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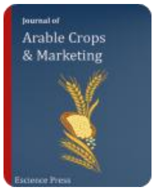

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Plant Diseases Associated with Insect-Transmitted Phloem-Limited Bacteria

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ABSTRACT

Phloem-limited, insect-transmitted bacteria represent one of the most destructive groups of plant pathogens affecting global agriculture. These pathogens including *Candidatus Phytoplasma* and *Candidatus Liberibacter* species reside exclusively in sieve elements, where nutrient-rich phloem sap supports their survival, systemic movement, and rapid spread through host plants. Their transmission is primarily mediated by phloem-feeding insects such as psyllids, leafhoppers, and planthoppers, which facilitate dissemination across a wide range of economically important crops. Phytoplasmas are associated with disorders such as witches' broom, phyllody, flavescence dorée, and lethal yellowing, while *Candidatus Liberibacter* species cause citrus Huanglongbing (HLB), zebra chip disease in potato, and other destructive conditions. These pathogens manipulate plant and insect physiology through secreted effector molecules that interfere with developmental regulators, defense pathways, and hormonal balance. Despite significant advances in genomics and molecular diagnostics, management remains challenging due to long latency periods, asymptomatic infections, lack of culturable isolates, and the complexity of vector–host–pathogen interactions. Understanding phloem biology, pathogen effector functions, and plant immune responses including PAMP-triggered and effector-triggered immunity is essential for developing durable resistance. This review synthesizes current knowledge on the biology, transmission, virulence mechanisms, and host responses associated with phloem-limited bacteria, highlighting the global threat they pose and the need for integrated management strategies.

Keywords: Phloem-limited bacteria, PAMP, Candidatus Phytoplasma, effector-triggered immunity.

INTRODUCTION

Over the past thirty years, plant diseases linked to phloem-dwelling, insect-transmitted bacteria have risen sharply across the globe, resulting in major economic damage (Bertaccini, 2023). The phloem serves as the central channel for distributing photosynthates and signaling compounds throughout the plant, enabling coordination between organs. Its nutrient-rich environment provides an ideal niche for many pathogens, shielding them from external stresses while supplying abundant metabolic resources. Consequently, phloem-feeding insects, bacteria, fungi, and viruses exploit this system for nutrition, often causing serious diseases and yield reductions (Haider et al., 2024). The term phloem-limited, insect-transmitted refers to pathogens such as phytoplasmas and some viruses that can survive only within phloem tissue and depend on phloem-feeding insects for movement between plants (Wang et al., 2024). Bacterial pathogens of this type are responsible for severe diseases in a wide range of agricultural crops and fruit trees worldwide (Vidhyasekaran, 2015), with global losses amounting to billions of dollars annually (Pimentel et al., 2001). Phytoplasmas were called MLOs before 1992; later, phytoplasmas were assigned to the 'Ca. Phytoplasma' genus in the class Mollicutes (IRPCM., 2004). Two major groups of such bacteria are *Candidatus Phytoplasma* and *Candidatus Liberibacter*. Phytoplasmas, which lack a cell wall, are transmitted mainly by leafhoppers, planthoppers, and psyllids and cause disorders such as lethal yellowing, witches' broom, phyllody, and flavescence dorée (Ashwathappa et al., 2024). In contrast, *Candidatus Liberibacter* species are Gram-negative bacteria that possess a cell wall and are also spread primarily by psyllids. Species such as *Ca. L. asiaticus*, *Ca. L. americanus*, and *Ca. L. africanus* cause citrus Huanglongbing (HLB), while *Ca. L. solanacearum* is linked to potato zebra chip disease. All are phloem-restricted pathogens that require psyllid vectors for entry into the plant (Sugio et al., 2011; Firrao et al., 2004).

