韧皮部防卫反应调控植物抗刺吸类昆虫的研究进展*

樊彦珍[1**] 王新翔[2] 张 悦[3,4] 姚露琴[1] 谢睿智[1] 张志勇[1] 郭洪刚[1***]

（1. 北京农学院生物与资源环境学院，农业农村部华北都市农业重点实验室，北京 102206；2. 保山市动物疫病预防控制中心，保山 678000；3. 沧州市农林科学院，沧州 061001；4. 河北省土壤昆虫学重点实验室，沧州 061001）

摘 要 韧皮部取食性刺吸类昆虫是全球农业生产中危害最为严重的害虫类群之一，蚜虫等以韧皮部为主要取食部位的刺吸类昆虫通常在植物叶背、嫩茎以及花内等幼嫩组织取食为害，以特化的口针刺入植物韧皮部持续吸取汁液，导致植物营养成分流失，严重时可直接导致植株死亡。鉴于韧皮部是韧皮部取食性刺吸类昆虫最重要的取食部位，研究植物韧皮部防卫反应在抵御该类昆虫取食过程的作用机制则尤为重要。基于此，本文梳理了韧皮部防卫反应的作用方式（胼胝质沉积、韧皮部蛋白凝集）、调控机制（激素信号传导、转录调控、防卫相关基因表达等）、以及害虫唾液蛋白（激发子与效应子）在调控韧皮部防卫反应中的作用，系统性的从植物韧皮部防御激活、昆虫反防御两个方面，归纳了韧皮部防卫反应调控植物——韧皮部取食性刺吸类昆虫的互作过程，旨在为深入解析植物韧皮部抗虫机制，为基于韧皮部防卫反应的绿色防控技术研发提供理论参考，也为作物抗虫品种的分子设计与培育提供新思路。

关键词 韧皮部取食性刺吸类昆虫；韧皮部防卫反应；作用方式；调控机制；害虫唾液蛋白

Progress in research on phloem-based plant resistance to piercing-sucking insects

FAN Yan-Zhen[1**] WANG Xin-Xiang[2] ZHANG Yue[3,4] YAO Lu-Qin[1]
XIE Rui-Zhi[1] ZHANG Zhi-Yong[1] GUO Hong-Gang[1***]

(1. Key Laboratory of Urban Agriculture in North China, Ministry of Agriculture and Rural Affairs, College of Biology, Resources and Environment, Beijing University of Agriculture, Beijing 102206, China; 2. Baoshan Animal Disease Prevention and Control Center, Baoshan 678000, China; 3. Cangzhou Academy of Agricultural and Forestry Sciences, Cangzhou 061001, China; 4. Key Laboratory of Soil Entomology in Hebei Province, Cangzhou 061001, China)

Abstract Phloem-feeding, piercing-sucking insects are one of the most destructive pests in global agricultural production. These insects, such as aphids, generally feed on tender plant tissues, including leaf undersides, young stems, and flowers. By penetrating the plant phloem and continuously ingesting phloem sap via specialized stylets, these pests consume plant nutrients and can even cause plant death. Given that plant phloem is the primary feeding site for phloem-feeding, piercing-sucking insects, it is important to investigate the mechanisms underlying the phloem-based defense (PBD) of plants against these pests. This review summarizes the functional modes of PBD (callose deposition and P protein plugging), their regulatory mechanisms (hormone signaling, transcriptional regulation, and the expression of defense-related genes), as well as the role of insect salivary proteins (elicitors and effectors) in modulating PBD. We elaborate on the interaction between plants and

*资助项目 Supported project：北京市昌平区“科技副总”专项资助（202506003055）；北京市高等教育学会 2024 年立项重点课题，“岗课赛”融通的《作物昆虫学》产教融合实践体系建设（ZD202433）；北京农学院教改课题，《作物昆虫学》虚拟仿真实验平台建设探索

**第一作者 First author，E-mail：19510337542@163.com

***通讯作者 Corresponding author，E-mail：guohonggang1@163.com

收稿日期 Received：2026-06-22；接受日期 Accepted：2026-07-28

phloem-feeding, piercing-sucking insects from the perspective of PBD activation and insect counter-defense. This review aims to provide a theoretical basis for further understanding the defense mechanisms of plants against piercing-sucking insects, and for developing green pest management strategies based on PBD. It also offers new insights for the molecular design and breeding of insect-resistant crop varieties.

Key words phloem-feeding, piercing-sucking insects; phloem-based defense; functional mode; regulation mechanism; insect salivary protein

蚜虫等以韧皮部为主要取食部位的刺吸类害虫依靠其特化口针刺破植物表皮，口针在组织内反复刺探，直至口针与韧皮部筛管细胞联通后，开始被动吸取筛管细胞内部的汁液，造成植物营养物质流失，导致植物生长势衰弱（Will and van Bel, 2006）。鉴于植物韧皮部是蚜虫等韧皮部取食性刺吸类昆虫最重要的取食部位，研究和解析植物韧皮部防御途径在抵御蚜虫等韧皮部取食性刺吸类昆虫韧皮部取食阶段的作用机制则极为重要（Will *et al*., 2013; Jiang *et al*., 2019）。韧皮部取食性刺吸类昆虫口针到达植物韧皮部后，植物会启动以韧皮部为核心的防御反应，称为韧皮部防卫反应（Phloem-based defense）（耿东灿, 2017; 黄丽娜等, 2025），阻止韧皮部取食性刺吸类昆虫从韧皮部获取营养物质。

1 韧皮部防卫反应的作用方式

当遭受蚜虫等韧皮部取食性刺吸类昆虫取食时，植物会启动韧皮部防卫反应，通过堵塞韧皮部筛管来阻止害虫持续取食。韧皮部防卫反应产生的筛管阻塞主要有两方面的作用机制，一类是胼胝质沉积作用（Callose depositing），另一类是韧皮部蛋白凝集作用（Protein plugging）；而且韧皮部蛋白（Phloem protein，PP，简称 P 蛋白）PP1-PP2 蛋白复合体形成过程中，常伴随筛板部位的胼胝质沉积，二者共同构成物理屏障，阻碍昆虫韧皮部取食，抑制韧皮部取食性刺吸类昆虫在植株上的定殖与种群繁殖（Will and van Bel, 2006; Louis and Shah, 2013; Furch *et al*., 2015; Walker, 2022）。

1.1 胼胝质沉积作用

胼胝质是一类以 β-1, 3-葡聚糖为核心骨架结构的功能性多糖，当植物遭受韧皮部取食性刺吸类昆虫取食胁迫后，胼胝质会大量合成，新合成的胼胝质通过韧皮部的转运沉积于筛管两端的筛板处，逐步覆盖筛板上的筛孔，形成致密的物理屏障（Wang *et al*., 2021a），而且这一沉积过程具有高度的针对性，仅发生在害虫取食的侵染部位及周边筛管。

胼胝质沉积已被报道通过限制蚜虫等韧皮部取食性刺吸类昆虫韧皮部取食过程而增加植物对韧皮部取食性刺吸类昆虫抗性。研究发现，寄主植物韧皮部胼胝质沉积会阻碍韧皮部取食性刺吸类昆虫如俄罗斯小麦蚜 *Diuraphis noxia*、褐飞虱 *Nilaparvata lugens* 等从韧皮部吸取植物汁液，进而降低昆虫适合度（谭晓玲等, 2025）。黄甘蔗蚜虫 *Sipha flava* 取食为害柳枝稷 *Panicum virgatum* 叶片后，抗虫品种胼胝质积累更显著，导致抗性品种上取食的蚜虫韧皮部取食时间明显缩短（Koch *et al*., 2018）。桃蚜 *Myzus persicae* 在抗虫辣椒 *Capsicum annuum* 品种上取食会在筛管处显著积累胼胝质，阻碍桃蚜的韧皮部取食而表现出抗性，然而感虫品种正好相反，说明不同辣椒品种表现出蚜虫感、抗差异与胼胝质沉积差异有关（Sun *et al*., 2018）。褐飞虱取食不同抗性水稻 *Oryza sativa* 品种后，抗性品种水稻的胼胝质含量更高，阻止营养物质向口针插入点的运输，最终表现为褐飞虱韧皮部持续取食时间显著缩短（Yang *et al*., 2013b）。水稻植株上外源喷施脱落酸（Abscisic acid, ABA）后，水稻叶片胼胝质含量显著增加，致使褐飞虱的产卵量显著降低（Liu *et al*., 2017）。β-氨基丁酸预处理提高大豆 *Glycine max* 植株胼胝质沉积而显著降低大豆蚜 *Aphis glycines* 数量、相对增长率以及相对生殖速率（Yao *et al*., 2020）。增高的 CO_2 显著增加菜豆 *Phaseolus vulgaris* 胼胝质沉积而提高对西花蓟马 *Frankliniella occidentalis* 抗性（Qian

et al., 2019; 郑晓斌等, 2025)。因此，韧皮部胼胝质沉积会显著增强植物对韧皮部取食性刺吸类昆虫抗性。

1.2　韧皮部蛋白凝集作用

① 韧皮部蛋白包括韧皮部蛋白 1（PP1）和韧皮部蛋白 2（PP2）两种类型，其中 PP2 属于植物凝集素家族，在调控植物与韧皮部取食性刺吸类昆虫互作过程中发挥作用（张春玲等, 2012)。研究发现，植物受到韧皮部取食性刺吸类昆虫取食胁迫后，PP1 分子单体与 PP2 二聚体通过二硫键结合形成 PP1-PP2 蛋白质高分子聚合物，封闭筛孔，阻止韧皮部取食性刺吸类昆虫韧皮部取食（Dinant *et al*., 2003; Kehr, 2006; Fu *et al*., 2014; Peng and Walker, 2020)。外源诱抗剂 Harpin 可同时诱导小麦 *Triticum aestivum* 韧皮部蛋白基因（*PP2-A1*, *PP2-A2* ）和胼胝质合成酶基因（*GSL2*, *GSL10*, *GSL12* ）表达，致使 PP 蛋白与胼胝质同时堵塞韧皮部筛板的筛孔，进而阻碍蚜虫从韧皮部取食，说明韧皮部蛋白与胼胝质两者可以协同提高植物对韧皮部取食性刺吸类昆虫的抗性（Fu *et al*., 2014)。

