Emergence and Spread of *Tobacco streak virus* Menace in India and Control Strategies

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Abstract

Since the first outbreak of Tobacco streak virus *(TSV), genus* Ilarvirus *as sunflower necrosis disease (SND) on sunflower and peanut stem necrosis disease(PSND) on groundnut in late 1990s, the virus has been a subject of much research in India. This review considers main features of TSV in India. The virus epidemics are very damaging to several crops in South India. Natural occurrence of TSV was recorded on bottle gourd, chilli, crossandra, cotton, cowpea, cucumber, gherkin, ixora, marigold, mungbean, niger, okra, pumpkin, safflower, sesame, soybean, sunn hemp, urdbean, and several weed species. Coat protein gene sequence of TSV isolates from various locations and hosts are 97-100% identical. The virus is transmitted through pollen assisted by thrips (Thysanoptera: Thripidae). Epidemiological studies indicate TSV as a monocyclic disease in annual crops and asymptomatic weeds such as parthenium serve as TSV inoculum source. Attempts on identification and deployment of host resistance met with limited success. Phytosanitation and cultural methods of control were effective in reducing virus incidence but not popularly adopted by farmers. Major efforts are on-going to develop transgenic varieties using TSV coat protein gene. Additional research is required to determine the extent of TSV spread to other crops and its economic importance, understand disease epidemiology and development of host resistance for effective virus control, success of which will bring benefits to millions of farmers in India.*

Keywords: *Tobacco streak virus*, ilarvirus, thrips, pollen transmission, sunflower, groundnut, disease control, India

Introduction

Tobacco streak virus (TSV), first described by Johnson (1936), is the type species of the genus *Ilarvirus*, of the family *Bromoviridae* that includes viruses having tripartite quasi-isometric particles of size 27 to 35 nm (Fauquet *et al*., 2005). The virus has three nucleoprotein particles designated T (to four to five single stranded positive sense RNA designated as RNA-1 (3.5 kb), RNA-2 (3.0 kb), RNA-3 (2.3 kb), RNA-4 (1.0 kb) and RNA-4a (0.9 kb) and a coat protein of c. 28 kDa (Xin *et al*., 1998; Scott, 2001). RNAs 1 to 3 are genomic and encodes proteins 1a (119 kDa), 2a (91 kDa) and 3a (32 kDa), respectively; whereas RNA-4a and RNA-4 are subgenomic expressed from RNA-2 and RNA-3 which encodes 2b (22 kDa) and coat proteins (28 kDa), respectively. TSV genome is infectious only in presence of its coat protein or RNA-4 (Fulton, 1985; Sanchez-Navarro and Pallas, 1994; Ansel-McKinney *et al*., 1996). Several TSV variants that differ in host range, symptom expression, serological properties and transmissibility through seed was reported (Kaiser *et al*., 1982; Stenger *et al*., 1987; Walter *et al*., 1992).

Host range of TSV is wide, infecting more than 200 plant species belongs to 30 dicotyledonous and monocotyledonous plant families (Fulton, 1985; EPPO, 2005). TSV occurrence was reported from over 26 countries worldwide (EPPO, 2005). In India, TSV was first identified from sunflower necrosis disease(SND) affected sunflower and peanut stem necrosis disease (PSND)-affected groundnut during 1999-2000 from Andhra Pradesh state (Prasadarao *et al*., 2000; Reddy *et al*., 2002). Since then virus was found to be responsible for causing serious damage to groundnut, sunflower and several other annual crops in Andhra Pradesh, Karnataka, Maharastra and Tamil Nadu states (Kumar *et al*., 2006; Jain *et al*., 2008). Although the virus is widespread around the world, but it is not known to cause destructive

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epidemics as observed in India (Prasadarao *et al*., 2000) and very recently in Australia (Report, 2006; Sharman *et al.,* 2008). In this review we present main features of TSV status in India.