The first evidence of these pathogens came in 1967 when Doi et al. observed mycoplasma-like organisms (MLOs) in sieve tubes of plants showing yellowing and witches' broom symptoms, suggesting a causal role (Doi et al., 1967). The name phytoplasma was formally adopted in 1992, and the genus *"Candidatus Phytoplasma"* was created for these unculturable prokaryotes (IRPCM, 2004). Under natural conditions, phytoplasmas are spread mainly by insects and also by grafting, manipulating both plant and insect hosts through secreted effectors (Bertaccini et al., 2014). Once inside a plant, they induce various physiological disorders, including chloroplast disruption and hormonal imbalances (Dickinson et al., 2013). Phytoplasmas infect more than 700 plant species across diverse families, producing symptoms such as witches' broom, phyllody, virescence, yellowing, stunting, shortened internodes, leaf deformation, and in severe cases, plant decline or death (Omar & Foissac, 2012; Wei et al., 2022). Because they cannot be grown in artificial media, molecular methods especially analysis of 16S rRNA sequences are essential for their detection and classification (Ramos et al., 2020; Mori et al., 2020). Phylogenetic studies have placed phytoplasmas as a monophyletic group within the class Mollicutes (Bertaccini & Duduk, 2010). Based on RFLP and phylogenetic analysis of 16S rRNA, Seemüller et al. (1998) identified 20 major phytoplasma groups. Advances in research have since expanded genomic resources, and more than 240 phytoplasma genomes have now been fully or partially sequenced (Wang et al., 2024). Phytoplasmas reside specifically in sieve elements and are transmitted mainly by phloem-feeding insects such as psyllids, planthoppers, and leafhoppers (Asudi et al., 2021; Huang et al., 2022). The parasitic plant dodder can also transfer these pathogens (Akhtar et al., 2009). Vegetative propagation methods such as grafting of apple, pear, and jujube, or stem-based propagation of strawberry and grape can further spread infection (Bertaccini, 2007). Seed transmission has also been documented in some species (Kirdat et al., 2023a). Infected plants typically show yellowing, stunting, witches' broom, phyllody, small leaves, purple tops, and sometimes plant death, leading to considerable agricultural losses (Safarova et al., 2016; Kirdat et al., 2023b).

The genus "*Candidatus Liberibacter*" comprises multiple species detected in plants worldwide. These include *Ca. L. asiaticus* (Las), *Ca. L. africanus* (Laf), and *Ca. L. americanus* (Lam), which cause citrus HLB; *Ca. L. solanacearum* (Lso), associated with potato zebra chip and diseases in other solanaceous crops (Table 1); *Ca. L. europaeus* (Leu), which infects various Rosaceae hosts (often without symptoms); and *Liberibacter crescens*, found in Babaco (a hybrid mountain papaya) (various sources cited). Diseases associated with *Candidatus Liberibacter* species have gained increasing global attention, particularly due to the rapid and destructive spread of HLB, which has nearly collapsed the citrus industry in regions such as Florida, USA. The spread of zebra chip disease in potatoes across the Americas and New Zealand has further emphasized the significant threat posed by these pathogens.

Citrus Huanglongbing (HLB) Disease Caused by *Candidatus Liberibacter* spp.

Citrus Huanglongbing (HLB), also known as citrus greening, is a major threat to the global citrus industry, causing severe economic losses annually (*Singerman and Rogers* et al., 2020). HLB is caused by *Candidatus Liberibacter asiaticus* (CLas), *Ca. L. americanus* (Lam), and *Ca. L. africanus* (Laf), with CLas being the most prevalent. Las and Lam are transmitted by the Asian citrus psyllid (ACP; *Diaphorina citri*), while Laf is transmitted by the African citrus psyllid (*Trioza erytreae*) (Phahladira et al., 2012). CLas is restricted to the sieve tubes, where it blocks the transport of photoassimilates and other molecules, resulting in vascular obstruction [Wang and Trivedi, 2013]. HLB symptoms include shoot yellowing, blotchy mottled leaves, corky veins, malformed and discolored fruits, premature fruit drop, root loss, and eventual tree death [Yang and Ancona, 2022]. In advanced stages, the disease decreases plant carbohydrate metabolism and severely impairs root growth due to reductions in starch transport and accumulation [Johnson et al., 2014]. HLB has not been identified in Mediterranean or Australian citrus regions, the presence of Las and ACP in Papua New Guinea and Indonesia poses a threat to the Australian citrus industry (Deng et al., 2019).

Table 1 Diseases caused by *C. Liberibacters* their hosts, and distributions.

