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Research article

Carbohydrate Interfaces in Plant-Fungal Interactions: A Scoping Review

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Abstract: Carbohydrates play important roles in plant–fungal interactions, contributing to fungal adhesion, immune evasion, and host recognition**.** During fungal infection in plants, carbohydrate-based structures play a significant role in fungal adhesion, immune evasion, and host recognition. This scoping review aims to consolidate current evidence on the role of carbohydrate interfaces, including both structural polysaccharides and protein-linked carbohydrates, in plant–fungal interactions. This study followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) Extension for Scoping Reviews guidelines. A total of 451 articles were retrieved from Scopus, Web of Science, PubMed, and ScienceDirect using keywords such as "carbohydrate", "fungal", "glycan", "infection", and "plant", from which 20 articles were selected for analysis based on inclusion criteria. Chitin-related glycans were the most frequently investigated carbohydrate type (n = 10), followed by *N*-glycans (n = 4) and β-glucans (n = 4), particularly in major crop systems. In contrast, protein-linked carbohydrates, especially *N*-glycans, remain limited, while studies specifically addressing *O*-glycans are largely absent. Most research has also focused on staple crops and laboratory-based experimental systems. These gaps suggest the need for greater focus on functional and dynamic analyses of glycan modifications during infection, broader representation of crops, and the application of advanced glycomic and molecular approaches.

Keywords: Carbohydrate; fungi; glycan; plant; scoping review

1. Introduction

Carbohydrates, including structural polysaccharides and glycan moieties, play essential roles in plant–fungal interactions by mediating recognition, adhesion, and defense responses [1]. For example, they are involved in metabolic activities, cellular functions, and the synthesis of essential biomolecules such as glycoproteins and nucleic acids [2]. Carbohydrates, also known as saccharides, encompass a wide range of simple sugars to more complex sugars, such as oligosaccharides [3]. Polysaccharides are complex, high-molecular-weight carbohydrates consisting of extended chains of monosaccharide units joined together through glycosidic linkages [4]. Their complex structures enabled them to perform many biological functions, including host-pathogen interactions [2].

When fungi infect plants or plants are subjected to experimental infection, multiple biological processes occur. These processes include complex

interactions between defense-challenged plants and the pathogen, resulting in immune response activation, cellular alterations, and the production of defensive compounds that inhibit infection [5]. For instance, it induces pattern-triggered immunity (PTI), in which pathogen-associated molecular patterns (PAMPs) are detected by pattern recognition receptors (PRRs) on the plant's surface. This initiates a signaling cascade that generates antibacterial substances and physical barriers to restrict pathogen infiltration [6]. Therefore, carbohydrates are studied because of their involvement in plant immune responses. Despite growing research on plant–fungal interactions, evidence on carbohydrate-mediated mechanisms remains poorly integrated across studies. A comprehensive synthesis is required to identify the types of carbohydrates studied, the plant–fungal systems investigated, and underexplored areas in current studies. Therefore, this scoping review aims to map current research on carbohydrate interfaces in plant–fungal interactions and identify key research trends and knowledge gaps.

This scoping review aimed to systematically map and characterize the existing base evidence on carbohydrate-mediated interfaces in plant–fungal interactions. Specifically, this review aimed to identify the types of carbohydrate involved, summarize the experimental methods used to investigate these interactions, examine their functional roles in fungal pathogenicity and plant defense, and identify current knowledge gaps in the literature. To further define the scope of this review, a Population–Concept–Context (PCC) framework was applied. Population: plant species affected by fungal pathogens. Concept: carbohydrate-mediated interfaces involved in plant–fungal interactions, including structural polysaccharides such as chitin, cellulose, and β-glucans, protein-linked glycans (e.g., *N*-glycosylation), and carbohydrate-binding proteins or lectins involved in pathogen recognition. Context: experimental studies investigating plant–fungal interactions under controlled laboratory or field conditions.

Based on this framework, this scoping review addressed the following research question: What types of carbohydrates are reported in plant–fungal interactions? What experimental methods are used to study carbohydrate-mediated plant–fungal interactions? What functional roles of carbohydrate structures play in fungal pathogenicity and plant defense?