TSV in India

First identification

Since 1996 outbreaks of SND were recognized on sunflower across a large area around Bangalore, Karnataka State (Annual Report, 1998 and 2000). The disease spread rapidly to adjoining regions and caused severe epidemics on sunflower in subsequent years. In 2000, PSND epidemic was recognized on groundnut grown in 225,000 ha in Anantapur and Kurnool districts of Andhra Pradesh, resulting in crop losses exceeding Rs 300 crores (Prasadarao *et al*., 2000; Reddy *et al*., 2002). Based on symptoms, *Peanut bud necrosis virus* (PBNV, genus *Tospovirus*) or a necrotic strain of *Cucumber mosaic virus* (CMV, genus *Cucumovirus*) was thought to be involved in PSND etiology. But either of these viruses was detected in the diseased plants (Reddy *et al*., 2002). Jain *et al*., (2000) and Venkata-Subbaiah *et al*. (2000) reported an association of a tospovirus that has serological affinities to PBNV, but its etiology in SND was not established. A collaborative research work between ICRISAT and NBPGR Regional Station, Hyderabad, has first isolated TSV from SND-affected sunflower plants obtained from Bellary (Karnataka), Anantapur, Hyderabad (Andhra Pradesh) and PSND-affected groundnut plants obtained from Anantapur (Prasadarao *et al*., 2000; Reddy *et al*., 2002). Further characterization has conclusively proved TSV as the causal agent of SND and PSND (Prasadarao *et al*., 2000; Ramiah *et al*., 2001; Ravi *et al*., 2001; Bhat *et al*., 2002b,c; Reddy *et al*., 2002).

Virus properties

The TSV isolate purified from PSND-affected groundnut has properties similar to the strains reported previously (Reddy *et al*., 2002). Purified virus particle preparations have four RNA species of estimated size 3.7 (RNA-1), 3.1 (RNA-2), 2.2 (RNA-3) and 0.9 (RNA-4) kb; a major coat protein of estimated size 28 kDa; tripartite quasi-isometric particles of 25-35 nm in diameter; and serological relatedness [in enzyme-linked immunosorbent assay (ELISA) and immunosorbent electron microscope (ISEM)] with TSV-WC and TSV-black raspberry strains (Reddy *et al.*, 2002). TSV coat protein and movement protein gene sequences had 89% similarities with TSV-WC strain (Reddy *et al*., 2002; Bhat *et al*., 2002b). The virus isolated from groundnut differed from the isolates reported by Fulton (1948) in not infecting *Lycopersicon esculentum* (cv Pusa Ruby and Maruthi), *Pisum sativum* (cv. Bonneville) and *Nicotiana tabacum* (cv. Xanthi-nc) (Reddy *et al*., 2002). On the basis of symptoms on *Chenopodium amaranticolor, C. quinoa* and *Vigna unguiculata*, the TSV isolate from groundnut was classified as 'Pathotype-1' (Reddy *et al*., 2002). TSV coat protein genes from about 60 isolates originating from different hosts and locations in India are available in the NCBI GenBank (www.ncbi.nlm.nih.gov/genbank). These sequences were 97-100% identical at protein and nucleic acid level indicating that various TSV isolates are similar and may have a common lineage (PL Kumar, unpublished).

Distribution and host range

TSV was identified on several crops and weeds in the peninsular India (Table 1) (Prasadarao *et al*., 2003b; Kumar *et al.*, 2006; Jain *et al*., 2008). It was also reported on chilli from Uttar Pradesh (Jain *et al*., 2005) and on okra in Haryana and Madhya Pradesh (Krishnareddy *et al*., 2003a). It is likely that TSV may occur in other parts of India.

The virus has become a menace on sunflower, groundnut, okra, cucurbits and several other annual and horticrops. TSV epidemic in 2002 on sunflower in Karnataka was reported to cause yield loss of Rs 110 crores; an epidemic in 2004 on groundnut in Andhra Pradesh resulted in an estimated yield loss of Rs 93 crores; virus epidemic in gherkin in 2001-02, resulted in reduction in cropping area from 257 ha to 105 ha (Krishnareddy *et al*., 2003b). In 2005, TSV outbreak was reported on 20,000 ha of cotton fields grown in Khammam and Warangal districts of Andhra Pradesh. Critical studies on diseased cotton plants detected TSV in a fewer leaves and many symptomatic leaves of the same plant tested negative to virus (PL Kumar and RDVJ Prasadarao, unpublished). Seedlings of several cotton varieties (both bt and non-bt) inoculated with TSV in greenhouse experiments revealed virus infection only in the inoculated leaves without any systemic spread (RDVJ Prasadarao and PL Kumar, unpublished). These observation warrants for careful evaluation of cotton disorder attributed to TSV.

