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Phloem: The Hidden Battleground of Vascular Pathogens

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INTRODUCTION

Plants may seem calm and still, yet beneath their surface thrives a world of constant activity, communication and conflict. Among the most intriguing and hidden battlegrounds lies the phloem-a network of microscopic pipelines that transports sugars, hormones, and signalling molecules throughout the plant. Acting as a secret highway system, the phloem sustains life by distributing nutrients, but it also serves as a vulnerable arena where destructive pathogens wage a silent war. Bacteria, phytoplasmas and viruses infiltrate this nutrient-rich passage hijacking its transport routes to move stealthily from leaf to root. Sheltered deep within plant tissues, these invaders evade pesticides and external defense mechanism making them exceptionally difficult to control.

Recent research reveals that the phloem is far more than a passive conduit, it is a dynamic defended interface where plants, pathogens and insect vectors continuously interact. This intricate crossroads plays a critical role in the spread of vascular diseases that threaten global food security. Gaining deeper insight into how phloem-resident microbes invade, move and overcome plant defense is essential for developing innovative surveillance systems, resistance breeding strategies and vector management approaches to safeguard major crops.

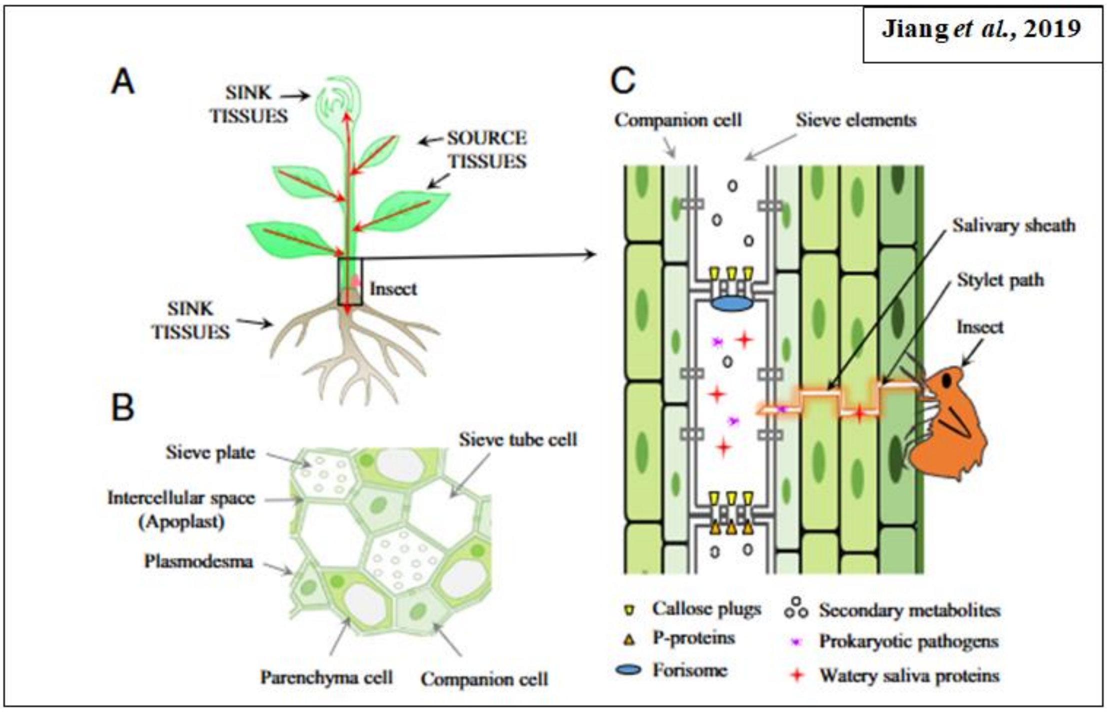
Phloem: niche and gateway

Phloem consists of sieve elements (SEs), companion cells (CCs), phloem parenchyma and sometimes fibres forming a pressurized, microaerophilic conduit enriched in sucrose, amino acids, signalling RNAs, proteins and defence metabolites. Sieve Elements (SE's) lose their nucleus, tonoplast and most organelles during differentiation, becoming metabolically dependent on Companion Cells through specialized plasmodesmata which constrains local immune perception but enables long-distance signalling via hormones such as salicylic acid, jasmonates, peptides and mobile RNAs.

