pupa and pupa which are inactive non feeding stages. Sometimes the latter leave the plant and live in the soil below their host plant. The inactive stages often remain in the flowers of ornamental plants (Greene & Paralla, 1992). The adult thrips are superficially similar to the nymphs except that they have two pairs of fringed wings which are a diagnostic feature of the order Thysanoptera (Lewis, 1973).

Thrips have a unique mode of feeding which combines a piercing and sucking action

(Mound, 1971; Chisholm & Lewis, 1984; Hunter & Ullman, 1989; 1992). The principal feeding structures are contained within the mouthcone. They consist of the salivary pump, a mandibular stylet and two maxillary stylets (Heming, 1978). When a thrips prepares to feed, it presses the mouthcone against the plant substrate and uses the single mandibular stylet to punch a hole through the plant cuticle. The mandibular stylet lacks an opening or food channel and is used only to make the initial opening before the insertion of the paired maxillary stylets followed by the commencement of feeding. The paired maxillary stylets are equipped with a longitudinal groove that, when the two stylet are interlocked, provides a hollow tube for withdrawing food material from the underlying cells. Saliva is injected into the plant tissue through the opening of the maxillary stylets and cellular contents are drawn up the feeding channel by a pumping action. This feeding pattern is central to acquisition and subsequent transmission of virus particles.

Direct damage to many parts of the plant results from both the feeding and ovipositing activity on flower and leaf buds, developing leaves, flowers and fruit. The damage which results in blemishing, scarring, distortion, leaf drop or the abortion of flowers and fruitlets often only becomes apparent as the affected leaf, flower or fruit develops and matures. Thrips are small and strongly thigmotactic and consequently prefer to hide between closed petals or leaflets on floral or leaf buds, between frond sheaths or at the bases of developing flower ovaries. Injury is not often readily apparent because the effects of thrips feeding are often insidious or delayed. When thrips feed on the cells of developing terminal foliage or flowers they cause cell death which later results in distortion due to the inability of the dead cells to expand in the same way as normal living tissue (Robb, 1992). Sometimes the pest may not even be present when damage becomes evident.

Indirect damage results from the transmission of diseases. Tospoviruses are the only viruses transmitted by thrips in a persistent, circulative manner (Ullman *et al.*, 1992a), involving a highly specific virus-vector interaction. A number of viruses other than tospoviruses are transmitted by thrips (Mumford *et al.*, in press). Infection results from the mechanical transmission of these viruses where thrips feeding wounds become infected either by viruses being carried in the thrips mouthparts or in infected pollen carried by thrips (Sdoodee & Teakle, 1987; Hardy & Teakle, 1992). Thrips are also known to carry bacterial infection (*Erwinia*) and fungal spores (*Uncinula, Sphaerotheca, Erisyphe, Alternaria* and *Botrytis*) which can give rise to infections (Tommasini & Maini, 1995).

Thrips Acquisition and Transmission of Tospoviruses

The virus acquisition-transmission cycle is influenced by the host plant, the distribution pattern of the virus within the plant combined with the internalisaton and replication of the virus within its thrips vector (Hsu & Lawson, 1991a; Parker *et al.*, 1995). The efficiency of viral acquisition relies on the feeding activity of the vector and the distribution of virus within the plant. One of the most notable features of the thrips-tospovirus relationship is the inability of adult thrips to acquire the virus. It is only the first larval stage that acquires the virus (van der Wetering *et al.*, 1995) which persists in the thrips in a circulatitive manner by penetrating and replicating within the internal organs. Only the adult thrips, or more rarely the late second instar larva, which have become infected as first instar larvae can transmit the virus (Sakimura, 1963). Once a host plant is determined as suitable, the thrips larvae ingest larger quantities of cytoplasm, empty more plant cells and increase the size of feeding scars, than when a plant host is perceived as less favourable (Broadbent *et al.*, 1990). The increased consumption of plant fluids by vigorous feeding leads to an increased number of virus particles being ingested by the insect vector. The probability of efficient acquisition of virus is greater when the distribution of virus-infected cells in the plant tissue is uniform, because more virus particles will be ingested, than when thrips feeding is high but virus distribution in the plant is not uniform (Cho *et al.*, 1988; German *et al.*, 1992; Ullman *et al.*, 1992a). Thus, both thrips feeding preference and the distribution of virus particles in the plant cells both govern the amount of virus ingested from a particular plant host.

Once ingested, virus particles penetrate the cells of the thrips through the midgut by a receptor-mediated mechanism which is probably sensitive to the membrane glycoproteins of the virus (Ullman *et al.*, 1989, 1991, 1995a; German *et al.*, 1992; Bandla *et al.*, 1995). Virus particles pass from the midgut into the body cavity and from there to the surrounding cell and organs (Ullman *et al.*, 1989, 1991, 1995a, 1995b). Virus particles also pass into the salivary glands which, in WFT, are unusual in that they are connected directly to the midgut via paired ducts (Ullman *et al.*, 1989). Virus replication and multiplication occurs within the cells of the midgut, the adjacent organs and the salivary glands (Cho *et al.*, 1991; German *et al.*, 1991; Urban *et al.*, 1991; Ullman *et al.*, 1993; Wijkamp *et al.*, 1993a, 1995b). Tospoviruses are therefore not just circulative but are propagative, with the virus replicating inside the vector. The virus persists within infected individuals transtadially through the different life stages and accompanying skin moults of the developing thrips. Multiplication of the virus within the thrips vector is probably a critical aspect to the successful acquisition and subsequent transmission of tospoviruses (German *et al.*, 1992; Ullman *et al.*, 1995a).

Although it has been shown that both adult and larval thrips ingest virus particles when feeding on infected plant material (Ullman *et al.*, 1992b) the adults do not acquire the virus or become infective (Sakimura, 1963; Ullman, 1992b; van der Wetering *et al.*, 1995). Virus particles ingested by adult thrips are accumulated but are prevented from invading the internal organs of the thrips and are degraded within the gut lumen (Ullman, 1992b). It has been postulated (Day & Irzykiewicz, 1954; Ullman *et al.*, 1992b) that changes in the pH of the midgut, and its affect on the activity of proteolytic enzymes, between larval and adult thrips results in a mid gut barrier to virus acquisition in the adults. It is only when a larval thrips has been feeding on infected plant material that the virus can be acquired and become circulative causing the vector to become viruliferous and subsequently infective as a late larva or adult.

In direct contrast to tospovirus acquisition, where efficiency increases with increased plant feeding, transmission of the virus occurs more readily during brief and shallow probing which may involve little or no ingestion of plant material by thrips (Sakimura, 1962b, 1963). This feeding activity is accompanied by increased salivation and presumably increased release of virus particles. It results in less extensive cell damage and more viable cells which are required for the initiation of the infection are exposed to virus than during vigorous feeding.

Different host plant suitability may influence not only the feeding pattern but also the activity and dispersal of thrips which may in turn affect the development of a virus epidemic (German *et al.*, 1992). Infective thrips which land on a favourable host plant are likely to stay on the plant and although infection of that plant may occur it will not be spread further if the thrips settles and does not disperses. Further virus spread will only occur through secondary spread by offspring which have developed on the infected plant (German *et al.*, 1992). Thrips which land on a less suitable host plant are likely to make a series of shallow probes and move on to other plants. This pattern of feeding and dispersal on unsuitable host plants favours the spread of the virus. Pesticides and repellents may increase both the shallow probing feeding pattern and thrips dispersion which in turn will aggravate a virus epidemic (German *et al.*, 1992; Broadbent & Allen, 1995). Some products have been investigated for their effect on reducing thrips feeding and reproduction to control viral epidemics (Allen *et* *al.*, 1993; Broadbent & Allen, 1995).

Other factors such as plant resistance to virus infection may also interact with feeding behaviour to alter transmission efficiency. In several studies on chrysanthemum, resistance to virus was found to be more significant than feeding preference on the epidemiology of the virus (Broadbent *et al.*, 1990; Allen *et al.*, 1991; Broadbent & Allen, 1995).

A significant reduction has been reported in the survival, development and reproductive potential of WFT which has been exposed to tospovirus through feeding on INSV-infected lobelia (DeAngelis *et al.*, 1993). Pathological changes which occur in the vector as a consequence of the circulative viral infection probably cause the slower developmental period, lower survival and reduced reproductive potential of the adult thrips (DeAngelis *et al.*, 1993). This is an important finding as even small changes in survival can significantly affect the number of infective vectors and ultimately the epidemiology of the disease.

Host Plant Resistance to Tospoviruses

The difficulty in controlling the diseases caused by *Tospovirus* species and containing some of the most damaging epidemics has, in part, been due to the problem of identifying genetic resistance to tospoviruses. Early research on breeding cultivars resistant to *Tospovirus* concentrated on resistance to TSWV in tomato (Best, 1968). Initial efforts to breed resistant cultivars were not successful (Reddy & Wightman, 1988). Sources of resistance have been found from screening beyond available crop cultivars (Paterson *et al.*, 1989; Kumar *et al.*, 1993) and has now been incorporated into commercial tomato lines (Stevens *et al.*, 1992; Boiteux & Giordano, 1993). However, strains of the virus have emerged that are capable of overcoming the resistance (Thompson & van Zijl, 1995). The situation is mirrored in pepper with extensive screening of cultivated and wild species revealing some immunity to TSWV (Black *et al.*, 1991; Boiteux *et al.*, 1993b; Boiteux & de Avila, 1994). However, resistance may have been short lived as it subsequently broke down with tests using other isolates of TSWV (Boiteux & Nagata, 1993). Resistance has also been detected in lettuce (Wang *et al.*, 1992a, b) and tobacco (Kennedy & Nielsen, 1993). The limited number of sources of natural resistance to tospoviruses may be a consequence of their probable recent evolution as plant viruses from an arthropod vectored, animal infecting virus, within the family Bunyaviridae (Goldbach & Peters, 1994).

Laboratory cultures of viruses which are maintained by mechanical inoculation can develop into defective forms which have lost essential segments of the viral genome (Resende *et al.*, 1991a,b). The most important of these are the so called "defective interfering" viruses (DIs) which interfere with the replication of normal virus infections in their hosts by competing for resources and are often associated with disease modulation in susceptible hosts (Huang, 1973). Defective forms have been reported for TSWV (Ie, 1982; Resende *et al.*, 1991a,b; Verkleij & Peters, 1983) and their effect on symptom attenuation may provide new ways to protect host plants (Resende, 1993).

The use of genetically engineered resistance has been successful in developing virus resistance in plants (Beachy & Loesch-Fries, 1990; Fitchen & Beachy, 1993). Initial studies have shown that transgenic tobacco, which express a gene for a coat protein of the virus (the N gene of TSWV), has significant resistance to the virus in terms of symptom expression and reduction in systemic accumulation of the virus (Gielen *et al.*, 1991; MacKenzie & Ellis, 1992; Pang *et al.*, 1992). The transgenic plants all expressed a viral nucleocapsid protein and it was assumed that the resistance was a coat-protein mediated resistance *sensu* Fitchen & Beachy (1993). Subsequent studies have shown that the resistance is also mediated by the expression of viral RNA and not a viral protein (de Haan *et al.*, 1992; Pang *et al.*, 1993; Kim *et al.*, 1994; Prins *et al.*, 1995). Although the mechanisms of resistance are not resolved fully (Pang *et al.*, 1994) it is evident that two processes are involved, one mediated by low levels of RNA and a second by high levels of coat protein, with resistance breaking down if levels are increased or decrease respectively. In addition, resistance which is highly effective against homologous isolates, even when thrips vectored (de Haan, *et al.*, 1992), may break down when plants are challenged with the heterologous tospoviruses GRSV, INSV and TCSV (de Haan *et al.*, 1992; Pang *et al.*, 1993). However, transgenic tobacco which express high levels of coat protein has shown moderate levels of resistance to both TSWV and INSV but in lines expressing low level of either coat-protein or viral RNA resistance was significantly higher to TSWV but not detectable against INSV (Pang *et al.*, 1994).

Resistance has been achieved in a number of commercial crops including tomato (Kim *et al.*, 1994; Gonsalves, C. *et al.*, 1995; Gonsalves, D. *et al.*, 1995), lettuce (Wang *et al.*,

1993) and chrysanthemum (Urban *et al.*, 1994; Gonsalves, D. *et al.*, 1995; Sherman *et al.*, 1995). Although the application of biotechnological approaches to control *Tospovirus* infection holds great promise for the future the only current practical means of control is to reduce the spread of the disease by controlling thrips populations and to use tested virus free motherstock in vegetatively propagated plants.

Biological Control Agents

As a consequence of their global occurrence and spread the pest species of thrips have been exposed to frequent applications of a wide range of pesticides. This fact, combined with their short generation time, has lead to a rapid development of a broad spectrum of resistance to pesticides (Robb *et al.*, 1988a, b; Helyer & Brobyn, 1992). The pest status of the thrips is heightened because they are vectors of tospoviruses. Attempts to control tospoviruses by means of chemical treatments against the vector have not been entirely successful and insecticides can cause residue and phytotoxicity problems when used intensively (Marchoux, 1990). Biological methods of pest control may provide a more suitable solution to controlling both the thrips population and virus incidence (Riudavets, 1995). Integrated pest management (IPM) which combines biological control with the integration of selective chemicals and physical controls provides a practical approach to pest control in commercial horticulture (Jacobson, 1995). In ornamental crops where little cosmetic damage can be tolerated a preventative pest control or "Keep-Down" pest strategy needs to be adopted (Brødsgaard, 1995). There are a number of natural enemies of thrips which have been proposed as biological control agents including predators, parasites and pathogens.

A range of pathogens are known to attack thrips including some products which are marketed commercially (Brownbridge, 1995). One of the principal drawbacks to the use of entomopathogenic fungi is their dependence on high humidity, in excess of 95% for good control (Helyer *et al.*, 1992). There is considerable potential to overcome this requirement with alternative formulations, including the use of various classes of adjuvants, combined with different application techniques such as ULV treatments (Brownbridge, 1995).

A number of parasites are known from thrips species worldwide but only two species, *Ceranisus menes* and *C. americensis*, are known to attack WFT and related thrips species (Loomans & van Lentern, 1995). Their potential in thrips control is unclear and the full range of biotypes need to be evaluated more fully (Loomans & van Lentern, 1995).

The most significant advances in the use of natural enemies in the control of thrips has been through the use of predatory arthropods (Riudavets, 1995). Predatory mites, of the family Phytoseiidae, and predatory flower bugs of the family Anthocoridae are commercially produced biological control agents for thrips control (Ramakers, 1995).

Phytoseiid mites of the genus *Amblyseius* are polyphagous predators which feed on a wide range of microarthropods including spider mites, tarsonemid mites (cyclamen mite and broad mite) and thrips (Riudavets, 1995). Of the small range of species which are known to include thrips as their prey, only two, *A. cucumeris* and *A. degenerans*, are in commercial production. Only the first larval instar of thrips are attacked by these small mites and control is based on large scale or innundative introductions of the mites to the crop (Riudavets, 1995). Both species are known to feed and develop on pollen and its presence promotes the successful use of these predatory mites in the control of thrips. The extent to which environmental factors and the characteristics of different crop plants effect the successful use of natural enemies is poorly understood but is of critical importance to the full development of biological and integrated control in ornamental crops (de Courcy Williams, 1993).

With the difficulties in controlling WFT with phytoseiid mites, recent attention has been focused on the use of predatory flower bugs of the genus *Orius*. They are larger than phytoseiid mites and attack a broader range of prey including all the life stages of thrips (Riudavets, 1995). A number of species have been reported as thrips predators on vegetable and ornamental crops (Riudavets, 1995). The principal species in Europe include *O. laevigatus, O. majusculus, O. niger* and *O. minutus*. Other species are reported as thrips predators in different geographic regions. Substantial opportunities still exist to determine the full potential of these predators which have only recently been commercially produced in the biological control of thrips on ornamental crops.