② 筛管堵塞蛋白（Sieve element occlusion protein, SEO)/筛管堵塞相关蛋白(Sieve element occlusion-related protein，SEOR ）是植物筛管分子的重要结构组分，由于学界对二者命名曾存在分歧，本文中 SEO 指豆科植物中的门体蛋白，SEOR 指与门体蛋白同源的蝶形亚科的非门体蛋白和非豆科的筛管堵塞蛋白。健康筛分子中 SEO/SEOR 蛋白沿细胞壁周缘分布，筛管受损后游离至筛管腔，聚集堵塞筛板(程琳琳等, 2023)。例如，F 蛋白体/韧皮蛋白体（Forisome，本文后续统一使用 F 蛋白体）是豆科植物特化的 SEO 蛋白，能够发生可逆性构象重塑，由浓缩纺锤形（低体积状态，几乎不会干扰筛管内汁液的运输）快速变为弥散栓状（高体积状态，堵塞筛管分子内腔并阻断汁液流动）堵塞筛管，阻碍蚜虫从植物韧皮部吸取汁液。但是 F 蛋白体介导的防御作用仅在部分蚜虫-寄主组合中限制非适应性蚜虫取食。如马铃薯长管蚜 *Macrosiphum euphorbiae* 和桃蚜取食蚕豆 *Vicia faba* 会触发 F 蛋白体介导的筛管堵塞，最终蚜虫只能撤回口针，无法吸食韧皮部汁液；豌豆蚜 *Acyrthosiphon pisum* 取食蚕豆并不会诱发 F 蛋白体堵塞，能够顺利取食韧皮部汁液。后续研究进一步证实，豌豆蚜可以抑制豆科植物 F 蛋白体介导的筛管堵塞，而且该抑制作用的有效性受到蚜虫寄主专化型、植物种类及植株发育阶段的综合影响（Medina-Ortega and Walker, 2015; Paulmann *et al*., 2023)。目前，关于 SEOR 蛋白介导筛孔堵塞以抵御韧皮部取食性刺吸类昆虫危害的相关研究仅在甜瓜 *Cucumis melo* 中有所报道。研究表明，抗性甜瓜品种 TGR-1551 在遭受瓜蚜 *Aphis gossypii* 取食后，其筛孔堵塞率高达 96%，而感虫品种的筛孔堵塞率仅为 28%（Peng *et al*., 2020)。鉴于前期研究在南瓜 *Cucurbita moschata* 筛分子堵塞物中检测到 PP1 蛋白与 SEO 蛋白（Clark *et al*., 1997; Ernst *et al*., 2012)，但在黄瓜属中尚未发现已知的 PP1 同源基因，因此推测抗性甜瓜中的筛管堵塞主要是由 SEOR 蛋白介导（Peng and Walker, 2020)。然而，部分研究结果与 SEO 蛋白作为抗虫屏障这一传统认知相反：与野生型相比，拟南芥 *Arabidopsis thaliana* SEOR 敲除突变体（*Atseor1-1* 和 *Atseor2-1* ）上桃蚜繁殖周期更短、单头总产若蚜数量下降（Anstead *et al*., 2012)；烟草 *Nicotiana tabacum* SEO RNA 干扰突变体（*irSEO* ）上桃蚜唾液分泌频率增加、韧皮部平均取食时间缩短，并伴随着黄瓜花叶病毒系统性侵染水平降低（Guo *et al*., 2025; 史清云等, 2026)。以上结果表明 SEO/SEOR 蛋白有利于蚜虫取食与种群繁衍，甚至可被黄瓜花叶病毒“劫持”以实现其在植株内的长距离运输。因此，SEO/SEOR 蛋白在植物与蚜虫等昆虫互作中兼具双重功能，既是植物抗虫防御的物理屏障，又可能被蚜虫等昆虫利用营造适宜取食的微环境。

综上所述，游离的韧皮部蛋白会通过自身聚合，或与其他蛋白质、糖蛋白相互结合，形成不溶性的高分子聚合物，这些不溶性聚合物会在害虫取食部位快速积累并形成物理屏障，直接阻

碍韧皮部取食性刺吸类昆虫口针的刺入与持续取食。

2 韧皮部防卫反应调控机制

韧皮部防卫反应涉及激素信号传导、转录调控及防卫相关基因表达等多个过程(Saberi *et al*., 2025)，本文从这 3 个层面，综述了胼胝质沉积与韧皮部蛋白凝集的调控机制。

2.1 胼胝质沉积介导韧皮部取食性刺吸类昆虫抗性的调控机制

植物胼胝质稳态由胼胝质合成酶（ Callose synthase, CalS，也叫做 Glucan synthase-like，GSL ）与 β-1,3-葡聚糖酶（胼胝质水解酶）协同调控，其中合成酶促进胼胝质生成，水解酶降解胼胝质，二者动态平衡直接决定胼胝质沉积量与抗虫水平。现有研究表明，钙离子（ Ca^{2+} ）、植物内源激素、多种转录因子从不同层面调控两类关键酶基因表达，进而调控胼胝质沉积与寄主植物抗虫性。

① 胼胝质合成酶基因与 β-1,3-葡聚糖酶基因协同调控胼胝质沉积

胼胝质是以 UDP-葡聚糖为底物，由一类与细胞膜结合的胼胝质合成酶催化合成(Schneider *et al*., 2016; Sanmartín *et al*., 2020)。*CalS* 基因通过调控胼胝质时空特异性积累，参与调控植物韧皮部防卫反应过程。例如，褐飞虱取食野生型和 Bph14 转基因水稻后维管束细胞壁和筛管上有明显的胼胝质沉积，并且胼胝质合成酶基因（*GSL1*, *GSL5* 和 *GSL10* ）明显上调，增强水稻的抗虫性（ Du *et al*., 2009)。西花蓟马侵染显著诱导胼胝质积累，进一步分析其诱导的胼胝质沉积与胼胝质合成酶基因 *CalS3* 和 *CalS10* 正相关（ Qian *et al*., 2019)。使用硅预处理水稻植株，会显著诱导胼胝质合成酶基因 *OsGSL1* 表达，增加筛管的胼胝质积累而降低褐飞虱适合度(Yang *et al*., 2017)。棉花 *Gossypium hirsutum GhCalS5* 基因在棉蚜 *Aphis gossypii* 取食后诱导表达，该基因可通过介导胼胝质积累，参与调控棉花对蚜虫的抗性（ Mbiza *et al*., 2022)。外源绿叶挥发物（*Z*）-3-hexenol 依赖胼胝质合成酶基因 *Cals12* 促进番茄 *Solanum lycopersicum* 植株的胼胝质沉积，增强植株对携带番茄黄化曲叶病毒的烟粉虱 *Bemisia tabaci* 抗性（ Yang *et al*., 2022)。

β-1,3-葡聚糖酶作为胼胝质水解酶，能够特异性内切水解 1,3-β-D-糖苷键，将胼胝质降解为 β-1,3-葡聚糖单体，与胼胝质合成酶协同调控胼胝质沉积介导的韧皮部取食性刺吸类昆虫抗性过程。例如丝氨酸/苏氨酸激酶（ Oxidative signal inducible 1 ）通过调控胼胝质合成/降解平衡介导拟南芥抗桃蚜，明确 β-1,3-葡聚糖酶基因 *AtGNS2* 为拟南芥的感蚜关键基因，胼胝质合成酶基因 *AtGSL5* 为抗蚜关键基因（ Shoala *et al*., 2018)。施硅处理诱导了 *OsGSL1* 和 *OsGns5* 基因上调表达，但 *OsGSL1* 基因表达量显著高于 *OsGns5* 基因表达量，促使水稻在褐飞虱侵害早期（ 48 h ）快速、大量沉积胼胝质，增强水稻对褐飞虱抗性（ Yang *et al*., 2017)。外源 ABA 处理显著提升水稻植株胼胝质合成酶活性但抑制 β-1,3-葡聚糖酶活性，引起水稻筛管等部位胼胝沉积增多而不利于褐飞虱取食与发生（ Liu *et al*., 2017)。褐飞虱取食能显著上调抗虫、感虫水稻 *OsGSL1/3/5* 基因表达，但是感虫水稻的 *Osg1*、*Gns5* 基因显著上调，快速降解胼胝质，抗虫水稻 *Osg1*、*Gns5* 几乎不表达，胼胝质持续堵塞筛管，决定了水稻抗/感褐飞虱的差异（ Hao *et al*., 2008)。以上结果表明，在植物与韧皮部取食性刺吸类昆虫互作过程中，胼胝质沉积的稳态依赖于胼胝质合成酶与 β-1,3-葡聚糖酶的协同作用。

② 钙信号介导上游调控

在部分植物中，Ca^{2+}信号是胼胝合成酶发挥活性的必需因子。韧皮部取食性刺吸类昆虫取食会打破植物静息状态下钙稳态，植物胞外 Ca^{2+} 快速内流至胞质（ Ca^{2+}内流 ）和胞内液泡中储存的 Ca^{2+}大量释放，形成 Ca^{2+}信号峰，进而引起胼胝合成酶基因上调表达、β-1,3-葡聚糖酶基因下调表达，最终胼胝质沉积(Hattori *et al*., 2012; Wu *et al*., 2022)。而且研究发现褐飞虱、蚜虫等韧皮部取食性刺吸类昆虫取食过程中向寄主分泌唾液蛋白，扰乱寄主植物胞质 Ca^{2+}稳态，进而激活

促分裂原活化的蛋白激酶（Mitogen activated protein kinase，MAPK）通路级联响应、茉莉酸（Jasmonic acid，JA）信号通路以及胼胝质大量沉积（Hao *et al*., 2008; Musetti *et al*., 2013; Shangguan *et al*., 2018; Cui *et al*., 2023; Gao *et al*., 2023）。以上研究表明，韧皮部取食性刺吸类昆虫取食引起 Ca^{2+}稳态的改变可同步触发上述多条防御路径，但 Ca^{2+}信号是分别独立调控 MAPK、JA 等途径进而引起胼胝质沉积，还是 Ca^{2+}信号作为上游枢纽依次启动 MAPK、JA 信号，最终协同调控胼胝质沉积仍有待解析。

③ 胼胝质沉积的激素信号传导机制

水杨酸（Salicylic acid，SA）、茉莉酸（JA）、脱落酸（ABA）、乙烯（Ethylene，ET）等植物激素是胼胝质沉积的重要上游调控信号，不同激素通过差异化调控胼胝质合成酶基因与 β-1,3-葡聚糖酶基因表达，动态调控胼胝合成与降解平衡，进而决定筛管或胞间连丝处胼胝质沉积水平。其中，SA 信号多正向诱导胼胝质沉积（Li *et al*., 2017; Zhang *et al*., 2023），通过上调胼胝质合成酶基因表达（Dong *et al*., 2008）或抑制 β-1,3-葡聚糖酶基因表达阻碍胼胝质降解（Song *et al*., 2024），促使胼胝大量沉积。ABA 信号以正向促进胼胝质沉积为主，一方面依赖 PYR/PYL-PP2C-SnRK2-ABI5/ABF 核心模块，转录激活胼胝合成酶基因和抑制 β-1,3-葡聚糖酶基因表达，从而调控胼胝质沉积（Oide *et al*., 2013; Lim *et al*., 2014; Liu *et al*., 2017; Singh *et al*., 2019; Guo *et al*., 2020; Yao *et al*., 2023; Liang *et al*., 2024）。JA 信号依赖于 JA-Ile-COI1-JAZ-MYC2 核心路径，上调胼胝质合成酶基因（*OsCslF6* 等）表达，可显著诱导胼胝质的沉积（Varsani *et al*., 2019; Grover *et al*., 2020; Dai *et al*., 2023）；也有研究发现 JA 合成前体 12-氧代植物二烯酸（12-Oxo-phytodienoic acid，OPDA）与活性产物茉莉酸-异亮氨酸（JA-Ile）对胼胝沉积存在相反调控效应，OPDA 可独立作为信号分子促进胼胝质积累，而 JA-Ile 则抑制胼胝质生成（Scalschi *et al*., 2015）。ET 信号通过 ETR/EIN2、EIN3/EIL 直接结合胼胝质合成酶基因（*GSL5*，*GSL10*，*GSL2* 和 *GSL12*）的启动子，双向调控胼胝质沉积，进而介导植物对韧皮部取食性刺吸类昆虫的防御响应。部分研究表明，低浓度（内源 ET 浓度< 0.3 nmol/g；外源 ET 浓度 0.1-1 μmol/L ACC）可上调胼胝质合成酶基因表达，提升胼胝质沉积，增强抗蚜性；高浓度（内源 ET 浓度> 0.4 nmol/g，外源 ET 浓度> 10 μmol/L ACC）抑制胼胝质合成酶基因表达，抑制胼胝质沉积，降低抗蚜性（Fu *et al*., 2014; Casteel *et al*., 2015; Zhu *et al*., 2018; Lu *et al*., 2023）。值得注意的是，在植物与病原菌互作中多种激素信号间协同（JA/ABA 协同）与拮抗互作（SA/ABA 拮抗，SA/JA、ET 拮抗）共同调控了胼胝质沉积过程（García-Andrade *et al*., 2011; Oide *et al*., 2013; Yi *et al*., 2014），但在植物与韧皮部取食性刺吸类昆虫的互作中，不同激素信号调控胼胝质沉积是否也存在着协同与拮抗机制仍有待进一步探究。

