

Multilocus Characterization of 'Candidatus Phytoplasma asteris' (16SrI-B) Associated with Phyllody and Witches' Broom in Sesamum latifolium, S. angolense and S. angustifolium

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Abstract

Phytoplasma diseases are threat to sesame and its wild relatives, but information on their occurrence in exotic *Sesamum* species is limited. During field evaluation, *Sesamum angolense*, *S. angustifolium*, and *S. latifolium* exhibited characteristic phyllody and witches' broom symptoms, including virescence, leafy floral organs, polysepalous calyx, polypetalous corolla, flattened stamens, shortened internodes, excessive shoot proliferation, and leaf twisting and curling. Molecular detection using universal phytoplasma primers P1/P7 and *tuf* gene-specific primers fTufAy/rTufAy amplified products of approximately 1.8 kb and 940 bp, respectively, from symptomatic plants. Sequence analysis of the 16S rRNA and *tuf* genes revealed 99–100% nucleotide identity with members of the '*Candidatus* Phytoplasma asteris' group. Phylogenetic reconstruction based on both loci consistently assigned the isolates to the 16Srl-B subgroup of 'Ca. Phytoplasma asteris'. To the best of our knowledge, this is the first report of phytoplasma infection in *S. angolense*, *S. angustifolium*, and *S. latifolium*, characterized at the strain level using both 16S rRNA and *tuf* gene sequences. The findings expand the known host range of 16Srl-B phytoplasmas and demonstrate that these wild *Sesamum* species, which are valuable components of the tertiary gene pool of cultivated sesame, can serve as natural reservoirs of phytoplasma inoculum.

Introduction

Sesame (*Sesamum indicum* L.), a member of the family Pedaliaceae is one of the oldest oilseed crops cultivated by humans. The Indian subcontinent is considered the primary center of domestication and diversity of cultivated sesame, whereas the genus *Sesamum* exhibits its greatest species diversity in Africa (Bedigian 2015; Dossa et al. 2017). According to the latest taxonomic treatment in Plants of the World Online (POWO, Royal Botanic Gardens, Kew), Pedaliaceae comprises 11 genera and 81 species of annual and perennial herbs distributed throughout the Old-World tropics and subtropics. The genus *Sesamum* currently includes 31 accepted species, of which *S. indicum* is the only cultivated species.

Several wild *Sesamum* species, including *S. angustifolium*, *S. latifolium*, *S. triphyllum*, *S. alatum*, *S. radiatum*, *S. angolense*, and *S. sesamoides*, constitute the tertiary gene pool of cultivated sesame and are important genetic resources for crop improvement (Nimmakayala et al. 2011). These species possess valuable agronomic traits and have been reported as sources of resistance or tolerance to various biotic stresses, including phyllody disease and insect pests, as well as abiotic stresses such as drought, waterlogging, and seed shattering (Miao et al. 2024).

Phyllody, caused by phytoplasmas, is one of the most destructive diseases affecting sesame cultivation worldwide. The host range of phytoplasmas is not restricted to cultivated sesame but extends to related and wild *Sesamum* species. Phytoplasma-associated phyllody and witches' broom symptoms have been reported in *S. indicum* (Al-Sakeiti et al. 2005; Akhtar et al. 2009; Nabi et al. 2015; Singh et al. 2016; Kalita et al. 2018; Junior et al. 2019), as well as in *S. malabaricum*, *S. mulayanum*, *S. prostratum*, *S. laciniatum*, *S. alatum*, and *S. radiatum* (Thirumalaisamy et al. 2023). Nevertheless, the degree of susceptibility varies according the species. Species of sesame, viz., *S. alatum*, *S. triphyllum* and amphidiploids derived from crossing of *S. alatum* and *S. indicum* were found field resistance to phytoplasma (Rajeswari et al. 2010 and Thirumalaisamy et al. 2024).