Pathogens	**Disease**	**Plant hosts**	**Insect vector**	**Reference**
Candidatus Liberibacter asiaticus (Las)	H L B	Citrus and citrus relatives	Asian citrus psyllid (Diaphorina citri)	(Bove, 2006).
Ca. L. africanus (Laf)	H L B	Citrus and citrus relatives	African citrus psyllid (*Trioza erytreae*)	(Garnier et al. 2000; Jagoueix et al. 1994).
Ca. L. africanus subsp. capensis (LafC)	Unknown	Cape chestnut (*Calodendrum capense*)	*T. erytreae*	(Garnier et al. 2000).
Ca. L. africanus subsp. clausenae (LafCl)	Unknown	Horsewood (Clausena)	*T. erytreae*	(Robert and Pietersen, 2017).
Ca. L. africanus subsp. zanthoxyli (LafZ)	Unknown	Small forest knobwood (Zanthoxylum)	*T. erytreae*	(Roberts et al. 2015)
Ca. L. africanus subsp. vepridis (LafV)	Unknown	White ironwood (Vepris)	*T. erytreae*	(Roberts et al. 2015)
Ca. L. africanus subsp. tecleae (LafT)	Unknown	Flaky cherry-orange (*Teclea gerrardii*)	*T. erytreae*	(Roberts et al. 2015)
Ca. L. americanus (Lam)	H L B	Citrus and citrus relatives	*D. citri*	(Teixeira et al. 2005).
Ca. L. solanacearum (Lso) Haplotype A	Z C	Solanaceous crops	*Bactericera cockerelli*	(Nelson et al. 2011; Liefting et al. 2008; Hansen et al. 2008).
Lso haplotype B	Z C	Solanaceous crops	*B. cockerelli*	(Nelson et al. 2011)
Lso haplotype C	Yellows decline and vegetative disorders	Carrot	*Trioza apicalis*	(Nelson et al. 2011)
Lso haplotype D	Yellows decline and vegetative disorders	Carrot	*Bactericera trigonica*	(Nelson et al. 2013).
Lso haplotype E	Vegetative disorders	Celery and carrots	*Bactericera trigonica* (likely)	(Tahzima et al. 2014; Teresani et al. 2014; Teresani et al. 2015)
Ca. L. europaeus (Leu)	Asymptomatic	Rosaceae plants, including apple (*Malus domestica*), blackberry (*Rubus plicatus*), hawthorn (*Crataegus monogyna*), and pear (*Pyrus*)	*Cacopsylla pyri* (L.)	Raddadi et al. 2011).

Similarly, the establishment of Las in Ethiopia, Mauritius, and Réunion threatens African citrus production. Due to the long latency period of HLB, Ca. *Liberibacter*–infected citrus trees often do not show visible symptoms at the initial stage. The latency period may last several months (Pandey et al., 2022) and varies with citrus variety, tree age, health status, and environmental factors (Rosales and Burns, 2011), which contributes to asymptomatic spread. Infected citrus plants typically display stunted growth, root decay, thinner canopy, yellow shoots, blotchy mottled leaves, upright and small leaves, early flowering, and overall tree decline (Johnson and Graham, 2013). Infected fruits are often small, lopsided, and unevenly colored (Graça et al., 2016). Some mandarin varieties develop "red nose fruit" or "red shoulder fruit," characterized by orange-red coloration on the fruit shoulder and a cyan, dull color on other parts. The disease cycle of HLB is illustrated in Figure 1.

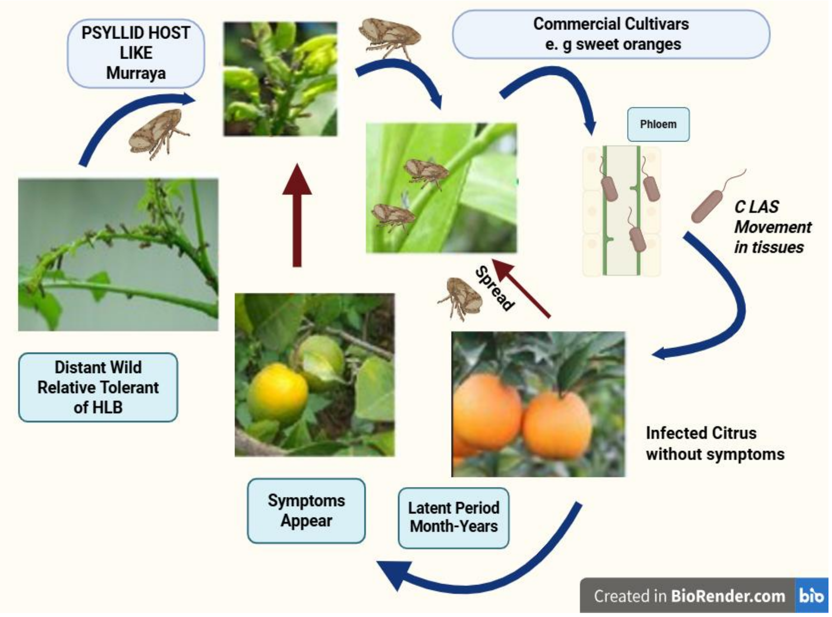

Figure 1. This diagram illustrates the **disease cycle of Huanglongbing (HLB)** and the movement of *Candidatus Liberibacter asiaticus* (CLas) within citrus hosts.