④ 胼胝质沉积的转录调控机制

已有多个不同的转录因子（如 WRKY、MYB、bZIP 等）被证实参与胼胝质沉积介导的韧皮部取食性刺吸类昆虫抗性过程。例如，水稻转录因子 *OsWRKY46* 和 *OsWRKY72* 可直接结合 *OsCalS* 基因（Callose synthase 5 isoform X1）提高褐飞虱抗性（Hu *et al*., 2017）。SA 信号通路通过 *SlWRKY70* 转录因子调控病程相关蛋白基因 *PR1* 的表达，同时激活胼胝质沉积防御通路，进而增强烟草（*N. tabacum* cv. NC89, *Nicotiana benthamiana*）对烟粉虱卵的抗性（Song *et al*., 2024）。高粱 *Sorghum bicolor SbWRKY86* 通过转录调控碳氮代谢与免疫信号通路，促进叶片及韧皮部胼胝质沉积，阻碍蚜虫取食，正调控对高粱蚜 *Melanaphis sacchari* 的抗性（Poosapati *et al*., 2022）。小麦 3 个 MYB 转录因子（*TaMYB19*, *TaMYB29*, *TaMYB44*）协同调控麦长管蚜 *Sitobion avenae* 诱导的胼胝质合成酶基因 *GSL2*、*GSL10* 和 *GSL12* 表达以及胼胝质沉积过程（Zhai *et al*., 2017）。拟南芥转录因子 *AtMYB44*（v-Myb avian myeloblastosis viral oncogene homolog）诱导 *AtCalS12*（*AtGSL5*）基因表达和胼胝质沉积，不利于桃蚜韧皮部取食（Lü *et al*., 2011）。另有研

究发现，过表达拟南芥 *AtMYB102* 基因显著抑制蚜虫诱导的胼胝质沉积，增加拟南芥对桃蚜的敏感性（Zhu *et al*., 2018）。除上述转录因子外，*ARF*[*AtARF17*（花粉发育）、*AtARF7*（向光性、向重力性）]、AtNHL3（灰霉菌抗性）、bZIP52（花粉管生长）、NAC100L1（嫁接亲和性）、LoNFYA7（鳞茎发育）等其他类型转录因子，已被报道参与调控病害胁迫、非生物胁迫及生长发育过程中的胼胝质合成与沉积（Yang *et al*., 2013a; Han *et al*., 2014; Wu *et al*., 2018; Pan *et al*., 2023; Tee *et al*., 2023; Xia *et al*., 2023; Yuan *et al*., 2023），这些转录因子是否也参与胼胝质沉积介导的韧皮部取食性刺吸类昆虫抗性过程，仍有待进一步解析。

2.2 韧皮部蛋白凝集介导韧皮部取食性刺吸类昆虫抗性的调控机制

① 韧皮部蛋白介导韧皮部取食性刺吸类昆虫抗性的调控机制

植物 PP2 蛋白由 *PP2* 基因家族编码，如南瓜属 *Cucurbita* 植物 *PP2* 基因家族包括 2-8 个成员（Bostwick *et al*., 1994）；芹菜 *Apium graveolens* 包含 6 个家族成员，拟南芥 *PP2* 基因家族拥有 30 个成员，包括 *AtPP2-A1-15* 和 *AtPP2-B1-15*（Dinant *et al*., 2003）。尽管不同植物 *PP2* 基因家族成员数量差异显著，但现有研究已证实多种作物的 *PP2* 基因参与植物-韧皮部取食性刺吸类昆虫的互作过程。例如，蚜虫取食可诱导苎麻 *Boehmeria nivea BnPP2-15* 基因在取食位点附近表达（Guo *et al*., 2018）。拟南芥 *AtPP2-A1* 基因是 Harpin 诱导拟南芥抗桃蚜的关键功能基因，*AtPP2-A1* 过表达株系显著缩短桃蚜韧皮部取食时长、减少蚜虫定殖（Zhang *et al*., 2011）。但进一步分析发现桃蚜分泌 Mp1、HL（类穿孔蛋白）两类不同唾液效应蛋白，与 AtPP2-A1 发生特异性互作，以此解除该蛋白的抑制作用，帮助蚜虫顺利完成取食（钟静, 2020; Wang *et al*., 2021b）。与野生型黄瓜 *Cucumis sativus* 相比，*CsPP2-A1* 过表达黄瓜对瓜蚜的抗性显著增强，而 *CsPP2-A1* 干扰后的黄瓜对瓜蚜的抗性最弱，进一步分析发现黄瓜 *CsPP2-A1* 基因通过维持黄瓜植株的活性氧稳态，调控营养组成并积累酚类、黄酮等次生代谢物，多途径抑制瓜蚜取食、定殖与繁殖（Li *et al*., 2023, 2025）。综上所述，*PP2* 基因作为编码 PP2 蛋白的关键基因，不仅通过 PP2 蛋白凝集堵塞筛管这一经典的韧皮部防卫方式，还可通过调控次生代谢合成等过程，综合介导植物抵御韧皮部取食性刺吸类昆虫危害。

② 筛管堵塞蛋白（SEO）/筛管堵塞相关蛋白（SEOR）介导韧皮部取食性刺吸类昆虫抗性的调控机制

目前针对 SEO/SEOR 蛋白调控韧皮部取食性刺吸类昆虫抗性的研究以豆科植物为主，重点解析了 F 蛋白体的抗虫机制。蚜虫等韧皮部取食性刺吸类昆虫取食引起 Ca^{2+}内流会触发 F 蛋白体蛋白构象改变，促使分散的蛋白单体快速聚集、交联，在筛板筛孔处形成致密蛋白栓，物理堵塞韧皮部筛管，达到与胼胝质相似的抗虫效果，说明胞内 Ca^{2+}浓度的动态变化是激活 F 蛋白体抗虫功能的核心信号（Furch *et al*., 2009; Medina-Ortega and Walker, 2015; Vincent *et al*., 2017）；而蚜虫通过唾液蛋白钙离子结合蛋白螯合 Ca^{2+}或唾液鞘结构蛋白阻断 Ca^{2+}内流，降低胞内 Ca^{2+}浓度，抑制 F 蛋白体的分散或使分散的 F 蛋白体转换回原始紧密的结构，进而顺利取食（Will *et al*., 2007, 2009; Will and Vilcinskas, 2015; Paulmann *et al*., 2023）。

3 韧皮部取食性刺吸类昆虫唾液蛋白调控韧皮部防卫反应

在植物与昆虫长期协同进化过程中，昆虫（包括蚜虫等韧皮部取食性刺吸类昆虫）进化出依靠唾液组分调控寄主防御反应的反防御策略（Guo *et al*., 2023; Pang *et al*., 2024; 吕子豪等, 2025）。蚜虫等韧皮部取食性刺吸类昆虫在刺探和取食过程中会向植物组织内分泌两类唾液：胶状唾液（Gel saliva）与水状唾液（Watery saliva）（Huang *et al*., 2015; van Bel and Will, 2016）。其中胶状唾液中的唾液鞘蛋白（Salivary sheath protein）、类黏蛋白（Mucin-like protein）被分泌到植物细胞间隙后固化形成唾液鞘（Salivary

sheath），发挥保护和润滑口针的作用，帮助蚜虫等刺吸类昆虫建立通向韧皮部的取食通道，保障持续取食（Huang *et al*., 2017; 黄海剑等, 2025; 张洪祥等, 2025）；水状唾液组分与生理功能更为复杂，包含多种水解酶、钙结合蛋白等，会在刺探与取食阶段直接注入植物细胞内，协助昆虫分解植物有毒次生物质和调控植物防御反应（Kettles and Kaloshian, 2016）。无论是胶状唾液还是水状唾液，其中可以被植物识别并诱导植物防御反应的唾液组分称为激发子（Hu *et al*., 2025; Wang *et al*., 2025），而抑制植物防御反应的唾液组分称为效应子（Xu *et al*., 2019; Peng *et al*., 2023）。

3.1　韧皮部取食性刺吸类昆虫唾液蛋白激活韧皮部防卫反应

韧皮部取食性刺吸类昆虫唾液蛋白中的激发子可以被植物免疫系统识别，进而激活植物韧皮部相关的防卫反应（表 1）。褐飞虱在取食水稻时分泌的 Nl12、Nl16、Nl28、Nl32、Nl40 和 Nl43 等唾液蛋白在植物韧皮部表达，能够显著增强胼胝质沉积，并且诱导 SA 和 JA 信号通路下游防卫相关基因的表达（Rao *et al*., 2019）。获草谷网蚜 *Sitobion miscanthi* 唾液蛋白激发子 SmCSP4 在取食过程中被分泌到小麦细胞中激活 SA 介导的防御通路，同时伴随过氧化氢爆发、胼胝质大量沉积（Zhang *et al*., 2023）。另外，获草谷网蚜的唾液中还包含来源于初级共生菌的 GroES 蛋白，也可以诱导小麦叶片的过氧化氢积累与胼胝质沉积（Li *et al*., 2022）。伊氏叶螨 *Tetranychus evansi* 唾液激发子 Te16 可诱导本氏烟活性氧爆发、胼胝质沉积以及 JA 防御通路激活（Cui *et al*., 2024）。值得一提的是，桃蚜唾液蛋白葡萄糖脱氢酶（Glucose dehydrogenase，GLD）分泌到烟草韧皮部内，在韧皮部筛管腔内

表 1　激活韧皮部防卫反应的韧皮部取食性刺吸类昆虫唾液组分（激发子）

Table 1　Salivary proteins (elicitor) of phloem-feeding, piercing-sucking insects for activating the phloem-based defense