During field evaluation of sesame germplasm and wild relatives under a crop improvement programme, plants of *S. angolense*, *S. angustifolium*, and *S. latifolium* were observed exhibiting typical phyllody, witches' broom and leaf curling and twisting symptoms. Therefore, the present study was undertaken to investigate the association of phytoplasmas with these symptomatic plants. Molecular detection was performed using 16S rRNA gene amplification and sequencing, which is the standard marker for phytoplasma identification and classification. In addition, sequencing of the *tuf* (elongation factor Tu) gene was carried out to achieve finer strain-level characterization and to assess the genetic diversity of the associated phytoplasma.

Materials and Methods

Sample Collection

Plants of *Sesamum angolense*, *S. angustifolium*, and *S. latifolium* exhibiting phyllody and witches' broom symptoms, characteristic of phytoplasma infection, were collected from the experimental fields of the Sesame Crop Improvement Programme (2023 & 2024) at ICAR–National Bureau of Plant Genetic Resources (NBPGR), Regional Station, Vellanikkara, Thrissur, Kerala, India (10.55215°N, 76.27514°E; 55 m above mean sea level). Symptomless plants of the respective species were also collected and used as healthy controls.

Nucleic Acid Extraction

Total nucleic acids were extracted from symptomatic and asymptomatic leaf tissues using the cetyltrimethylammonium bromide (CTAB) method described by Doyle and Doyle (1990) with minor modifications. DNA quality and concentration were assessed by agarose gel electrophoresis and spectrophotometry. DNA isolated from sesame plants previously confirmed to be infected with phytoplasma was included as a positive control, while DNA from healthy plants served as a negative control.

PCR Amplification of 16S rRNA and tuf Genes

Phytoplasma detection was carried out by polymerase chain reaction (PCR) using universal phytoplasma primers P1 (5'-AAGAGTTTGATCCTGGCTCAGGATT-3') and P7 (5'-CGTCCTTCATCGGCTCTT-3'), which amplify approximately 1.8 kb of the phytoplasma 16S rRNA gene region (Deng and Hiruki 1990; Schneider et al. 1995). Following confirmation of phytoplasma infection, the elongation factor Tu (*tuf*) gene was amplified using primer pair fTufAy (5'-CCTGAAGAAAGAGAACGTGG-3') and rTufAy (5'-CGGAAATAGAATTGAGGACG-3'), yielding an amplicon of approximately 940 bp (Schneider and Gibb, 1997). PCR reactions were performed in a Mastercycler Pro-thermal cycler (Eppendorf, Hamburg, Germany). The reaction mixture and thermal cycling conditions were as described previously by Thirumalaisamy et al (2023). Amplified products were resolved by electrophoresis on 1.0% agarose gels stained with ethidium bromide and visualized under UV illumination. PCR products corresponding to the expected sizes of approximately 1.8 kb (16S rRNA gene) and 940 bp (*tuf* gene) were purified and subjected to bidirectional sequencing.

Nucleotide Sequencing and Analysis

PCR amplicons of the 16S rRNA and *tuf* genes were purified using the QIAquick PCR Purification Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. Purified products were sequenced in both directions using the same primers employed for PCR amplification on an ABI PRISM 3730 automated DNA sequencer (Applied Biosystems, Foster City, CA, USA) at Eurofins Genomics India Pvt. Ltd., Bengaluru, India. Raw sequence chromatograms were inspected manually, and low-quality terminal regions and primer sequences were trimmed. Forward and reverse sequences were assembled into consensus sequences using BioEdit version 7.2. The resulting sequences were compared with reference phytoplasma sequences available in the National Center for Biotechnology Information (NCBI) database using the BLASTn algorithm. Consensus sequences generated in this study were deposited in the GenBank database, and the corresponding accession numbers are provided in Table 1. The 16S rRNA gene sequences were subjected to virtual restriction fragment length polymorphism (RFLP) analysis using the online tool iPhyClassifier (Zhao et al. 2013) to determine phytoplasma group and subgroup affiliations.

