Phytoplasma on sesame: etiology, insect vectors, molecular characterization, transmission and integrated management

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Sesame phyllody disease is of serious concern in many sesame-growing areas. It significantly diminishes crop production, especially in warm environments causing up to 80% yield loss. We observed various symptoms of phyllody disease, viz. flowery phyllody, virescence, flower bud proliferation, ovivipary and cracking of seed capsules. *Orosius albicinctus* (Distant) was identified as the vector of sesame phyllody. Sesame phyllody phytoplasma 16SrI strain sequences of India, Egypt and Thailand were associated in one group; 16SrII strains were grouped separately, comprising sequences from India, Iran, Taiwan, Turkey and Oman. 16SrIX stains of Iran (MW27256, KF774193 and MW272565) and Turkey (KC139791) sequences were clearly distinguished from the phylogenetic tree. This result clearly shows the presence of different sesame phyllody phytoplasma strains and diversity in the Indian subcontinent. Sesame phytoplasma was effectively transmitted to the healthy plants from infected plants of sesame through *O. albicinctus*, grafting and dodder. The most sustainable and viable alternative for managing sesame phyllody can be an integrated strategy by combining cultural, host plant resistance, biological, physical and chemical methods. Sesame phyllody has become a potential threat to sesame cultivation. Hence, it is necessary to take steps to reduce its further spread. In this article, extensive details on distribution, taxonomy, symptomatology, etiology, transmission, molecular characterization, genetic diversity, host plant resistance and management methods on phytoplasma infecting sesame are provided.

Keywords: Host plant resistance, insect vectors, molecular characterization, sesame phyllody, symptoms.

SESAME (*Sesamum indicum* L.) is an important oilseed crop belonging to the Pedaliaceae family. It originated in Africa and is the oldest oilseed crop grown in many places around the world. It was first mentioned around 4000 years ago in ancient Babylon and Assyria. Sudan (1,525,104 tonnes), Myanmar (740,000 tonnes), the United Republic of Tanzania (710,000 tonnes), India (658,000 tonnes), and Nigeria (490,000 tonnes) are the top global sesame seed producers[1]. Sesame seeds are a good source of edible oil (50%) and protein (20%), with approximately 39% linolenic acid and 47% oleic acid[2]. Phyllody disease in sesame is of serious concern in many cultivation areas, which significantly diminishes its production, especially in warm environments, causing up to 80% yield loss[3,4]. It was first recorded in Mirpur Khas (Sindh Pakistan Province) in the Indo-Pakistan subcontinent in 1908 (ref. 5). In subtropical and tropical regions of the world, sesame phyllody is a major disease that causes substantial loss to the economy[6,7]. The disease poses a major threat to production in the world's largest sesame-producing areas. In India, infected sesame crops are partially or fully sterile, resulting in complete yield loss and incidence ranging from 10% to 100% (ref. 8).

Phytoplasmas are pathogens linked with several diseases in both wild and cultivated plants. They are mostly spread in a propagative and persistent manner by insect vectors. By consuming on a diseased plant, the insect vectors obtain the phytoplasmas and then transfer them to fresh/healthy sesame plants after a latent time, where the phytoplasmas pass and develop in the insect vector bodies. Many phytoplasma vectors are found in three major taxonomic groups, viz. leafhoppers (Cicadellidae), psyllids (Psyllidae) and planthoppers (Fulgoromorpha). In this article, extensive details on the distribution, symptomatology, diagnosis, host range, epidemiology, molecular characterization, transmission and integrated management of phytoplasma infecting sesame are provided.

