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Review article

Proteomics in Downy Mildew and Related Oomycete Pathogens: Current Knowledge and the Unexplored Proteome of *Plasmopara halstedii*

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Abstract

Downy mildew pathogens are obligate biotrophic oomycetes responsible for destructive diseases in many agricultural crops. Among them, *Plasmopara halstedii*, the causal agent of sunflower downy mildew, represents a major threat to sunflower production worldwide. While extensive research has focused on the genetics of host resistance and the pathogenic variability of this organism, information regarding the proteins involved in its infection process remains limited. Proteomic approaches have increasingly been used to study plant–pathogen interactions, as they enable the direct identification of proteins produced during infection. In oomycete pathogens such as *Phytophthora* species, proteomic studies have revealed numerous proteins associated with host colonization, virulence, and stress adaptation. However, comparable large-scale proteomic investigations are still scarce for downy mildew pathogens, particularly for *P. halstedii*. This review summarizes current knowledge on proteomic studies in oomycete plant pathogens and discusses the limited information available on proteins of *P. halstedii*. The review also highlights key research gaps and potential directions for future proteomic investigations.

Keywords: Downy Mildew, Oomycete Pathogens, *Plasmopara halstedii*, Proteomics, Sunflower

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INTRODUCTION

Oomycetes constitute a diverse group of filamentous eukaryotic microorganisms belonging to the Stramenopiles and include numerous plant pathogens of major agricultural importance. Although they share morphological similarities with fungi, their evolutionary origin and cellular organization are fundamentally different. For instance, oomycete cell walls are primarily composed of cellulose rather than chitin, and phylogenetic analyses place them closer to certain algal lineages than to true fungi (Thines, 2014).

Within this group, downy mildew pathogens represent an important lineage of obligate biotrophic organisms capable of infecting a wide range of plant species. These pathogens frequently cause severe yield losses in agriculture. One notable example is *Plasmopara halstedii (P. halstedii),* the causal agent of sunflower downy mildew (Sackston & Vimard, 1988; Tourvieille de Labrouhe et al., 2008; Viranyi et al., 2015).

Sunflower (*Helianthus annuus L.)* ranks among the most widely cultivated oilseed crops worldwide (Kaya et al., 2012). Consequently, diseases affecting sunflower production can have considerable economic impact. Among these diseases, downy mildew caused by Plasmopara halstedii remains one of the most economically important constraints to sunflower production in many regions of the world (Gascuel et al., 2016; Molinero-Ruiz, 2022; Kaya et al., 2012). Infection by *P. halstedii* typically results in symptoms such as plant dwarfism, chlorosis, and reduced seed formation, which can significantly decrease yield under favorable environmental conditions (Gascuel et al., 2016; Molinero-Ruiz, 2022). The pathogen infects plants mainly through the roots during early developmental stages and subsequently colonizes aerial tissues, where sporulation occurs and new infections can develop.

Over the past decade, advances in genomic research have substantially improved our understanding of the molecular biology of downy mildew pathogens. Genome sequencing of *P. halstedii* revealed numerous genes associated with pathogenicity, including members of the RXLR and CRN effector families commonly found in oomycete pathogens (Sharma et al., 2015). These effectors are thought to play important roles in host colonization and in the modulation of plant immune responses. More recent phylogenomic studies have further shown that genomic rearrangements and recombination events contribute to the rapid evolution of virulence in this pathogen (Pecrix et al., 2026).

Despite the progress achieved through genomic and transcriptomic analyses, knowledge of the proteins involved in *P. halstedii* infection remains limited. Proteins ultimately carry out the biological functions encoded by genes and directly mediate processes such as host invasion, nutrient acquisition, and suppression of plant defense responses. For this reason, proteomic approaches provide an important complementary perspective for understanding plant–pathogen interactions.