Table 1
Symptoms of phytoplasma infection in sesame species, disease incidence and associated phytoplasma group

S. No.	Sesamum Species	NBPGR-NGB Accession No.	Major Symptoms	Disease Incidence (%)		GenBank Accession No.		Candidatus Phytoplasma association		Putative Vectors
				2023	2024	16Sr RNA	Tuf gene	Species	Group-Subgroup	
1	<i>S. latifolium</i>	EC1076128	Phyllody, virescence, excessive proliferation of axillary shoots	66.6	58.3	PP048624	PZ699744	<i>Ca. P. asteris</i>	16Sr-IB	<i>Orosius albicinctus</i> Distant <i>Hishimonus phycitis</i> Distant
2	<i>S. angolense</i>	EC1076117	Phyllody, virescence, witches' broom, excessive proliferation of axillary shoots	33.3	60.0	PP048626	PZ699743	<i>Ca. P. asteris</i>	16Sr-IB	
3	<i>S. angustifolium</i>	EC1076121	Witches' broom, excessive proliferation of axillary shoots	85.7	44.4	PP048625	PZ699742	<i>Ca. P. asteris</i>	16Sr-IB	

Phylogenetic Analysis

For phylogenetic analysis, the 16S rRNA and *tuf* gene sequences generated in this study, together with representative phytoplasma reference sequences retrieved from GenBank, were aligned using the ClustalW algorithm implemented in MEGA version 11 (Tamura et al. 2021). Phylogenetic trees were constructed using the Neighbor-Joining (NJ) method with 1,000 bootstrap replications to assess branch support. Separate phylogenetic analyses were performed for the 16S rRNA and *tuf* gene datasets to determine the evolutionary relationships and strain-level affiliations of the phytoplasmas associated with phyllody and witches' broom symptoms in wild *Sesamum* species.

Results

During field evaluation, plants of *Sesamum angolense*, *S. angustifolium*, and *S. latifolium* exhibited symptoms characteristic of phytoplasma infection. Affected plants showed typical phyllody and witches' broom symptoms. Floral organs were transformed into green, leaf-like structures. The calyx became polysepalous with multicostate venation and prominent vein clearing, unlike the gamosepalous calyx observed in healthy flowers. Sepals were enlarged and exhibited pronounced foliar characteristics. The corolla became polypetalous with thickened and conspicuous veins. Stamens and filaments were flattened and showed varying degrees of phyllody. In addition, infected plants exhibited shortened internodes, reduced leaf size, excessive shoot proliferation, and leaf deformation manifested as twisting and curling (Fig. 1). Leafhoppers, *Orosius albicinctus* Distant and *Hishimonus phycitis* Distant, were observed in the field and may serve as potential vectors of the phytoplasma. PCR amplification using the universal phytoplasma primer pair P1/P7 produced amplicons of approximately 1.8 kb from all symptomatic samples of *S. angolense*, *S. angustifolium*, and *S. latifolium*. Similarly, amplification with the *tuf*-specific primer pair fTufAy/rTufAy yielded products of approximately 940 bp. No amplification was detected in asymptomatic plants or negative controls. The amplified products were sequenced, and the resulting sequences were deposited in the GenBank database (Table 1).

BLASTn analysis of the 16S rRNA gene sequences obtained from *S. latifolium* (PP048624), *S. angustifolium* (PP048624), and *S. angolense* (PP048626) revealed 99–100% nucleotide identity with phytoplasma strains belonging to the aster yellows group (16SrI), including mulberry dwarf phytoplasma (AB639064) reported from Japan. Virtual RFLP analysis using *iPhyClassifier* indicated that the sequences shared more than 99% similarity with the reference strain of '*Candidatus Phytoplasma asteris*' (M30790), confirming their affiliation with the 16SrI group.