Distribution

Sesame phyllody has been mostly documented in African and Asian countries; so far, it has been reported in Uganda[9], Sudan[10], Burkina Faso[11], Israel[12], Nigeria, Ethiopia, Tanzania, Venezuela, Mexico[13], Iraq[14], Thailand[15], Oman[16], Pakistan[17], Myanmar[18], Turkey[19], Taiwan[20] and India[21]. Sesame phyllody in India has a larger geographic distribution. Still, it has been primarily recorded thus far from the south (Tamil Nadu, Karnataka, Andhra Pradesh, Telangana, Maharashtra), north (Madhya Pradesh, Rajasthan, Gujarat, Uttar Pradesh, Delhi, Haryana), east (Odisha, Chhattisgarh,

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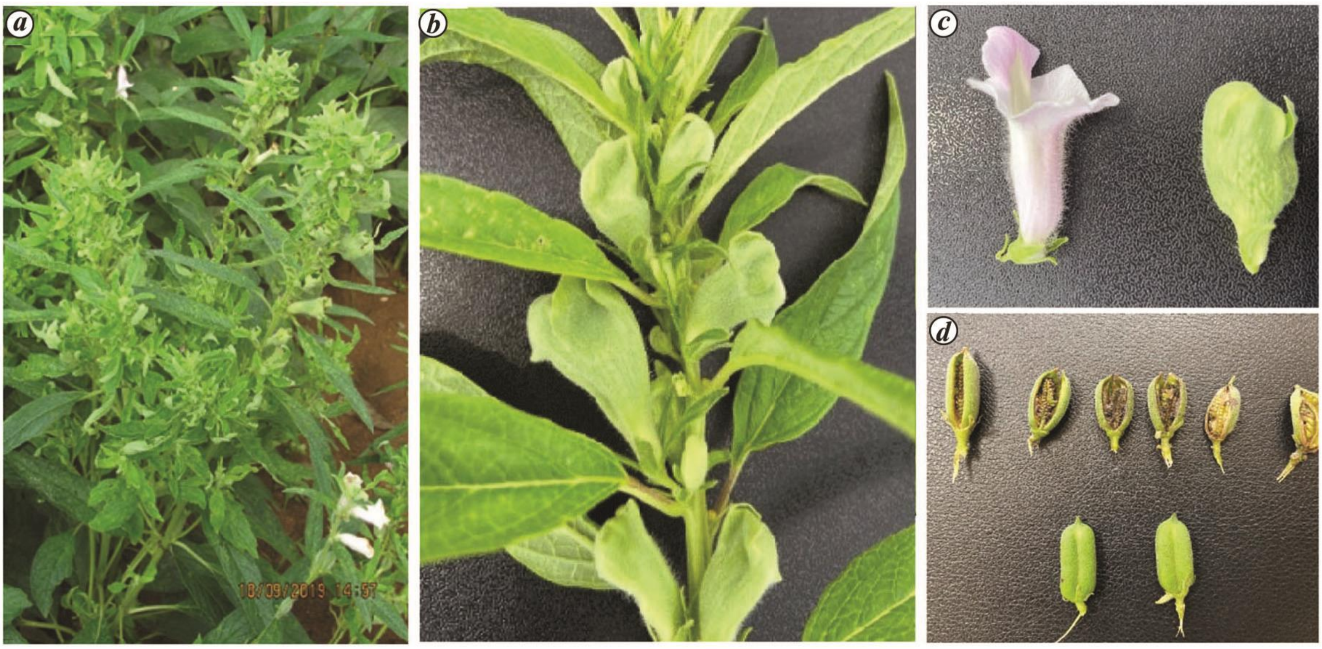

Figure 1. Sesame plants showing different types of phyllody symptoms: (***a***) little leaf symptom; (***b***, ***c***) flower virescence (healthy and infected flowers) and (***d***) seed capsule cracking (healthy and infected capsules).

West Bengal) and North East (NE) India (Assam, Mizoram, Tripura, Manipur, Nagaland, Arunachal Pradesh, Meghalaya).