序号 No.	昆虫种类 Insect species	唾液蛋白 Salivary protein		功能 Function
		蛋白类型 Protein type	名称 Name	
1	获草谷网蚜 *Sitobion miscanthi*	小分子伴侣蛋白 Small chaperone protein	GroES	过氧化氢积累与胼胝质沉积 H_2O_2 accumulation and callose deposition (Li *et al*., 2022)
2	获草谷网蚜 *Sitobion miscanthi*	化学感受蛋白 Chemosensory protein	SmCSP4	激活 SA 防御通路，同时伴随过氧化氢爆发与胼胝质沉积 Activating SA-dependent defense pathway, H_2O_2 burst, and callose deposition (Zhang *et al*., 2023)
3	豌豆蚜 *Acyrthosiphon pisum*	化学感受蛋白 Chemosensory protein	ApCSP4	
4	棉蚜/瓜蚜 *Aphis gossypii*	化学感受蛋白 Chemosensory protein	AgCSP4	
5	桃蚜 *Myzus persicae*	化学感受蛋白 Chemosensory protein	MpCSP4	
6	桃蚜 *M. persicae*	葡萄糖脱氢酶 Glucose dehydrogenase	GLD	在韧皮部筛管腔内营造氧化微环境，驱动 SEO 从分散态向高度有序聚合态的构象转换 Establishing an oxidative micro-environment in phloem sieve tube lumen and triggering the transition of SEO proteins from the dispersed state to the aggregated state (Guo *et al*., 2025)
7	褐飞虱 *Nilaparvata lugens*	唾液蛋白 Salivary protein	Nl12 Nl16 Nl28 Nl32 Nl40 Nl43	诱导胼胝质沉积，SA 和 JA 防御通路防卫相关基因表达 Inducing callose deposition and the expression of SA- and JA-dependent defense-related genes (Rao *et al*., 2019)

续表 1 (Table 1 continued)

序号 No.	昆虫种类 Insect species	唾液蛋白 Salivary protein		功能 Function
		蛋白类型 Protein type	名称 Name	
8	褐飞虱 *N. lugens*	唾液蛋白 Salivary protein	NlSP1	诱导细胞凋亡、过氧化氢积累、防卫相关基因表达以及胼胝质沉积 Inducing programmed cell death, H_2O_2 accumulation, the expression of defense-related genes, and callose deposition (Huang *et al*., 2020)
9	褐飞虱 *N. lugens*	唾液蛋白 Salivary protein	NlG14	诱导活性氧积累、细胞凋亡、胼胝质沉积与 JA 防御通路 Inducing ROS accumulation, programmed cell death, callose deposition, and JA-dependent defense pathway (Gao *et al*., 2022)
10	褐飞虱 *N. lugens*	唾液分子伴侣蛋白 Salivary molecular chaperone	NlDNAJB9	激活 Ca^{2+}信号和 MAPK 级联反应、活性氧积累、JA 防御通路与胼胝质沉积 Activating Ca^{2+} signaling, MAPK cascades, ROS accumulation, JA-dependent defense pathway, and callose deposition (Gao *et al*., 2023)
11	褐飞虱 *N. lugens*	类黏蛋白 Mucin-like protein	NlMLP	诱导细胞凋亡、防卫相关基因表达以及胼胝质沉积 Inducing programmed cell death, the expression of defense-related genes, and callose deposition (Shangguan *et al*., 2018)
12	灰飞虱 *Laodelphax striatellus*	蛋白二硫化物异构酶 Protein disulfide isomerase	LsPDI1	诱导活性氧积累、细胞凋亡、胼胝质沉积与 JA 防御通路 Inducing ROS accumulation, programmed cell death, callose deposition, and JA-dependent defense pathway (Fu *et al*., 2021)
13	伊氏叶螨 *Tetranychus evansi*	唾液蛋白 Salivary protein	Te16	活性氧积累、胼胝质沉积以及 JA 防御通路激活 ROS accumulation, callose deposition, and activating JA-dependent defense pathway (Cui *et al*., 2024)
14	伊氏叶螨 *T. evansi*	蛋白二硫化物异构酶 Protein disulfide isomerase	TePDI	活性氧积累、胼胝质沉积以及抗性相关基因表达 ROS accumulation, callose deposition, and the expression of defense-related genes (Cui *et al*., 2023)

营造氧化微环境，驱动 SEO 从分散态向高度有序聚合态的构象转换，反而可能有利于蚜虫取食（Guo *et al*., 2025; 史清云等, 2026）。

3.2 韧皮部取食性刺吸类昆虫唾液蛋白抑制韧皮部防卫反应

除激活植物韧皮部防卫反应的唾液激发子外，更多的研究关注于能够抑制植物韧皮部防卫反应过程的韧皮部取食性刺吸类昆虫唾液效应子（表 2）。褐飞虱唾液蛋白 NlVRSP1（稻飞虱中高度保守唾液效应子），能够与水稻胞间连丝胼胝质结合蛋白 OsPDCB1 直接互作，破坏 OsPDCB1 与胼胝质结合活性，抑制胼胝质沉积介导的褐飞虱抗性（Yang *et al*., 2026）。沉默灰

表 2　抑制韧皮部防卫反应的韧皮部取食性刺吸类昆虫唾液组分（效应子）

Table 2　Salivary proteins (effector) of phloem-feeding, piercing-sucking insects for suppressing the phloem-based defense

序号 No.	昆虫种类 Insect species	唾液蛋白 Salivary protein		功能 Function
		蛋白类型 Protein type	名称 Name	
1	豌豆蚜 *Acyrthosiphon pisum*	巨噬细胞移动抑制因子 Macrophage migration inhibitory factor	ApMIF1	抑制胼胝质沉积 Suppressing callose deposition (Naessens *et al*., 2015)
2	豌豆蚜 *A. pisum*	唾液鞘蛋白 Structural sheath protein	ApSSP	在外封堵伤口，阻断胞间外源 Ca^{2+}进入筛管，抑制 F 蛋白体的分散，使筛管不封堵 Sealing extracellular wounds to prevent Ca^{2+} influx into the sieve tube lumen, thereby suppressing the forisome dispersion to avoid sieve- tube occlusion (Will and Vilcinskas, 2015)
3	麦长管蚜 *Sitobion avenae*	类细胞周期蛋白依赖性激酶 Cyclin-dependent kinase-like	SaCDKL	抑制胼胝质沉积，SA、JA 防御通路下游防卫相关基因表达
4	获草谷网蚜 *Sitobion miscanthi*	唾液蛋白 Salivary protein	Sm10 SmC002 Sm9723	Suppressing callose deposition and the expression of SA- and JA-dependent defense-related genes (Zhang *et al*., 2022a, 2022b, 2024; Fu *et al*., 2023)
5	麦二叉蚜 *Schizaphis graminum*	唾液蛋白 Salivary protein	Sg2204	
6	桃蚜 *Myzus persicae*	唾液蛋白 Salivary protein	Mp55	抑制 4-甲氧基吲哚-3-甲基硫代葡萄糖苷积累、过氧化氢积累和胼胝质沉积 Suppressing the accumulation of 4-methoxyindol-3-ylmethyl glucosinolate and H_2O_2, as well as inhibiting callose deposition (Elzinga *et al*., 2014)
7	桃蚜 *M. persicae*	唾液蛋白 Salivary protein	Mp1	Mp1 与 AtPP2-A1 特异性结合，抑制 AtPP2-A1 介导的防御功能，解除拟南芥韧皮部防御 Mp1 specifically binds to AtPP2-A1, which suppresses AtPP2-A1-mediated defense activity and consequently attenuates phloem defense responses in *Arabidopsis thaliana* (Wang *et al*., 2021b)
8	桃蚜 *M. persicae*	类穿孔蛋白 Perforin-like protein	HL	唾液蛋白 HL 与 PP2-A 互作，抑制凝集素类韧皮部蛋白在筛管细胞壁、筛板表面和筛孔边缘沉积 The salivary protein HL interacts with PP2-A, and thereby inhibiting the deposition of lectin-like phloem proteins on the sieve tube cell walls, sieve plate surfaces, and sieve pore margins (钟静, 2020)
9	桃蚜 *M. persicae*	巨噬细胞移动抑制因子 Macrophage migration inhibitory factor	MpMIFs	抑制胼胝质沉积、细胞凋亡以及病程相关蛋白基因表达 Suppressing callose deposition, cell apoptosis, and the expression of pathogenesis-related genes (Naessens *et al*., 2015)

续表 2 (Table 2 continued)

序号 No.	昆虫种类 Insect species	唾液蛋白 Salivary protein		功能 Function
		蛋白类型 Protein type	名称 Name	
10	马铃薯长管蚜 *Macrosiphum euphorbiae*	金属蛋白酶 Metalloproteinase	MMP	高效降解韧皮部蛋白 PP1，但无法降解凝集素属性的 PP2 Efficiently degrading the phloem protein PP1, but failing to degrade the lectin-like protein PP2 (Furch *et al*., 2015)
11	巢菜修尾蚜 *Megoura viciae*	钙离子结合蛋白 Calcium-binding protein	MvCBP	促进 F 蛋白体构象变化，使分散的 F 蛋白体转换回原始紧密的结构 Accelerating the conformational transition of forisomes from the dispersed state to the aggregated state (Will *et al*., 2009)
12	巢菜修尾蚜 *M. viciae*	钙离子结合蛋白 Calcium-binding protein	43-kD protein	与 Ca^{2+}结合，降低 Ca^{2+}浓度，抑制 F 蛋白体的分散，使筛管不封堵 Decreasing cellular Ca^{2+} concentration by binding to Ca^{2+}, inhibiting forisome dispersion, and consequently preventing sieve tube occlusion (Will *et al*., 2007)
13	褐飞虱 *Nilaparvata lugens*	钙离子结合蛋白 Calcium-binding protein	SG-8F6 SG-8C10 SG-4C4	不分泌到水稻内，调控自身唾液腺细胞中 Ca^{2+}平衡，间接调控唾液中各类效应蛋白的合成与分泌 Un-secreting into rice plants and stabilizing itself Ca^{2+} homeostasis of salivary gland to indirectly modulate the synthesis and secretion of various salivary effector proteins (Wang *et al*., 2015)
14	褐飞虱 *N. lugens*	唾液蛋白 Salivary protein	NlSP1	与 OsPDCB1 直接互作破坏其与胼胝质结合活性 Interacting with OsPDCB1 directly to impair its callose-binding capacity (Yang *et al*., 2026)
15	褐飞虱 *N. lugens*	碳酸酐酶 Carbonic anhydrase	NICA	抑制韧皮部筛板上的胼胝质沉积，降低防御基因表达 Suppressing callose deposition on phloem sieve plates and down-regulating the expression of defense-related genes (Jiang *et al*., 2024)
16	灰飞虱 *Laodelphax striatellus*	DNA 酶Ⅱ Deoxyribonuclease Ⅱ	DNase Ⅱ	降解胞外 DNA，降低过氧化氢水平和抑制胼胝质沉积 Degrading extracellular DNA, decreasing H_2O_2 levels, and inhibiting callose deposition (Huang *et al*., 2019)
17	灰飞虱 *L. striatellus*	钙调蛋白 Calmodulin	LsCaM	抑制过氧化氢积累、胼胝质沉积等 Suppressing H_2O_2 accumulation and callose deposition (Fu *et al*., 2022)
18	灰飞虱 *L. striatellus*	钙离子结合蛋白 Calcium-binding protein	LsECP1	与 Ca^{2+}结合，降低 Ca^{2+}浓度，抑制 JA、过氧化氢积累 Decreasing cellular Ca^{2+} concentration and suppressing JA and H_2O_2 accumulation by binding to Ca^{2+}(Tian *et al*., 2021）

续表 2 (Table 2 continued)