Symptoms and yield losses

Most common symptoms of TSV include chlorosis and necrosis of leaves, necrotic streaks on petioles, stems, floral parts and stunted growth (Fig. 1). TSV infection at seedling stage results in premature death of the plant. Infection during mid-stage of the plant growth may result in necrosis of the leaves and severe reduction in yield. Infection at late stage of the plant growth results in mild chlorotic symptoms, with little effect on plant growth and yield. In several weed hosts, such as parthenium, TSV causes asymptomatic infection. Premature death of plant was the main reason for enormous yield losses during the SND epidemics.

TSV transmission

TSV is transmitted through pollen assisted by thrips

Table 1. Natural host range of TSV in India*

Cultivated species:

Bottle gourd (*Luffa cylindrica*), chilli (*Capsicum annuum*), cotton (*Gossypium hirsutum*), cowpea (*Vigna unguiculata*), Crossandra (*Crossandra infundibuliformis*), cucumber (*Cucumis sativus*), gherkin (*Cucumis anguria*), groundnut (*Arachis hypogaea*), ixora (*Ixora coccinea*), jute (*Hibiscus cannabinus* L.), marigold (*Tagetes erecta*), mungbean (*Vigna radiata*), niger (*Guizotia abyssinica*), okra (*Abelmoschus esculentus*), pumpkin (*Cucurbita pepo*), safflower (*Carthamus tinctorius*), sesame (*Sesamum indicum*), soybean (*Glycine max*), sunflower (*Helianthus annuus*), sunhemp (*Crotalaria juncea*) and urdbean (*Vigna mungo*).

Weed species:

Abutilon indicum, Acalypha indica, Achyranthes aspera, A. hispidium, Calotropis gigante, Cleoma viscose, Commelina benghalensis, Croton bonplandianum, C. sparsiflorus, Digera arvensis, Euphorbia hirta, E. geniculata, Lagasca mollis, Leucas aspera, Parthenium hysterophorus, Tridax procumbens and *Xanthium strumarium*.

*As of reports in India up to 2007 (Ravi *et al*., 2001; Reddy *et al*., 2002; Chander-Rao *et al*., 2003; Krishnareddy *et al*., 2003b; Prasadarao *et al*., 2003b; Jain *et al*., 2005; Santha-lakshmi-Prasad *et al.,* 2005; Kumar *et al*., 2006; Ladhalakshmi *et al*., 2006;)

Figure 1. TSV infected groundnut (A), sunflower (B) and okra (C)

(Thysanoptera: Thripidae) and experimentally by mechanical sap inoculation, grafting and dodder (*Cuscuta campestris*), but not by contact or soil (Fulton, 1985). Adults and nymphs of several thrips species were shown to transmit TSV-infected pollen from the infected plants by a mechanical mechanism whereby virus from pollen carried externally or released from inside the pollen infects plants through feeding wounds caused by the thrips (Sdoodee and Teakle, 1987, 1993). A similar mechanism was shown in TSV transmission to groundnut by three species of thrips, *Frankliniella schultzei* Trybom, *Megalurothrips usitatus* Bagnall and *Scirtothrips dorsalis* Hood (Reddy *et al*., 2002; Prasadarao *et al.,* 2003a; Shukla *et al*., 2005).

Seed transmission of TSV was reported in several crop species elsewhere in the world (Kaiser *et al*., 1982, 1991; Fulton, 1985; Sdoodee and Teakle, 1987, 1993). Seed transmission was not found in naturally or experimentally infected groundnut, sunflower, parthenium or several other annual crops infected with TSV in India (Prasadarao *et al*., 2003a; Reddy *et al*., 2007). However, a recent report suggests seed transmission of TSV to an extent of 2.7 – 65.7% in cucumber and gherkin in Southern Karnataka (M. Krishnareddy, personal communication; Jain *et al*., 2008). It is not known whether this phenomenon is confined to these hosts or a different strain of TSV is involved. Careful monitoring is necessary to assess seed transmission of TSV isolates occurring in India.