Recommendations

1. The threshold levels of thrips and their virus loading which are required to initiate significant disease spread should be assessed in comparison to tolerance thresholds of thrips in the absence of virus.

2. The epidemiology of thrips mediated spread of tospoviruses in selected protected crops should be more fully described particularly in regard to the seasonal variation in disease epidemics.

3. The development and verification of simulation models to describe the epidemiology of thrips movement, thrips population development and virus spread, with the aim of designing decision support systems (DSS), would improve the control of thrips and virus spread in protected ornamentals.

4. Current, commonly owned commercial varieties of selected crops, particularly AYR chrysanthemums, should be screened for tospovirus tolerance and thrips preference, using methods already or currently under development.

5. Design an improved sampling strategy for virus indexing stock plants used in vegetatively propagated ornamental crops.

6. Compile an information booklet and poster showing a more comprehensive range of symptoms of tospovirus infection on ornamental plants.

7. In the event of the establishment of other thrips species, such as *T. palmi*, or other tospoviruses, then work should be undertaken to develop control strategies for these new virus and vector combinations.

Plant Families with Recorded Hosts For *Tospovirus* Species

Acanthaceae
Agavaceae
Aizoaceae
Amaranthaceae
Amaryllidaceae
Apocynaceae
Araceae
Araliaceae
Aristolochiaceae
Asclepiadaceae
Balsaminaceae
Begoniaceae
Boraginaceae
Bromeliaceae
Cactaceae
Campanulaceae
Cannaceae
Caricaceae
Caryophyllaceae
Chenopodiaceae
Compositae
Convolvulaceae
Crassulaceae
Cruciferae
Cucurbitaceae
Dipsacaceae
Euphorbiaceae
Gentianaceae
Geraniaceae
Gesneriaceae
Gramineae
Iridaceae
Labiatae
Leguminosae
Liliaceae
Lobeliaceae
Malvaceae
Martyniaceae
Moracea
Nolanaceae
Onagraceae
Paeoniaceae
Papaveraceae
Pedaliaceae
Phytolaccaceae
Planlaginaceae
Plumbaginaceae
Polemoniaceae
Polygonaceae
Portulacaceae
Primulaceae
Ranunculaceae
Rubiaceae
Saxifragaceae
Scrophulariaceae
Solanaceae
Tetragoniaceae
Tropaeolaceae
Umbelliferae
Urticaceae
Verbenaceae
Violaceae
Zygophyllaceae

Tospovirus Host-Plant Species List, Arranged Alphabetically By Scientific Name

Botanical Name	Common Name	Source
Abelia x *grandiflora* (André) Rehd.		
'Edward Goucher'		Ruter & Gitaitis, 1993b
Acanthospermum hisipidum DC	Ageratum sp.	Greber & McCarthy, 1977
Agathea spp.		Vaira *et al.*, 1992
Ageratum sp.		Linford, 1932*[1]
A. houstonianum Milly.	Ageratum	Gumpf & Weathers, 1972
Agrostemma githago L.	Purple cockle	Stobbs *et al.*, 1992
Alliaria officinalis Andrz.	Garlic Mustard	Stobbs *et al.*, 1992
Allium cepa L.	Onion	Hall *et al.*, 1993
Alstroemeria sp.	Perovian Lily	Tehrani *et al.*, 1990
Amaranthus sp.		Costa & Forster, 1942*[2]
A. caudatus L.	Tassel Flower	Best. 1968
A. graecizans L.		Best, 1968
A. hybridus L.	Green Amaranth; Pigweed	Cho *et al.*, 1986
A. paniculata L.		Wingard, 1928*[3]
A. retroflexus L.	Redroot Plgweed	Milbrath, 1939*[4]
A. spinosus L.	Spiny Amaranth	Cho *et al.*, 1986
A. viridis L.	Slender Amaranth	Cho *et al.*, 1984
Amaryllis sp.	Barbados Lily	Gardener *et al.*, 1935
Ambrosia artemisiifolia L.	Small Ragweed	Wingard, 1928*[3]
A. trifida L.	Giant Ragweed	Wingard, 1928*[3]
Anagallis arvensis L.	Scarlet Pimpernel	Stobbs *et al.*, 1992
Ananas comosus (L.) Merr.	Pineapple	Illingsworth, 1931*[1]
'Cayenne'		Linford, 1932*[1]
Anemone sp.	Anemone	Smith, 1937
A. coronana L.		Hurtt, 1985
Anthurium andraeanum Lind	Flamingo Lily	Cho *et al.*, 1989
Antennaria neglecta Greene	Field pussytoes	Stobbs *et al.*, 1992
Antirrhinum sp.	Snapdragon	Tompkins & Gardner, 1934
A. majus L.		Wingard, 1928*[3]
Aphelandra squarrosa Nees	Zebra Plant	Halliwell & Barnes, 1987
Apium graveolens L.	Celery	Gardner *et al.*, 1935
'Golden Self Blanching'		Sakimura, 1940
Aquilegia vulgaris L	Common Columbine	Smith, 1937
Arachis hypogaea L.	Peanut	Costa, 1941
'Gangapuri'		Amin, 1985
'Robut 33-1' *[a]		Amin, 1985
'Red Spanish'		Helms *et al.*, 1961
'TMV 2'		Amin, 1985
'Virginia Bunch'		Helms *et al.*, 1961
Arctium lappa L.	Burdock	Cho *et al.*, 1986
A. minus Bernh.	Common burdock	Stobbs *et al.*, 1992
Aristolochia elegans Mast.	Calico Flower	Matteoni *et al.*, 1988a
Arum palaestinum Boiss	Black Calla	Tompkins & Severin, 1950
Asarum canadense L.	Wild ginger	Stobbs *et al.*, 1992

Asplenium nidus-avis L.	Bird's Nest Fern	Lavina & Batlle, 1994
Aster sp.	Michaelmas Daisy	Smith, 1932 3
A. cordifolius L.	Bluewood aster	Stobbs *et al.*, 1992
A. laevis L.	Ostrich Plume Aster	Wingard, 1928*[3]
A. laterifolus (L.) Britton	Calico Aster	Stobbs *et al.*, 1992
A. novae-angliae L.	New England Aster	Stobbs *et al.*, 1992
Atropa belladonna L.	Deadiy Nightshade	Smith, 1932
Barbarea vulgaris R. Br.	Winter Cress	Wingard, 1928*[3]
Begonia sp.	Begonia	Gardner *et al.*, 1935
B. x hiemalis Fotsch	Elatior or Reiger Begonia	Barnes & Halliwell, 1985
'Whisper O'Pink'		Green *et al.*, 1988
'Renaissance'		Green *et al.*, 1988
'Schwabenland Red'		Green *et al.*, 1988
'Improved Schwabenland Orange'		Green *et al.*, 1988
'Non Stop'		Green *et al.*, 1988
B. semperflorens Link and Otto	Begonia	Gardner *et al.*, 1935
B. x *tuberhybrida Voss*	Hybrid Tuberous Begoma	Middleton, 1939
B. tuberosa see *B.* x *tuberhybrida*		
Belamcanda chinensis (L.) DC	Blackberry Lily	Yamamota & Ohata, 1977
Beta vulgaris L.	Beet	Priode, 1928*[3]
B. vulgaris var. *cicla L.*	Swiss Chard	Wingard, 1928*[3]
Bidens discoidea Brit.	Spanish Needle	Wingard, 1928*[3]
B. pilosa L.	Spanish Needle	Linford, 1932*[1]
B. p. var. *minor* (Bl.) Sherf	Spanish Needle	Cho *et al.*, 1984
B. vulgata Greene	Tall Beggarticks	Stobbs *et al.*, 1992
Brassaia actinophylla Endl.	Umbrella Tree	Matteoni *et al.*, 1989
Brassica campestris L. subsp. *chinensis*	White Stem Cabbage	Cho *et al.*, 1986
B. oleracea L. var. *botrytis* L.	Cauliflower	Gardner *et al.*, 1935
Browallia sp.	Bush Violet	Gardner *et al.*, 1935
B. americana L.	Browallia	Gardner *et al.*, 1935
B. speciosa Hook		Smith, 1957
B. speciosa cv major	Amethyst Flower	Smith, 1937
Calceolaria sp.	Slipperwort	Smith, 1937
C. crenatifolia Cav.	Calceolaria	Allen & Matteoni, 1988
C. herbaceibybrida Voss	Florists' Calceolaria	Noordam, 1952
C. hybrida see *C. herbaceltybrlda*		
Calendula offlcinalis L.	Pot Marigold	Wingard, 1928*[3]
Callistephus chinensis (L.) Nees	China Aster	Wingard, 1928*[3]
Calycanthus floridus L.		Ruter & Gitaitis, 1993b
Campanula sp.	Bellflower	Gardner *et al.*, 1935
C. rapunculoides L.	Creeping bellflower	Stobbs *et al.*, 1992
C. americana L.	Tall Bellflower	Gardner *et al.*, 1935
C. isophylla Moretti	Italian Bellfower	Noordam, 1952
C. pyramidalis L.	Chimney Bellflower	Smith, 1937
Canna L.	Canna Lily	Matteoni *et al.*, 1988a
Capsella sp.		Green *et al.*, 1988
C. bursa-pastoris (L.) Medic.	Shepherd's Purse	Best, 1968
Capsicum sp.	Pepper	Smith, 1931b
C. annuum L.	Bell Pepper	Smith, 1932
var. *anglosum* (L.) Sendt.		Iwaki *et al.*, 1984
'California Wonder'		Pontis & Feldman, 1967

'Chinese Giant'		Sakimura, 1940
'Fordhook'		Ferguson, 1951
var. *grossum* (L.) Sendt.		Yudin *et al.*, 1986
C. frutescens L.	Tabasco Pepper	Costa & Forster, 1942*[2]
Cardamine oligosperma Nutt.	Bitter cress	Stobbs *et al.*, 1992
Carduus acanthoides L.	Plumeless Thistle	Stobbs *et al.*, 1992
Carica papaya L.	Papaya	Cook, 1972
cv. Solo		Gonsalves & Trujillo, 1986
Carum carvii L.	Caraway	Stobbs *et al.*, 1992
Cassia occidentalis L.	Coffee Senna	Stobbs *et al.*, 1992
Catharanthus roseus (L.) G. Don.	Madagascar Periwinkle	Ie, 1970
Centaurea cyanus L.	Bachelor's Button	Matteoni *et al.*, 1988a
Cerastium vulgatum L.	Mouse-ear chickweed	Stobbs *et al.*, 1992
Cheiranthus sp.	Wallflower	Gardner *et al.*, 1935
Chenopodium album L.	Lamb's Quarter	Wingard, 1928*[3]
C. amaranticolor Coste & Reynier		Iwaki *et al.*, 1984
C. ambrosioides L.	Mexican Tea	Cho *et al.*, 1986
C. gigantospermum Aellen	Maple-leaf goosefoot	Stobbs *et al.*, 1992
C.glaucum L.	Oak-leaf goosefoot	Stobbs *et al.*, 1992
C. murale L.	Nettleleaf Goosefoot	Cho *et al.*, 1986
C. quince Wilid.		Paliwal, 1974
Chondrilla sp.	Skeleton Weed	Best, 1968
Chrysanthemum sp.	Chrysanthemum	Gardner & Whipple, 1934
Chrysanthemum leucanthemum L.	Oxeye Daisy	Stobbs *et al.*, 1992
C. coronarium L.	Garland Chrysanthemum	Cho, *et al.*, 1986
C. frutescens L.	Marguerite Daisy	Matteoni *et al.*, 1988a
C. maximun Ramond	Shasta Daisy	Brown, 1988
C. x *morifolium* Ramat	Florist's Chrysanthemum	Gardner & Whipple, 1934
cv. Accent		Matteoni & Allen, 1989
cv. Amber		Matteoni & Allen, 1989
cv. Blue Marble		Matteoni & Allen, 1989
cv. Chardonnay		Matteoni & Allen, 1989
cv. Charlie		Matteoni & Allen, 1989
cv. Charisma		Matteoni & alien, 1989
cv. Dark Yellow		Matteoni & Allen, 1989
cv. Dynamo		Matteoni & Allen, 1989
cv. El Charo		Matteoni & Allen, 1989
cv. Florida Marble		Matteoni & Allen, 1989
cv. Foxy		Matteoni & Allen, 1989
cv. Goldcap		Matteoni & Allen, 1989
cv. Golden Polaris		Matteoni & Allen, 1989
cv. Iceberg		Matteoni & Allen, 1989
cv. Icecap		Matteoni & Allen, 1989
cv. Maximo		Matteoni & Allen, 1989
cv. May Shoesmith		Matteoni & Allen, 1989
cv. Mellow		Matteoni & Allen, 1989
cv. Omegan		Matteoni & Allen, 1989
cv. Palisade		Matteoni & Allen, 1989
cv. Polaris		Green *et al.*, 1988
cv. Super White		Matteoni & Allen, 1989
cv. Super Yellow		Matteoni & Allen, 1989

cv. White Delight		Matteoni & Allen, 1989
cv. White Marble		Matteoni & Allen, 1989
cv. Yellow Dynamo		Matteoni & Allen, 1989
cv. Yellow Palisade		Matteoni & Allen, 1989
cv. Yellow Polaris		Matteoni & Allen, 1989
C. x *superbum* Berg. ex. Ingram	Shasta Daisy	Tehrani *et al.*, 1990
Cichorium endivia L.		
'Large Green Curled'	Endive	Sakimura, 1940
C. intybus L. 'Witloaf'	Chicory	Sakimura, 1940
Cineraria sp. see *Senecio cineraria*		
C. cruenta Mass. see Senecio cruentus		
Cirsium lanceolatum see Cirsium vulgare		
Cirsium arvense (L.) Scop.	Canada Thistle	Stobbs *et al.*, 1992
C. vulgare (Savi) Ten.	Bull Thistle	Best, 1968
Citrullus lanatus (Thun) Matsum & Nakai	Watermelon	Iwaki *et al.*, 1984
C. vulgaris Shrad.	Monte Cristo Watermelon	Wingard, 1928*[3]
Clarkia sp.	Clarkia	Gardner *et al.*, 1935
C. amoena subsp. *lindleyi* (Dougl)		Gardner *et al.*, 1935
Coleus sp.	Coleus	Matteoni *et al.*, 1988a
Columnea sp.		Bellardi *et al.*, 1993
Conium maculatum L.	Poison-hemlock	Stobbs *et al.*, 1992
Consolida ambigua (L.) Ball & Heyw.	Annual Delphinium, Larkspur	Matteoni *et al.*, 1988a
Convolvulus sp.	Morning Glory	Best, 1968
C. arvensis L.	Field Bindweed	Sherf, 1948
C. sepium L.	Hedge bindweed	Stobbs *et al.*, 1992
Conyza bonariensis L.	Hairy Horseweed	Cho *et al.*, 1986
(=*Engeron bonanensis* L.)		
Cordyline terminalis (L.) Kunth.	Ti, Ki	Cho *et al.*, 1986
Coreopsis sp.	Coreopsis	Matteoni *et al.*, 1988a
C. basalis (Otto & Diet.) Blake	Tickseed, Coreopsis	Smith, 1937
C. drummondii see *Coreopsis basalis*		
C.lanceolata L.	Tickseed	Stobbs *et al.*, 1992
Coriandrum sativom L.	Coriander	Best, 1968
Coronopus didymus (L.) Smith	Swinecress	Cho *et al.*, 1986
Cosmos sp.	Cosmos	Smith, 1937
C. bipinnatus Cav.		Smith, 1957
Crepis capillaris (L.) Wallr.	Hawksbeard	Best, 1968
C. divaricata (Lowe) F. Schuitz		Best, 1968
C. pulchra L.		Best, 1968
C. pumila Rydb.		Best, 1968
C. rhoeadifolia Bieb.(*C. foetida* L. subsp. *rhoeadifolia* (Bieb) Celak)		Best, 1968
Crotalaria incana L.	Fuzzy Rattlepod	Cho *et al.*, 1984
Cucumis mucronata Desv.	Smooth Rattlepod	Cho *et al.*, 1984
C. melo L.	Melon	Iwaki *et al.*, 1984
Conomon Group		
conomon (Thunb.) Mak.		Iwaki *et al.*, 1984
Cantalupensis Group		
cantalupensis Naud.	Honey Dew Canteloupe	Wingard, 1928*[3]
C. sativus L.	Cucumber	Ie, 1970
cv. Chicago Pickling		Barnes & Halllwell, 1985
cv. Everbearing		Wingard, 1928*[3]