Symptomatology

We observed various types of symptoms for phyllody disease to be associated with phyllody-infected sesame plants, viz. flowery phyllody, virescence, intense leaf and flower bud proliferation, ovivipary condition on sesame plant and cracking of seed capsules (Figure 1). However, virescence and phyllody were registered more often compared to floral proliferation. Of this major class of symptoms, phyllody refers to the development of leafy structures in flowers instead of the corolla, while virescence refers to corolla changes from pink to green or white to green. Subsequently, the disease is associated with the cracking of seed capsules, dark exudates forming on floral and foliage parts, seeds germinating within capsules, and yellowing occasionally. The symptoms of phyllody-infected plants of sesame vary depending on the stage of the crop and infection time. An early stage of growth infection, the phyllody infection produced inter-nodal elongation cessation, stunting and leaf size reduction (to approximately two-thirds of the plant height). The whole inflorescence was transformed into reduced leaves tightly arranged at the stem top, twisted, with shorter internodes[22]. Before flowering, the infected plants displayed severe symptoms that spread over the entire plant, whereas infected plants during flowering showed severe symptoms on the top portion, and sometimes rudimentary flowers formed tiny capsules with morphed seeds. Infected capsules were also cracked longitudinally[12,22].

Diagnosis

Prior to the 1970s, sesame phyllody was primarily identified by symptoms, the presence of mycoplasma-like bodies (MLOs) under electron microscopy and the blue colour of phloem tissues in infected plants by Diene's stain under a light microscope[12,22,23]. Several observations of pleomorphic bodies of 300–800 nm were made using transmission electron microscopy (TEM) in infected plants[14,20,22–24]. Sesame phytoplasma was also observed by Southern hybridization with specific DNA probes[25]. Researchers identified the phytoplasma one or two decades ago using molecular techniques like PCR assays and restriction fragment length polymorphism (RFLP)[6,16,21,26]. Genes such as *secA*, *tuf* and *groEL* for phytoplasma characterization associated with sesame phyllody were used, in addition to 16S rDNA (ref. 21). Primers of the *secA* gene were found to be more specific in identifying different sesame phyllody phytoplasma strains[21]. A restriction endonuclease digestion step followed by a virtual PCR RFLP analysis of 16S rDNA (1.25 kb) was used to classify the phytoplasma strain to the ribosomal subgroup[21].

Etiology

Phytoplasmas causing sesame phyllody are microscopic and obligate parasites and have never been grown in an axenic culture. They are provisionally known as Candidatus Phytoplasma. Species are delineated by genome size and phylogeny, as well as ribosomal RNA. They are systemic and limited to phloem cells within the plant. Thin hand

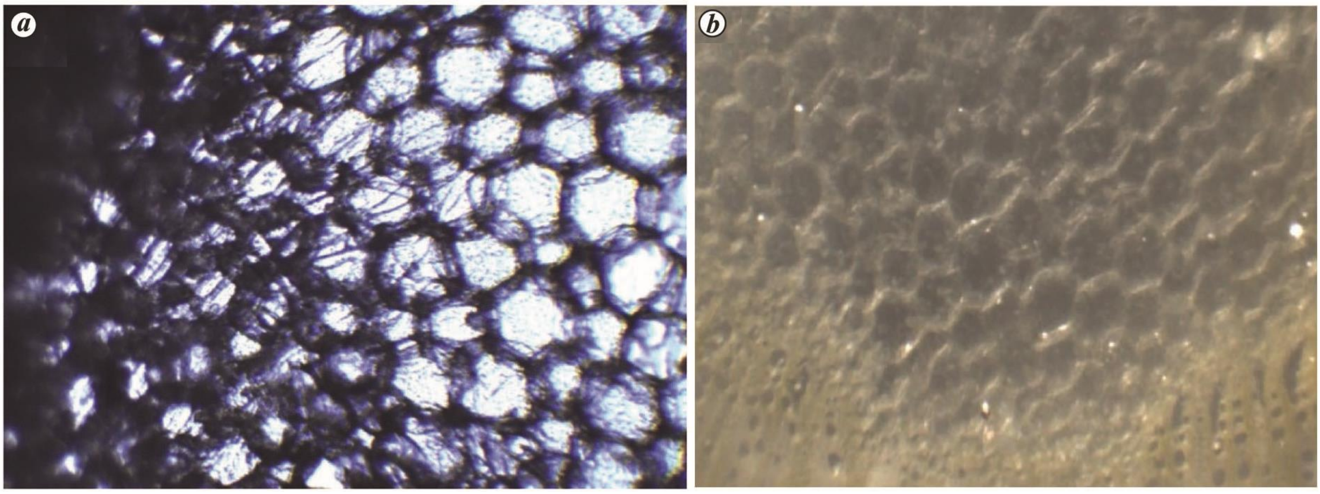

Figure 2. Variations in the plant cell structure in (***a***) infected and (***b***) healthy sesame plants under light microscopy.