Downy mildew diseases are major problems in crops such as sunflower, grapevine, pearl millet, maize, sorghum, and pea. Although these pathogens have been studied for many years, proteomic studies

are still very limited. Most studies have focused mainly on pathogenic variability, resistance breeding, genomics, and transcriptomics, while proteins involved in infection have received much less attention. Proteomics has already contributed valuable insights into several plant pathogens. For example, studies on *Phytophthora infestans* revealed complex extracellular proteomes containing enzymes, effectors, and other proteins associated with host colonization and pathogenicity (Meijer et al., 2014). In contrast, large-scale proteomic analyses are still scarce for downy mildew pathogens.

For *P. halstedii* in particular, comprehensive proteomic data remain largely unavailable. Only a few studies have attempted to identify pathogen-derived proteins directly. One example is the identification of an elicitor protein using mass spectrometry combined with molecular approaches (Jung et al., 2010). While such findings provide an important starting point, the overall proteome of *P. halstedii* remains poorly characterized.

Given the agricultural importance of sunflower downy mildew and the remarkable adaptability of the pathogen, a deeper understanding of its molecular biology is clearly needed. Combining genomic, transcriptomic, and proteomic approaches may therefore help clarify the mechanisms underlying pathogen virulence and host adaptation. This review therefore summarizes current knowledge on proteomic studies in oomycete plant pathogens and highlights the largely unexplored proteome of *P. halstedii*, with particular emphasis on potential directions for future research.

Literature Search Strategy

Relevant literature on downy mildew pathogens and proteomic studies related to *Plasmopara halstedii* was retrieved from the Web of Science Core Collection and Scopus databases.

Searches were conducted using combinations of keywords including *Plasmopara halstedii,* downy mildew, sunflower, *Helianthus annuus,* proteomics, secretome, effector proteins, transcriptomics, genomics, virulence, and host–pathogen interaction. The search was performed in titles, abstracts, and keywords.

All retrieved records were exported and imported into EndNote 21 reference management software. Duplicate entries were removed automatically and subsequently verified manually. After duplicate removal, records classified as non-English publications, errata, or non-research article types were excluded.

The remaining publications were screened based on their titles and abstracts in order to determine their relevance to downy mildew pathogens and related molecular studies. The literature selection followed the general principles of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework. After screening and eligibility assessment, 129 publications were retained and used as the primary literature set for this review. The overall selection process is summarized in the PRISMA flow diagram presented in Fig. 1.