Diagnosis

Symptoms of TSV on several host species can be confused with those caused by CMV or PBNV. Therefore, confirmatory testing by serological or nucleic acid-based diagnostic assays is necessary. Polyclonal antibodies raised against TSV were used for virus detection by ISEM and ELISA (Reddy *et al*., 2002). TSV isolates in India were serologically related and antiserum raised against one isolate could be useful for the detection of other isolates. Reverse transcription-polymerase chain reaction (RT-PCR) assay was also described for the detection of TSV (Bhat *et al*., 2002a; Reddy *et al*., 2002).

TSV can also be identified based on the symptoms on indicator hosts such as, *N. tabacum, C. quinoa, V. unguiculata* (cv. C-152)*, C. tetragonoloba* (cv. S-51)*, G. globosa* and *P. vulgaris* (cv. Topcrop). Diagnostic hosts such as *V. unguiculata* cv. C-152 and *P. vulgaris* cv. Topcrop help to differentiate TSV from PBNV. TSV produces necrotic local lesions and venial necrosis on inoculated primary leaves of these indicator plants, whereas PBNV produces only concentric chlorotic/necrotic local lesions.

Epidemiology

TSV epidemiology in groundnut in Anantapur district was well studied (Prasadarao *et al.,* 2003a,b). Since virus is not seed-borne in groundnut it has to be introduced from external sources. Weeds, *Parthenium hysterophorus, Abutilon indicum, A. conyzoides*, *Croton sparsiflorous*, *Commelina benghalensis, Cleome viscose, Euphorbia hirta, Lagasca mollis* and *Tridax procumbense* were found to be the most common TSV sources in the fields. Of these, parthenium is most widely distributed and is a symptomless carrier of TSV and produces several flushes of flowers during its life cycle ensuring continuous supply of pollen. Heavy westerly winds that occur during August and September facilitate deposition of virus-carrying pollen on to groundnut plants from the infected parthenium, and other weed sources and virus transmission occurs when such plants are colonized by the thrips (Prasadarao *et al*., 2003a). Cliestogamous species like groundnut are dead-end hosts.

A similar situation may be contributing to the initiation of TSV infection in other susceptible crops like sunflower, mung bean and okra. Early infected susceptible plants prematurely die. It is conceivable that late-infected plants may produce flowers and pollen from such flowers could serve as inoculum source for further plant-to-plant spread in presence of thrips. Even if this situation occurs, is unlikely to contribute significant increase in disease incidence or yield loss as crop attains maturity by that time. Nevertheless, this phenomenon requires a study.

Evidence suggests that TSV is monocyclic virus in highly susceptible species (eg. sunflower, groundnut) and polycyclic in asymptomatic species (eg. parthenium) (Fig. 2). Asymptomatic weeds that host the virus as well as thrips and produce copious pollen throughout season act as a primary source of inoculum initiating and sustaining the TSV infection during a crop season. Thrips colonizing flowers of these plants can become externally contaminated with pollen and movement of these thrips to new hosts results in introduction of the virus into fields (Sdoodee and Teakle, 1987, 1993; Prasadarao *et al.*, 2003a,b). Wind blown pollen of parthenium contaminates the leaves and thrips arriving independently may well contribute to infection (Greber *et al.,* 1991; Shukla *et al*., 2005). Environmental conditions that favor thrips multiplication contribute to the rapid spread of virus leading to devastating epidemics in susceptible crops. Although TSV is seed-borne in certain host species, a study on soybean in USA demonstrated that seed-borne TSV did not contribute to epidemics but inoculum sources originated from outside the fields and high vector movement was shown to be responsible for the TSV epidemics (Rabedeaxu *et al*., 2005).

The conditions found favorable for TSV epidemics in fields include pre-monsoon showers during late May or early June that encourage germination and growth of TSV reservoir hosts like parthenium; sowing crops during July by which time parthenium is in full bloom; and dry spells that encourage thrips multiplication and movement (Prasadarao *et al.,* 2003a). Appearance of TSV in fields where no known sources of TSV in the vicinity could be due to the migratory thrips carrying TSV-infected pollen on their body parts contributing to the long distance spread of the virus.