cv. Ideal White Spine Cucumber		Wingard, 1928*[3]
cv. Windermoor Wonder		Allen & Broadbent, 1986
Cucurbita maxima Duch.	Squash	Iwaki *et al*., 1984
C. m. x *C. moschata* (Duch.) Poir		Iwaki *et al*., 1984
C. moschata Dech.	Cushaw Pumpkin	Wingard, 1928*[3]
C. pepo L.	Cornfield Pumpkin	Wingard, 1928*[3]
var. *condense* Bailey	Gold. Sum. Crookneck Squash	Wingard, 1928*[3]
var. *ovifera* (L.) Aief	Yellow Flowered Gourd	Wingard, 1928*[3]
Cynara scolymus L.	Artichoke	Garcia & Feldman, 1978
Cyclamen persicum Mill	Cyclamen	Allen & Matteoni, 1988
cv. Carmen		Allen & Matteoni, 1988
Cymbidium sp.	Cymbidium Orchid	Matteoni *et al*., 1988a
Cynara scolymus L.	Globe Artichoke	Vaira *et al*., 1992
Cyperus esculentus L.	Yellow Nut Sedge	Stobbs *et al*., 1992
Cyphomandra sp.		Costa & Forster, 1942*[2]
C. betacea (Cav.) Sendt.	Tree Tomato	Costa & Forster, 1942*[2]
Dahlia sp.	Dahlia	Smith, 1932
D. pinnate x *D. coccinea* Cav. cv. Figaro		Allen & Broadbent, 1986
D. variabilis		Smith, 1937
'Jean'		Brunt, 1959
'Willy Den Ouden'		Brunt, 1959
Datura arborea L.	Angel's Trumpet	Costa & Forster, 1942*[2]
D. ferox L.		Greber & McCarthy, 1977
D. meter L.		Norris, 1946
D. stramonium L.	Jimson Weed	Wingard, 1928*[3]
D. tatula L. (*D. stramonium* L.)		Norris, 1946
D. wrightli ex. Regal (*D. inoxia* Mill.)		Smith, 1937
Delphinium sp.	Delphinium	Gardner *et al*., 1935
D. X cultorum Voss		Gardner *et al*., 1935
Desmodium uncinatum (Jac.) DC	Spanish Clover	Cho *et al*., 1986
Dichondra carolinensis Michx.	Lawn Leaf	Sakimura, 1961
Dieffenbachia sp.	Dumb Cane	Kaminska & Korbin, 1991
Digitalis purpurea L.	Foxglove	Ruter & Gitaitis, 1993a
Dolichos lablab L.	Broad Windsor Bean	Wingard, 1928*[3]
Dorotheanthus tricolor (Wilid.) Bolus	Tricolor Ice Plant	Best, 1968
Dracacna fragrans massangeana L. Ker-Gaw	Corn Plant	Tehrani *et al*., 1990
D. marginata L.	Spiker	Tehrani *et al*., 1990
Duboisia leichbardtii (Muel.)		McCarthy & Greber, 1978
D. 1. x *D. myoporoides* R. Br.		Greber & McCarthy, 1977
Echinocystis lobata (Michx.) Torr & A. Gray	Wild Cucumber	Stobbs *et al*., 1992
Eleusine indica (L.) Gaertn.	Goose Grass	Bailey, 1935
Emilia sp.		Gardner *et al*., 1935
E. javanica (Burm. f.) Robi.	Flora's Paintbrush	Linford, 1932*[1]
E. sagittata see *E. javanica*		
E. sonchifolia (L.) DC	Red Pualele	Sakimura, 1940
Erigeron bonariensis L.	Hairy Horseweed	Helms *et al*., 1961
E. canadensis	Horseweed	Stobbs *et al*., 1992
E. strigosus Muhl. ex Willd.	Rough Fleabane	Stobbs *et al*., 1992
E. canadensis L.	Small-leaf Horseweed	Wingard, 1928*[3]
Erysimum cheiranthoides L.	Woomseed Mustard	Stobbs *et al*., 1992

Eupatorum maculatum L.	Joe-Pye-Weed	Stobbs *et al*., 1992
Eustoma sp.	Lisianthus	Hsu & Lawson, 1991b
Eustoma grandiflorum (Raf.) Shinn.		Ruter & Gitaitis, 1993a
Exacum sp.	Persian Violet	Green *et al*., 1988
E. affine Balf. f.		Matteoni *et al*., 1988a
Fagopyrum esculentum Moench	Buckwheat	Stobbs *et al*., 1992
Farfugium japonicum (L.) Kitam.		Vaira *et al*., 1992
Fatsia japonica (Thunb) Duch & Plancn		Allen & Matteoni, 1991
Ficus elastica Roxb. ex Hornem. 'Decora'	Rubber Plant	Lavina & Batlle, 1993
'Varigata'		Lavina & Batlle, 1993
F. pumila L. 'Repens'	Creeping Fig	Lavina & Batlle, 1993
Franklinia alatamaha Marsh.		Ruter & Gitaitis, 1993b
Fucshia sp.	Fucshia	Green *et al*., 1988
F. x *hybrida* ex. Vilm.	Fucshia	Matteoni *et al*., 1989
Gaillardia sp.	Blanket Flower	Gardner *et al*., 1935
G. aristata Pursh.		Gardner *et al*., 1935
G. x *grandiflora* Van Houtte	Blanket Flower	Tehrani *et al*., 1990
Galinsoga ciliata (Raf.) Blake	Hairy Galinsoga	Stobbs *et al*., 1992
G. parviflora Cav.	Fuji Grass, Galinsoga	Cho *et al*., 1986
G. quadriradiata (Raf.) Blake	Peruvian Daisy	Cho *et al*., 1986
Gallium sp.		Bitterlich & MacDonald, 1993
Gazania spp.	Gazania, Treasure Flower	Ruter & Gitaitis, 1993a
Geranium sp.	Geranium	Brown, 1988
G. molle		Bitterlich & MacDonald, 1993
G. robertianum L.	Herb-robert	Stobbs *et al*., 1992
Gerbera sp.	African Daisy, Gerber Daisy	Best, 1968
G. jamesonii Bolus ex. Hook f.	Gerbera	Noordam, 1952
Gladiolus sp.	Gladiola	Smith, 1957
Gloxinia sp.	Gloxinia	Green, 1934
G. hybridum (*Sinningia speciosa* (Lodd.) Hiern.)		Noordam, 1943
Gnaphalium uliginosum L.	Low Cudweed	Stobbs *et al*., 1992
Godetia sp. see *Clarkia* sp.		
G. grandiflora see *Clarkia amoena* subsp. Lindleyi		
Gomphrena globosa L.	Globe Amaranth	Ie, 1970
'Dwarf Buddy'		Allen & Broadbent, 1986
Gossypium barbadense L.	Sea Island Cotton	Schuster & Halliwell, 1994*[d]
G. hirsutum L.	Upland Cotton	Schuster & Halliwell, 1994*[d]
Gynura aurantiaca (Blume) DC	Gynura, Purple Velvet	Matteoni *et al*., 1989
'Sarmentosa'		MacDonald *et al*., 1989
Gypsophila elegans Bieb.	Baby's Breath	Tehrani *et al*., 1990
G. paniculata L.	Baby's Breath	Best, 1968
Halesia carolina L.		Ruter & Gitaitis, 1993b
Helianthus annuas L.	Mammoth Russian Sunflower	Wingard, 1928*[3]
Helipterum manglesli (Lindl.) F.J. Muell.	Swan River Everlasting	Best, 1968
H. roseum (Hook) Benth.		Best, 1968
Hesperis matronalis L.	Dame's Rocket	Stobbs *et al*., 1992
Hibiscus esculentus L.	Okra	Wingard, 1928*[3]
H. tiliaceus L.	Mahoe	Schuster & Halliwell, 1994*[d]
Hippeastrum sp.	Amaryllis; Barbados Lily	Smith, 1937
H. x *hybridum*		Noordam, 1943
Hoya carnosa (L.f.) R. Br.	Wax Plant	Stubbs, 1960

Hybiscus trionum L.	Flower-of-an-Hour	Stobbs *et al.*, 1992
Hydrangea sp.		Matteoni *et al.*, 1988a
H. macrophylla 'Imaculata' Series	French Hydrangea	Ailen *et al.*, 1983
H. quercifolia W. Bartram		Ruter & Gitaitis, 1993b
Hydrocotyle asiatica Bert. ex Urban	Water Pennywort	Paliwal, 1974
Hyoscyamus niger L.	Henbane	Smith, 1932
Ilex glabra (L.) A. Gray 'Shamrock'		Ruter & Gitaitis, 1993b
Impatiens sp.	Impatiens, Touch-me-not	Broadbent *et al.*, 1987
I. balsamina L.	Garden balsam	Tehrani *et al.*, 1990
I. capensis Meerb.	Jewelweed	Stobbs *et al.*, 1992
I. holstii Engl. & Warb.		Noordam, 1952
I. sultanli Hook.f.		DeBruin-Brink *et al.*, 1953
I. wallerana Hook f.		
New Guinea cultivars	New Guinea Impatiens	Matteoni *et al.*, 1988a
Ipomoea congesta R. Br.	Blue Morning Glory	Cho *et al.*, 1986
I. hederacea Jacq. cv. Superba		Sakimura, 1961
I. hederifolia L.	Star Ipomoea	Sakimura, 1961
I. purpurea L.	Morning Glory	Wingard, 1928*[3]
Jacquemontia tamnifolia (L.) Griseb.		Schuster & Halliwell, 1994
Kalanchoe sp.	Kalanchoe	Tehrani *et al.*, 1990
Lactuca canadensis L.	Canada lettuce	Stobbs *et al.*, 1992
L. sativa L.	Lettuce	Gardner & Whipple, 1934
'Grand Rapid'		Sakimura, 1940
'Parris Island Cos'		Cho *et al.*, 1988
'Minetto'		Cho *et al.*, 1988
'Morada'		Pontis & Feldman, 1967
L. s. var. *capitata* L.	Crisphead Lettuce	Wingard, 1928*[3]
L. s. var. *crispa* L.	Leaf lettuce	Cho *et al.*, 1986
L. s. var. *longifolia* Lam.	Romaine or Cos	Thompkins & Gardner, 1934
L. scariola see *L. serriola*		
L. serriola L.	Prickly Lettuce	Wingard, 1928*[3]
Lagenaria leucantha see *L. siceraria*		
L. siceraria (Mol.) Standl.	White Flowering, Dipper Gourd	Wingard, 1928*[3]
Lamium ampexicaule L.	Henbit	Stobbs *et al.*, 1992
Lathyrus odoratus L.	Sweet Pea	Snyder & Thomas, 1936
Layia ex DC sp.	Tidytips	Gardner *et al.*, 1935
L. elegans see *L. platyglossa*		
L. platyglossa (Fisch. & Mey.) Gray		Gardner *et al.*, 1935
Leonotis nepeteefolia (L.) R. Br.	Lion's Ear	Cho *et* al., 1986
Ligularia kaempferi see *Farfugium japonicum*		
Lilium lancifolium Thunb.	Tiger Lily	Best, 1968
L. longiflorum Thunb.	Easter Lily	Tehrani *et al.*, 1990
L. tigrinum see *L. lancifolium*		
Limonium latifolium (Sm.) Ktze.	Statice	Cho *et al.*, 1986
Lobelia sp.	Lobelia	Smith, 1937
L. erinus L.	Trailing Lobelia	DeAngelis *et al.*, 1993
Lufla cylindrica Roem.	Dishcloth Gourd	Wingard, 1928*[3]
Lupinus sp.	Lupine	Smith, 1932
L. albus L.	White Lupine	Gardner & Whipple, 1934
L. angustifolius L.		Smith, 1932
L. leucophyllus Dougl. ex Lindl.		Smith, 1937

L. subcarnosus Hook.	Texas Bluebonnet	Schuster & Halliwell, 1994
Lychnis alba Mill.	White cockle	Stobbs *et al.*, 1992
L. coronaria (L.) Desr.	Dusty Miller; Mullein Pink	Best, 1968
Lycium ferocissimum Miers	Matrimony-vine; Boxthron	Smith, 1937
Lycopersicon esculentum see *L. lycopersicum*		
L. lycopersicum (L.) Karst. ex Farw.	Tomato	Brittlebank, 1919
'Ahahu'		von der Pahlen, 1970
'Bonny Best'		Hutton & Peak, 1953
'Bounty'		Kikuta *et al.*, 1945
'Break o'Day'		Bald, 1937
'Buffalo'		Allen & Broadbent, 1986
'Burbank'		Sakimura, 1940
'Burwood Prize'		Bald, 1937
'Centennial'		Allen & Broadbent, 1986
'Currant'		Bald, 1937
'Dombello'		Allen & Broadbent, 1986
'Dombito'		Allen & Broadbent, 1986
'Dwarf Champion'		Bald, 1937
'Early Dwarf Red'		Bald, 1937
'Early Dwarf Red x. Break O'Day'		Best, 1937
'First Early'		Sakimura, 1940
'Foremost 21'		Gonsalves & Trujillo, 1986
'Glamour'		Allen & Broadbent, 1986
'Globe'		Sakimura, 1940
'Heinz 1370'		DaGraca *et al.*, 1985
'Jumbo'		Allen & Broadbent, 1986
'Kolea-C'		von der Pahlen, 1970
'Laura'		Allen & Broadbent, 1986
'Marglobe'		Bald, 1937
'Maui'*[b]		von der Pahlen, 1970
'Ohio'		Matteoni *et al.*, 1988a
'Ohio MR13'		Allen & Broadbent, 1986
'Pearson'		Frazier *et al.*, 1950
'Ponderosa'		Best, 1946
'Potentate'		Finlay, 1953
'Pritchard'		Gonsalves & Trujillo, 1986
'Red Plum'		Sakimura, 1940
'Rey de los Tempranos'*[b]		Hutton & Peak, 1953
'Rutgars'		Sakimura, 1940
'San Marsano'		Pontis & Feldman, 1967
'Sensation'		Bald, 1937
'Stone'		Sakimura, 1940
'Vendor'		Allen & Broadbent, 1986
'Vision'		Allen & Broadbent, 1986
L. hirsutum H.B.K.		Smith, 1944
L. peruvianum (L.) Mill.*[c]		Norris, 1946
L. pimpinellifolium (Jusl.) Mill.	Small Red-Currant Tomato	Smith, 1937
Maianthemum canadense Desf.	Wild-Lily-of-the-Valley	Stobbs *et al.*, 1992
Malcolmia maritime (L.) R. Br.	Virginia Stock	Best, 1968
Malva nicaeenis All.	Mallow	Sakimura, 1961
M. neglecta Wallr.	Common Mallow	Stobbs *et al.*, 1992