Zebra Chip (ZC) Disease Caused by *Candidatus Liberibacter solanacearum* (Lso)

Zebra chip (ZC) is the best-characterized disease caused by *Candidatus Liberibacter solanacearum* (Lso), and all commercial potato (*Solanum tuberosum*) varieties are susceptible. The name refers to the major tuber symptom: brown discoloration of the phloem and medullary rays, visible when sliced and intensified upon frying, which makes tubers unsuitable for producing potato chips or French fries. ZC was first reported in Mexico in 1994, in Texas in 2000, and in the Pacific Northwest of the United States in 2010 (Munyaneza, 2012). It is also reported from Central America, including Guatemala and Honduras, and from New Zealand (Munyaneza et al. 2009). Symptoms first appear aboveground, including leaf curling, purpling, and chlorosis; as the disease progresses, plants become stunted, develop swollen internodes, and may form aerial tubers. Severe infections reduce tuber production and often cause plant death (Crosslin et al. 2012). Lso can be transmitted to the next generation through infected tubers used as seed pieces (Swisher Grimm et al. 2020) and its role as the causal agent of ZC was confirmed by graft transmission studies (Conrad et al. 1995). Five Lso haplotypes (A, B, C, D, and E) have been identified infecting different crops (EPPO, 2013) and were distinguished using SNP genotyping of the 16S rRNA, 16S/23S ISR, and the 50S rplJ and rplL ribosomal protein genes (Aakra et al. Nes, 1999) multilocus sequence typing markers, and simple sequence repeats (Burgess et al. 2001). Lso A and Lso B, vectored by the tomato/potato psyllid *Bactericera cockerelli*, cause ZC (Thinakaran, 2014). Both haplotypes occur in the Americas and may be found separately or together in vectors and plant hosts; Lso A is the only haplotype present in New Zealand. Besides ZC, Lso A and B infect other economically important solanaceous crops including tomato, pepper, eggplant, tamarillo, tobacco, and cape gooseberry (*Physalis peruviana*) in North and Central America and New Zealand, likely transmitted by *B. cockerelli*. Lso is seed transmitted in several crops, as demonstrated in chili pepper (Rojas-Martínez et al. 2016), and various weedy solanaceous species host Lso A and B with reduced or no symptoms (Platt, 1999). Lso C and Lso D cause disease in carrot in Europe and Africa, vectored by the carrot psyllids *Trioza apicalis* and *Bactericera trigonica*, respectively (Antolinez et al. 2017). Haplotype E causes disease in carrot and celery in Spain, although no confirmed psyllid vector is known (Moreno et al. 2021). Recent reports suggest that *B. trigonica*, *Bactericera tremblayi*, *Bactericera nigricornis*, and another *Bactericera* species in Spain may carry Lso and could serve as vectors (Ben Othmen, 2019). Lso can also be seed transmitted in both carrot and celery (Fujikawa et al. 2020).

Grapevine Flavescence Dorée (FD) Disease Caused by Phytoplasmas

Flavescence dorée (FD) is a grapevine quarantine disease associated with phytoplasmas and transmitted to healthy plants by insect vectors, mainly *Scaphoideus titanus* (Oliveira et al., 2023). Although symptoms of FD had been observed in France since the beginning of the 20th century, the disease was formally named around 1950 after it spread through vineyards in southwest France, particularly in Gascogne and Armagnac (Caudwell, 1990). More recently, FD has also been reported in other wine-producing European regions, including Austria, Croatia, Hungary, Portugal, and Switzerland (CABI, 2016). Both FD phytoplasma strains are vectored by the leafhopper *Scaphoideus titanus* (Mori et al., 2002), which acquires the phytoplasma during its first larval stage while feeding on infected plants (EFSA, 2014). The sap-feeding process of *S. titanus* was recently studied using electropenetrography (Chuche et al., 2017). Previously described as a phloem-feeding insect, this technique revealed that *S. titanus* ingests a mix of both xylem and phloem sap, suggesting that it may also be capable of spreading *Xylella fastidiosa* in vineyards. The main host plants for FD are *Vitis vinifera* and *V. riparia*, although the two FD phytoplasma strains differ in host specificity. For the 16SrV-D strain, no alternative plant hosts or insect vectors have been reported. However, for the 16SrV-C strain, alternative host plants such as *Clematis vitalba*, *Alnus glutinosa* (Malembic-Maher et al., 2011), and *Ailanthus altissima* (Filippin et al., 2011) have been identified. Infected plants typically develop symptoms including leaf rolling, yellowing or reddening (depending on berry color), stunted growth, unripe canewood, and shriveled berries. Shoots of susceptible grapevine varieties may also fail to lignify, becoming thin, rubbery, and hanging pendulously