Disease management

Host resistance

The most economical and convenient way to manage TSV is to grow resistant varieties. However, resistance to TSV was not found in cultivated species in India. For instance, 150 groundnut cultivars and advanced breeding lines evaluated for TSV were found to be susceptible (Prasadarao *et al*., 2003b; Kalyani *et al*., 2005). Three breeding lines, ICGV # 92267, 99029 and 01276 showed delayed symptom expression but they succumbed under high disease pressure (Prasadarao *et al*., 2003b; Kalyani *et al*., 2005). Large number of sunflower germplasm evaluated for TSV under field conditions at Regional Agricultural Research Station, Nandyal, Andhra Pradesh, were found to be susceptible (RDVJ Prasada Rao, unpublished). However, difference in symptom expression was observed in various genotypes of groundnut and sunflower indicating that not all the cultivars are equally susceptible to TSV.

Recently, TSV resistance was found in 8 of the 56 wild *Arachis* accessions evaluated (Kalyani *et al*., 2007). These are, ICG # 8139, 8195, 8200, 8203, 8205 and 11550 belonging to *Arachis duranensis*, ICG 8144 belonging to *A. villosa* and ICG 13210 belonging to *A. stenosperma*. Similarly, resistance to TSV was found in a wild tomato, *Lycopersicon pimpinellifolium* (Govorova, 1989) and in one ancestral soybean line 'Tanner' (Wang *et al*., 2005). These sources can be used to transfer resistance into cultivated varieties through breeding programs. Resistance against thrips, *F. occidentalis*, was found to offer partial resistance to TSV in chrysanthemum cv. Kan-komichi in Japan (Ohta,

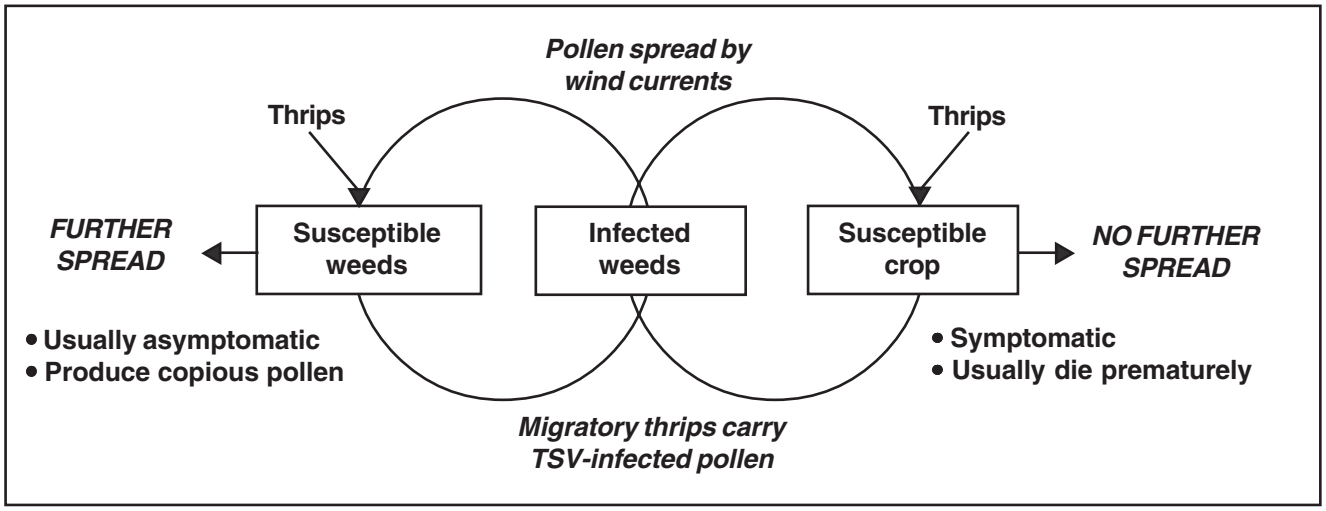

Figure 2. Probable TSV cycle. Virus is polycyclic in asymptomatic weeds that host the virus as well as thrips, and act as a primary source of inoculum initiating several disease cycles during a crop season. Due to pre-mature death of infected plants, virus is monocyclic symptomatic (highly susceptible) in crops

2002). Such resistance to thrips may occur in other TSV host species, if found can be exploited to reduce TSV incidence in the fields.