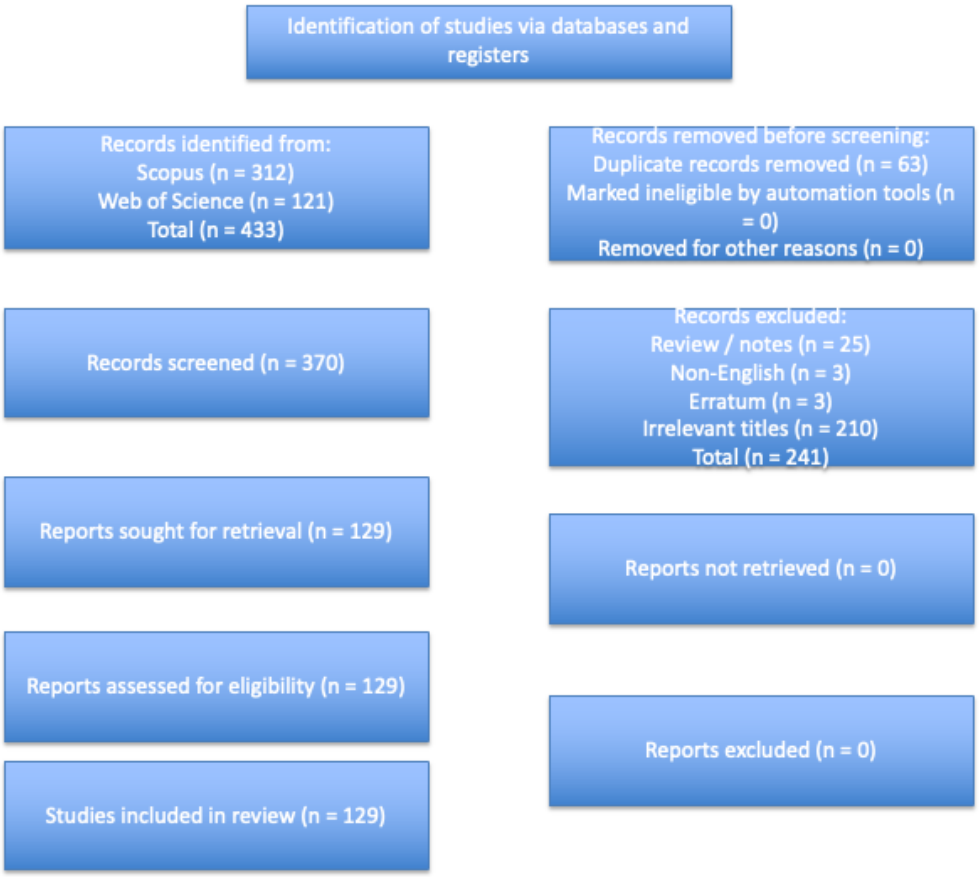

Fig. 1. PRISMA flow diagram illustrating the identification, screening, eligibility assessment, and final inclusion of publications used in this review.

Genomic and molecular insights into *Plasmopara halstedii*

In recent years, molecular studies have considerably improved our understanding of the biology and pathogenicity of *Plasmopara halstedii*. Genome sequencing has played a key role in this progress by providing the first comprehensive overview of the genetic repertoire of the sunflower downy mildew pathogen. Analysis of the draft genome revealed numerous candidate effector genes, including members of the RXLR and CRN families that are widely associated with virulence in oomycete pathogens (Gascuel et al., 2016; Sharma et al., 2015). Comparative analyses further indicated that many of these effector genes show signs of rapid evolution, reflecting the ongoing molecular arms race between the pathogen and its host.

Functional studies have also begun to explore the role of specific pathogenicity factors involved in host–pathogen interactions. Several effector candidates identified in *P. halstedii* have been shown to induce hypersensitive-like responses in resistant sunflower lines, suggesting that these proteins may contribute to host recognition and the activation of plant defense mechanisms (Gascuel et al., 2016).

These findings highlight the importance of effector-mediated processes in determining compatibility between *P. halstedii* and sunflower and provide initial insights into how the pathogen may manipulate host cellular functions during infection.

In parallel with pathogen-focused research, numerous studies have investigated the genetic basis of sunflower resistance to downy mildew. A large number of resistance genes have been identified and incorporated into breeding programs aimed at controlling the disease. Nevertheless, populations of *P. halstedii* display considerable pathogenic variability, and new virulent races frequently emerge that are capable of overcoming previously effective resistance genes (Molinero-Ruiz, 2022; Viranyi et al., 2015). This situation illustrates the continuous evolutionary interplay between pathogen adaptation and host resistance deployment.

Despite these advances in genomics and host–pathogen genetics, considerably less information is available regarding the proteins that are produced during infection. Genomic and transcriptomic studies provide important clues about potential virulence factors, but they do not fully reveal which proteins are actually present during the infection process or how they function within the host environment. Because proteins represent the functional molecules that drive biological processes such as host invasion, signaling, and suppression of plant defense responses, proteomic approaches offer an important complementary perspective. Integrating proteomic data with existing genomic knowledge may therefore help to clarify the molecular mechanisms underlying the interaction between *P. halstedii* and sunflower.

Proteomics in oomycete plant pathogens

Proteomic approaches have become an important tool for investigating plant–pathogen interactions. While genomic and transcriptomic analyses reveal the presence and potential expression of genes, proteomics enables the direct identification of proteins that are produced during infection. Because proteins ultimately mediate biological processes such as host colonization, nutrient acquisition, and the modulation of plant defense responses, proteomic analyses provide valuable insights into the molecular mechanisms underlying pathogenicity.

Recent advances in mass spectrometry have greatly improved the sensitivity and accuracy of protein identification, making it possible to analyze complex protein mixtures at a large scale. In addition, the development of subcellular proteomics has expanded the ability to study protein localization and dynamics within specific cellular compartments during plant–pathogen interactions.