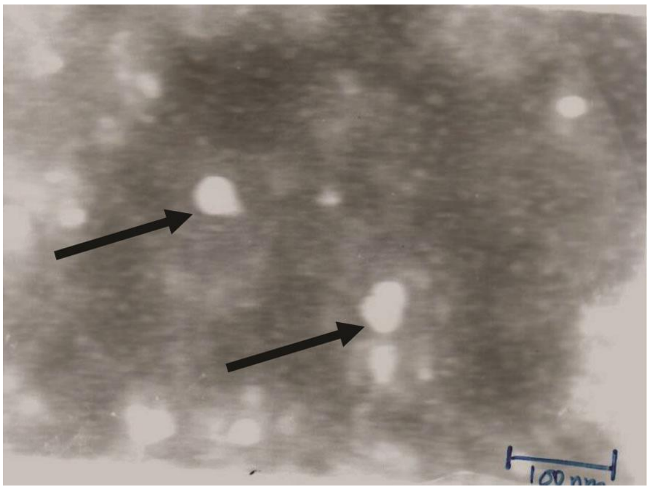

Figure 3. Transmission electron photomicrographs showing phytoplasma in sieve tubes in the phloem of infected sesame leaves. Black arrows indicate pleomorphic bodies of the phytoplasma.

sections of phyllody-infected and healthy sesame leaves treated with Diene's stain showed blue areas in the phloem region under the light microscope, indicating phytoplasma in the phyllody-infected tissues. However, the healthy leaf sections did not show any blue colour though treated with Diene's stain in our study (Figure 2). Colour differentiation was observed in the phloem of phyllody-infected plants but not in other tissues. Many pleomorphic bodies of the phytoplasma in sieve elements of companion cells, xylem cells, and cells of the phloem parenchyma of diseased plants were observed using TEM (Figure 3). They were mainly spherical, but beaded, elongated, dumb-bell shaped and curved structures were also observed. Ribosome-like granules next to the unit membranes were found in large bodies. In the central region of some cells, dark strands, probably DNA, were found[27]. Thread-like structures were possibly protein structures among MLDs bodies[28].

Host range

Phytoplasma can affect >600 various plant species. Phyllody is not confined to cultivated sesame, *Sesamum indicum*. It has also been found in *Sesamum alatun*, *Sesamum radiatum*, *Sesamum occidentale* and *Sesamum indicatum*[10]. We also reported alternate hosts, such as *Croton* sp., *Parthenium hysterophorus* and *Crotalaria juncea*, which served as inoculums (Figure 4). In India, *Sclerocarpus africanus* and *Cannabis sativa* have been recently noticed as natural hosts of sesame phyllody disease[29]. The phytoplasma detected in sesame was also detected in eggplant and pepper[6].

Epidemiology

Climate variability and change may have a major effect on vector-borne plant diseases. Rainfall, relative humidity and temperature are highly correlated with the onset of sesame phyllody and reproduction, development, behaviour and population dynamics of vectors[30]. The decrease or increase in the occurrence of phyllody will mostly depend on the weather conditions as well as on ecological and epidemiological factors. Although it is difficult to predict the precise effect of phyllody disease from sustained weather change, its impact could be complicated by adjusting the vector (insect)–host (sesame)–pathogen balance. The frequent precipitation and lower temperature with high relative humidity are favourable conditions for disease occurrence.

Insect vectors

Psyllids, planthoppers and leafhoppers are considered vectors of phytoplasmas, which are mainly categorized in the order Hemiptera[31]. Among insect vectors, *Orosius albicinctus* (Distant; Figure 5) was identified as a main vector of sesame

Figure 4. Phyllody disease reported in (***a***) *Parthenium hysterophorus*, (***b***) *Croton* sp. and (***c***) *Crotalaria juncea.*

Figure 5. Sesame phyllody vector *Orosius albicinctus* (Distant).

phyllody[6,12,13,32]. Sesame phyllody was also transmitted by *Orosius cellulosus*[11], *Hishimonus phycitis* Distant[29] and *Circulifer haematoceps* (Mulsant and Rey)[32].