M. parviflora L.	Cheeseweed	Sakimura, 1961
M. rotundifolia L.	Common Mallow	Milbrath, 1939*[4]
Marrubium vulgare L.	Common Hoarhound	Best, 1968
Martynia annua L.		Gardner & Whipple, 1934
Matricaria maritma L.		
var. *agrestis* (Knaf.) Wilm.	Scentless Chamomile	Stobbs *et al.*, 1992
M. matricarioides (Lees.) C.L. Porter	Pinapple weed	Stobbs *et al.*, 1992
Matthiola incana R. Br.	Stock	Best, 1968
Medicago lupulina L.	Black Medick	Stobbs *et al.*, 1992
M. polymorpha L.	Bur Clover	Cho *et al.*, 1986
Melilotus officinalis (L.) Pall.	Yellow Sweet Clover	Wingard, 1928*[3]
Mentha arvensis L.	Field Mint	Stobbs *et al.*, 1992
M. piperita L. 'Black Mitcham'	Peppermint	Sether *et al.*, 1991
M. spicata L.	Spearmint	Allen in Sether *et al.*, 1992
Mesembryanthemum tricolor see *Dorotheanthus tricolor*		
Moluccella laevis L.	Bells of Ireland	Vaira *et al.*, 1992
Monarda fistulosa L.	Wild Bergamot	Stobbs *et al.*, 1992
Montia sp.		Best, 1968
Myosotis alpestris Schmidt	Forget-me-not	Best, 1968
Nepeta cataria L.	Catnip	Milbrath, 1939*[4]
Nerium oleander L.	Oleander	Franki & Grivell, 1970
Nicandra sp.		Gardner & Whipple, 1934
N. physalodes (L.) Gaertn.	Apple of Peru	Wingard, 1928*[3]
Nicotiana acuminate (R.C. Grah.) Hook		Wingard, 1928*[3]
N. alata Link & Otto	Jasmine Tobacco	Gardner & Whipple, 1934
N. a. var. *grandiflora* Comes		Norris, 1946
N. angustifolia Mill.		Smith, 1937
N. atropurpureum		Smith, 1937
N. benthamiana Domin.		Gonsalves & Trujillo, 1986
N. bigelovii (Torr.) S. Wats.		Smith, 1937
N. bonariensis Lehm.		Best, 1968
N. calyciflora		Smith, 1937
N. campanulata see N. *rustica* subsp. *texana*		
N. caudigera Phil.		Smith, 1937
N. chinensis Fisch.		Smith, 1937
N. clevelandii A. Gray		Wingard, 1928*[3]
N. clevelandii x *N. glutinosa*		Francki & Hatta, 1981
N. dedneyi Domin		Best, 1968
N. exigua Wheeler		Best, 1968
N. excelsior J.M. Black		Norris, 1946
N. glauca Graham	Tree Tobacco	Smith, 1931b
N. glutinosa L.		Fromme *et al.*, 1927*[3]
N. goodspeedii Wheeler		Best, 1968
N. langsdortfi Weinm.		Fromme *et al.*, 1927*[3]
N. longiflora Cav.	Long-flowered Tobacco	Wingard, 1928*[3]
N. macrophylla Spreng		Smith, 1937
N. maritime Wheeler		Norris, 1946
N. miersli Remy.		Norris, 1946
N. multivalvis Gray		Wingard, 1928*[3]
N. nudicaulis S. Wats.		Costa & Forster, 1942*[2]
N. palmeri Gray		Norris, 1946

N. paniculata L.		Fromme *et al.*, 1927*[3]
N. plumbaginifolia Viv.		Wingard, 1928*[3]
N. quadrivalvis Pursh.		Wingard, 1928*[3]
N. q. var. *multivalvis* Gray		Wingard, 1928*[3]
N. repanda Wilid.		Wingard, 1928*[3]
N. rotundifolia Lindl.		Norris, 1946
N. rustica L.	Wild Tobacco	Smith, 1932
'America'		de Haan *et al.*, 1989a
'English'		Wingard, 1928*[3]
'lowa'		Wingard, 1928*[3]
'Jamaicensis'		Wingard, 1928*[3]
texana Comes		Norris, 1946
N. x *sanderae* W. Wats.		Wingard, 1928*[3]
N. solanifolia Walp.		Best, 1968
N. suaveolens Lehm.		Wingard, 1928*[3]
N. s. var. *longiflora*		Norris, 1946
N. sylvestris Speg. & Comes		Fromme *et al.*, 1927*[3]
N. tabacum L.	Turkish Tobacco	Smith, 1931b
'Adock'		Wingard, 1928*[3]
'Atropurpurea'		Fromme *et al.*, 1927*[3]
auriculata		Fromme *et al.*, 1927*[3]
'Big Burley'		Wingard, 1928*[3]
'Blue Pryor'		Best, 1936
brasiliensis		Fromme *et al.*, 1927*[3]
'Bright Yellow'		Iwaki *et al.*, 1984
'Burley'		Fromme *et al.*, 1927*[3]
calycina		Wingard, 1928*[3]
calcyciflora		Fromme *et al.*, 1927*[3]
cavala		Wingard, 1928*[3]
colossea		Fromme *et al.*, 1927*[3]
'Connecticut Havanna'		Milbrath, 1939*[4]
gigantea		Fromme *et al.*, 1927*[3]
'Greens'		Fromme *et al.*, 1927*[3]
'H423'		Gonsalves & Trujillo, 1986
'Harrow Velvet'		Allen & Broadbent, 1986
'Hickory Pryor'		Norris, 1946
'Kentucky Yellow'		Wingard, 1928*[3]
lacerate		Fromme *et al.*, 1927*[3]
latissima		Fromme *et al.*, 1927*[3]
'Little Orinoco'		Fromme *et al.*, 1927*[3]
'Lizard Tail'		Wingard, 1928*[3]
'Macedonian'		Fromme *et al.*, 1927*[3]
macrophylla		Fromme *et al.*, 1927*[3]
'Maryland'		Fromme *et al.*, 1927*[3]
microphylla		Fromme *et al.*, 1927*[3]
purpurea		Wingard, 1928*[3]
'Samsun'		Pontis & Feldman, 1967
'Samsun NN'		Ie, 1970
sanguinea		Wingard, 1928*[3]
'Stabdup Burley'		Wingard, 1928*[3]
'Turkish'		Black *et al.*, 1963

'Virginia'		Smith, 1931b
'Warne'		Wingard, 1928*[3]
'White Burley'		Smith, 1931b
'White Burley 21'		Hagan *et al.*, 1990
'Wildfire Resistant'		Fromme *et al.*, 1927*[3]
'Xanthi nc.'		Pontis & Feldman, 1967
N. t. x *N. glutinosa*		Costa & Forster, 1942
N. tomentosa Ruiz. & Pav.		Wingard, 1928*[3]
N. tomentosiformis Goodspeed		Best, 1968
N. trigonophylla Dun.		Wingard, 1928*[3]
N. undulate Ruiz & Pav.		Norris, 1946
N. veluttina Wheeler		Norris, 1946
N. wigandioides Koch & Fint		Best, 1968
Nolana sp.	Nolana	Tehrani *et al.*, 1990
Ocimum basilicum L.	Common Basil; Sweet Basil	Vaira *et al.*, 1992
Oenothera sp.	Evening Primrose	Best, 1968
O. biennis L.	Yellow Evening-primrose	Stobbs *et al.*, 1992
Oncidium sp.		Wang *et al.*, 1992c
Oxalis stricta L.	European Woodsorrel	Stobbs *et al.*, 1992
Oxydendrum arboreum (L.) DC.		Ruter & Gitaitis, 1993b
Paeonia sp.	Peony	Smith, 1937
Papavar sp.	Poppy	Smith, 1937
P. nudicaule L.	Iceland Poppy	Bald & Samuel, 1931
P. orientale L.	Oriental Poppy	Gardner *et al.*, 1935
Pelargonium x *hortorum* Bailey	Geranium	Allen & Broadbent, 1986
Penstemon sp.	Beard-Tongue	Gardner *et al.*, 1935
Penstemon hirsutus (L.) Willd		Gardner *et al.*, 1935
Petunia sp.	Petunia	Smith, 1932
Petunia x *hybrida* Vilm.	Petunia	Priode, 1928*[3]
'Calypso'		Allen & Broadbent, 1986
'Minstrel'		Ie, 1970
'Pink Beauty'		Van Kammen *et al.*, 1966
'Purple Plum'		Cho *et al.*, 1987b
P. violacea Lindl.		Wingard, 1928*[3]
Phalaenopsis sp.		Mayhew *et al.*, 1992
Phaseolus lunatus L	Small Lima or Sieva Bean	Wingard, 1928*[3]
P. vulgaris L.	Snap or French Bean	Smith, 1937
Phlox divaricata L.		Ruter & Gitaitis, 1993a
P. drummondii Hook	Annual Phlox	Best, 1968
Photinia x *faseri* Dress		Ruter & Gitaitis, 1993b
Physalis sp.	Ground Cherry	Tompkins & Gardner, 1934
P. angulata L.	Ground Cherry	Wingard, 1928*[3]
P. brasiliensis Cos. & For.		Costa & Forster, 1942*[2]
P. floridana Rydb.		Helms *et al.*, 1961
P. heterophyla Nees	Clammy Ground Cherry	Stobbs *et al.*, 1992
P. hygrophylla Mart		Costa & Forster, 1942*[2]
P. ixocarpa Brot. ex Hornem.	Tomatillo	Valverde *et al.*, 1993
P. peraviana L.	Cape Gooseberry	Smith, 1937
P. pruinosa L.	Dwarf Cape Gooseberry	Costa & Forster, 1942*[2]
P. pubescens L.	Downy Ground Cherry	Gardner & Whipple, 1934
Phytolacca decandra L.	Pokeweed	Priode, 1928*[3]

Pilea pumila (l.) A. Gray	Clearweed	Stobbs *et al.*, 1992
Pisum sativom L.	Garden Pea	Smith, 1937
'Yellow Admiral'		Whipple, 1936
'Kelvedon Wonder'		DeGraca *et al.*, 1985
Plantago major L.	Broad-leaved Plantain	Smith, 1932
Plectranthus australis R. Br.		
Polygonum sp.	Knotweed; Jointweed	Smith, 1937
P. aviculare L.	Prostrate Knotweed	Stobbs *et al.*, 1992
P. convolvulus L.	Black Bindweed	Smith, 1937
P. hydropiper L.	Smartweed	Wingard, 1928*[3]
P. persicaria L.	Lady's Thumb	Stobbs *et al.*, 1992
Portulaca oleracea L.	Common Purslane	Costa & Carvalho, 1960
Primula sp.	Primrose	Smith, 1937
P. malacoides Franch.	Fairy Primrose	Smith, 1937
P. obconica Hance	German Primrose	Gardner *et al.*, 1935
P. sinensis Sab. ex. Lindl.	Chinese Primrose	Smith, 1937
P. vulgaris Huds.		Tehrani *et al.*, 1990
Plantago lanceolata L.	Narrow-leaved Plantain	Stobbs *et al.*, 1992
P. rugelii Decne	Rugel's Plantain	Stobbs *et al.*, 1992
Quamoclit coccinea 'Hederifolia' see *Ipomoea hederifolia*		
Ranunculus sp.	Buttercup	Smith, 1937
R. acris L.	Tall Buttercup	Stobbs *et al.*, 1992
R. abortivus L.	Small-flowered Buttercup	Stobbs *et al.*, 1992
R. arvensis L.	Corn Buttercup	Stobbs *et al.*, 1992
R. sardous Crantz		Hobbs *et al.*, 1993
Rhapiolepis indica (L.) Lindl. 'Clara'		Ruter & Gitaitis, 1993b
Richardia africana see *Zantedeschia aethiopica*		
R. scabra L.	Mexican Clover	Linford, 1932*[1]
Ricinus communis L.	Castor-oil Plan	Wingard, 1928*[3]
Rudbeckia hirta L.	Black-eyed Susan	Schuster & Halliwell, 1994
Rumex acetosella L.	Sheep's Sorrel	Bitterlich & MacDonald, 1993
R. crispus L.	Curly Dock	Stobbs *et al.*, 1992
Saintpaulia ionantha Wendl.	African Violet	Broadbent *et al.*, 1987
Salpiglossis sp.		Tompkins & Gardner, 1934
S. sinuata Ruiz & Pav	Painted Tongue	Gardner & Whipple, 1934
Salsola pestifer A. Nels.	Russian-thistle	Stobbs *et al.*, 1992
Salvia sp.	Salvia	Gardner *et al.*, 1935
S. splendens Sel ex. Roem & Schult.	Scarlet Sage	Wingard, 1928*[3]
Saponaria officinalis L.	Bouncing Bet	Best, 1968
Saxilraga sp.	Rockfoil	Best, 1968
Scabiosa sp.	Pincushion Flower	Smith, 1937
S. atropurpurea L.	Sweet Scabiosa	Wingard, 1928*[3]
Schefflera sp.	Umbrella Tree	Jones & Baker, 1989
S. arboricola Ayata	Tree or Dwarf Schefflera	MacDonald *et al.*, 1989
Schizanthus sp.	Poor Man's Orchid	Tompkins & Gardner 1934
S. pinnatus Ruiz. & Pav.	Pincusion Flower	Gardner & Whipple, 1934
Schlumbergera bridgesli (Lem) Lofgr.	Christmas Cactus	Tehrani *et al.*, 1990
S. truncate (Haw.) Moran.	Thanksgiving Cactus	Hausbeck & Gildow, 1991
Scutelleria sp.	Scullcap	Allen in Sether *et al.*, 1992
Sedum sp.	Sedum	Stobbs *et al.*, 1992
Senecio cineraria	Dusty Miller	Gardner & Whipple, 1934

S. cruentus (Masson) DC.	Cineraria	Jones, 1944
S. x *hybridus* (Wilid.) Regal		Matteoni *et al.*, 1988a
S. jacobaea L.	Tansy Ragwort	Allen *et al.*, 1983
S. vulgaris L.	Common Groundsel	Stobbs *et al.*, 1992
Sesamum indicum L.	Sesame	Costa & Forster, 1942*[2]
Sinningia speciosa (Lodd.) Hiern.	Gloxinia	Gardner *et al.*, 1935
'Imperial Red Velvet'		Allen & Matteoni, 1991
S. tigrina		Allen & Broadbent, 1986
Solanum aculeatissimum Jacq.	Cockroach Berry	Smith, 1932
S. americanum Mill	American Nightshade	Stobbs *et al.*, 1992
S. atriplicifolium Gill. ex Nees (Rio Negro)		Garcia & Feldman, 1989
S. auriculatum Ait.		Costa & Forster, 1942*[2]
S. aviovlare Forst. f.	Kangaroo Apple	Smith, 1931b
S. capsicastrum Link ex. Schauer	Winter Cherry; Orange Flower	Smith, 1931b
S. carolinense L.	Horse Nettle	Wingard, 1928*[3]
S. dulcamara L.	Bittersweet, Deadly Nightshade	Smith, 1932
S. grandiflorum Ruiz. & Pav.		Costa & Forster, 1942*[2]
S. laciniatum see S. *aviculare*		
S. marginatum L.		Smith, 1932
S. melongena L.	Eggplant	Smith, 1932
'Black Beauty'		Ferguson, 1951
esculentum Nees		Wingard, 1928*[3]
'New York Improved'		Sakimura, 1940
S. miniatum Bernh. ex Wilid.		Smith, 1937
S. nigrum L.	Black Nightshade	Wingard, 1928*[3]
S. nodiflorum Jacq.		Smith, 1931b
S. pseudo-capsicum L.	Jerusalem Cherry	Costa & Forster, 1942*[2]
S. ptycanthum Dunal in DC.	Eastern Black	Stobbs *et al.*, 1992
S. sanitwongsii Craib.		Smith, 1937
S. seaforthianum Andr.		Smith, 1937
S. sodomoum L.	Apple of Sodom	Smith, 1937
S. spinosissimum Lodd.		Costa & Forster, 1942*[2]
S. triflorum Nutt.	Cutleaf Nightshade	Allen *et al.*, 1983
S. tuberosum L.	Potato	Smith, 1931b
'Arran Victory'		Smith, 1937
'Bismark'		Hutton & Peak, 1952
'Bliss Triumph'		Milbrath, 1939*[1]
'Brownell'		Hutton & Peak, 1952
'Factor'		Hutton & Peak, 1952
'Katahdin'		Hutton & Peak, 1952
'President'		Hutton & Peak, 1952
'Sebage'		Hutton & Peak, 1952
'Sequoia'		Hutton & Peak, 1952
'Snowflake'		Hutton & Peak, 1952
'Up To Date'		Norris, 1946
S. viarum	Tropical Soda Apple	McGovern *et al.*, 1993
Sonchus asper (L.) J. Hill	Spiny Annual Sowthistle	Stobbs *et al.*, 1992
S. oleraceus L.	Common Sowthistle	Helms *et al.*, 1961
Spergula arvensis L.	Corn spurry	Stobbs *et al.*, 1992
Spinacia oleracea L.	Spinach	Sakimura, 1940
'Viroflay'		Sakimura, 1940