Phylogenetic analyses based on both the 16S rRNA and *tuf* gene sequences consistently grouped the phytoplasma isolates from *S. angolense*, *S. angustifolium*, and *S. latifolium* within the 16SrI-B subgroup of '*Candidatus Phytoplasma asteris*'. The isolates clustered closely with other members of the aster yellows phytoplasma group and formed a well-supported clade distinct from phytoplasmas belonging to other 16Sr groups (Figs. 2 and 3). The congruent clustering patterns obtained from the two gene datasets further confirmed the identity and subgroup assignment of the phytoplasma associated with phyllody and witches' broom disease in these wild *Sesamum* species.

Discussion

Members of the '*Candidatus Phytoplasma asteris*' group, particularly those belonging to the 16SrI-B subgroup, are widely distributed in India and have been reported from numerous economically important crops, including cultivated sesame and several wild *Sesamum* species (Singh et al. 2016; Thirumalaisamy et al. 2023). The present study identified phytoplasma isolates associated with phyllody and witches' broom symptoms in *S. latifolium*, *S. angolense*, and *S. angustifolium* as members of the 16SrI-B subgroup based on analyses of both the 16S rRNA and *tuf* genes. To the best of our knowledge, this is the first report of phytoplasma association in *S. latifolium*, *S. angolense*, and *S. angustifolium* and characterized up to strain level.

The *tuf* gene has been widely employed as an informative housekeeping marker for phytoplasma classification because it exhibits greater sequence variability than the 16S rRNA gene (Schneider et al. 1995; Schneider et al. 1997; Martini et al. 2007). Phylogenetic analyses based on both 16S rRNA and *tuf* gene sequences consistently placed the phytoplasma isolates within the 16SrI-B subgroup of '*Ca. Phytoplasma asteris*', confirming the identity of the pathogen. The congruence of phylogenetic relationships inferred from two independent loci provides strong evidence that the phytoplasma infecting these wild sesame species belongs to the aster yellows group. Multigene characterization has become increasingly important for distinguishing closely related phytoplasma strains and understanding their evolutionary relationships, epidemiology, and host adaptation (Lee et al. 2004; Wei et al. 2008; Zhao et al. 2009).

These findings expand the known host range of 16SrI-B phytoplasmas and demonstrate the susceptibility of additional wild *Sesamum* species to phytoplasma infection. The identification of these wild species as natural hosts has important implications for sesame disease management and breeding programmes, as they may function both as reservoirs of inoculum and as valuable genetic resources for

studying host-pathogen interactions. The detection of 16Srl-B phytoplasma in *S. angolense*, *S. angustifolium*, and *S. latifolium* is particularly significant because these species constitute important components of the tertiary gene pool of cultivated sesame. Wild *Sesamum* species are increasingly utilized in breeding programmes as sources of resistance to biotic and abiotic stresses, including insect pests, diseases, drought, waterlogging, and seed shattering (Parameswarappa et al. 2009; Dossa et al. 2017). The occurrence of phytoplasma infection in these valuable genetic resources suggests that they may act as natural reservoirs for phytoplasma survival and dissemination in sesame-growing ecosystems. Such reservoir hosts can contribute to disease persistence by providing inoculum sources for insect vectors during periods when cultivated sesame is absent from the field.

The occurrence and persistence of phytoplasma diseases within a region are strongly influenced by the availability of alternate host plants, weed reservoirs, and competent insect vectors. Wild *Sesamum* species growing in and around cultivated fields may serve as important reservoirs for phytoplasmas, facilitating pathogen survival during off-seasons and acting as sources of inoculum for subsequent infections. Previous studies have demonstrated that phytoplasma strains belonging to the 16Srl group possess a broad host range and are capable of infecting diverse cultivated and wild plant species, thereby enhancing their epidemiological significance (Lee et al. 2000; Weintraub and Beanland 2006; Hogenhout et al. 2008; and Bertaccini et al. 2014).