Among oomycete pathogens, most proteomic studies have focused on species of the genus *Phytophthora*. One of the early large-scale investigations characterized the extracellular proteome of the potato late blight pathogen *Phytophthora infestans*. This study identified numerous secreted proteins, including glycoside hydrolases, proteases, and other cell-wall-degrading enzymes that are likely involved in host tissue colonization and nutrient acquisition (Meijer et al., 2014). Several proteins

associated with carbohydrate metabolism and cell wall modification were also detected, emphasizing the importance of enzymatic degradation of host cell walls during infection.

Subsequent proteomic studies expanded these findings by examining proteins expressed during different developmental stages of the pathogen. These analyses revealed proteins involved in energy metabolism, stress responses, and signaling pathways that may contribute to pathogen growth and infection processes (Resjö et al., 2017).

More recently proteomic analyses have provided additional insights into intracellular mechanisms associated with pathogenicity. For example, characterization of intracellular vesicles in *P. infestans* revealed several vesicle-associated proteins that may participate in secretion and intracellular transport (Pham et al., 2026). Vesicle-mediated secretion is particularly important because it is thought to play a central role in the delivery of effector proteins and other virulence factors during infection.

Proteomic approaches have also been applied to other oomycete species. In Phytophthora parasitica, shotgun proteomic analyses identified proteins associated with primary metabolism, oxidative stress responses, and protein folding, suggesting that metabolic adaptation and stress tolerance contribute to successful host colonization (Hannat et al., 2023). Similarly, proteomic studies in the Phytophthora capsici pathosystem revealed host proteins associated with defense signaling, reactive oxygen species metabolism, and stress-related pathways during infection (Mahadevan et al., 2016).

Compared with *Phytophthora,* proteomic studies of downy mildew pathogens remain relatively limited. A few additional studies related to downy mildew pathosystems have also been reported in crops such as pearl millet and sorghum, although proteome-level data in these systems are still limited (Anup et al., 2015; Jadhav et al., 2018). Nevertheless, several investigations have examined proteomic changes during interactions between grapevine and *Plasmopara viticola.* These studies revealed substantial changes in host proteins during the early stages of infection, including proteins involved in defense responses, redox regulation, and stress signaling (B. Santos et al., 2020). Comparative analyses of compatible and incompatible interactions further showed differential accumulation of proteins associated with plant immunity, such as pathogenesis-related proteins, antioxidant enzymes, and proteins involved in hormone-mediated defense signaling (Liu et al., 2021).

Because only a limited number of proteomic studies are available for downy mildew pathogens, Table 1 also includes studies performed in other oomycete pathogens such as Phytophthora spp. in order to provide a broader perspective on oomycete proteomics.

Table 1. Representative proteomic studies in oomycete pathogens, including available studies on downy mildew pathosystems.

Pathogen	Host	Proteomic approach	Main findings	Reference
Phytophthora infestans	Potato	**Shotgun LC-MS/MS (gel-free proteomics)**	Characterization of extracellular proteins associated with virulence and host colonization	(Meijer et al., 2014)
Phytophthora infestans	Potato	**Label-free quantitative LC-MS/MS**	Identification of proteins associated with developmental stages and infection processes	(Resjö et al., 2017)
Phytophthora infestans	Potato	**Shotgun LC-MS/MS proteomics**	Characterization of intracellular vesicle proteome involved in secretion pathways	(Pham et al., 2026)
Phytophthora parasitica	Various hosts	**Gel-free LC-MS/MS proteomics**	Identification of metabolic and pathogenicity-related proteins	(Hannat et al., 2023)
Phytophthora capsici	Pepper	**iTRAQ quantitative proteomics**	Host proteins associated with stress and defense responses during infection	(Mahadevan et al., 2016)
Plasmopara viticola	Grapevine	**Shotgun LC-MS/MS proteomics**	Early modulation of host defense proteins during infection	(B. Santos et al., 2020)
Plasmopara viticola	Grapevine	**iTRAQ quantitative proteomics**	Differential protein accumulation in compatible vs incompatible interactions	(Liu et al., 2021)
Plasmopara halstedii	Sunflower	**Gel-free LC-MS/MS protein identification**	Identification of an elicitor protein involved in plant–pathogen interaction	(Jung et al., 2010)

Compared with other oomycete pathogens such as Phytophthora, proteomic studies in downy mildew pathosystems are still quite limited. Most of the available studies have focused on the grapevine–Plasmopara viticola interaction, while proteomic data for other downy mildew diseases, including sunflower, pearl millet, sorghum, maize, and pea, remain scarce. A few additional studies related to these pathosystems have been reported (Anup et al., 2015; Jadhav et al., 2018), but proteome-level information is still very limited for obligate downy mildew pathogens.