Stachys sp.	Hedge Nettle	Linford, 1932*[1]
S. arvensis L.	Staggerweed	Greber & McCarthy, 1977
Stellaria sp.	Chickweed	Best, 1968
S. media (L.) Cyr.	Common Chickweed	Holmes, 1948
Stephanotis floribunda Brong.	Madagascar Jasmine	Green *et al.*, 1988
Streptosolen jamesonii (Berth,) Miers	Firebush; Yellow Heliotrope	Smith, 1937
Tagetes erecta L.	African Marigold	Wingard, 1928*[3]
T. minute L.	Marigold	Helms *et al.*, 1961
T. patula L.	French Marigold	Allen & Broadbent, 1986
'Petite Harmony'		Allen & Broadbent, 1986
Taraxacum officinale Wigg.	Dandelion	Stobbs *et al.*, 1992
Tetragonia expanse see *T. tetragonioides*		
T. tetragonioides (Pall.) Kuntze	New Zealand Spinach	Priode, 1928*[3]
Tithonia rotundifolia (Mill.) S.F. Blake	Mexican Sunflower	Ruter & Gitaitis, 1993a
Trachelium sp.	Throatwort	Smith, 1937
T. caeruleum L.		Smith, 1937
Trachymene coerulea R.C. Grah.	Blue Lace Flower	Best, 1968
Trevesia palmata (Roxb. ex Lindl.)		Vaira *et al.*, 1992
Tribulus terrestris L.	Punture Vine	Allen *et al.*, 1983
Trifolium repens L.	Wild Clover	Paliwal, 1976
T. subterraneum L.		Helms *et al.*, 1961
Tropaeolum sp.	Nasturtium	Gardner & Whipple, 1934
T. majus L.	Garden Nasturtium	Smith, 1937
'Golden Gleam'		Best, 1937
Troximon sp.		Best, 1968
Tussilago farara L.	Coltsfoot	Stobbs *et al.*, 1992
Urtica dioica L.	Stinging Nettle	Gardner & Whipple, 1934
Verbascum thapsus L.	Common Mullein	Stobbs *et al.*, 1992
Verbena sp.	Vervain	Gardner *et al.*, 1935
V. hastata L.	Blue Vervain	Stobbs *et al.*, 1992
V. hybrida Voss	Garden Verbena	Gardner *et al.*, 1935
V. litoralis HBK	Oi	Cho *et al.*, 1986
V. rigida Spreng.	Vervain	Cho *et al.*, 1984
Verbesina encelioides (Cav.) B. & H	Golden Crownbeard	Cho *et al.*, 1984
Vicia faba L.	Broad Bean	Gardner & Whipple, 1934
Vigna mungo (L.) Hepper cv UPU-1	Urd Bean	Amin *et al.*, 1981
V. sinensis Endl.	Cowpea	Wingard, 1928*[3]
'Queen Anne Black'		Allen & Broadbent, 1986
V. sesquipedalis (L.) W. F. Wright		Iwaki *et al.*, 1984
V. unguiculata (L.) Walp. cv. 'Blackeye'		Iwaki *et al.*, 1984
Vinca rosea see *Catharanthus roseus*		
Viola papilionacea see *V. sororia*		
V. sororia Wilid.	Woolly Blue Violet	Wingard, 1928*[3]
V. tricolor L.	Field or European Pansy	Wingard, 1928*[3]
Viola x *witterockiana* Gams.		Ruter & Gitaitis, 1993a
Weigela florida (Bunge) A. DC. 'Variegata Nana'		Ruter & Gitaitis, 1993b
Xanthium saccharatum Wallr. (x *strumanum* L.)	Cocklebur	Cho *et al.*, 1986
Youngia japonica (L.) DC.		Kobatake *et al.*, 1984
Yucca baccata L.	Yucca	Tehrani *et al.*, 1990
Zantedeschia aethiopica (L.) Spreng	White Calla Lily; Arum	Ogilvie, 1935

Z. albomaculata (Hook.) Baill.	Spotted Calla	Tompkins & Severin, 1950
Z. elliottiana (W. Wats.) Engler	Yellow Calla	Tompkins & Severin, 1950
Z. melanoleuca Engler (Z. *albomaculata)*	Black-throated Calla	Tompkins & Severin, 1950
Z. rehmannli Engler	Pink Calla	Tompkins & Severin, 1950
Zinnia sp.	Zinnia	Smith, 1932
Z. elegans Jacq.	Zinnia	Wingard, 1928*[3]

*[1] Originally identified as pineapple yeliow-spot; virus, later identified as TSWV by Sakimura (1940).
*[2] Originally identified as 'vira-cabeca' virus, later identified as TSWV by Costa & Forster (1942).
*[3] Originally identified as ring spot, later identified as TSWV by Smith (1932).
*[4] Originally identified as tomato tip-blight virus.

*[a] Conflicting reports of susceptibility. TSWV resistance reported in this variety by Amin (1985).
*[b] Conflicting reports of susceptibility. TSWV resistance reported by Frazier *et al.*, (1950) in 'Maui', 'Manzana', 'Pearl Harbor', and 'Rey de los Tempranos'.
*[c] Conflicting reports of susceptibility. Strong resistance, approaching immunity was reported by Norris, 1946.
*[d] Record based only on artificially infected host.

References

Adam, G., Lesemann, D.E. & Vetten, H.J. (1991) Monoclonal antibodies against tomato spotted wilt virus: characterisation and application. *Annals of Applied Biology* **118:** 87-104.

Adam, G., Yeh, S.D., Reddy, D.V.R. & Green, S.K. (1993) Serological comparison of *Tospovirus* isolates from Taiwan and India with impatiens necrotic spot virus and different tomato spotted wilt isolates. *Archives of Virology* **130:** 237-250.

Adam, G., Peters, D. & Goldbach, R. (1995) Serological comparison of *Tospovirus* isolates using polyclonal and monoclonal related antibodies. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* pp 15-16. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Allen, T.C., McMorran, J.P. & Locatelli, E.A. (1983) Isolation of tomato spotted wilt virus from Hydrangea and four weed species. *Plant Disease* **67:** 429-431.

Allen, W.R. & Broadbent, A.B. (1986) Transmission of tomato spotted wilt virus in Ontario greenhouses by *Frankliniella occidentalis. Canadian Journal of Plant Pathology* **8:** 33-38.

Allen, W.R. & Matteoni, J.A. (1988) Cyclamen ringspot: Epidemics in Ontario greenhouses caused by the tomato spotted wilt virus. *Canadian Journal of Plant Pathology* **10:** 41-46.

Allen, W.R. & Matteoni, J.A. (1991) Petunia as an indicator plant for use by growers to monitor for thrips carrying the tomato spotted wilt virus in greenhoses. *Plant Disease* **75:** 78-82.

Allen, W.R., Matteoni, J.A. & Broadbent, A.B. (1991) Factors relating to epidemiology and symptomatology in florist's chrysanthemum infected with the tomato spotted wilt virus. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 28-45. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Allen, W.R., Tehrani, B. & Luft, R. (1993) Effects of horticultural oil, insecticidal soap, and film-forming products on the western flower thrips and the tomato spotted wilt virus. *Plant Disease* **77:** 915-918.

Amin, P.W. (1985) Apparent resistance of ground cultivar Robut 33-1 to bud necrosis disease. *Plant Disease* **69:** 718-719.

Amin, P.W., Reddy, D.V.R., Ghanekar, A.M. & M.S. Reddy (1981) Transmission of tomato spotted wilt virus, the causal agent of bud necrosis of peanut, by *Scirtothrips dorsalis* and *Frankliniella scultzei. Plant Disease* **65:** 663-665.

Anonymous (1959) Tomato spotted wilt. MAFF, Advisory leaflet 238. HMSO, London.

Anonymous (1989a) EPPO Data sheets on quarantine organisms No. 175, *Thrips palmi* Karny. *Bulletin OEPP/EPPO Bulletin* **19:** 717-720.

Anonymous (1989b) EPPO Data sheets on quarantine organisms No. 177, *Frankliniella occidentalis* (Perg.). *Bulletin OEPP/EPPO Bulletin* **19:** 725-731.

Ascerno, M.E. (1988) Working the bugs out. *Grower Talks* **52(8):** 102.

Ascerno, M.E. (1989) Working the bugs out. *Grower Talks* **52(10)**: 74.

Bailey, S.F. (1935) Thrips as vectors of plant disease. *Journal of Economic Entomology* **28:** 856-863.

Bald, J.G. (1937) Investigations on "spotted wilt" of tomatoes. III. Infection in field plots. *Bulletin. Council for Scientific and Industrial Research, Australia* **106**: 1-32.

Bald, J.G., & Samuel, G. (1931) Investigations on "spotted wilt" of tomatoes. II. *Bulletin. Council for Scientific and Industrial Research, Melbourne* **54:** 24 pp.

Bandla, M.D., Westcot, D.M., Chenault, K.D., Ullman, D.E., German, T.L. & Sherwood, J.L. (1994) Use of monoclonal antibody to the nonstructural protein encoded by the small RNA of tomato spotted wilt *Tospovirus* to identify viruliferous thrips. *Phytopathology* **84:** 1477-1431.

Bandla, M.D., Westcot, D.M., Ullman & Sherwood, J.L. (1995) A thrips midgut protein that binds to tomato spotted wilt virus glycoprotein. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* pp 42. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Barker, I. (1989) Beware spotted wilt. *Grower* **111(9):** 17-19.

Baker, J.R. & Jones, R.K. (1990) Tomato spotted wilt and western flower thrips 1990 update. *North Carolina Flower Growers' Bulletin* **35:** 13-15.

Baker, R.H.A., Bartlett, P.W. & Cheek, S. (1993) *Thrips palmi* (The Palm thrips) an alien thrips recently arrived in Europe. *CSL Plant Pest Notice* **No.15**, 2 pp.

Barnes, L.W. & Halliwell, R.S. (1985) Tomato spotted wilt virus infecting Begonia hybrids in Texas. *Plant Disease* **69:** 613.

Beachy, R.N., Loesch-Fries, S. & Tumer, N.E. (1990) Coat protein-mediated resistance against virus infection. *Annual Review of Phytopathology* **28:** 451-474.

Bellardi, M.G., Vicchi, V. & Bertaccini, A. (1993) Tospoviruses infecting *Kalanchoe* sp. and *Columnea* sp. in Italy. *Advances in Horticultural Sceince* **7:** 99-102.

Best, R.J. (1946) Thermal inactivation of tomato spotted wilt virus. Part I. *Australian Journal of Experimental Biology* **24:** 21-25.

Best, R.J. (1968) Tomato spotted wilt virus. *Advances in Virus Research* **13:** 65-146.

Best, R.J. & Gallus, H.P.C. (1953) Strains of tomato spotted wilt virus. *Australian Journal of Science* **15:** 212-214.

Bitterlich, I. & MacDonald, L.S. (1993) The prevalence of tomato spotted wilt virus in weeds and crops in southwestern Columbia. *Canadian Plant Disease Survey* **73:** 137-142.

Black, L.L., Hobbs, H.A. & Gatti, J.M. (1991) Tomato spotted wilt virus-resistance in *Capsicum chinense* PI 152225 and 159236. *Plant Disease* **75:** 863.

Black, L.L., Brakke, M.K. & Vatter, A.E. (1963) Purification and electron microscopy of tomato spotted wilt virus. *Virology* **20:** 120-130.

Boiteux, L.S. & de Avila, A.C. (1994) Inheritance of a resistance specific to tomato spotted wilt tospovirus in *Capsicum chinense* PI-159236. *Euphytica* **75:** 139-142.

Boiteux, L.S., de Avila, A.C. & Dutra, W.P. (1993a) Natural infection of melon by a *Tospovirus* in Brazil. *Plant Disease* **78:** 102.

Boiteux, L.S. & Giordano, D.E.B. (1993) Genetic basis of resistance against two *Tospovirus* species in tomato (*Lycopersicon esculentum*). *Euphytica* **71:** 151-154.

Boiteux, L.S. & Nagata, T. (1993) Susceptibility of *Capsicm chinense* PI 159236 to tomato spotted wilt virus. *Plant Disease* **77:** 210.

Boiteux, L.S., Nagata, T., Dutra, W.P. & Fonseca, M.E.N. (1993b) Sources of resistance to tomato spotted wilt virus (TSWV) in cultivated and wild species of *Capsicum*. *Euphytica* **67:** 89-94.

Bournier, A. & Bournier, J.-P. (1987) L'introduction en France d'un nouveau ravageur: *Frankliniella occidentalis*. *Phytoma* **388:** 14-17.

Brittlebank, C.C. (1919) Tomato diseases. *Journal of Agriculture, Victoria* **17:** 213-235.

Broadbent, A.B. & Allen, W.R. (1995) Interactions within the western flower thrips/tomato spotted wilt virus/host plant complex on virus epidemiology. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 185-196. Plenum Press, London, 636pp.

Broadbent, A.B., Allen, W.R. & Foottit, R.G. (1987) The association of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) with greenhose crops and the tomato spotted wilt virus in Ontario. *Canadian Entomologist* **119:** 501-503.

Broadbent, A.B., Matteoni, J.A. & Allen, W.R. (1990) Feeding preferences of the western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), and incidence of tomato spotted wilt virus among cultivars of florist's Chrysanthemum. *Canadian Entomologist* **122:** 1111-1117.

Brødsgaard, H.F. (1995) "Keep-down" a concept of thrips biological control in ornamental plants. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 221-224. Plenum Press, London, 636pp.

Brown, L.G. (1988) Tomato spotted wilt virus in ornamentals. *Plant Pathathology Circular* **No. 313:** 4 pp.

Brown, L.G. Simone, G.W. & Christie, R.G. (1991) Diagnostic strategy development for tomato spotted wilt virus. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 94-100. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Brownbridge, M. (1995) Prospects for mycopathogens in thrips management. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 281-295. Plenum Press, London, 636pp.

Brunt, A.A. (1959) Leaf enations in *Dahlia variabilis* Desf., induced by tomato spotted wilt virus. *Nature* **183**: 627-628.

Chamberlin, J.R., Culbreath, A.K., Todd, J.W. & Demski, J.W. (1993) Detection of tomato spotted wilt virus in tobacco thrips (Thysanoptera: Thripidae) overwintering in harvested peanut fields. *Journal of Economic Entomology* **86:** 40-45.

Chamberlin, J.R., Todd, J.W., Beshear, R.J., Culbreath, A.K. & Demski, J.W. (1992) Overwintering hosts and wingform of thrips, *Frankliniella* spp., in Georgia (Thysanoptera: Thripidae): implications for management of spotted wilt disease. *Environmental Entomology* **21:** 121-128.