Molecular characterization of phytoplasma

Figure 6 presents a phylogenetic tree based on 16S rDNA, showing the relationships among sesame phyllody phytoplasma strains constructed by the neighbor-joining method using Mega 7.0 software. GenBank accession numbers are specified in the tree, while the numbers on branches are bootstrap values obtained for 2000 replicates. The tree has grouped the sequences in the 16SrI, 16SrII and 16SrIX subgroups. Sesame phyllody phytoplasma 16SrI strain sequences of India, Egypt and Thailand were associated in one group. 16SrII strains were grouped separately, comprising sequences from India, Iran, Taiwan, Turkey and Oman. 16SrIX stains in Iran (MW27256, KF774193 and MW272-565) and Turkey (KC139791) sequences can be clearly distinguished from the tree. This result clearly shows the presence of different sesame phyllody phytoplasma strains and diversity in the Indian subcontinent (Supplementary Table 1).

Draft genome sequence of *Candidatus* Phytoplasma australasia

Candidatus Phytoplasma is an intracellular bacterial plant pathogen transmitted by insect vectors. Among the phytoplasma group, the 16SrII group or peanut witch's broom of phytoplasma, which is associated with different diseases, causes huge yield losses in India. The *Candidatus* Phytoplasma sp. strain SS02 has been implicated in the phyllody disease of sesame collected in New Delhi, India. The genome sequence of strain SS02 was obtained using its genomic DNA enrichment and hybrid assembly of sequences generated on the Illumina and Oxford Nanopore Technologies MinION platforms. The hybrid assembly strategy generated a draft genome with 60 contigs having a total length of 553,228 bp with more than 400 × depth coverage and 95.21% estimated completeness[33]. The SS02 draft genome sequence contained 465 protein-coding genes, 17 tRNA genes and three rRNA genes. The draft genome availability also provided a basis for genome-scale genotypic analyses.

Transmission of sesame phyllody phytoplasma

Sesame phyllody phytoplasma was successfully transmitted by insect vectors, grafting and dodder (*Cuscuta campestris*). The following methods were used for efficient transmission of sesame phyllody phytoplasma.

Insect transmission

In the present study, sesame phytoplasma was effectively transmitted to healthy plants from infected plants of sesame through *O. albicinctus* under net-house conditions, which is in line with earlier studies[22,26,34–36]. Hogenhout *et al*.[37] reported that the symptoms might occur seven days after phytoplasma introduction by a vector (host insect) but