Current knowledge on proteins of *Plasmopara halstedii*

Despite the agricultural importance of sunflower downy mildew, information on proteins produced by *Plasmopara halstedii* remains limited. One major obstacle is the obligate biotrophic lifestyle of the pathogen, which makes experimental studies challenging. Because *P. halstedii* cannot be maintained in axenic culture, most early research focused primarily on disease development, pathogenic variability, and sunflower resistance rather than on the direct characterization of pathogen proteins (Sackston & Vimard, 1988; Viranyi & Spring, 2011).

The development of genomic and molecular approaches has gradually improved our understanding of the pathogen. Genome-based analyses revealed numerous genes predicted to encode secreted proteins that may function as effectors during infection. Large repertoires of candidate secreted proteins have been identified, many of which are likely involved in virulence and host colonization (Sharma et al., 2015; Zhang et al., 2020). Several of these proteins show similarities to effector families

described in other oomycete pathogens, suggesting that related infection strategies may operate across different downy mildew species.

Comparative studies have further highlighted the diversity of predicted effector proteins in *P. halstedii.* Analyses of effector families such as RxLR and CRN revealed substantial sequence variation that may contribute to pathogen adaptation and race differentiation (Gascuel et al., 2016). In addition, comparative analyses of oomycete secretomes have identified conserved structural features among proteins associated with host colonization and pathogenicity (Kamoun, 2006). Broader studies of oomycete pathogens have also emphasized several groups of proteins commonly linked to virulence, including secreted enzymes, effector proteins, and proteins involved in the suppression of plant immune responses (Guo et al., 2024; Rivera et al., 2016).

Transcriptomic studies have provided additional insights into genes potentially involved in infection. Early transcriptomic analyses of the sunflower–*P. halstedii* interaction showed that several genes encoding secreted proteins are expressed during host colonization (As-Sadi et al., 2011). More recent high-throughput expression analyses confirmed that groups of genes associated with infection processes and pathogen development are actively expressed during interaction with sunflower (Bharti & Thines, 2023). These findings highlight a number of candidate proteins that may contribute to pathogenicity, although their precise biological functions remain largely unknown.

Overall, most of the available knowledge about proteins in *P. halstedii* is derived from genomic and transcriptomic studies, while direct proteomic characterization remains scarce. Identifying pathogen-derived proteins during infection and understanding their roles in host–pathogen interactions therefore remain important research challenges. Proteome-wide analyses of infected plant tissues may provide new insights into pathogen virulence mechanisms and host defense responses in the sunflower–*P. halstedii* pathosystem (Fig. 2).