Chen, C.C. & Chiu, R.J. (1995) A tospovirus causing chlorotic fan-spot on peanut in Taiwan. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* pp 18. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Childers, C.C. & Achor, D.S. (1995) Thrips feedng and oviposition injuries to economic plants, subsequent damage and host response to infestation. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 31-51. Plenum Press, London, 636pp.

Chisholm, I.F. & Lewis, T (1984) A new look at thrips (Thysanoptera) mouthparts, their action and effects of feeding on plant tissue. *Bulletin of Entomological Research* **74:** 663-675.

Cho, J.J., Mau, R.F.L., German, T.L., Hartmann, R.W., Yudin, L.S., Gonsalves, D. & Provvidenti, R. (1989) A multidisciplinary approach to management of tomato spotted wilt virus in Hawaii. *Plant Disease* **73:** 375-383.

Cho, J.J., Mau, R.F.L., Gonsalves D. & Mitchell, W.C. (1986) Reservoir weed hosts of tomato spotted wilt virus. *Plant Disease* **70:** 1014-1017.

Cho, J.J., Mau, R.F.L., Hamasaki, R.T. & Gonsalves, D. (1988) Detection of the tomato spotted wilt virus in individual thrips by enzyme-linked immunosorbent assay. *Phytopathology* **78:** 1348-1352.

Cho, J.J., Mau, R.F.L., Mitchell, W.C., Gonsalves, D. & Yudin, L.S. (1987a) Host list of plants susceptible to tomato spotted wilt virus. *Research Extension Series, Hawaii Institute Of Tropical Agriculture & Human Resources.* **1987:** 10pp.

Cho, J.J., Mau, R.F.L., Ullman, D.E. & Custer, D.M. (1991) Detection of tomato spotted wilt virus (TSWV) in thrips. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-thrips-plant interactions of Tomato Spotted Wilt Virus,* pp 144-152. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Cho, J.J., Mitchell, W.C., Mau, R.F.L. & Sakimura, K. (1987b) Epidemiology of tomato spotted wilt virus disease on crisphead lettuce in Hawaii. *Plant Disease* **71:** 505-508.

Cho, J.J., Mitchell, W.C., Yudin, L.S. & Takayama, L. (1984) Ecology and epidemiology of tomato spotted wilt virus (TSWV) and its vector, *Frankliniella occidentalis. Phytopathology* **74:** 866.

Cook, A.A. (1972) Virus diseases of papaya. *University of Florida Agricultural Experimental Station Bulletin* **No. 750**: 19pp.

Costa, A.S. (1941) Uma molestia de virus de amendoim *(Arachis hypogaea* L.) *Biologico* **7**: 249-251.

Costa, A.S. & Carvalho, A.M.B. (1960) Common puslane, a reservoir of tomato spotted wilt virus. *Bragantia* **19:** 21-27I.

Costa, A.S., & Forster, R. (1942) Lista de hospedeiras de virus vira-cabeca. *Bragantia* **2:** 83-91.

Crowley, N.C. (1957) Studies on the seed transmission of plant virus diseases. *Australian Journal of Biological Sciences* **10:** 449-464.

Davis, R.F., DeHerrera, V., Gonzales, L. & Sutula, C. (1991) Use of strain specific monoclonal and polyclonal antibodies to detect two serotypes of tomato spotted wilt virus. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions* *of Tomato Spotted Wilt Virus,* pp 153-161. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Day, M.F. & Irzykiewicz, H. (1954) Physiological studies on thrips in relation to transmission of tomato spotted wilt virus. *Australian Journal of Biological Sciences* **7:** 274-281.

DeAngelis, J.D., Sether, D.M. & Rossignol, P.A. (1993) Survival, development, and reproduction in western flower thrips (Thysanoptera: Thripidae) exposed to impatiens necrotic spot virus. *Environmental Entomology* **22:** 1308-1312.

de Avila, A.C., de Haan, P., Kitajima, E.W., Kormelink, R., Resende, R. de O., Goldbach, R.W. & Peters, D. (1992) Characterization of a distinct isolate of tomato spotted wilt virus (TSWV) from Impatiens sp. in the Netherlands. *Journal of Phytopathology* **134:** 133-151.

de Avila, A.C., de Haan, P., Kormelink, R., Resende, R. de O., Goldbach, R.W. & Peters, D. (1993a) Classification of tospoviruses based on phylogeny of nucleoprotein gene sequences. *Journal of General Virology* **74:** 153-159.

de Avila, A.C., de Haan, P., Smeets, M.L.L., Resende, R. de O., Kormelink, R., Kitajima, E.W., Goldbach, R.W. & Peters, D. (1993b) Distinct levels of relationships between *Tospovirus* isolates. *Archives of Virology* **128:** 211-227.

de Avila, A.C., Huguenot, C., Resende, R. de O., Kitajima, E.W., Goldbach, R.W. & Peters, D. (1990) Serological differentiation of 20 isolates of tomato spotted wilt virus. *Journal of General Virology* **71:** 2801-2807.

De Bruin-Brink, G., Maas Geesteranus, H.P. & Noordam, D. (1953) *Lycopersicum* virus 3 (tomato spotted wilt virus), on *Nicotiana tabacum* and *Impatiens holstii.* Tijdschr. PIZiekt. 59: 240-244.

de Courcy Williams, M. (1993) *Amblyseius cucumeris* (Acari: Phytoseiidae) in the control of western flower thrips (*Frankliniella occidentalis*) on Cyclamen. *IOBC/WPRS Bulletin* **16(8):** 48-52.

DaGraca, J.V., Trench, T.N. & Martin, M.M. (1985) TSWV in commercial Cape gooseberry *(Physalis peruviana)* in Transkei. *Plant Pathology* **34:** 451-453.

de Haan, P., Gielen, J.J.L., Prins, M. Wijkamp, I.G., van Schepen, A., Peters, D., van Grinsven, M.Q.J.N. & Goldbach, R.W. (1992) Characterisation of RNA-mediated resistance to tomato spotted wilt virus in transgenic tobacco plants. *Biotechnology* **10:** 1133-1137.

de Haan, P., Wagemakers, L., Goldbach, R.W. & Peters, D. (1989a) Tomato spotted wilt virus, a new member of the *Bunyaviridae*? *In:* Kolakofsky, D. & Mahy, B.W.J. (editors) *Genetics and Pathogenicity of Negative Strand Viruses,* pp. 287-291.

Elsevier, Amsterdam.

de Haan, P., Wagemakers, L., Peters, D. & Goldbach. R. (1989b) Molecular cloning and terminal sequence determining of the S and M RNAs of tomato spotted wilt virus. *Journal of General Virology* **70:** 3469-3473.

Elliott, R.M. (1990) Molecular biology of the *Bunyavaridae. Journal of General Virology* **71:** 501-522.

Feldman, J.M. & Boninsega, J.A. (1968) Antiserum to tomato spotted wilt virus. *Nature* **219:** 183-184.

Ferguson, I.A.C. (1951) Four virus diseases of solanaceous plants in Trinidad. *Plant Disease Reporter* **35:** 102-105.

Finlay, K.W. (1953) Inheritance of spotted wilt resistance in the tomato. II. Five genes controlling spotted wilt resistance in four tomato types. *Australian Journal of Biological Sciences* **6:** 153-163.

Fitchen, J.H. & Beachy, R.N. (1993) Genetically engineered protection against viruses in transgenic plants. *Annual Review of Microbiology* **47:** 739-763.

Fletcher, J (1990) Severe losses after the return of an old enemy. *Grower* **113(1):** 19-23

Franki, R.I.B., Fauquet, C.M., Knudson, D.L. & Brown, F. (1991) Classification and nomenclature of viruses. Fifth report of the International Committee on Taxonomy of Viruses. *Archives of Virology* **Supplement 2:** 1-450.

Francki, R.I.B., & Grivell, C.J. (1970) An electron microscope study of the distribution of tomato spotted wilt virus in systemically infected *Datura stramonium* leaves. *Virology* **42:** 969-978.

Franki, R.I.B. & Hatta, T. (1981) Tomato spotted wilt virus. *In:* E. Kurstak, (editor) *Handbook of Plant Virus Infections and Comparative Diagnosis*, pp. 491-512. Elsevier/North Holland Biomedical Press, Amsterdam.

Frazier, W.A., Dennett, R.K., Hendrix, J.W., Poole C.F. & Gilbert. J.C. (1950) Seven new tomatoes Varieties resistant to spotted wilt, fusarium wilt, and grey leaf spot. *Bulletin of the Hawaii Agricultural Experimental Station* **103:** 1-22.

Fromme, F.D., Wingard, S.A. & Priode. C.N. (1927) Ring spot of tobacco; an infectious disease of unknown cause. *Phytopathology* **17:** 321-328.

Fujisawa, I., Tanaka, K. & Ishii, M. (1988) Tomato spotted wilt virus transmission by three species of thrips, *Thrips setosus, Thrips tabaci* and *Thrips palmi. Annals of the Phytopathological Society of Japan* **54:** 392.

Garcia, O. & Feldman, J.M. (1978) Natural infection of artichoke by tomato spotted wilt virus. *Plant Disease Reporter* **62:** 1076-1077.

Garcia, O. & Feldman, J.M. (1989) First report of tomato spotted wilt virus on celery and three weed species in Argentina. *Plant Disease* **73:** 859.

Gardner, M.W., Tomkins, C.M. & Whipple, O.C. (1935) Spotted wilt of truck crops and ornamental plants. *Phytopathology* **25:** 17.

Gardner, M.W. & Whipple, O.C. (1934) Spotted wilt of tomatoes and its transmission by thrips. *Phytopathology* **24:** 1136.

Gebre-Selassie, K., Chabrièrs, C. & Marchoux, G. (1989) Un virus qui se réveille, Le tomato spotted wilt sur cultures légumières et florales. *Phytoma* **410:** 30-35.

German, T.L., Hu, Y., Mau, R.F.L. & Ullman, D.E. (1991) Detection of tomato spotted wilt virus RNA in plants and thrips using strand specific probes. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 137-143. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

German, T.L., Ullman, D.E. & Moyer, J.W. (1992) *Tospoviruses*: diagnosis, molecular biology, phylogeny and vector relationships. *Annual Review of Phytopathology* **30:** 315-348.

Ghanekar, A.M., Reddy, D.V.R., Izuka, N., Amin, P.W. & Gibbons, R.W. (1979) Bud necrosis of groundnut *Arachis hypogaea* in India caused by tomato spotted wilt virus. *Annals of Applied Biology* **93:** 173-179.

Gielen, J.J.L., de Haan, P., Peters, M.R., van Grinsven, N.Q.J.M. & Goldbach, R.W. (1991) Engineered resistance to tomato spotted wilt virus, a negative-stranded RNA virus. *Biotechnology* **9:** 1363-1367.

Goldbach, R.W. & Peters, D. (1994) Possible causes of the emergence of *Tospovirus* diseases. *Seminars in Virology* **5:** 113-120.

Gonsalves, C. Xue, B., Pang, S.Z., Provvidenti, R., Slightom, J.L. & Gonsalves, D. (1995) Breeding transgenic tomatoes for resistance to tomato spotted wilt and cucumber mosaic viruses. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 22. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Gonsalves, D., Pang, S.Z., Gonsalves, C., Xue, B., Yepes, M. & Jan, F.J. (1995) Developing transgenic crops that are resistant to Tospoviruses. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 23. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Gonsalves, D. & Trujillo, E.E. (1986) Tomato spotted wilt virus in Papaya and detection of the virus by ELISA. *Plant Disease* **70:** 501-506.

Greber, R.S. & McCarthy, G.J.P. (1977) A disease of *Duboisia* caused by tomato spotted wilt virus (TSWV). *Australian Plant Pathology Society Newsletter* **6:** 54-55.

Green, D.E. (1934) The virus of spotted wilt in Gloxinias. *Gardeners' Chronical* **96:** 159.

Green, J.L., Allen, T.C. & Fischer, S. (1988) Tomato spotted wilt virus in Stephanotis in an Oregon greenhouse. *Plant Disease* **72:** 912.

Greene, I. & Parrella, M. (1992) An eye on control. *Greenhouse Grower* **October:** 55-58.

Greenough, D.R., Black, L.L., Story, R.N., Newsom, L.D. & Bond, W.P. (1985) Occurrence of *Frankliniella occidentalis* in Louisiana: a possible cause for the increased incdence of tomato spotted wilt. *Phytopathology* **75:** 1362.

Gumpf, D.J. & Weathers, G. (1972) Identification and purification of tomato spotted wilt virus isolated from Ageratum. *Plant Disease Reporter* **56:** 869-872.

Hagan, A.K., Weeks, J.R., French, J.C., Gudauskas, R.T., Mullen, J.M., Gazaway, W.S. & Shelby, R. (1990) Tomato spotted wilt virus in peanut in Alabama. *Plant Disease* **74:** 615.

Hall, J.M., Mohan, K., Knott, E.A. & Moyer, J.W. (1993) Tospoviruses associated with scape blight of onion (*Allium cepa*) seed crops in Idaho. *Plant Disease* **77:** 952.

Halliwell, R.S. & Barnes, L.W. (1987) Tomato spotted wilt virus infection of commercial *Aphelandra* sp. *Journal of Environmental Horticulture* **5:** 120-121.

Hardy, V.G. & Teakle, D.S. (1992) Transmission of a sowbane mosaic vrus by *Thrips tabaci* in th epresence and absence of virus-carrying pollen. *Annals of Applied Biology* **121:** 315-320.

Hausbeck, M.K. & Gildow, F.F. (1991) Report of tomato spotted wilt virus on Thanksgiving Cactus. *Plant Disease* **75:** 215.

Hausbeck, M.K., Welliver, R.A., Derr, M.A. & Gildow, F.E. (1992) Tomato spotted wilt virus survey amongst greenhouse ornamentals in Pennsylvania. *Plant Disease* **76:** 795-800.

Helms, K., Grylls, N.E. & Purss, G.S. (1961) Peanut plants in Queensland infected with tomato spotted wilt virus. *Australian Journal of Scientific Research* **12:** 239-246.

Helyer, N.L. & Brobyn, P.J. (1992) Chemical control of western flower thrips (*Frankliniella occidentals* Pergande). *Annals of Applied Biology* **121:** 219-231.

Helyer, N.L., Gill, G., Bywater, A. & Chambers, R. (1992) Elevated humidities for control of chrysanthemum pests with *Verticillium lecanii*. *Pesticide Science* **36:** 373-378.

Heming, B.S. (1978) Structure and function of the mouthparts in the larvae of *Haplothrips verbasci* (Osborn) (Thysanoptera, Tubilifera, Phlaeothripidae). *Journal of Morphology* **156:** 1-37.

Hill, M. (1994) *Western flower thrips*. Institute for Horticultural Development, Knoxfield, Australia.

Hobbs, H.A., Black, L.L., Story, R.N., Valverde, R.A., Bond, W.P., Gatti, J.M., Schaeffer, D.O. & Johnson, R.R. (1993) Transmission of tomato spotted wilt virus from pepper and three weed hosts by *Frankliniella fusca*. *Plant Disease* **77:** 797-799.

Holmes, F.O. (1948) Resistance to spotted wilt in tomato. *Phytopathology* **38:** 467-473.

Hsu, H.-t. & Lawson, R.H. (editors) (1991a) *Virus-thrips-plant interactions of TSWV*. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Hsu, H.-t. & Lawson, R.H. (1991b) Direct tissue blotting for detection of tomato spotted wilt virus in *Impatiens*. *Plant Disease* **75:** 292-295.

Huang, A.S. (1973) Defective interfering viruses. *Annual Review of Microbiology* **27:** 101-117.