Phloem colonization strategies

Mature sieve elements, vital for cell integrity, protein turnover, and chemical defense, rely on companion cells for support. These sieve elements exhibit unique structural and functional relationships and employ mechanical defense mechanisms alongside biochemical methods **(Dalio et al., 2021).** While a pathogen infecting a single leaf may not threaten the entire plant, specific pathogens that infiltrate neighboring cells and reach the phloem for systemic infection pose a significant danger. Plants employ two specialized phloem-specific defense mechanisms to counter such infections. The first is long-term occlusion by the accumulation of callose. Callose, a β-1,3-glucan polymer, acts universally in plants in response to cellular damage **(Verma and Hong, 2001).** Callose synthase CalS7, located near plasmodesmata, induces sieve element occlusion during injury (Fig. 2). By extracting sugars from the sieve tube lumen, the enzyme produces callose for the extracellular environment. The process of sieve element occlusion through callose deposition is relatively slow **(Noll et al., 2022),** with reported rates on the sieve pore cell wall ranging from 25 to 60 nm/s **(Oparka and Turgeon, 1999).** The second mechanism is short-term occlusion by the accumulation of P-protein and forisomes. Short-term occlusion results from the rapid accumulation of P-proteins and forisomes in response to phloem damage. P-proteins, such as PP1 and PP2 in cucurbits, play a key role in repairing phloem tissue wounds by forming a gel-like substance that temporarily blocks sap flow **(Golecki et al., 1999).** PP2, a phloem lectin protein, binds filaments to the plasma membrane or sieve element endoplasmic reticulum via glycoproteins. Simultaneously, PP1 forms filaments connected to PP2 by disulfide bridges, with both encoded by genes associated with sieve element occlusion (SEOR) **(Clark et al., 1997).** Forisomes in legumes regulate sap flow by transforming into a condensed shape in response to stimuli, leading to reversible phloem occlusion. This rapid redirection of sap optimizes nutrient distribution and facilitates wound healing. Both P-proteins and forisomes, along with their respective genes (SEO-F), contribute to short-term phloem blocking under various conditions, ensuring plant defense and efficient nutrient transport while presenting significant obstacles to phloem-colonizing pathogens.

Bacterial effector molecules

Phytoplasma genomes retain genes needed for essential functions such as DNA replication, transcription, translation, and glycolysis [Miura et al., 2015], but they lack many metabolic pathways including amino acid and fatty acid biosynthesis, the tricarboxylic acid cycle, and oxidative phosphorylation. Their metabolic capacity is even more limited than that of mycoplasmas [Mushegian and Koonin, 1996]. Despite having such reduced genomes, phytoplasmas are able to cause distinctive developmental disorders in plants, such as phyllody and witches' broom, making their host-manipulation strategies a subject of considerable interest. Many Gram-negative plant and animal pathogens employ Type III secretion systems (T3SSs) to deliver virulence effectors into host cells [Grant et al., 2006]. Phytoplasmas, however, do not encode T3SS machinery. Instead, they possess genes for a Sec-dependent protein translocation system [Kakizawa et al., 2004], which they use to secrete proteins directly into the cytoplasm of host cells, as they lack a cell wall and reside intracellularly. These Sec-secreted proteins are predicted to function as effectors that influence host–parasite interactions and contribute to virulence [Wei et al., 2004]. The phytoplasma Sec pathway recognizes and cleaves N-terminal signal peptides in a manner similar to other bacterial Sec systems (Kakizawa et al. 2004). Therefore, signal peptide prediction tools such as SignalP (Nielsen et al. 1997; Garcion et al. 2021) and PSORT (Nakai and Kanehisa, 1991) can be used to identify potential effector proteins encoded in phytoplasma genomes. To date, a substantial number of candidate effectors have been identified. For example, approximately 56 putative effectors have been predicted in the genome of the 'Ca. Phytoplasma asteris' AY-WB strain and around 45 in the OY strain (Bai et al. 2009). Although the precise molecular mechanisms underlying phytoplasma-induced symptoms remain only partially understood, several effectors have already been confirmed to manipulate host factors or trigger characteristic disease phenotypes (Table 1).