Because of high turgor and deep location, direct penetration of phloem by most pathogens is rare instead, phloem-feeding hemipterans (aphids, whiteflies, leafhoppers and psyllids) introduce pathogens directly into sieve elements while probing and sustained feeding. Once inside the continuous sieve tube network allows pathogen to achieve systemic colonization, often moving more slowly than bulk sap flow yet efficiently reaching sinks, roots and reproductive tissues that are crucial for symptom development and transmission (Bendix and Levis, 2018).

Sieve element defence architecture

SEs, though enucleate, participate in fast, largely mechanical defence responses that are tightly coordinated with CCs and parenchyma via calcium fluxes, reactive oxygen species (ROS) and phloem-mobile signals. These defences aim primarily to restrict pathogen and insect movement rather than to eliminate established infections, trading local transport for systemic protection (Lewis *et al*., 2022).


Jiang *et al.*, 2019

A) A schematic showing source-to-sink translocation of metabolites and signalling molecules through the phloem (red arrows). B) A cross-section of the phloem illustrating the spatial arrangement of major cell types. C) A longitudinal view depicting interactions between phloem tissues, insect vectors, and invading pathogens.

1. P-proteins and Forisomes

P-proteins play a crucial role in the plant's rapid defense response within the phloem. Many angiosperms produce structural P-proteins, including sieve element occlusion-related (SEOR) proteins, which can quickly assemble into aggregates at sieve plates when the plant experiences wounding, pressure changes or strong electrical or chemical signals. In legumes, a specialized form of P-proteins known as forisomes function like biological safety plugs. These spindle-shaped complexes can undergo reversible calcium-dependent shape changes, allowing them to swell and block sieve pores within milliseconds. This provides a rapid energy-independent mechanism to temporarily seal the phloem against sap loss or pathogen entry during herbivore attack or early infection. However, studies suggest that SEOR-type P-proteins may not always completely block phloem transport, indicating that their effectiveness and function might differ among plant species and may operate alongside callose-based occlusion systems for redundancy and added protection (Lewis *et al*., 2022)

2. Callose deposition and cell wall dynamics

Callose deposition at sieve plates and plasmodesmata, largely mediated by callose synthases such as Callose synthase 7 (CalS7), is a hallmark of phloem stress responses, reducing pore aperture and symplastic connectivity between SEs and CCs. Enhanced callose accumulation has been correlated with restricted long-distance movement of several phloem-limited viruses and with reduced phloem conductivity in susceptible hosts, illustrating its dual role as a protective barrier and a contributor to disease-associated carbohydrate and nutrient imbalances (Xie *et al*., 2011).

3. Cell wall swelling

Sieve elements cell walls can also show rapid swelling and thickening following mechanical disturbance or severe turgor changes, narrowing the conductive lumen and physically constraining microbe movement. Together with phloem-located defensive metabolites and proteins (e.g., secondary metabolites, lectins, and protease inhibitors) these architectural responses help shape a dynamic barrier against both herbivores and microbes (Lewis *et al*., 2022).

Phloem- restricted pathogens: biology and strategies

1. Phloem-limited bacteria

Phloem-limited bacteria, including *Candidatus liberibacter asiaticus* and phytoplasmas, exhibit highly reduced genomes and obligate biotrophy, relying on both plant and insect hosts for amino acids, vitamins and other essential metabolites. Their movement through sieve tubes tends to be slow and directional, sometimes even counter to bulk flow, suggesting active interactions at sieve plates and potential use of host cytoskeletal or membrane structures for passage (Pandey *et al.*, 2022).