Huguenot, C., van deen Dobbelsteen, G., de Haan, P., Wagenmakers, C.A.M., Drost, G.A., Osterhaus, A.D.M.E. & Peters, D. (1990) Detection of tomato spotted wilt virus using monoclonal antibodies and riboprobes. *Archives of Virology* **110:** 47-62.

Hunter, W.B. & Ullman, D.E. (1989) Analysis of mouthpart movements during feeding of *Frankliniella occdentalis* (Pergande) and *F. scultzei* Trybom (Thysanoptera: Thripidae). *International Journal of Insect Morphology and Embryology* **18:** 17-35.

Hunter, W.B. & Ullman, D.E. (1992) Anatomy and ultrastructure of the piercing-sucking mouthparts and paraglossal sensilla of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae). *International Journal of Insect Morphology and Embryology* **21:** 17-35.

Hurtt, S.S., Trees, S.C. & Watterson, J.C. (1985) Tomato spotted wilt virus associated with a lethal disease of *Anentone coronaria*. *Phytopathology* **75:** 1359.

Hutton, E.M. & Peak, A.R. (1952) The selection of-spotted wilt resistant phenotypes in the potato (*Solanum tuberosum*). *Australian Journal of Agricultural Research* **3:** 137-147.

Hutton, E.M. & Peak, A.R. (1953) Spotted-wilt development in resistant and susceptible *Lycopersicum* species. *Australian Journal of Agricultural Research* **4:** 160-167.

Ie, T.S. (1970) Tomato spotted wilt virus. C.M.I./A.A.B. *In:* Descriptions of plant viruses No. 39. Commonwealth Mycological Institute/Association of Applied Biology, Kew, Surrey, England.

Ie, T.S. (1982) A sap transmissible, defective form of tomato spotted wilt virus. *Journal of General Virology* **59:** 387-391.

Illingworth, J.F. (1931) Yellow spot of pineapples in Hawaii. *Phytopathology* **21:** 865-880.

Iwaki, M., Honda, Y., Hanada, K., Tochihara, H., Yonaha, T., Hokama, K. & Yokoyama, T. (1984) Silver wattle disease of watermelon caused by tomato spotted wilt virus. *Plant Disease* **68:** 1006-1008.

Jacobson, R.J. (1995) Resources to implement biologcal control in greenouses. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 211-219. Plenum Press, London, 636pp.

Jones, L.K. (1944) Streak and mosaic of cineraria. *Phytopathology* **34:** 941-953.

Jones, R.K. & Baker, J.R. (1987) Beware: WFT can transmit damaging virus. *Greenhouse Grower* May 1987:76-79.

Jones, R.K. & Baker, J.R. (1989) Tomato spotted wilt virus: prospects for 1989. *North Carolina Flower Growers Bulletin* **34:** 12-15.

Jones, R.K. & Baker, J.R. (1991) TSWV: symptoms, host range and spread. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 89-93. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Kaminska, M. & Korbin, M. (1991) The occurence of tomato spotted wilt virus in Polish glasshouses. *Phytopathologica Polonica* **12:** 9-14.

Kato, K. (1995) Some properties of melon spotted wilt virus isolated from netted melon (*Cucumeris melo*) in Japan. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 28. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Kennedy, B.S. & Nielsen, M.T. (1993) Characterisation of tomato spotted wilt virus (TSWV) resistance in the tobacco cultivar 'Polalta'. *Phytopathology* **83:** 1420.

Kikuta, K., Hendrix, J.W. & Frazier, W.A. (1945) Pearl Harbor, a tomato variety resistant to spotted wilt in Hawaii. *Hawaii Agricultural Experimental Station Circular* **24:** 6 pp.

Kim, J.W., Sun, S.S.M. & German, T.L. (1994) Disease resistance in tobacco and tomato plants transformed with the tomato spotted wilt virus nucleocapsid gene. *Plant*

Disease **78:** 615-621.

Kobatake, H., Osaki, T. & Inouye, T. (1984) The vector and reservoirs of tomato spotted wilt virus in Nara Prefecture. *Annals of the Phytopathological society of Japan* **50:** 541-544.

Kumar, N.K.K., Ullman D.E. & Cho, J.J. (1993) Evaluation of *Lycopersicon* germ plasm for tomato spotted wilt *Tospovirus* resistance by mechancal and thrips transmission. *Plant Disease* **77:** 938-941.

Lavina, A. & Batlle, A. (1993) First report of tomato spotted wilt virus infection *Ficus* species in Spain. *Plant Disease* **77:** 536.

Lavina, A. & Batlle, A. (1994) First report of impatiens necrotic spot virus in *Asplenium nidis-avis* in Spain. *Plant Disease* **78:** 316.

Law, M.D. & Moyer, J.W. (1989) Physiochemical properties analysis of a serologically distinct tomato spotted wilt virus strain. *Phytopathology* **79:** 1157.

Law, M.D. & Moyer, J.W. (1990) A tomato spotted wilt-like virus with a serologically distinct N protein. *Journal of General Virology* **71:** 933-938.

Law, M.D., Seck, J. & Moyer, J.W. (1991a) Genomic organisatin of the impatiens necrotic spot virus M RNA. *Phytopathology* **81:** 1192.

Law, M.D., Seck, J. & Moyer, J.W. (1991b) Nucleotide sequence of the 3' non-coding region and N gene of the S RNA of a serologically distinct *Tospovirus*. *Journal of General Virology* **72:** 2597-2601.

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

Lewis, T. (1973) *Thrips: their biology, ecology, and economic importance.* Academic Press, London. 349pp.

Linford, B. (1932) Transmission of the pineapple yellow-spot virus by *Thrips labaci. Phytopathology* **22:** 301-324.

Loomans, A.J.M. & van Lentern, J.C. (1995) Biological control of thrips pests: a review on thrips parasitoids. *Wageningen Agricultural University Papers* **95-1:** 89-201.

Lublinkhof, J & Foster, D.E. (1977) Development and reproductive capacity of *Frankliniella occidentalis* (Thysanoptera:Thripidae) reared at three temperatures. *Journal of the Kansas Entomological Society* **50:** 313-316.

MacDonald, L.S., Stace-Smith, R.R., Allen W.R. & Matteoni, J.A.. (1989) Incidence of tomato spotted wilt virus in British Columbia. *Canadian Plant Disease Survey* **69:** 87-88.

MacGovern, R.J., Polston, J.E. & Mullahey, J.J. (1993) Tropical soda apple: newly identifed host of tomato, pepper and tobacco viruses in Florida. *Citrus and Vegetable Magazine* **56:** 10-12.

MacKenzie, D.J. & Ellis, P.J. (1992) Resistance to tomato spotted wilt virus infection in tobacco expressing the viral nucleocapsid gene. *Molecular Plant-Microbe Interactions* **5:** 34-40.

Marchoux, G. (1990) La transmission de virus par *Frankliniella occidentalis* et autre thrips. *Phytoma* **422:** 40-45.

Marchoux, G., Gebre-Selassie, K & Villevieille, M. (1991) Detection of tomato spotted wilt virus and transmission by *Frankliniella occidentalis* in France. *Plant Pathology* **40:** 347-352.

Matteoni, J.A. & Allen, W.R. (1989) Symptomatology of tomato spotted wilt virus infection in florist's Chrysanthemum. *Canadian Journal of Plant Pathology* **11:** 373-380.

Matteoni, J.A., Allen, W.R. & Broadbent, A.B. (1988a) Host range and symptoms of tomato spotted wilt virus. pp 84-93 *In* Ali, A.D. (editor) *Proceedings of the Fourth Conference on Insect and Disease Management on Ornamentals. Kansas City, MO.*

Matteoni, J.A., Allen, W.R. & Broadbent, A.B. (1988b) Tomato spotted wilt virus in greenhouse crops in Ontario. *Plant Disease* **72:** 801.

Matteoni, J.A., Allen W.R. & Tehrani, B. (1989) Diseases of ornamentals: diagnostic summary, Vineland Research Station. *Canadian Plant Disease Survey* **69:** 90-93.

Matthews, R.E.F. (1982) Classification and nomenclature of viruses: Fourth report of the International Committee on Taxonomy of Viruses. *Intervirology* **17:** 1-200.

Matthews, R.E.F. (1991) *Plant Virology (3rd edition).* Academic Press, New York.

Mau, R.F.L., Bautista, R., Cho, J.J., Ullman, D.E., Gusukuma-Minuto, L. & Custer, D. (1991) Factors affecting the epidemiology of TSWV in field crops: comparative virus acquisition efficiency of vectors and suitability of alternative hosts to *Frankliniella occidentalis* (Pergande). *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 21-27. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Mayhew, D.E., Cooke, A.L. & Raabe, R.D. (1992) A new virus is reported for *Phalaenopsis. American Orchid Society Bulletin* **61:**575-577.

McCarthy, G.J.P.& Greber, R.S. (1978) Tomato spotted wilt virus in *Duboisia*. *Queensland Agricultural Journal* **104:** 336-338.

Mertelík, J., Mokrá, V & Götzová, B. (1995) Occurence of tomato spotted wilt virus infection in vegetables in the Czech republic. *In: Advances in Vegetable Virus Research,* pp. 158-161. Proceedings of the 8th conference on virus diseases of vegetables,Czech Academy of Agricultural Sciences, Prague.

Middleton, J.T. (1939) Occurrence of spotted wilt in Missouri. *Plant Disease Reporter* **23:** 204.

Milbrath, J.A. (1939) Tomato tip-blight virus. *Phytopathology* **29:** 156-168.

Milne, R.G. & Franki, R.I.B. (1984) Should tomato spotted wilt virus be considered as a possible member of the family *Bunyaviridae*? *Intervirology* **22:** 72-76.

Mitchell, F.L. & Smith Jr., J.W. (1991) Epidemiology of tomato spotted wilt virus relative to thrips populations. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 46-52. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Mound, L.A. (1971) The feeding apparatus of thrips. *Bulletin of Entomological Research* **60:** 547-548.

Mound, L.A., Morison, G.D., Pitkin, B.R. & Palmer, J.M. (1976) Thysanoptera. *Handbooks for the Identification of British Insects* **1(11):**79pp.

Mound, L.A. & Teulon, D.A.J. (1995) Thysanoptera as phytophagous opportunists. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 3-19. Plenum Press, London, 636pp.

Moyer, J.W., Law, M.D. & Urban, L.A. (1991) Characterization of a serologically distinct TSWV-like virus from Impatiens. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 53-59. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Mumford, R.A., Barker, I. & Wood, K.R. (1994) The detection of tomato spotted wilt virus using the polymerase chain reaction. *Journal of Virological Methods* **46:** 303-311.

Mumford, R.A., Barker, I. & Wood, K.R. (In press) The biology of the *Tospoviruses*. *Annals of Applied Biology*.

Nameth, S.T., Powell, C.C. & Lindquist, R.K. (1988) Tomato spotted wilt virus: a serious threat to greenhouse crops. *Ohio Florists' Association Bulletin* **704:** 2-4.

Nameth, S.T., Lindquist, R.K. & Powell. C.C. (1989) *Tomato spotted wilt virus: a serious threat to greenhouse crops.* Extension Plant Pathology, Ohio Cooperative Extension Service, The Ohio State University.

Noordam, D. (1943) On the occurrence of 'spotted wilt' in Holland. *Tijdschrift Plantziekten* **49:** 117-119.

Noordam, D. (1952). *Lycopersicum*-virus 3 (tomato spotted wilt) on some ornamental plants. *Tijdschrift Plantziekten.* **58:** 89-96.

Norris, D.O. (1946) The strain complex and symptom variablility of tomato spotted wilt virus. *Bull. Coun. Sci. Ind. Res. Aust.* **202:** 1-51.

Ogilvie, L. (1935) Spotted wilt and its control. *Annual Report of the Long Ashton Research Station* **1934:** 170-174.

Paliwal, Y.C. (1974) Some properties and thrip transmission of tomato spotted wilt virus in Canada. *Canadian Journal of Botany* **52:** 1177-1182.

Paliwal, Y.C. (1976) Some characteristics of the thrips vector relationship of tomato spotted wilt virus in Canada. *Canadian Journal of Botany* **54:** 402-405.

Pang, S.Z., Bock, J.H., Gonsalves, C., Slightom, J.L. & Gonsalves, D. (1994) Resistance of transgenic *Nicotiana benthamiana* plant to tomato spotted wilt and impatens necrotic spot *Tospoviruses*: evidence of the involment of the N gene RNA in resistance. *Phytopathology* **84:** 243-249.

Pang, S.Z., Nagpala, P., Wang, M., Slightom, J.L. & Gonsalves, D. (1992) Resistance to heterologous isolates of tomato spotted wilt virus in transgenic tobacco expressing its nucleocapsid protein gene. *Phytopathology* **82:** 1223-1229.

Pang, S.Z., Slightom, J.L & Gonsalves, D. (1993) Different mechanisms protect transgenic tobacco plants against tomato spotted wilt and impatiens necrotic spot *Tospoviruses. Biotechnology* **11:** 819-824.

Parker, B.L., Skinner, M. & Lewis, T. (editors) (1995) *Thrips Biology and Management.* Plenum Press, London, 636pp.

Paterson, R.G., Scott, S.J. & Gergerich, R.C. (1989) Resistance in two *Lycopersicon* species to an Arkansas isolate of tomato spotted wilt virus. *Euphytica* **43:** 173-178.

Peters, D., de Avila, A.C. Kitajima, E.W., Resende, R. de O., de Haan, P. & Goldback, R.W. (1991) An overview of tomato spotted wilt virus. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 1-14. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Pittman, H.A. (1927) Spotted wilt of tomatoes. *Journal of the Australian Council for Science and Industrial Research* **1:** 74-77.

Pontis, R.E. & Feldman, J.M. (1967) Tomato spotted wilt virus in lettuce in Argentina. *Plant Disease Reporter* **51**:225.

Powell, C.C. (1990) Viruses - a growing threat to greenhouse crops. *Ohio Florists' Association Bulletin* **731:** 5-9.

Prins, M., de Haan, P & Goldbach, R. (1995) Molecular basis of gene specific RNA-mediated resistance to tomato spotted wilt virus in transgenic tomato plants. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 37. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Priode, C.N. (1928) Further studies in the ringspot disease of tobacco. *American Journal of Botany* **15:** 88-93.

Pundt, L. (1993) Petunias: Effective indicator plants for detecting TSWV. *Professional Plant Growers Association News* **March 1993:** 2-3.

Ramakers, P.M.J. (1995) Biological control using oligophagous predators. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 225-229. Plenum Press, London, 636pp.

Reddy, D.V.R., Sudarshana, M.R., Ratna, A.S., Reddy, A.S., Amin, P.W., Kumar, I.K. & Murthy, A.K. (1991) The occurence of yellow spot virus, a member of tomato spotted wilt virus group, on peanut (*Arachis hypogaea*) in India. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 77-88. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Reddy, D.V.R. & Wightman, J.A. (1988) Tomato spotted wilt virus: thrips transmission and control. *Advances in Disease Vector Research* **5:** 203-220.

Resende, R. de O. (1993) *Generation and characterisation of mutants of tomato spotted wilt virus.* PhD. Thesis, Wageningen Agricultural University, Wageningen.

Resende, R. de O., de Haan, de Avila, A.C., Kitajima, E.W., Kormelink, R., Goldbach, R. & Peters, D. (1991a) Generation of envelope and defective infering RNA mutants of tomato spotted wilt virus bymechanical passage. *Journal of General Virology* **72:** 2375-2383.

Resende, R. de O., Kitajima, E.W., de Avila, A.C., Goldbach, R.W. & Peters, D. (1991) Defective isolates of tomato spotted wilt virus. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 71-76. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Resende, R. de O., Posser, L., Nagata, T., Bezerra, I.C., Lima, M.I., Kitajima, E.W. & de Avila, A.C. (1995) Diversity of *Tospoviruses* in Brazil. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 39. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Rice, D.J., German, T.L., Mau, R.F.L. & Fujimoto, F.M. (1990) Dot blot detection of tomato spotted wilt virus RNA in plant and thrips tissues by cDNA clones. *Plant Disease* **74:** 274-276.