Phyllogen

Flower deformities including phyllody, where floral organs take on leaf-like characteristics; virescence, marked by the greening of floral tissues; and abnormal shoot proliferation are well-known indicators of phytoplasma infection [Himeno et al., 2011]. A distinct group of phytoplasma effector genes, termed the phyllogen or phyllody-inducing gene family, has been identified as the cause of these abnormalities, first demonstrated in *Arabidopsis* [Yang et al., 2015]. These effectors have also been shown to trigger phyllody symptoms in several other eudicot species representing multiple plant families [Kitazawa et al., 2017]. Phyllogen genes are present in numerous *'Ca. Phytoplasma'* species and appear to undergo horizontal transfer among phytoplasma lineages [Iwabuchi et al., 2020], supporting the idea that they function as broadly conserved phyllody-inducing effectors. Members of the phyllogen family, including SAP54 and PHYL, interfere with floral homeotic proteins defined in the floral quartet model (Singh and Lakhanpaul, 2020), which are encoded by MADS-domain transcription factors (MTFs). Phyllogens promote the degradation of A- and E-class MTFs through a proteasome-dependent mechanism [Maejima et al., 2015], indicating that they recognize a conserved structural motif shared among these transcription factors. Structural studies have shown that the K-domain of MTFs—the region bound by phyllogens [Puranik et al., 2014]—contains two α-helices with conserved hydrophobic amino acids that are required for MTF multimer formation [Omenge et al., 2021]. These conserved residues are also essential for phyllogen recognition [Kitazawa et al., 2022], explaining why these effectors can target MTFs across diverse plant hosts (Fig. 1; adapted from Oshima et al., 2023). Two specific phyllogens, PHYLOY and PHYLPnWB, produced by the OY strain of *'Ca. Phytoplasma asteris'* and the PnWB strain of *'Ca. Phytoplasma aurantifolia'*, respectively, similarly possess two α-helices that are critical for their activity [Liao et al., 2019]. Comparative sequence analysis indicates that a single amino acid variation in the second α-helix determines the extent of their phyllody-inducing capability.

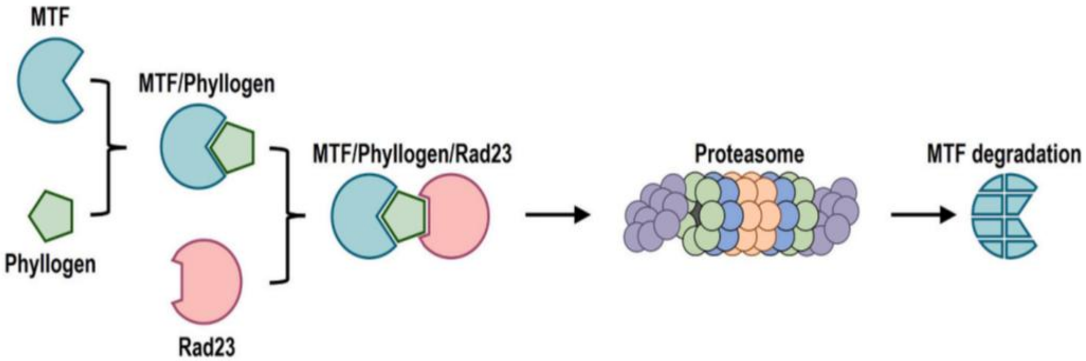

Figure 2. Phyllogen-mediated stepwise formation of ternary complex with MADS-box transcription factor (MTF) and Rad23 leads proteasomal degradation of MTF. (Oshima et al., 2023).

SAP05

SAP05 is a secreted effector protein identified in the '*Ca. Phytoplasma asteris*' AY-WB strain (MacLean et al. 2011). When expressed in *A. thaliana*, SAP05 induces witches' broom-like clusters of leaves and sterile shoots. SAP05-expressing plants also continue growing for more than 12 weeks much longer than GFP-control plants indicating that this effector suppresses normal senescence. Yeast two-hybrid analyses have shown that SAP05 interacts with both SPL and GATA transcription factors in *Arabidopsis*. SPL proteins play a central role in regulating developmental phase transitions in vascular plants (Ding et al., 2015), whereas GATA transcription factors influence organ formation, branching patterns, and flowering time (Huijser and Schmid, 2011). SAP05 additionally binds to the 26S proteasome subunit RPN10 and promotes the degradation of SPL and GATA factors through this ubiquitin receptor. As a result, SAP05 disrupts developmental progression and leads to excessive vegetative proliferation and delayed aging. Under normal conditions, RPN10 serves as a key ubiquitin receptor that directs ubiquitinated proteins to the proteasome. Remarkably, SAP05 enables degradation of SPL and GATA transcription factors without requiring ubiquitination, instead acting as a molecular bridge that brings these transcription factors to RPN10 (Huang et al., 2021). Some phytoplasma species carry one or two SAP05 homologs, each capable of selectively degrading either SPL or GATA proteins. Furthermore, *A. thaliana* plants engineered to carry an RPN10 variant differing by only two amino acids exhibited neither severe leaf malformations nor excessive lateral shoot formation after phytoplasma infection. This finding suggests that disrupting SAP05–RPN10 interaction can reduce the susceptibility of the host to phytoplasma infection.