In phytoplasma-endemic regions, the simultaneous occurrence of multiple phytoplasma strains has been reported, although confirmed mixed infections within individual plants are comparatively rare. The close proximity of cultivated sesame, wild *Sesamum* species, alternate hosts, and potential insect vectors in experimental and natural ecosystems may favour the maintenance and spread of phytoplasma populations. Further studies employing multilocus sequence analysis and vector transmission assays would provide greater insights into the diversity and population structure of phytoplasmas infecting sesame and its wild relatives. The present study underscores the need for further investigations on the epidemiology of phytoplasma diseases in wild *Sesamum* species, with particular emphasis on the identification of insect vectors, characterization of alternate host plants, assessment of pathogen transmission dynamics, and evaluation of the role of wild germplasm in the long-term survival and dissemination of phytoplasmas in sesame-growing ecosystems.

From a germplasm conservation perspective, phytoplasma infection poses an additional challenge for the maintenance and exchange of wild sesame accessions. Because phytoplasmas are transmitted by phloem-feeding insect vectors and may persist in perennial or volunteer hosts, infected accessions can facilitate long-term pathogen survival in field gene banks. Consequently, regular phytosanitary monitoring and molecular indexing of sesame germplasm collections are essential to prevent inadvertent dissemination of phytoplasma-associated diseases through germplasm movement and breeding programmes.

Declarations

Funding

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Compliance with Ethical Standards

This study did not involve human participants or animals.

Conflict of Interest

The authors declare that they have no conflict of interest.

Author Contributions

TPP conceived the study, conducted the experiments. PB, KL and SK generated molecular data. KS and TPP contributed to data analysis and manuscript preparation. SA, PK, PKS and RY reviewed the manuscript. All the authors approved the final manuscript.

Data Availability Statement

The datasets generated during this study are available in publicly accessible repositories. Sequence data have been deposited in GenBank, and all relevant data are included within the manuscript.

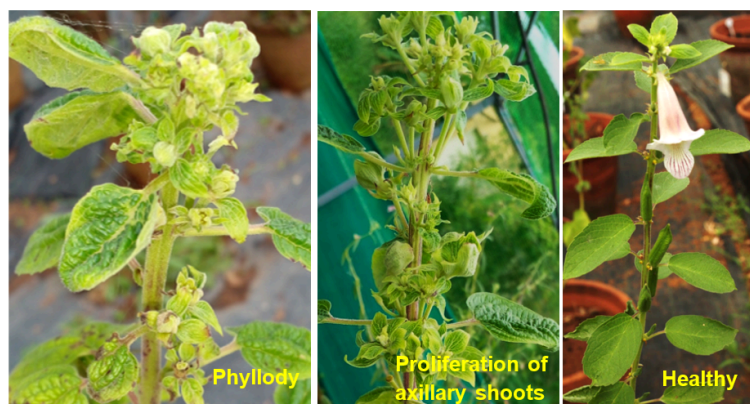
Acknowledgements

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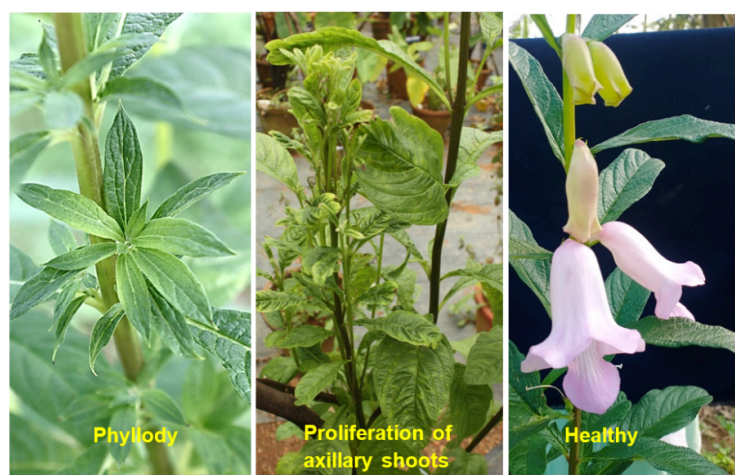
Figures



A) *S. latifolium*



B) *S. angustifolium*



C) *S. angolense*

Figure 1

Symptoms of phytoplasma infection in *Sesamum* species. A) Phyllody, virescence and proliferation of axillary shoots in *S. latifolium*. B) Witches' broom, twisting and curling of leaves, scaly leaves in *S. angustifolium*. C) Phyllody and virescence, witches' broom in *S. angolense*.