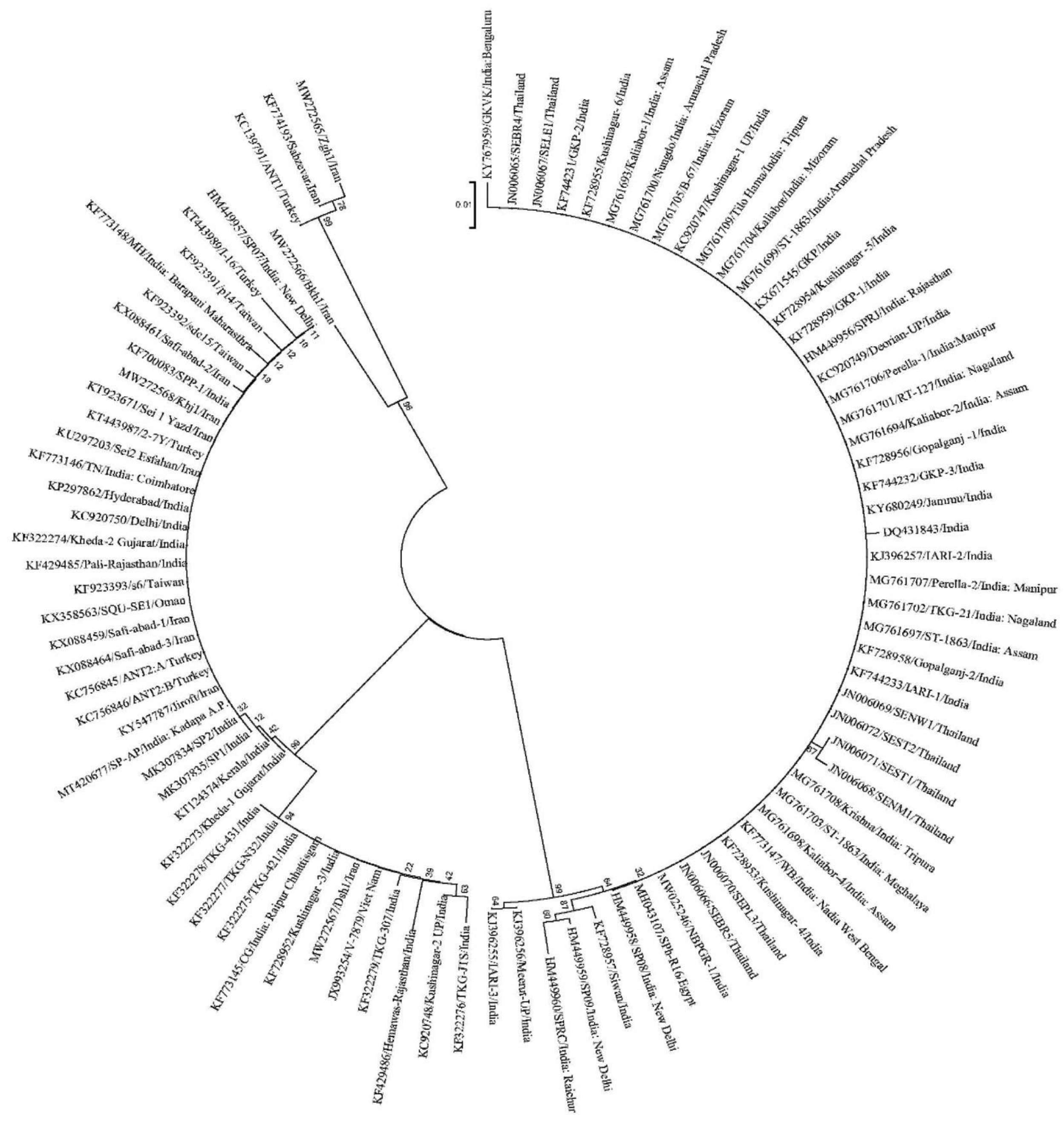

Figure 6. Phylogenetic tree of sesame phyllody distribution across the world.

may be much longer, based on the plant species and phytoplasma.

Graft transmission

In the present study, the sesame phyllody phytoplasma transmission from the infective to healthy sesame plants was successfully carried out by grafting (Figure 7 *a*), which aligns with earlier studies[23,24,35,36]. The symptoms began within 30 days of grafting and continued until 40 days, and phyllody phytoplasma was transmitted to 80% of the grafted plants. In all the grafted plants, the causative agent (phytoplasma) was successfully transmitted to healthy plants, producing phyllody disease symptoms within 25–35 days[22]. Phytoplasmas travel from source to sink in plants and can pass through the phloem tissue over sieve-tube elements[38].

Dodder transmission

Sesame phytoplasma was effectively transferred from phyllody-infected plants to healthy sesame plants in net-house

Figure 7. Transmission of phyllody disease in sesame plants through (***a***) grafting and (***b***) dodder (*Cuscuta campestris*).

Table 1. Resistant and tolerant cultivars of sesame to sesame phyllody

Cultivar	Reaction	Country	Reference
Sesamum alatum	Resistant	India	45, 52, 53
Sesamum mulayanum	Tolerant	India	44, 45
Sesamum yanaimalaiensis	Resistant	India	45
SVPR 1	Resistant	India	45
JT-21, Swetha, Rama, Sekhar	Tolerant	India	46
GTG-30, GT-10	Moderately resistant	India	54
KMR14, Pragati, KMR14 × RT54, Pragati × ORM17 and Pragati × KMR75	Resistant	India	53
OSC-366, JLW-620	Moderately resistant	India	55
Argane, T-85	Moderately resistant	Ethiopia	56
TMV 4	Resistant	India	57

conditions by dodder (*C. campestris*, Figure 7*b*), which aligns with earlier studies[22,24,35,36]. It took 35–50 days for the dodder-transmitted plants of sesame to show symptoms after phyllody transmission. Seven of the ten plants used to transmit the dodder displaced clear phyllody symptoms, accompanied by floral virescence and yellowing of the leaves. Disease transmission by dodder was noticed in only 20% of disease transmission[22]. Dodder could be an efficient means of natural disease transmission in the field.