Plant defense mechanisms against phloem-feeding insects and pathogens

Our current knowledge of plant interactions with leaf mesophyll cell-infecting pathogens reveals the activation of two main branches of immunity: pathogen-associated molecular pattern (PAMP) triggered immunity (PTI) and effector-triggered immunity (ETI). PTI is initiated by plasma membrane-localized pattern recognition receptors (PRRs) detecting PAMPs (Couto and Zipfel 2016). Virulent pathogens employ effectors to suppress PTI defense responses (Toruno et al. 2016). A list of reported gene products associated with host interactions in the case of vector-borne plant pathogens has been enlisted in (Table 1). Plants employ ETI mainly through nucleotide-binding leucine-rich repeat (NLR) proteins recognizing pathogen effectors (Jones et al. 2024). Plants respond to insect feeding through a PTI-like mechanism, where herbivore-associated molecular patterns (HAMPs) and damage-associated molecular patterns (DAMPs) trigger immune responses (Howe and Jander 2008). For example, AtPeps induce PTI-like responses in Arabidopsis through PEP-Receptors 1 and 2 (PEPR1 and PEPR2) (Howe & Jander 2008). GroEL homologues from aphid endosymbiont bacteria induce PTI responses (Chaudhary et al. 2014). FlaLas from Ca. Liberibacter asiaticus (CLas) initiates PTI responses, and phytoplasmas may elicit PTI-like reactions through internal PAMPs (Shi et al. 2019) (Fig. 3). Phloem-restricted pathogens pose a considerable threat due to their elusive presence in plants and the delayed or latent development of symptoms in infected plants. Moreover, these pathogens often engage in complex tritrophic interactions involving plant hosts and insect vectors. The inability to satisfy Koch's postulates and the challenge of culturing most phloem-limited bacteria in vitro have led to classifying these bacterial species as Candidatus. Nevertheless, many of them have been identified as causative agents of plant diseases (Fredericks and Relman 1996).

Table 2 Target, host factor and function of secreting effectors of phytoplasmas.

Effector	**Organism(s)**	**Target(s)**	**Other Host Factors**	**Function**	**References**
TENGU	*'Ca. P. asteris'* OY strain	Unknown	–	Suppresses auxin signaling; promotes excessive stem formation; induces sterility	(Hoshi *et al.* 2009).
SAP11 / SWP1	*'Ca. P. asteris'* AY-WB strain; *'Ca. P. tritici'*	CIN-TCPs, TB/CYC-TCPs	–	Destabilizes TCP transcription factors; reduces jasmonic acid biosynthesis; promotes stem proliferation	(Sugio et al. 2011; Berry, 2022).
Phyllogen (PHYL / SAP54)	*'Ca. P. asteris'* OY strain; *'Ca. P. asteris'* AY-WB strain	A- and E-class MADS-domain transcription factors (MTFs)	RAD23	Degrades A- and E-class MTFs via ubiquitin-independent pathway; induces phyllody	(MacLean et al. 2014; Oshima et al. 2023).
SAP05	*'Ca. P. asteris'* AY-WB strain	SPL and GATA transcription factors	RPN10	Degrades SPL/GATA via ubiquitin-independent mechanism; enhances stem formation	(Wang and Zeng, 2022).
SWP12	*'Ca. P. tritici'*	TaWRKY74	–	Degrades TaWRKY74 via ubiquitin-dependent pathway; reduces plant resistance	(Bai et al. 2023).
SWP16	*'Ca. P. tritici'*	Unknown	–	Inhibits RNA silencing in the host plant	(Oshima et al. 2023).
PM19_00185	*'Ca. P. mali'*	E2 UBC09, E2 UBC10	–	Possesses E3 ligase activity; suppresses basal plant defense	(Oshima et al. 2023).