Candidatus liberibacter asiaticus and HLB (Citrus Greening)

Candidatus liberibacter asiaticus (CLas), the major causal agent of citrus Huanglongbing/ citrus greening (HLB), colonizes sieve elements in leaves, stems and roots and is associated with massive callose deposition and narrowing of sieve pores, ultimately disrupting carbohydrate export and source-sink balance. CLas lacks a canonical type III secretion system but encodes several alternative secretion pathways, *viz*., SECP8 Sec-dependent effector proteins that can modulate host immunity, ROS signalling and phloem function, including those that suppress hypersensitive-like cell death and reduce callose formation at early infection stages (Lewis *et al*., 2022). HLB alters hormone signalling,carbohydrate partitioning and micronutrient distribution leading to starch accumulation in leaves, phloem collapse and root decline, even before visible canopy symptoms appear. Comparative transcriptomics show that tolerant citrus genotypes often upregulate NBS-LRR immune receptors, RLKs and pathogenesis-related genes rather than over-accumulating callose, suggesting that maintaining phloem transport while enhancing immune surveillance may underlie partial tolerance (Shen *et al*., 2022).

2. Phytoplasmas as developmental manipulator

Phytoplasmas are wall-less Mollicutes that reside almost exclusively in sieve elements and are transmitted primarily by leafhoppers and planthoppers. In addition to suppressing basal immunity, phytoplasmas secrete effectors that hijack transcription factors and hormone pathways, leading to dramatic developmental changes such as phyllody, witches’ broom and sterility which often increase vector access and feeding. Effectors like TENGU have been shown to interfere with auxin and jasmonic acid signalling, resulting in dwarfing and floral defects that alter plant architecture and volatile profiles thereby, enhancing vector attraction and pathogen transmission efficiency. Other phytoplasma effectors target TCP and MADS-box transcription factors controlling meristem identity and leaf morphology, illustrating how phloem-resident microbes can reprogram whole-plant development from within the vascular system (Minato *et al*., 2014).

3. Phloem-limited viruses and tissue remodelling

Numerous plant viruses, particularly within the families Reoviridae and Geminiviridae, are phloem-associated at least during early systemic infection and often rely on CC–SE interfaces, plasmodesmata and modified cellular junctions for movement. Some rice-infecting reoviruses, such as Rice black streaked dwarf virus, Rice gall dwarf virus and Rice ragged stunt/stripe viruses, induce hyperplasia of sieve elements and parenchyma, as well as formation of enlarged or "flexible" intercellular connections between SE–SE and SE–parenchyma domains. Electron microscopy frequently reveals virion aggregates aligned within these expanded channels and membrane-bound structures, supporting their role as high-capacity routes for both longitudinal and radial viral spread. Viral non-structural proteins can act as movement proteins and scaffolds, remodelling plasmodesmata and recruiting host cytoskeletal elements, thereby overcoming callose-based restrictions and allowing persistent colonization of young, developing tissues (Lv *et al.*, 2014).

CONCLUSION

The phloem represents both a lifeline and a battleground within vascular plants—a dynamic environment where nutrient transport, signalling, defense, and microbial invasion converge. Far from being a passive transport system, the phloem actively participates in defense through structural components like P-proteins, forisomes, and callose deposition, supported by calcium fluxes and reactive oxygen species signalling. These mechanisms enable rapid sealing, pathogen containment, and sustained protection of systemic transport integrity. Yet, phloem-resident pathogens such as *Candidatus liberibacter asiaticus*, phytoplasmas, and phloem-limited viruses have evolved sophisticated strategies to circumvent these defenses by manipulating host signalling pathways, modifying cell structures, and exploiting insect vectors for dissemination. The interplay between plant defense responses and pathogen virulence factors underscores the phloem's role as a critical interface influencing the success or failure of vascular diseases**.**

Future prospects

Research must delve deeper into the molecular dialogues occurring within phloem tissues. High-resolution imaging, single-cell transcriptomics, and phloem-specific proteomics can unveil dynamic interactions between companion cells, sieve elements, and invading microbes. Understanding how effectors manipulate host immune signalling and transport networks will guide the development of resistant genotypes through advanced breeding and biotechnological interventions. Additionally, exploiting vector behaviour, engineering phloem-targeted antimicrobial peptides, and designing early diagnostic sensors based on phloem biomarkers offer promising avenues for integrated disease management. Future progress in unravelling the hidden complexity of this vascular network will not only strengthen plant defense strategies but also contribute significantly to global food security by mitigating losses from phloem-restricted diseases.

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