Integrated management of phyllody and its vector

The most sustainable and viable alternative method for managing phyllody and its vector can be an integrated strategy by combining cultural, host-plant resistance, biological, physical and chemical methods[39].

Cultural control

Some cultural methods, crop rotation, removal and destruction of infected plants, late sowing, intercropping with pigeon pea (1 : 1), etc. could control or prevent phyllody disease[40–42].

Host plant resistance

Table 1 presents several resistant and tolerant cultivars of sesame against sesame phyllody. Sesame collections from

Figure 8. Reaction of (***a***) resistant (cv. GT-10) and (***b***) susceptible (cv. RJR-170 showing leafhopper damage in lower leaves) genotypes of sesame against sesame phyllody and leafhopper.

NE India recorded minimum phyllody incidence compared to the other regions[43]. *S. alatum*, *S. yanaimalaiensis*, *S. mulayanum* Burm and *S. prostratum* were resistant to sesame phyllody[44,45]. Sesame cultivars, viz. JT-21, Rama, Swetha and Sekhar have been reported to tolerate phyllody disease[46]. In the present study, the genotypes, viz. GTG-30 and S-05-27 recorded low leafhopper population and were also tolerant to phyllody (Figure 8).

Botanical control

Leafhopper incidence was substantially decreased by the application of natural and indigenous products[47]. Seed treatment with imidacloprid + neem oil @ 3% application and karanj oil was found to be more efficient in reducing the incidence of phyllody disease[48]. Kumar *et al.*[49] examined the efficacy of neem oil and NSKE in controlling sesame phyllody disease.

Antibiotic control

Antibiotic sprays (tetracycline and oxytetracycline) in combination with insecticide seed treatment were found to be highly efficient in the prevention of phyllody incidence[22,48].

Chemical control

Seed treatment with imidacloprid (@ 6g/kg) followed by spraying of imidacloprid (2 ml/10 l) or thiamethoxam (2 g/10 l) or clothianidin (0.5 g/l) substantially reduced the incidence of insect vector (leafhopper) and phyllody infection[48,50,51]. The application of dimethoate 30 EC @ 0.1% combined with pigeon pea + sesame intercropping (1: 6) effectively controlled the insect vector. Pathak *et al.*[34] recorded a substantial reduction in insect vector population by application of methyl-o-demeton @0.025%.

Future line of work

Sesame phyllody has become a potential threat to sesame cultivation. Hence it is necessary to take steps to reduce its further spread. Some of them are as follows:

- Extensive survey of sesame growing areas of the country to identify regions and seasons free from phyllody disease.
- Identifying the alternate hosts and weeds which would serve as potential reservoirs for the phytoplasma and insect vectors during the season and off-seasons.
- Leafhoppers are important vector species responsible for disease spread. More information regarding vector–phytoplasma and vector–plant interactions is important for enhanced control of phytoplasma-associated diseases in sesame.
- Identifying critical factors priming phyllody development.
- It is important to study the genetic diversity of sesame phyllody in other sesame-growing countries to identify the various phytoplasmas infecting this species.
- To eradicate alternative plant hosts and control insect vectors to avoid further spread of the disease, epidemiological studies should also be performed.
- Sesame phyllody management approaches also need attention for developing resistant genotypes.
- Incorporation of intrinsic or transgenic resistance into agronomically superior cultivars.
- Development of a sustainable integrated phyllody management package for adoption by the farmers.

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Received 23 June 2022; revised accepted 5 June 2023

doi: 10.18520/cs/v125/i4/383-391