序号 No.	昆虫种类 Insect species	唾液蛋白 Salivary protein		功能 Function
		蛋白类型 Protein type	名称 Name	
19	烟粉虱 *Bemisia tabaci*	钙离子结合蛋白 Calcium-binding protein	BtCaBP1 BtCaBP2	不分泌到寄主植物中，稳定自身胞内钙稳态 Un-secreting into the host plant and stabilizing itself intracellular Ca^{2+} homeostasis (Guo *et al*., 2019)
20	烟粉虱 *B. tabaci*	铁蛋白 1 Ferritin 1	BtFer1	抑制植物氧化信号、胼胝质沉积、蛋白酶抑制剂的激活以及 JA 防御通路 Suppressing oxidative signaling, callose deposition, protease-inhibitor activation, and the JA-dependent defense pathway (Su *et al*., 2019)
21	亚洲柑橘木虱 *Diaphorina citri*	唾液蛋白 Salivary protein	DcE13 DcE1	抑制植物超敏反应，减弱胼胝质沉积，并下调 JA 防御通路抗性基因的表达 Suppressing the plant hypersensitive response, reducing callose deposition, and down-regulating the expression of JA-dependent defense-related genes (Kuang *et al*., 2025; Shangguan *et al*., 2025)
22	伊氏叶螨 *Tetranychus evansi*	唾液蛋白 Salivary protein	Te28 Te84	抑制活性氧暴发和胼胝质沉积 Suppressing ROS burst and callose deposition (Cui *et al*., 2023)
23	黑尾叶蝉 *N. cincticeps*	钙离子结合蛋白 Calcium-binding protein	NcSP84	进入筛管与 Ca^{2+}结合，降低 Ca^{2+}浓度，抑制胼胝质合成 Entering the sieve tube and binding to Ca^{2+}, thereby decreasing Ca^{2+} (Hattori *et al*., 2012)concentration and inhibiting callose synthesis
24	西花蓟马 *Frankliniella occidentalis*	碳酸酐酶 Carbonic anhydrase	FoCA2	抑制 JA 与 SA 防御通路相关基因表达，胼胝质合酶基因及胼胝质沉积 Suppressing the expression of JA- and SA-dependent defense-related genes and callose synthase genes, as well as inhibiting callose deposition (Tian *et al*., 2025)

表 1、表 2 中所列伊氏叶螨（螯吸式口器）与西花蓟马（锉吸式口器），在分类学上并不属于典型的刺吸式口器昆虫。但鉴于两点原因仍将其一并纳入表 1、表 2 展示：①在植物-昆虫互作及抗虫性相关研究中，这两类害虫常被归为刺吸类害虫进行统一分析与讨论；②已有文献明确证实，二者取食为害同样能够诱导植物产生韧皮部防卫反应，其为害机制与本研究聚焦的韧皮部取食性刺吸类昆虫具有高度相似性。

The pests *Tetranychus evansi* (cheliceral-sucking mouthparts) and *Frankliniella occidentalis* (rasping-sucking mouthparts) in Table 1 and Table 2 are not classified as typical piercing-sucking insects under taxonomic criteria. Nevertheless, they are still included in Table 1 and Table 2 for two reasons: ① Both pests are commonly grouped into piercing-sucking pests for analysis and discussion in researches on plant-insect interactions and plant resistance against herbivorous insects; ② Previous studies have confirmed that both pests can trigger phloem-based defense of plants, with the underlying defense-related mechanisms overlapping those of the phloem-feeding, piercing-sucking insects discussed in the present study.

飞虱 *Laodelphax striatellus* 唾液蛋白-DNA 酶Ⅱ，灰飞虱取食会诱导更高的胼胝质沉积，但不影响 JA、SA 以及 ET 信号通路介导的抗性响应，说明唾液组分 DNA 酶Ⅱ作为一种效应子抑制水稻植株的胼胝质沉积（Huang *et al*., 2019）。沉默西花蓟马碳酸酐酶家族成员 FoCA2 可显著抑制其

取食和降低其繁殖与存活率，同时诱导胼胝质合成酶基因表达及胼胝质沉积（Tian *et al*., 2025）。巢菜修尾蚜 *Megoura viciae* 唾液中含有钙结合蛋白，可以阻止钙与筛分子蛋白结合，进而抑制筛分子中钙依赖信号的级联反应，促使堵塞在筛孔附近分散的 F 蛋白体转换回原始紧密的结构，从而恢复韧皮部汁液的流动，帮助蚜虫成功取食（Will *et al*., 2009; Vincent *et al*., 2017）。蚜虫唾液中含有的金属蛋白酶等蛋白酶类组分，可降解植物韧皮部关键结构蛋白 PP1，破坏筛管封堵防御，使得口针更容易插入植物韧皮部（Furch *et al*., 2015）。而且后续研究表明，不同蚜虫（豌豆蚜、桃蚜、麦长管蚜、禾谷缢管蚜 *Rhopalosiphum padi* 等）利用唾液组分抑制韧皮部筛板闭塞是一种普遍现象；但是发挥该功能的唾液组分在不同蚜虫物种间存在明显不同（Will *et al*., 2009）。

另外韧皮部取食性刺吸类昆虫唾液蛋白另一个重要功能是辅助其完成口针穿刺、构建取食通道，提升取食效率。韧皮部取食性刺吸类昆虫唾液中含有的果胶酶、纤维素酶等多种细胞壁降解酶，可降解植物细胞壁多糖成分，使得细胞壁降解和软化，有利于韧皮部取食性刺吸类昆虫口针的穿刺。并且唾液中的蔗糖酶、淀粉酶等可将植物多糖分解为单糖，提升汁液适口性与营养利用率。例如，褐飞虱唾液蛋白 NlSP5 和 NlSP7 可以形成“唾液鞘”，固定口针并密封穿刺伤口，有效阻止汁液外流与防御信号扩散，是保障其良好取食与种群适合度的关键蛋白（Liu *et al*., 2024）。

4 总结与展望

本文系统梳理了植物韧皮部防卫反应抵御韧皮部取食性刺吸类昆虫的研究进展。植物受到韧皮部取食性刺吸类昆虫取食危害后会启动韧皮部防卫反应，主要通过胼胝质沉积与韧皮部蛋白凝集两种方式形成物理屏障，堵塞筛管筛孔，阻碍害虫持续取食、定殖与繁殖，二者常协同发挥抗虫作用。

在植物层面，蚜虫等韧皮部取食性刺吸类昆虫取食会扰乱植物胞内 Ca^{2+} 稳态形成钙信号峰，进而激活 MAPK 通路级联响应以及激素信号通路（SA、JA、ET、ABA 等），动态调控胼胝质合成酶（CalS/GSL）和 β-1,3-葡聚糖酶基因表达，引起胼胝质沉积；同时 Ca^{2+} 稳态同样会影响韧皮部蛋白（PP2）与筛管堵塞蛋白（SEO/SEOR/F 蛋白体）介导的筛管封堵，进而影响植物抵御韧皮部取食性刺吸类昆虫取食。在昆虫层面，韧皮部取食性刺吸类昆虫演化出完善的反防御策略，其利用唾液效应子，如钙离子结合蛋白、碳酸酐酶等，螯合 Ca^{2+}，进而削弱甚至阻断植物韧皮部防卫反应，辅助口针穿刺与韧皮部取食。

综上所述，植物韧皮部防卫反应与韧皮部取食性刺吸类昆虫唾液介导的反防御构成了植物-韧皮部取食性刺吸类昆虫博弈的核心。未来，可依托多组学测序技术（基因组、代谢组、空间转录组、单细胞转录组、空间蛋白质组等）、冷冻电镜、CRISPR/Cas9 基因编辑等技术，从基础理论、生产应用两大维度开展深入研究：基础研究层面，①解析植物激活韧皮部防卫反应的完整调控通路：如 Ca^{2+} 信号作为上游开关，协同多条激素通路调控胼胝质沉积、韧皮部蛋白凝集等韧皮部防卫反应的级联机制；以及系统筛选并验证介导韧皮部防卫反应的核心转录因子，构建完整的韧皮部防卫反应转录调控网络。②揭示昆虫唾液蛋白反防御植物韧皮部防卫反应的机制，一方面进一步筛选、鉴定不同刺吸类昆虫中能够抑制寄主韧皮部防卫的唾液效应子，明晰各类效应子与植物筛管防御元件的靶向互作模式；另一方面不同昆虫物种抑制韧皮部防卫反应的唾液成分存在相似性，这可能是昆虫长期适应进化的特征，系统比较多个昆虫物种的唾液蛋白组，联合进化基因组学解析其演化规律，阐释不同昆虫唾液效应子趋同演化出抑制韧皮部防卫反应的进化逻辑。生产应用层面，①作物抗虫分子育种材料创制：基于已挖掘的韧皮部防卫反应关键基因，结合基因编辑、分子标记辅助育种、转基因等手段，培育具备稳定韧皮部抗性的新品系；以及兼顾抗虫性、产量与品质性状，培育多基因聚合、抗性持久的高产抗虫品种。②绿色防控技术方案的开发：基于植物韧皮部防卫反应的激活机

制，开发可诱导作物内源韧皮部抗性的植物免疫诱抗剂；针对害虫唾液效应子功能，研发靶向抑制效应子活性、阻断害虫反防御能力的新型生物制剂，构建“免疫诱抗+生物防控”的害虫绿色防控方案。上述研究成果既能完善植物-刺吸昆虫互作的基础理论体系，又可为作物抗虫分子育种、基于植物防御的绿色防控技术研发提供重要理论支撑，为保障农作物安全生产、推动绿色农业发展提供重要保障。

参考文献 (References)

Anstead JA, Froelich DR, Knoblauch M, Thompson GA, 2012. Arabidopsis P-protein filament formation requires both *AtSEOR1* and *AtSEOR2*. *Plant Cell Physiology*, 53(6): 1033–1042.

Bostwick DE, Skaggs MI, Thompson GA, 1994. Organization and characterization of cucurbita phloem lectin genes. *Plant Molecular Biology*, 26(3): 887–897.

Casteel CL, De Alwis M, Bak A, Dong H, Whitham SA, Jander G, 2015. Disruption of ethylene responses by turnip mosaic virus mediates suppression of plant defense against the green peach aphid vector. *Plant Physiology*, 169(1): 209–218.

Cheng LL, Wang X, An F, Xie GS, Wang JK, Peng WT, Zhou LJ, 2023. Advances in understanding the roles of SEO/SEOR proteins in plant growth development and stress responses. *Plant Physiology Journal*, 59 (7): 1265–1276. [程琳琳, 王璇, 安锋, 谢贵水, 王纪坤, 彭文涛, 周立军, 2023. SEO/SEOR 蛋白在植物生长发育及逆境响应中的功能研究进展. 植物生理学报, 59(7): 1265–1276.]

Clark AM, Jacobsen KR, Bostwick DE, Dannenhoffer JM, Skaggs MI, Thompson GA, 1997. Molecular characterization of a phloem-specific gene encoding the filament protein, phloem protein 1 (PP1), from *Cucurbita maxima*. *The Plant Journal*, 12(1): 49–61.

Cui JR, Bing XL, Tang YJ, Liu F, Ren L, Zhou JY, Liu HH, Wang MK, Hoffmann AA, Hong XY, 2023. A conserved protein disulfide isomerase enhances plant resistance against herbivores. *Plant Physiology*, 191(1): 660–678.