Riudavets, J. (1995) Predators of *Frankliniella occidentalis* (Perg.) and *Thrips tabaci* Lind.: a review. *Wageningen Agricultural University Papers* **95-1:** 43-87.

Robb, K.L. (1989) Analysis of *Frankliniella occidentalis* (Pergande) as a pest of floricultural crops in California greenhouses. *PhD. Thesis, University of California, Riverside, USA.* 135pp.

Robb, K.L. (1992) Profile of a pest. *Greenhouse Grower* **September:** 71-74.

Robb, K.L., Parrella, M.P. & Newman, J.P. (1988a) The biology and control of the western flower thrips. Part I. *Ohio florists' Association Bulletin* **699:** 2-5.

Robb, K.L., Parrella, M.P. & Newman, J.P. (1988b) The biology and control of the western flower thrips. Part II. *Ohio florists' Association Bulletin* **700:** 2-5.

Ruter, J.M. & Gitaitis, R.D. (1993a) First report of tomato spotted wilt virus on bedding plants in Georgia. *Plant Disease* **77:** 101.

Ruter, J.M. & Gitaitis, R.D. (1993b) Impatiens necrotic spot virus in woody landscape plants in Georgia. *Plant Disease* **77:** 318.

Sakimura, K. (1940) Evidence for the identity of the yellow-spot virus with the spotted wilt virus: Experiments with the vector, *Thrips tabaci. Phytopathology* **30:** 281-299.

Sakimura, K. (1961) Field observations on the thrips vector species of the tomato spotted wilt virus in the San Pablo Area, California. *Plant Disease Reporter* **45:** 772-776.

Sakimura, K. (1962a) *Frankliniella occidentalis* (Thysanoptera: Thripidae), a vector of the tomato spotted wilt virus, with special reference to colour forms. *Annals of the Entomological Society of America* **55:** 387-389.

Sakimura, K. (1962b) The present status of thrips-borne viruses. *In:* Maramorosch, K. (editor) *Biological Transmission of Disease Agents*, pp. 33-40. Academic Press, New York.

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

Sakimura, K. (1969) A comment on *Frankliniella schultzei* (Thysanoptera: Thripidae) in transmission of tomato spotted wilt virus. *Pacifc Insects* **11:** 761-762.

Samuel, G., Bald, J.G. & Pittman, H.A. (1930) Investigations on 'spotted wilt' of tomatoes. *Australian Council of Science and Industrial Research Bulletin* **44:** 64.

Schliephake, G. (1990) Zwei eingeschleppte Thysanopteren-Arten als neue Schädlinge in Gewächshäusern: *Frankliniella occidentalis* und *Thrips palmi. Entomologische Nachrichten Berichten* **34:** 29-32.

Schuster, G.L. & Halliwell, R.S. (1994) Six new hosts of tomato spotted wilt virus. *Plant Disease* **78:** 100.

Sdoodee, R & Teakle, D.S. (1987) Transmission of tobacco streak virus by *Thrips tabaci*: a new method of plant virus transmission. *Plant Pathology* **36:** 377-380.

Sether, D.M. & DeAngelis, J.D. (1992) *Tomato spotted wilt virus host list and Bibliography.* Special report 888, Agricultural Experiment Station, Oregon State University, 16pp.

Sether, D.M., DeAngelis, J.D.D. & Rossignol, P.A. (1991) First report of tomato spotted wilt virus in peppermint *(Mentha* x *piperita). Plant Disease* **75:** 644.

Sherf, A.F. (1948) Occurrence of tomato spotted wilt in Nebraska in 1948. *Plant Disease Reporter* **32:** 509.

Sherman, J.M., Moyer, J.W. & Daub, M.E. (1995) Genetically-engineered resistance to tomato spotted wilt virus in chrysanthemum (*Dendranthema grandiflora*): a model system for virus protection in ornamental crops. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 34. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Sherwood, J.L., Sandborn, M.R. Keyser, G.C. & Myers, L.D. (1989) Use of monoclonal antibodies in detection of tomato spottted wilt virus. *Phytopathology* **79:** 61-64.

Sing, S.J. & Krishnareddy, M. (1995) Diagnosis and epidemiology of a *Tospovirus* infecting watermelon in India. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 42. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Smith, I.M., McNamara, D.G., Scott, P.R. & Harris, K.M. (editors) (1992) *Quarantine Pests for Europe.* CABI & EPPO, Wallingford.

Smith, K.M. (1931a) *Thrips tabaci* as a vector of plant virus disease. *Nature* **127:** 852-853.

Smith, K.M. (1931b) Studies on potato virus diseases. VIII. On a ringspot virus affecting solanaceous plants. *Annals of Applied Biology* **18:** 1-15.

Smith, K.M. (1932) Studies on plant virus diseases. XI. Further experiments with a ringspot virus: its identification with spotted wilt of the tomato. *Annals of Applied Biology* **19:** 305-330.

Smith, K.M. (1933) Spotted wilt: an important virus disease of the tomato. *Journal of the Ministry of Agriculture* **39:** 1097-1103.

Smith, K.M. (1937) *A Textbook of Plant Virus Diseases.* P. Blakiston's Son & Co. Inc., Philadelphia, 615 pp.

Smith, K.M. (1957) *A Textbook of Plant Virus Diseases,* 2nd edition, Churchill, London, 572 pp.

Smith, P.G. (1944) Reaction of *Lycopersicon* spp. to spotted wilt. *Phytopathology* **34:** 504-505.

Snyder, W.C. & Thomas, H.R. (1936) Spotted wilt of the sweet pea. *Hilgardia* **10:** 257-262.

Spence, N. (1996) First steps to wilt control. *Grower* **125(8):** 13-15.

Stevens, M.R., Scott, S.J. & Gergerich, R.C. (1992) Inheritance of a gene for resistance to tomato spotted wilt virus (TSWV) from *Lycopersicon peruvianum* Mill. *Euphytica* **59:** 9-17.

Stobbs, L.W., Broadbent, A.B, Allen, W.R. & Stirling, A.L. (1992) Transmission of tomato spotted wilt virus by the western flower thrips to weeds and native plants found in southern Ontario. *Plant Disease* **76:** 23-29.

Stubbs, L.L. (1960) *Hoya carnosa* infected with tomato spotted wilt virus. *Australian Plant Disease Recorder* **12:** 33.

Tehrani, B., Allen, W.R. & Matteoni, J.A. (1990) Update on the incidence of tomato spotted wilt virus in greenhouses. *Canadian Plant Disease Survey* **70:** 102-103.

Thompson, G.J. & van Zijl, J.J.B. (1995) Control of tomato spotted wilt virus in tomatoes in sSouth Africa. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 43. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Tommasini, M.G. & Maini, S. (1995) *Frankliniella occidentalis* and other thrips harmful to vegetable and ornamental crops in Europe. *Wageningen Agricultural University Papers* **95-1:** vii-x, 1-42.

Tompkins, C.M. & Gardner, M.W. (1934) Spotted wilt of head lettuce. *Phytopathology.* **24:** 1135-1136.

Tompkins, C.M. & Severin, H.H.P. (1950) Spotted wilt of white, yellow, and pink callas. *Hilgardia* **20:** 207-232.

Ullman, D.E., Cho, J.J., Mau, R.F.L., Hunter, W.B. Westcot, D.M. & Custer, D.M. (1992a) Thrips-tomato spotted wilt virus interactions: morphological, behavioural and cellular components influencing thrps transmission. *Advances in Diseases Vector Research* **9:** 196-240.

Ullman, D.E., Cho, J.J., Mau, R.F.L., Westcot, D.M. & Custer, D.M. (1992b) A midgut barrier to tomato spotted wlt virus acquisition by adult Western flower thrips. *Phytopathology* **82:** 1333-1342.

Ullman, D.E., German, T.L., Sherwood, J.L. & Westcot, D.M. (1995a) Thrips transmission of *Tospoviruses*: future possibilities for management. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 135-151. Plenum Press, London, 636pp.

Ullman, D.E., German, T.L., Sherwood, J.L., Westcot, D.M. & Cantone, F.A. (1993) *Tospovirus* replication in insect vector cells: immunocytochemical evidence that the nonstructural protein encoded by the S RNA of tomato spotted wilt tospovirus is present in thrips vector cells. *Phytopathology* **83:** 456-463.

Ullman, D.E., Westcot, D.M., Hunter, W.B. & Mau, R.F.L. (1989) Internal anatomy and morphology of *Frankliniella occidentalis* (Pergande) (Thysanoptera: Tripidae) with special reference to interactions between thrips and tomato spotted wilt virus. *International Journal of Insect Morphology and Embryology* **18:** 289-310.

Ullman, D.E., Westcot, D.M., Hunter, W.B., Mau, R.F.L., Cho, J.J. & Custer, D. (1991) Tomato spotted wilt virus and one thrips vector: *Frankliniella occidentalis* (Pergande) internal morphology and virus location. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 127-136. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

Ullman, D.E., Westcot, D.M., Sherwood, J.L. & German, T.L. (1995b) Potential mechanisms for tomato spotted wilt tospovirus movement between thrips cells. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 47. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Urban, L.A., Huang, P. & Moyer, J.W. (1991) Cytoplasmic inclusions in cells infected with isolates L and I serogroups of tomato spotted wilt virus. *Phytopathology* **81:** 525-529.

Urban, L.A., Sherman, J.M., Moyer, J.W. & Daub, M.E. (1994) High-frequency shoot regeneration and *Agrobacterium*-mediated transformation of chrysanthemum (*Dendranthema grandiflora*). *Plant Science* **98:** 69-79.

Valverde, R.A., Can, F. & Rush, M.C. (1993) Yellow mottle of tomatillo (*Physalis ixocarpa*) caused by physalis mottle virus. *Plant Pathology* **42:** 657-660.

van Blockland, G.D. (1991) Consequences of avoiding TSWV in a breeding station in the temperate zone. *In:* Hsu, H.-t. & Lawson, R.H. (editors) *Virus-Thrips-Plant Interactions of Tomato Spotted Wilt Virus,* pp 162-165. Proceedings of a USDA workshop, United States Department of Agriculture, Agricultural Research Service, ARS-87, 170pp.

van der Wetering, F., Peters, D. & Goldbach, R. (1995) TSWV is transmitted by *Frankliniella occidentalis* only after acquisition during the first larval stage. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 47. Taiwan Agricultural Research Institute, Taichung, Taiwan.

van Kammen. A., Henstra, S. & Ie, T.S. (1966) Morphology of tomato spotted wilt virus. *Virology* **30:** 574-577.

von der Pahlen, A. (1970) Inheritance of the resistance in tomato (cv. Platense) to spotled wilt *(Lycopersicon* virus 3 Smith). *Revista Investigaciones agropecuarias, Serie 5, Pathologia Vegetal* **7:** 129-134.

Varia, A.M., Gallo, S. & Lisa, V. (1992) Nuove infezione da due *Tospovirus* (tomato spotted wilt and impatiens necrotic spot) in Liguria. *Informatore Fitopatologico* **42:** 37-42.

Vaira, A.M., Roggero, P., Luisoni, E., Masenga, V., Milne, R.G. & Lisa, V. (1993) Characterisation of two *Tospoviruses* in Italy: tomato spotted wilt and impatiens necrotic spot. *Plant Pathology* **42:** 530-542.

Verkleij, F.N. & Peters, D. (1983) Characterization of a defective form of tomato spotted wilt virus. *Journal of General Virology* **64:** 677-686.

Vierbergen, G. (1995) International movement, detection and quarantine of Thysanoptera pests. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 119-132. Plenum Press, London, 636pp.

Wang, M. & Cho, J.J., Provvidenti, R. & Hu, J.S. (1992a) Identification of resistance to tomato spotted wilt virus in lettuce. *Plant Disease* **76:** 642.

Wang, M., Cho, J.J. & Hu, J.S. (1992b) Identification and incorporation of TSWV resistance into commercial lettuce. *Phytopathology* **82:** 1087.

Wang, M., Ferreira, S. & Ogata, D. (1992c) Tomato spotted wilt virus on *Oncidium* Orchids in Hawaii. *Plant Disease* **76:** 426.

Wang, M. & Gonsalves, D. (1990) ELISA detection of various tomato spotted wilt virus isolates using specific antisera to structural proteins of the virus. *Plant Disease* **74:** 154-158.

Whipple, O.C. (1936). Spotted wilt of garden pea. *Phytopathology* **26:** 918-920.

Wijkamp, I. Almarza, N. & Peters, D. (1995a) Median latent period and transmission of Tospoviruses vectored by thrips. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 153-156. Plenum Press, London, 636pp.

Wijkamp, I. & Peters, D. (1993) Determination of the median latent period of two tospoviruses in *Frankliniella occidentalis*, using a novel leaf disk assay. *Phytopathology* **93:** 986-991.

Wijkamp, I., van Lent, J., Kormelink, R., Goldbach, R.W. & Peters, D. (1993a) Virus-vector interactions during the transmission of tospoviruses by thrips. *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society* **1993 No.4:** 193-198.

Wijkamp, I., van Lent, J., Kormelink, R., Goldbach, R.W. & Peters, D. (1993b) Multiplication of tomato spotted wilt virus in its insect vector, *Frankliniella occidentalis*. *Journal of General Virology* **74:** 341-349.

Wijkamp, I., van Lent, J., Kormelink, R., Goldbach, R. & Peters, D. (1995b) Multiplication of tomato spotted wilt virus in western flower thrips. *In:* Parker, B.L., Skinner, M. & Lewis, T. (editors) *Thrips Biology and Management*, pp 157-161. Plenum Press, London, 636pp.

Wingard, S.A. (1928) Hosts and symptoms of ring spot, a virus disease of plants. *Journal of Agricultural Research* **37:** 127-153.

Wood, K.R., Mumford, R.A., Weeks, R.J. & Barker, I. (1995) Diagnosis of tospoviruses by RT-PCR. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 48. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Yamamoto, C.M. & Ohata, K. (1977) Some properties and electron microscopy of tomato spotted wilt virus isolated from blackberry lily (*Belamcanda chinensis* DC.). *Bulletin of the Shikoku Agricultural Experimental Statio* **30:** 39-47.

Yeh, S.D. & Chang, T.F. (1995) Nucleotide sequence of the N gene of watermelon silver mottle virus, a proposed new member of the genus *Tospovirus*. *Phytopathology* **85:** 58-64.

Yeh, S.D., Lin, Y.C., Cheng, Y.H., Jih, C.L., Chen, M.J. & Chen, C.C. (1992) Identification of tomato spotted wilt-like virus on watermelon in Taiwan. *Plant Disease* **76:** 835-840.

Yeh, S.D., Chao, C.H., Chen, Y.H. & Chen, C.C. (1995) Serological comparison of four distinct tospoviruses by polyclonalantibodies to purified nucleocapsid proteins. (Abstract). *International Symposium on Tospoviruses and Thrips of Floral and Vegetable Crops,* p. 49. Taiwan Agricultural Research Institute, Taichung, Taiwan.

Yudin, L.S., Cho, J.J. & Mitchell, W.C. (1986) Host range of western flower thrips, *Frankliniella occidentalis* (Thysanoptera: Thripidae), with special reference to *Leucaena glauca*. *Environmental Entomology* **15:** 1292-1295.

Zitter, T.A., Daughtrey, L. & Sanderson, J.P. (1989) Vegetable/horticultural crops, Tomato spotted wilt virus. Cornell cooperative extension, Diseases of tomato, other vegetables, and ornamental crops. Fact sheet No. 735.90, Cornell University.