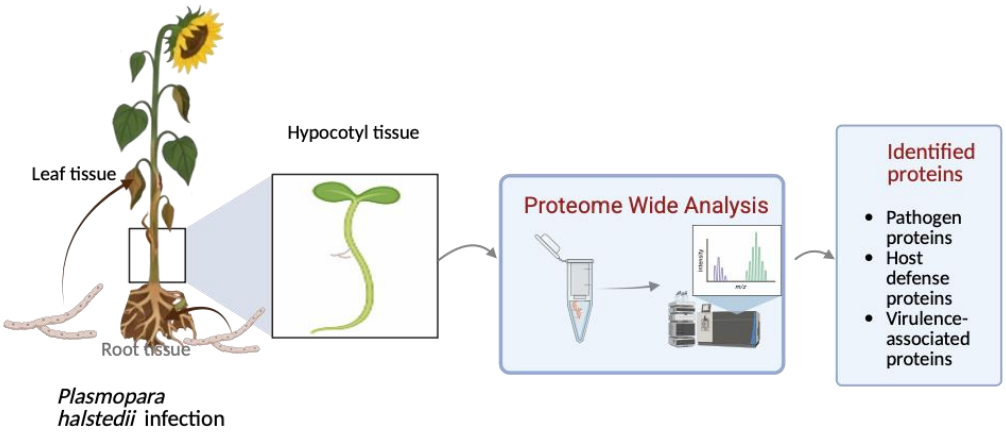

Fig. 2. Conceptual overview of the sunflower–Plasmopara halstedii interaction and potential sampling sites (root, hypocotyl, and leaf tissues) for proteomic analysis. Created with BioRender.com. Gunel, A. (2026) https://BioRender.com/0zxkb2z

Research gaps and future directions

Despite the increasing availability of genomic information for *Plasmopara halstedii, the* pathogen remains largely unexplored at the proteome level. One of the few studies that directly addressed proteins produced by the pathogen is the work of Jung et al. (2010), which reported the identification of an elicitor protein using peptide sequencing combined with molecular approaches. Although this study demonstrated that pathogen-derived proteins can be detected in infected sunflower tissues, it focused on the characterization of a single protein and did not attempt to explore the broader proteome of the pathogen. Consequently, many fundamental questions remain unanswered, including which pathogen proteins are actually produced during infection and how they contribute to virulence and host colonization.

Another notable aspect is that proteomic studies have been reported for some downy mildew pathosystems, such as the grapevine–*Plasmopara viticola* interaction, where several investigations have analyzed host proteome responses during infection. In contrast, similar proteomic studies are almost absent for *Plasmopara halstedii.* Several factors may contribute to this difference. First, much of the research on sunflower downy mildew has historically focused on pathogenic variability and resistance breeding because of its agricultural importance in sunflower production. As a result, molecular studies have largely emphasized pathogen races, resistance genes, and genomic analyses rather than protein-level investigations. Second, the early systemic infection of *P. halstedii* in sunflower seedlings, particularly in root and hypocotyl tissues, may complicate the isolation of pathogen proteins from infected plant material.

Importantly, the obligate biotrophic lifestyle of the pathogen alone does not fully explain the lack of proteomic studies. Proteomic analyses have been successfully applied in other obligate biotrophic plant pathogens, including rust fungi (Demirci et al., 2016) and powdery mildew fungi (Li et al., 2018), where infected host tissues have been used as a source for identifying pathogen-derived proteins. These studies demonstrate that proteomic investigations of obligate pathogens are technically feasible when appropriate experimental strategies are applied.

Future research should therefore focus on applying modern high-resolution proteomic approaches to infected sunflower tissues. Comparative proteomic analyses of infected and non-infected tissues, particularly from roots, hypocotyls, and leaves where the pathogen actively develops, may enable the identification of both pathogen-derived proteins and host defense responses associated with infection (Fig. 2). In addition, integrating proteomic analyses with genomic and transcriptomic data will be essential for validating predicted effector proteins and determining which candidate virulence factors are actually produced during infection.

Overall, expanding proteomic investigations of *P. halstedii* represents an important opportunity to bridge the current gap between genomic predictions and functional protein-level evidence, ultimately improving our understanding of the molecular mechanisms underlying sunflower downy mildew.

Conclusion

Although considerable progress has been made in genomic and transcriptomic studies of P. halstedii, knowledge of the pathogen at the proteome level remains very limited. Existing studies have primarily focused on predicted effectors and transcriptomic evidence, while direct identification of pathogen proteins during infection is still scarce. Expanding proteomic investigations in infected sunflower tissues may therefore provide valuable insights into pathogen virulence mechanisms and host defense responses. Integrating proteomic, genomic and transcriptomic approaches will be essential for a more comprehensive understanding of the sunflower–*P. halstedii* pathosystem.

Author contribution

The author has accepted responsibility for the entire content of this manuscript and approved its submission.

Conflict of interest

The author declares that there is no conflict of interest.

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