Cui JR, Zhou B, Tang YJ, Zhou JY, Ren L, Liu F, Hoffmann AA, Hong XY, 2024. A new spider mite elicitor triggers plant defence and promotes resistance to herbivores. *Journal of Experimental Botany*, 75(5): 1493–1509.

Dai YS, Liu D, Guo W, Liu ZX, Zhang X, Shi LL, Zhou DM, Wang LN, Kang K, Wang FZ, Zhao SS, Tan YF, Hu T, Chen W, Li P, Zhou QM, Yuan LY, Zhang Z, Chen YQ, Zhang WQ, Li J, Yu LJ, Xiao S, 2023. Poaceae-specific β-1,3;1,4-d-glucans link jasmonate signalling to OsLecRK1-mediated defence response during rice-brown planthopper interactions. *Plant Biotechnology Journal*, 21(6): 1286–1300.

Dinant S, Clark AM, Zhu Y, Vilaine F, Palauqui JC, Kusiak C, Thompson GA, 2003. Diversity of the superfamily of phloem lectins (phloem protein 2) in angiosperms. *Plant Physiology*, 131(1): 114–128.

Dong X, Hong Z, Chatterjee J, Kim S, Verma DP, 2008. Expression of callose synthase genes and its connection with Npr1 signaling pathway during pathogen infection. *Planta*, 229(1): 87–98.

Du B, Zhang W, Liu B, Hu J, Wei Z, Shi Z, He R, Zhu L, Chen R, Han B, He G, 2009. Identification and characterization of Bph14, a gene conferring resistance to brown planthopper in rice. *Proceedings of the National Academy of Sciences of the United States of America*, 106(52): 22163–22168.

Elzinga DA, De Vos M, Jander G, 2014. Suppression of plant defenses by a *Myzus persicae* (green peach aphid) salivary effector protein. *Molecular Plant-Microbe Interactions*, 27(7): 747–756.

Ernst AM, Jekat SB, Zielonka S, Müller B, Neumann U, Rüping B, Twyman RM, Krzyzanek V, Prüfer D, Noll GA, 2012. Sieve element occlusion (SEO) genes encode structural phloem proteins involved in wound sealing of the phloem. *Proceedings of the National Academy of Sciences of the United States of America*, 109(28): E1980–1989.

Fu J, Shi Y, Wang L, Zhang H, Li J, Fang J, Ji R, 2021. Planthopper-secreted salivary disulfide isomerase activates immune responses in plants. *Frontiers in Plant Science*, 11: 622513.

Fu J, Shi Y, Wang L, Tian T, Li J, Gong L, Zheng Z, Jing M, Fang J, Ji R, 2022. Planthopper-secreted salivary calmodulin acts as an effector for defense responses in rice. *Frontiers in Plant Science*, 13: 841378.

Fu M, Xu M, Zhou T, Wang D, Tian S, Han L, Dong H, Zhang C, 2014. Transgenic expression of a functional fragment of harpin protein Hpa1 in wheat induces the phloem-based defence against English grain aphid. *Journal of Experimental Botany*, 65(6): 1439–1453.

Fu Y, Liu X, Wang Q, Liu H, Cheng Y, Li H, Zhang Y, Chen J, 2023. Two salivary proteins Sm10 and SmC002 from grain aphid *Sitobion miscanthi* modulate wheat defense and enhance aphid performance. *Frontiers in Plant Science*, 14: 1104275.

Furch AC, van Bel AJ, Fricker MD, Felle HH, Fuchs M, Hafke JB, 2009. Sieve element Ca^{2+} channels as relay stations between remote stimuli and sieve tube occlusion in *Vicia faba*. *Plant Cell*,

21(7): 2118–2132.

Furch AC, van Bel AJ, Will T, 2015. Aphid salivary proteases are capable of degrading sieve-tube proteins. *Journal of Experimental Botany*, 66(2): 533–539.

Gao H, Lin X, Yuan X, Zou J, Zhang H, Zhang Y, Liu Z, 2023. The salivary chaperone protein NlDNAJB9 of *Nilaparvata lugens* activates plant immune responses. *Journal of Experimental Botany*, 74(21): 6874–6888.

Gao H, Zou J, Lin X, Zhang H, Yu N, Liu Z, 2022. *Nilaparvata lugens* salivary protein NlG14 triggers defense response in plants. *Journal of Experimental Botany*, 73(22): 7477–7487.

García-Andrade J, Ramírez V, Flors V, Vera P, 2011. *Arabidopsis* ocp3 mutant reveals a mechanism linking ABA and JA to pathogen-induced callose deposition. *Plant Journal*, 67(5): 783–794.

Geng DC, 2017. Piercing-sucking pests on landscape plants in north China mining areas: Common species and control measures. *Chinese Horticulture Abstracts*, 33(9): 123–124. [耿东灿, 2017. 华北矿区园林植物刺吸性害虫常见种类及防治方法. 中国园艺文摘, 33(9): 123–124.]

Grover S, Varsani S, Kolomiets MV, Louis J, 2020. Maize defense elicitor, 12-oxo-phytodienoic acid, prolongs aphid salivation. *Communicative & Integrative Biology*, 13(1): 63–66.

Guo J, Wang H, Guan W, Guo Q, Wang J, Yang J, Peng Y, Shan J, Gao M, Shi S, Shangguan X, Liu B, Jing S, Zhang J, Xu C, Huang J, Rao W, Zheng X, Wu D, Zhou C, Du B, Chen R, Zhu L, Zhu Y, Walling LL, Zhang Q, He G, 2023. A tripartite rheostat controls self-regulated host plant resistance to insects. *Nature*, 618(7966): 799–807.

Guo H, Sun Y, Yan H, Li C, Ge F, 2020. O_3-induced priming defense associated with the abscisic acid signaling pathway enhances plant resistance to *Bemisia tabaci*. *Frontiers in Plant Science*, 11: 93.

Guo H, Shi Q, Ling X, Wu Y, He L, Li D, Zhu-Salzman K, Sun Y, 2025. Viral systemic movement is enhanced by alteration of a structural phloem protein by the insect vector. *Advanced Science*, 12(45): e06990.

Guo L, Li C, Liang P, Chu D, 2019. Cloning and functional analysis of two Ca^{2+}-binding proteins (CaBPs) in response to cyantraniliprole exposure in *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Journal of Agricultural and Food Chemistry*, 67(40): 11035–11043.

Guo P, Zheng Y, Peng D, Liu L, Dai L, Chen C, Wang B, 2018. Identification and expression characterization of the phloem protein 2 (PP2) genes in ramie (*Boehmeria nivea* L. Gaudich). *Scientific Reports*, 8(1): 10734.

Han X, Hyun TK, Zhang M, Kumar R, Koh EJ, Kang BH, Lucas WJ, Kim JY, 2014. Auxin-callose-mediated plasmodesmal gating is essential for tropic auxin gradient formation and signaling. *Developmental Cell*, 28(2): 132–146.

Hao P, Liu C, Wang Y, Chen R, Tang M, Du B, Zhu L, He G, 2008. Herbivore-induced callose deposition on the sieve plates of rice: An important mechanism for host resistance. *Plant Physiology*, 146(4): 1810–1820.

Hattori M, Nakamura M, Komatsu S, Tsuchihara K, Tamura Y, Hasegawa T, 2012. Molecular cloning of a novel calcium-binding protein in the secreted saliva of the green rice leafhopper *Nephotettix cincticeps*. *Insect Biochemistry and Molecular Biology*, 42(1): 1–9.

Hu B, Feng X, Xu M, Huang Y, Guo C, Yuan R, Li Y, Wei Z, Chen J, Sun Z, 2025. A pentatomomorpha-specific salivary protein activates plant immunity and is critical for insect feeding. *Proceedings of the National Academy of Sciences of the United States of America*, 122(5): e2425190122.

Hu L, Wu Y, Wu D, Rao W, Guo J, Ma Y, Wang Z, Shangguan X, Wang H, Xu C, Huang J, Shi S, Chen R, Du B, Zhu L, He G, 2017. The coiled-coil and nucleotide binding domains of brown planthopper resistance14 function in signaling and resistance against planthopper in rice. *Plant Cell*, 29(12): 3157–3185.

Huang HJ, Liu CW, Cai YF, Zhang MZ, Bao YY, Zhang CX, 2015. A salivary sheath protein essential for the interaction of the brown planthopper with rice plants. *Insect Biochemistry and Molecular Biology*, 66: 77–87.

Huang HJ, Liu CW, Xu HJ, Bao YY, Zhang CX, 2017. Mucin-like protein, a saliva component involved in brown planthopper virulence and host adaptation. *Journal of Insect Physiology*, 98: 223–230.

Huang HJ, Cui JR, Xia X, Chen J, Ye YX, Zhang CX, Hong XY, 2019. Salivary DNase II from *Laodelphax striatellus* acts as an effector that suppresses plant defence. *New Phytologist*, 224(2): 860–874.

Huang HJ, Li JM, Chen JP, Zhang CX, 2025. Components, evolution and functions of salivary secretions in phytophagous insects. *Science China Life Sciences*, 55(8): 1646–1660. [黄海剑, 李俊敏, 陈剑平, 张传溪, 2025. 植食性昆虫唾液的成分、进化和功能. 中国科学: 生命科学, 55(8): 1646–1660.]

Huang J, Zhang N, Shan J, Peng Y, Guo J, Zhou C, Shi S, Zheng X, Wu D, Guan W, Yang K, Du B, Zhu L, Yuan L, He G, Chen R, 2020. Salivary protein 1 of brown planthopper is required for survival and induces immunity response in plants. *Frontiers in Plant Science*, 11: 571280.

Huang LN, Guo YH, Zhou ZL, Feng GT, Sun X, 2025. Defensive

evolution of invasive plants to herbivorous insects. *Chinese Journal of Applied Entomology*, 62(5): 1650–1657. [黄丽娜, 郭艳慧, 周泽立, 冯广涛, 孙晓, 2025. 入侵植物对植食性昆虫的防御演化. 应用昆虫学报, 62(5): 1650–1657.]

Jiang Y, Zhang CX, Chen R, He SY, 2019. Challenging battles of plants with phloem-feeding insects and prokaryotic pathogens. *Proceedings of the National Academy of Sciences of the United States of America*, 116(47): 23390–23397.

Jiang Y, Zhang XY, Li S, Xie YC, Luo XM, Yang Y, Pu Z, Zhang L, Lu JB, Huang HJ, Zhang CX, He SY, 2024. Rapid intracellular acidification is a plant defense response countered by the brown planthopper. *Current Biology*, 34(21): 5017–5027.

Kehr J, 2006. Phloem sap proteins: Their identities and potential roles in the interaction between plants and phloem-feeding insects. *Journal of Experimental Botany*, 57(4): 767–774.

Kettles GJ, Kaloshian I, 2016. The potato aphid salivary effector Me47 is a glutathione-s-transferase involved in modifying plant responses to aphid infestation. *Frontiers in Plant Science*, 7: 1142.

Koch KG, Donze-Reiner T, Baird LM, Louis J, Amundsen K, Sarath G, Bradshaw JD, Heng-Moss T, 2018. Evaluation of greenbug and yellow sugarcane aphid feeding behavior on resistant and susceptible switchgrass cultivars. *BioEnergy Research*, 11(3): 480–490.