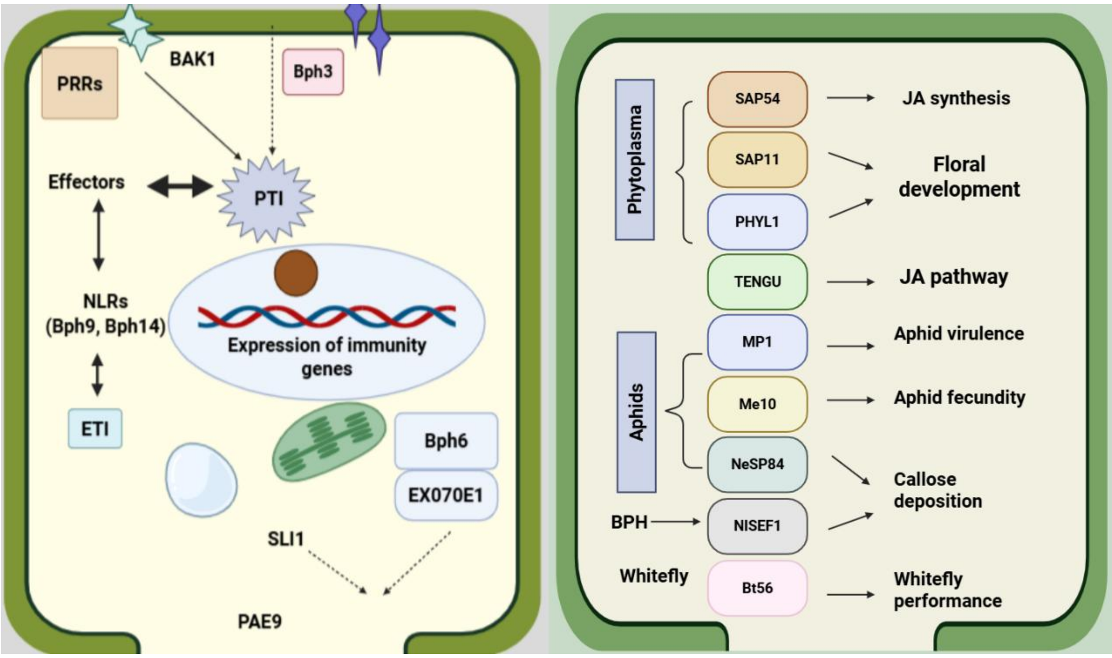

Fig. 3. A schematic representation of how plant cells respond to phloem-feeding insects and prokaryotic pathogens. a In resistant plants, membrane-anchored pattern recognition receptor Bph3, together with its coreceptor BAK1, detects insect- and pathogen-derived elicitors, triggering PAMP- and HAMP-mediated PTI. Plants carrying resistance proteins such as Mi-1.2, Bph14, and Bph9 further activate ETI by recognizing specific effectors. The association between EXO70E1 and Bph6 enhances the physical strength of the cell wall, restricting feeding by brown planthoppers (BPH). Important molecules participating in this defense include PAE9, EXOCYST70E1, ACETYLESTERASE 9, SIEVE ELEMENT-LINING CHAPERONE1, and PECTIN SLI1. b In susceptible plant cells that lack resistance proteins and therefore do not mount ETI, insect and pathogen effectors manipulate multiple phloem cellular functions, supporting pathogen growth and increasing insect reproduction. Key effectors and their host targets include SDE1 (Sec-delivered effector 1), SAP11 (secreted AY-WB protein 11), TCP transcription factors, SAP54, jasmonic acid (JA), MADS-box transcription factors (MTFs), PHYL1, Mp1 (M. persicae saliva protein 1), TENGU, ARF6/8 (AUXIN RESPONSE FACTOR 6/8), VPS52, Me10 (M. euphorbiae saliva protein 10), TFT7 (tomato 14–3–3 protein 7), NcSP84 (84-kDa Ca^{2+}-binding effector from N. cincticeps), Bt56 (B. tabaci salivary protein), NlSEF1 (EF-hand Ca^{2+}-binding protein of N. lugens), and NTH202.

CONCLUSIONS

Phloem-restricted, insect-transmitted bacteria continue to pose a major threat to global crop production due to their stealthy colonization of sieve elements, rapid systemic spread, and reliance on efficient insect vectors. Their ability to evade early detection, coupled with complex effector-mediated suppression of plant defenses, makes disease management exceptionally difficult. Pathogens such as *Candidatus Liberibacter asiaticus* the causal agent of citrus HLB and *Candidatus Liberibacter solanacearum* in zebra chip disease have devastated major industries and continue to expand into new regions. Likewise, phytoplasma-associated diseases such as flavescence dorée persist as quarantine concerns in high-value crops. Recent advances in genomics, molecular diagnostics, and effector biology have enhanced our understanding of pathogen strategies and plant immune responses, including the roles of callose deposition, P-proteins, forisomes, PTI, and ETI in restricting phloem colonization. However, the absence of effective curative treatments, limitations in culturing these organisms, and the adaptability of their insect vectors underline the urgent need for integrated approaches. Future efforts must combine vector management, resistant cultivar development, early detection tools, and a deeper mechanistic understanding of host pathogen interactions. Strengthening these strategies is essential to mitigate the escalating global impact of phloem-limited bacterial diseases and safeguard agricultural sustainability

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