Efforts are being made to develop TSV resistance by transgenic approach. Beachy (1990) has shown that plants transgenic for the virus coat protein are resistant to infection in a phenomenon termed as pathogen-derived resistance. Van Dun *et al.,* (1988) showed that resistance to TSV arises by inserting coat protein (CP) RNA. A similar approach was undertaken at ICRISAT to engineer resistance to TSV in popular groundnut cultivars JL 24, TMV-2 and ICGV 91114 using a TSV CP gene construct (Saivishnupriya *et al*., 2006, 2007). So far more than 150 putative transgenics events have been produced and events that resist systemic spread of TSV were identified. This work in progress at ICRISAT and other centers (Bag *et al*., 2007) may contribute to the development of durable TSV resistant cultivars.

Integrated approach management practices

Management strategies such as altering sowing dates, seed treatment with imidacloprid to control thrips vector, barrier crops with fast growing tall cereals to prevent vector movement, removal of TSV susceptible weed hosts and maintaining optimal plant population was found to significantly reduce disease incidence (Table 2) (Almeida and Corso, 1991; Almeida *et al*., 1994; Prasadarao *et al*., 2003a,b).

Outlook

TSV has emerged as major threat to several field and horticultural crops in less than a decade since first serious outbreak was recognized in India. Origin of this virus is unclear. Currently it is well established in peninsular states of Andhra Pradesh, Maharastra, Karnataka and Tamil Nadu. There is an urgent need to control the virus and prevent its spread into new niches. This requires surveillance surveys to identify the extent of TSV spread, its host range, identify thrips species present in the endemic areas and mechanisms of virus survival and plant-to-plant spread. This will contribute to the knowledge on virus distribution, dynamics of vector population, and distribution and abundance of sources of inoculum. This information combined with cropping patterns and weather parameters can be considered to predict the risk factors of TSV epidemics and develop a disease forecast system.

Most of the TSV reports in India are limited to first reports of new crop hosts. Information on extent of spread and yield loss, that demonstrates economic significance of the virus, was limited only to sunflower and groundnut. Similarly, genomic studies are limited to the portion encoding for coat protein gene. Genome of a TSV isolate needs to be fully characterized to understand the molecular attributes contributing to severe epidemics in India. Given the rarity of resistance to TSV in cultivated germplasm, alternative strategies are heavily pinned on developing transgenic resistance. Simultaneously, wild relatives known to possess TSV resistance can also be exploited to augment TSV resistance through breeding programs.

Studies have indicated that reservoir weed hosts and thrips play important role in TSV spread and SND is a polycyclic disease. These observations encourage phytosanitation to

Table 2. Options for the management of TSV

Destroy virus sources	Removal of virus sources (mostly weeds) germinated with early rains around can reduce TSV incidence. (Removal of infected groundnut plants from the field will have no effect, as infected plants do not contribute to secondary spread. Similarly, removal of early infected sunflower will not reduce disease incidence as early infected sunflower does not produce flowers).
Install barrier crops	Sow 7-11 rows of fast growing cereals (pearl millet, sorghum or maize) as border crop around fields which obstruct the movement of thrips from landing on crop plants thereby contributing to reduced disease incidence.
Maintain optimum plant population	Bare patches in the field attract thrips landing. Maintain optimum plant populations to discourage thrips landing on the crop.
Control thrips through chemical treatment	Seed treatment with imidaclorprid, followed by regular systemic insecticide spray in the early stages of the crop growth control thrips.

eradicate weed hosts and seed treatment with systemic insecticides as an effective option to control thrips to reduce the virus incidence early in the crop season and prevent SND epidemics.

There is a need for complementarity and synergism between the public and private sector organizations researching on TSV in India. Detailed research efforts through long-term coordinated support from funding agencies are critical for making rapid strides towards development of sustainable management strategies to combat TSV in India.

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