Kuang Y, Shangguan C, Wang C, Gao L, Yu X, 2025. Salivary effector DcE1 suppresses plant defense and facilitates the successful feeding of Asian citrus psyllid *Diaphorina citri*. *Pest Management Science*, 81(4): 1717–1726.

Li P, Shu YN, Fu S, Liu YQ, Zhou XP, Liu SS, Wang XW, 2017. Vector and nonvector insect feeding reduces subsequent plant susceptibility to virus transmission. *New Phytologist*, 215(2): 699–710.

Li Q, Fu Y, Liu X, Sun J, Hou M, Zhang Y, Chen J, 2022. Activation of wheat defense response by *Buchnera aphidicola*-derived small chaperone protein GroES in wheat aphid saliva. *Journal of Agricultural and Food Chemistry*, 70(4): 1058–1067.

Li Y, Fan H, Si Y, Guo Y, Wu Z, Du C, 2023. The phloem lectin PP2-A1 enhances aphid resistance by affecting aphid behavior and maintaining ROS homeostasis in cucumber plants. *International Journal of Biological Macromolecules*, 229: 432–442.

Li YP, Zhu Y, Dong LL, Wen YZ, Lv XL, Fan H, Du C, 2025. Influence of phloem lectin CsPP2-A1 on aphid development via mediation of phenylpropanoid and flavonoid biosynthesis in cucumber. *Pest Management Science*, 81(8): 4647–4656.

Liang X, Liao G, Li J, Fan W, Liu Y, Wang S, Chen L, Wang Y, Liu J, 2024. Exogenous ABA promotes resistance to *Sitobion avenae* (Fabricius) in rice seedlings. *Pest Management Science*, 80(7): 3389–3400.

Lim CW, Luan S, Lee SC, 2014. A prominent role for RCAR3-mediated ABA signaling in response to *Pseudomonas syringae* pv. *tomato* DC3000 infection in *Arabidopsis*. *Plant and Cell Physiology*, 55(10): 1691–1703.

Liu J, Du H, Ding X, Zhou Y, Xie P, Wu J, 2017. Mechanisms of callose deposition in rice regulated by exogenous abscisic acid and its involvement in rice resistance to *Nilaparvata lugens* Stål (Hemiptera: Delphacidae). *Pest Management Science*, 73(12): 2559–2568.

Liu XY, Cai XY, Wu HJ, Wan Y, Wei SF, Xu HJ, 2024. Salivary proteins NlSP5 and NlSP7 are required for optimal feeding and fitness of the brown planthopper *Nilaparvata lugens*. *Pest Management Science*, 80(9): 4297–4305.

Louis J, Shah J, 2013. *Arabidopsis thaliana-Myzus persicae* interaction: Shaping the understanding of plant defense against phloem-feeding aphids. *Frontiers in Plant Science*, 4: 213.

Lu K, Zhang L, Qin L, Chen X, Wang X, Zhang M, Dong H, 2023. Importin β1 mediates nuclear entry of EIN2C to confer the phloem-based defense against aphids. *International Journal of Molecular Sciences*, 24(10): 8545.

Lü B, Sun W, Zhang S, Zhang C, Qian J, Wang X, Gao R, Dong H, 2011. HrpN induced deterrent effect on phloem feeding of the green peach aphid *Myzus persicae* requires AtGSL5 and AtMYB44 genes in *Arabidopsis thaliana*. *Journal of Bioscience*, 36(1): 123–137.

Lü ZH, Ma HB, Zhang WQ, 2025. Insect RNAi: Two decades of retrospect and prospect. *Chinese Journal of Applied Entomology*, 62(5): 1299–1313. [吕子豪, 马海宾, 张文庆, 2025. 昆虫RNAi：二十年回顾与展望. 应用昆虫学报, 62(5): 1299–1313.]

Mbiza NIT, Hu Z, Zhang H, Zhang Y, Luo X, Wang Y, Wang Y, Liu T, Li J, Wang X, Zhang J, Yu Y, 2022. GhCalS5 is involved in cotton response to aphid attack through mediating callose formation. *Frontiers in Plant Science*, 13: 892630.

Medina-Ortega KJ, Walker GP, 2015. Faba bean forisomes can function in defence against generalist aphids. *Plant, Cell & Environment*, 38(6): 1167–1177.

Musetti R, Buxa SV, De Marco F, Loschi A, Polizzotto R, Kogel KH, van Bel AJ, 2013. Phytoplasma-triggered Ca^{2+} influx is involved in sieve-tube blockage. *Molecular Plant-Microbe Interactions*, 26(4): 379–386.

Naessens E, Dubreuil G, Giordanengo P, Baron OL, Minet-Kebdani N, Keller H, Coustau C, 2015. A secreted MIF cytokine enables

aphid feeding and represses plant immune responses. *Current Biology*, 25(14): 1898–1903.

Oide S, Bejai S, Staal J, Guan N, Kaliff M, Dixelius C, 2013. A novel role of PR2 in abscisic acid (ABA) mediated, pathogen-induced callose deposition in *Arabidopsis thaliana*. *New Phytologist*, 200(4): 1187–1199.

Pan W, Li J, Du Y, Zhao Y, Xin Y, Wang S, Liu C, Lin Z, Fang S, Yang Y, Zaccai M, Zhang X, Yi M, Gazzarrini S, Wu J, 2023. Epigenetic silencing of callose synthase by VIL1 promotes bud-growth transition in lily bulbs. *Nature Plants*, 9(9): 1451–1467.

Pang S, Zhai J, Song J, Rong D, Hong Y, Qiu Y, Ma J, Qi T, Huang H, Song S, 2024. bHLH19 and bHLH20 repress jasmonate-mediated plant defense against insect herbivores in *Arabidopsis*. *Plant Journal*, 120(6): 2623–2638.

Paulmann MK, Wegner L, Gershenzon J, Furch ACU, Kunert G, 2023. Pea aphid *Acyrthosiphon pisum* host races reduce heat-induced forisome dispersion in *Vicia faba* and *Trifolium pratense*. *Plants*, 12(9): 1888.

Peng HC, Walker GP, 2020. Sieve element occlusion provides resistance against *Aphis gossypii* in TGR-1551 melons. *Insect Science*, 27(1): 33–48.

Peng Z, Su Q, Ren J, Tian L, Zeng Y, Yang Y, Wang S, Xie W, Wu Q, Li Z, Zhang Y, 2023. A novel salivary effector, BtE3, is essential for whitefly performance on host plants. *Journal of Experimental Botany*, 74(6): 2146–2159.

Poosapati S, Poretsky E, Dressano K, Ruiz M, Vazquez A, Sandoval E, Estrada-Cardenas A, Duggal S, Lim JH, Morris G, Szczepaniec A, Walse SS, Ni X, Schmelz EA, Huffaker A, 2022. A sorghum genome-wide association study (GWAS) identifies a WRKY transcription factor as a candidate gene underlying sugarcane aphid *Melanaphis sacchari* resistance. *Plant*, 255(2): 37.

Qian L, Liu X, Huang Z, Wang L, Zhang Y, Gao Y, Gui F, Chen F, 2019. Elevated CO_2 enhances the host resistance against the western flower thrips *Frankliniella occidentalis*, through increased callose deposition. *Journal of Pest Science*, 93(1): 1–14.

Rao W, Zheng X, Liu B, Guo Q, Guo J, Wu Y, Shangguan X, Wang H, Wu D, Wang Z, Hu L, Xu C, Jiang W, Huang J, Shi S, He G, 2019. Secretome analysis and in planta expression of salivary proteins identify candidate effectors from the brown planthopper *Nilaparvata lugens*. *Molecular Plant-Microbe Interactions*, 32(2): 227–239.

Saberi RR, Fathi F, Gholizadeh Vazvani M, Vatankhah M, Kennedy JF, 2025. Defense-related callose deposition in plants against pathogens: A review. *International Journal of Biological Macromolecules*, 320(Pt 4): 146005.

Sanmartín N, Pastor V, Pastor-Fernández J, Flors V, Pozo MJ, Sánchez-Bel P, 2020. Role and mechanisms of callose priming in mycorrhiza-induced resistance. *Journal of Experimental Botany*, 71(9): 2769–2781.

Scalschi L, Sanmartín M, Camañes G, Troncho P, Sánchez-Serrano JJ, García-Agustín P, Vicedo B, 2015. Silencing of OPR3 in tomato reveals the role of OPDA in callose deposition during the activation of defense responses against *Botrytis cinerea*. *Plant Journal*, 81(2): 304–315.

Schneider R, Hanak T, Persson S, Voigt CA, 2016. Cellulose and callose synthesis and organization in focus, What's new? *Current Opinion in Plant Biology*, 34: 9–16.

Shangguan C, Kuang Y, Zhong L, Gao L, Yu X, 2025. Screening and functional analysis of a novel salivary effector DcE13 from the Asian citrus psyllid *Diaphorina citri*. *Journal of Agricultural and Food Chemistry*, 73(15): 8897–8906.

Shangguan X, Zhang J, Liu B, Zhao Y, Wang H, Wang Z, Guo J, Rao W, Jing S, Guan W, Ma Y, Wu Y, Hu L, Chen R, Du B, Zhu L, Yu D, He G, 2018. A mucin-like protein of planthopper is required for feeding and induces immunity response in plants. *Plant Physiology*, 176(1): 552–565.

Shoala T, Edwards MG, Knight MR, Gatehouse AMR, 2018. OXI1 kinase plays a key role in resistance of *Arabidopsis* towards aphids (*Myzus persicae*). *Transgenic Research*, 27(4): 355–366.

Shi QY, Guo HJ, Sun YC, 2026. Feeding behavioral characteristics and molecular regulatory mechanisms of aphids transmitting non-persistent plant viruses. *Acta Entomologica Sinica*, 69(4): 581–592. [史清云, 郭慧娟, 孙玉诚, 2026. 蚜虫传播非持久性植物病毒的取食行为特征与分子调控机制. 昆虫学报, 69(4): 581–592.]

Singh RK, Miskolczi P, Maurya JP, Bhalerao RP, 2019. A tree ortholog of short vegetative phase floral repressor mediates photoperiodic control of bud dormancy. *Current Biology*, 29(1): 128–133.

Song HD, Zhang FB, Ji SX, Wang XQ, Wang JX, Liu YX, Wang XW, Han WH, 2024. The SA-WRKY70-PR-callose axis mediates plant defense against whitefly eggs. *International Journal of Molecular Sciences*, 25(22): 12076.

Sun M, Voorrips RE, Steenhuis-Broers G, Van't Westende W, Vosman B, 2018. Reduced phloem uptake of *Myzus persicae* on an aphid resistant pepper accession. *BMC Plant Biology*, 18(1): 138.

Tan XL, Zhang Y, Fan J, Cheng JL, 2025. Major progress and prospect of wheat aphid research in China. *Chinese Journal of*

Applied Entomology, 62(5): 1189–1209. [谭晓玲, 张勇, 范佳, 陈巨莲, 2025. 我国小麦蚜虫研究的主要进展与展望. 应用昆虫学报, 62(5): 1189–1209.]

Tee EE, Johnston MG, Papp D, Faulkner C, 2023. A PDLP-NHL3 complex integrates plasmodesmal immune signaling cascades. *Proceedings of the National Academy of Sciences of the United States of America*, 120(17): e2216397120.