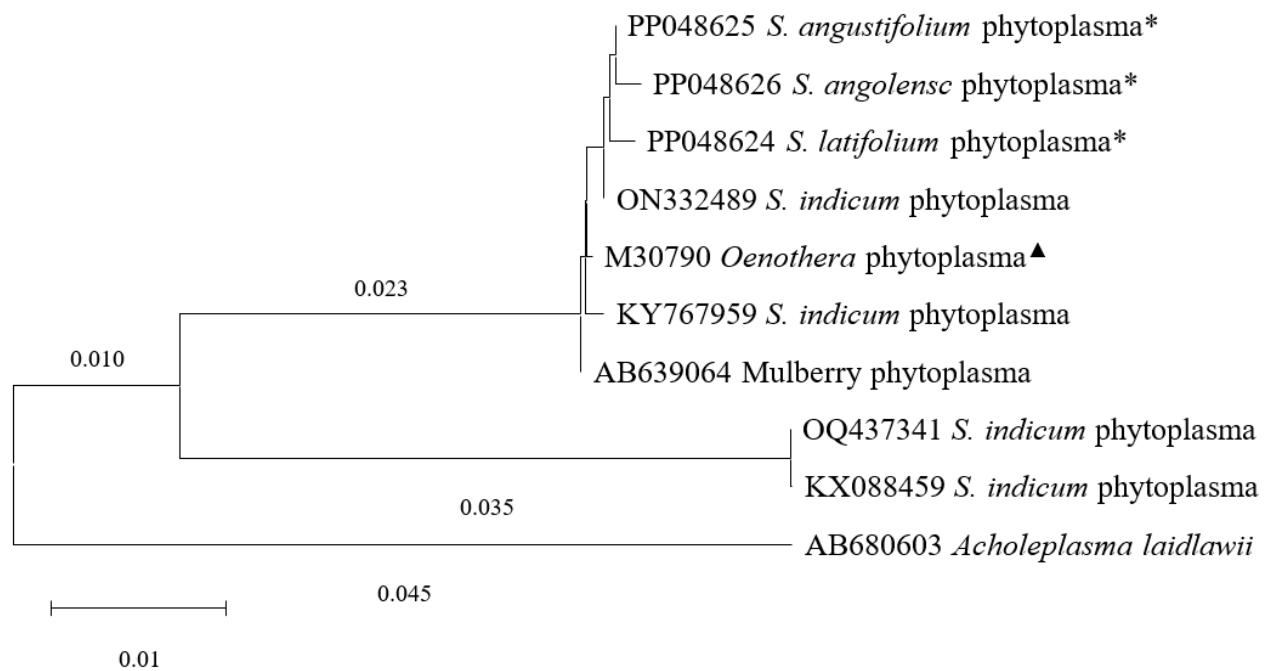


Fig. 2 Phylogenetic tree, based on 16S rRNA gene sequence, showing the relationship among phytoplasmas strains associate with phyllody in *Sesamum* species constructed by Neighbour-joining method using MEGA11 software. *Ascholeplasma laidlawii* (AB680603) was used as an outgroup. Numbers on the branches are boot-strap values obtained for 1000 replicates. The bar represents a phylogenetic distance of 1%. Symbols, * denotes strains identified in the present study and ▲ denotes reference stains.

Figure 2

See image above for figure legend.