Tian S, Yang Y, Li D, Yue W, Liu L, Zhi J, 2025. The role of salivary effector FoCA2 in modulating the interactions of the defense response of the kidney bean plant and the adaptability of *Frankliniella occidentalis* under dinotefuran exposure. *Pesticide Biochemistry and Physiology*, 209: 106336.

Tian T, Ji R, Fu J, Li J, Wang L, Zhang H, Yang S, Ye W, Fang J, Zhu-Salzman K, 2021. A salivary calcium-binding protein from *Laodelphax striatellus* acts as an effector that suppresses defense in rice. *Pest Management Science*, 77(5): 2272–2281.

van Bel AJ, Will T, 2016. Functional evaluation of proteins in watery and gel saliva of aphids. *Frontiers in Plant Science*, 7: 1840.

Varsani S, Grover S, Zhou S, Koch KG, Huang PC, Kolomiets MV, Williams WP, Heng-Moss T, Sarath G, Luthe DS, Jander G, Louis J, 2019. 12-oxo-phytodienoic acid acts as a regulator of maize defense against corn leaf aphid. *Plant Physiology*, 179(4): 1402–1415.

Vincent TR, Avramova M, Canham J, Higgins P, Bilkey N, Mugford ST, Pitino M, Toyota M, Gilroy S, Miller AJ, Hogenhout SA, Sanders D, 2017. Interplay of plasma membrane and vacuolar ion channels, together with BAK1, elicits rapid cytosolic calcium elevations in *Arabidopsis* during aphid feeding. *Plant Cell*, 29(6): 1460–1479.

Walker GP, 2022. Sieve element occlusion: Interactions with phloem sap-feeding insects. A review. *Journal of Plant Physiology*, 269: 153582.

Wang G, Hu B, Yao X, Wei Z, Chen J, Sun Z, 2025. A stinkbug salivary protein is indispensable for insect feeding and activates plant immunity. *Plant*, *Cell & Environment*, 48(3): 2329–2342.

Wang X, Zhang M, Feng F, He R, 2015. Differentially regulated genes in the salivary glands of brown planthopper after feeding in resistant versus susceptible rice varieties. *Archives of Insect Biochemistry and Physiology*, 89(2): 69–86.

Wang Y, Li X, Fan B, Zhu C, Chen Z, 2021a. Regulation and function of defense-related callose deposition in plants. *International Journal of Molecular Sciences*, 22(5): 2393.

Wang Z, Lü Q, Zhang L, Zhang M, Chen L, Zou S, Zhang C, Dong H, 2021b. Aphid salivary protein Mp1 facilitates infestation by binding phloem protein 2-A1 in *Arabidopsis*. *Biochemical and Biophysical Research Communications*, 572: 105–111.

Will T, Furch AC, Zimmermann MR, 2013. How phloem-feeding insects face the challenge of phloem-located defenses. *Frontiers in Plant Science*, 4: 336.

Will T, Kornemann SR, Furch AC, Tjallingii WF, van Bel AJ, 2009. Aphid watery saliva counteracts sieve-tube occlusion: A universal phenomenon? *Journal of Experimental Botany*, 60(20): 3305–3312.

Will T, Tjallingii WF, Thönnessen A, van Bel AJ, 2007. Molecular sabotage of plant defense by aphid saliva. *Proceedings of the National Academy of Sciences of the United States of America*, 104(25): 10536–10541.

Will T, van Bel AJ, 2006. Physical and chemical interactions between aphids and plants. *Journal of Experimental Botany*, 57(4): 729–737.

Will T, Vilcinskas A, 2015. The structural sheath protein of aphids is required for phloem feeding. *Insect Biochemistry and Molecular Biology*, 57: 34–40.

Wu SW, Kumar R, Iswanto ABB, Kim JY, 2018. Callose balancing at plasmodesmata. *Journal of Experimental Botany*, 69(22): 5325–5339.

Wu W, Yi G, Lv X, Mao Q, Wei T, 2022. A leafhopper saliva protein mediates horizontal transmission of viral pathogens from insect vectors into rice phloem. *Communications Biology*, 5(1): 204.

Xia Z, Wen B, Shao J, Zhang T, Hu M, Lin L, Zheng Y, Shi Z, Dong X, Song J, Li Y, Wu Y, Yuan Y, Wu J, Chen Q, Chen J, 2023. The transcription factor PbrbZIP52 positively affects pear pollen tube longevity by promoting callose synthesis. *Plant Physiology*, 191(3): 1734–1750.

Xu HX, Qian LX, Wang XW, Shao RX, Hong Y, Liu SS, Wang XW, 2019. A salivary effector enables whitefly to feed on host plants by eliciting salicylic acid-signaling pathway. *Proceedings of the National Academy of Sciences of the United States of America*, 116(2): 490–495.

Yang F, Zhang X, Xue H, Tian T, Tong H, Hu J, Zhang R, Tang J, Su Q, 2022. (Z)-3-hexenol primes callose deposition against whitefly-mediated begomovirus infection in tomato. *Plant Journal*, 112(3): 694–708.

Yang HH, Chen PF, Liu F, Zhang JL, Wei Q, He JC, Wang WX, Lai FX, Wei XJ, Fu Q, Wan PJ, 2026. OsPDCB1 mediates plasmodesmal callose defense and is targeted by a conserved planthopper effector. *Journal of Integrative Plant Biology*, 68(5): 1573–1589.

Yang J, Tian L, Sun MX, Huang XY, Zhu J, Guan YF, Jia QS, Yang ZN, 2013a. Auxin response factor17 is essential for pollen wall

pattern formation in *Arabidopsis*. *Plant Physiology*, 162(2): 720–731.

Yang L, Chen JM, Zhang HQ, Zhang JF, He YP, 2013b. Effects of brown planthopper *Nilaparvata lugens* (Stål) (Homoptera: Delphacidae) feeding on callose deposition in rice with different tolerance. *Chinese Journal of Rice Science*, 27(6): 624–632.

Yang L, Li P, Li F, Ali S, Sun X, Hou M, 2017. Silicon amendment to rice plants contributes to reduced feeding in a phloem-sucking insect through modulation of callose deposition. *Ecology and Evolution*, 8(1): 631–637.

Yao L, Guo X, Su J, Zhang Q, Lian M, Xue H, Li Q, He Y, Zou X, Song Z, Chen S, 2023. ABA-CsABI5-CsCalS11 module upregulates callose deposition of citrus infected with *Candidatus Liberibacter asiaticus*. *Horticulture Research*, 11(2): uhad276.

Yao L, Zhong Y, Wang B, Yan J, Wu T, 2020. BABA application improves soybean resistance to aphid through activation of phenylpropanoid metabolism and callose deposition. *Pest Management Science*, 76(1): 384–394.

Yi SY, Shirasu K, Moon JS, Lee SG, Kwon SY, 2014. The activated SA and JA signaling pathways have an influence on flg22-triggered oxidative burst and callose deposition. *PLoS ONE*, 9(2): e88951.

Yuan M, Jin T, Wu J, Li L, Chen G, Chen J, Wang Y, Sun J, 2023. IAA-miR164a-NAC100L1 module mediates symbiotic incompatibility of cucumber/pumpkin grafted seedlings through regulating callose deposition. *Horticulture Research*, 11(2): uhad287.

Zhai Y, Li P, Mei Y, Chen M, Chen X, Xu H, Zhou X, Dong H, Zhang C, Jiang W, 2017. Three MYB genes co-regulate the phloem-based defence against english grain aphid in wheat. *Journal of Experimental Botany*, 68(15): 4153–4169.

Zhang C, Shi H, Chen L, Wang X, Lü B, Zhang S, Liang Y, Liu R, Qian J, Sun W, You Z, Dong H, 2011. Harpin-induced expression and transgenic overexpression of the phloem protein gene AtPP2-A1 in *Arabidopsis* repress phloem feeding of the green peach aphid *Myzus persicae*. *BMC Plant Biology*, 11(1): 11.

Zhang CL, Fu MQ, Xu H, Dong HS, 2012. Transcriptional regulation of *Arabidopsis* phloem defense and wheat aphid resistance mechanisms. *Journal of Nanjing Agricultural University*, 35(5): 113–124. [张春玲, 付茂强, 徐衡, 董汉松, 2012. 拟南芥韧皮部防卫反应转录调控与小麦抗蚜虫机制. 南京农业大学学报, 35(5): 113–124.]

Zhang HX, Chen Q, Wei TY, 2025. Research progress on vector insects regulating plant defenses via salivary proteins to facilitate their feeding and virus transmission. *Chinese Bulletin of Life Sciences*, 37(5): 514–521. [张洪祥, 陈倩, 魏太云, 2025. 介体昆虫利用唾液蛋白调控植物防御促进自身取食和病毒传播的研究进展. 生命科学, 37(5): 514–521.]

Zhang Y, Fu Y, Liu X, Francis F, Fan J, Liu H, Wang Q, Sun Y, Zhang Y, Chen J, 2023. SmCSP4 from aphid saliva stimulates salicylic acid-mediated defence responses in wheat by interacting with transcription factor TaWKRY76. *Plant Biotechnology Journal*, 21(11): 2389–2407.

Zhang Y, Liu X, Francis F, Xie H, Fan J, Wang Q, Liu H, Sun Y, Chen J, 2022a. The salivary effector protein Sg2204 in the greenbug *Schizaphis graminum* suppresses wheat defence and is essential for enabling aphid feeding on host plants. *Plant Biotechnology Journal*, 20(11): 2187–2201.

Zhang Y, Liu X, Fu Y, Crespo-Herrera L, Liu H, Wang Q, Zhang Y, Chen J, 2022b. Salivary effector Sm9723 of grain aphid *Sitobion miscanthi* suppresses plant defense and is essential for aphid survival on wheat. *International Journal of Molecular Sciences*, 23(13): 6909.

Zhang Y, Liu X, Sun Y, Liu Y, Zhang Y, Ding T, Chen J, 2024. Salivary protein cyclin-dependent kinase-like from grain aphid *Sitobion avenae* suppresses wheat defense response and enhances aphid adaptation. *International Journal of Molecular Sciences*, 25(9): 4579.

Zheng XB, Wan YR, Zhang YJ, Wu QJ, 2025. Research progress on the interaction mechanism of tomato spotted wilt virus-thrips-host plant. *Chinese Journal of Applied Entomology*, 62(5): 1617–1628. [郑晓斌, 万岩然, 张友军, 吴青君, 2025. 番茄斑萎病毒-蓟马-寄主植物互作机制的研究进展. 应用昆虫学报, 62(5): 1617–1628.]

Zhong J, 2020. Perforin-like proteins of aphids: Impacts on phloem ingestion and plant phloem defense. Master dissertation. Nanjing: Nanjing Agricultural University. [钟静, 2020. 蚜虫的类穿孔蛋白对刺吸韧皮部与植物韧皮部防卫反应的影响. 硕士学位论文. 南京: 南京农业大学.]

Zhu L, Guo J, Ma Z, Wang J, Zhou C, 2018. *Arabidopsis* transcription factor MYB102 increases plant susceptibility to aphids by substantial activation of ethylene biosynthesis. *Biomolecules*, 8(2): 39.