2. Materials and Methods

This scoping review was performed following the principles established by the Preferred Reporting Items for Systematic Reviews and Meta-Analyses Extension for Scoping Reviews (PRISMA-ScR). There was no prior registration of a formal review methodology (e.g., Open Science Framework or PROSPERO). The review objectives, eligibility criteria, search strategy, and data extraction methodology were predetermined and are thoroughly documented to guarantee transparency and reproducibility.

2.1 Article selection

All the articles were selected and extracted from databases Scopus, Web of Science (WoS), ScienceDirect, and PubMed. The literature search was conducted on 22 December 2024. These databases were accessed via the university library (https://library.uitm.edu.my/collection) and can be easily obtained, as they are directly linked to the institution's login (Figure 1). The search strategy was developed using combinations of keywords and Boolean operators related to four main concepts: (1) glycoprotein or carbohydrate, (2) plants, (3) fungi, (4) infection or disease, and (5) carbohydrate-binding protein or lectin. The core search structure was:

("glycoprotein" OR "glycoproteins" OR "carbohydrate" OR "glycan" OR "sugar")
AND ("plant" OR "flora" OR "vegetation" OR "agriculture")
AND ("fungal" OR "fungus" OR "mycosis" OR "mycelium")
AND ("infection" OR "disease" OR "pathogen")
AND ("carbohydrate binding protein" OR "lectin" OR "binding protein" OR "CBP")

These keywords were applied to the database's advanced search, yielding 451 articles. Because each database uses different indexing systems and search interfaces, the search syntax was adapted to the database's requirements while maintaining a consistent conceptual search structure. The full search strategies for each database were provided in Supplementary Table S1. Each term keyword has a direct meaning and

connection, so the keywords have specific synonyms. Moreover, these keywords were carefully selected using combined terms (AND/OR) to capture all articles consistent with them. After identifying targeted keywords, the search filter was applied, and only research articles were included in this scoping study. No restrictions were applied to the publication year to capture the full breadth of available findings. The included studies spanned the period from 2005 to 2024, reflecting the distribution of relevant literature identified through the search. Although the search terms were comprehensive, the number of retrieved records was relatively focused because the search was restricted to the Title, Abstract, and Keywords fields to improve relevance. The search strategy was designed to capture studies specifically addressing carbohydrate or glycan components in plant–fungal interactions, which represents a specialized research area.

Supplemental Material Table S1
Search strategies used in each database.

Database	Search strategy
Scopus	TITLE-ABS-KEY ("glycoprotein" OR "glycoproteins" OR "carbohydrate" OR "glycan" OR "sugar") AND ("plant" OR "flora" OR "vegetation" OR "agriculture") AND ("fungal" OR "fungus" OR "mycosis" OR "mycelium") AND ("infection" OR "disease" OR "pathogen") AND ("carbohydrate binding protein" OR "lectin" OR "binding protein" OR "CBP")
Web of Science (WoS)	TS = ("glycoprotein" OR "carbohydrate") AND ("plant") AND ("fungal" OR "fungus") AND ("infection" OR "disease" OR "pathogen") AND ("carbohydrate binding protein" OR "lectin" OR "CBP")
PubMed	("glycoprotein" OR "glycoproteins" OR "carbohydrate" OR "sugar") AND ("plant" OR "agriculture") AND ("fungal" OR "fungus") AND ("infection" OR "disease" OR "pathogen") AND ("lectin" OR "carbohydrate binding protein" OR "CBP")
ScienceDirect	("glycoprotein" AND "plant" OR "agriculture" AND "fungus" AND "pathogen" AND "carbohydrate binding protein")

To enhance the robustness and completeness of the search process, the search strategy was pilot-tested for validation against a small set of known relevant articles identified during initial topic familiarization. The keywords and Boolean operators were refined to ensure these landmark studies could be retrieved across the selected databases. In addition, hand-searching was conducted by screening the reference lists of all included full-text articles to identify any additional relevant studies not captured in the database search.

All retrieved records were exported into Microsoft Excel for data organization and management. Duplicate records were identified and manually removed in Excel. The screening process was conducted in two stages: (i) title and abstract screening and (ii) full-text eligibility assessment. The primary reviewer performed the initial screening, and the supervising author independently checked it. Any uncertainties regarding study eligibility were discussed and resolved through consensus.

The number of articles extracted from each database varies depending on the breadth of a particular topic area. For example, Scopus provides abundant information on topics and offers wide-ranging insights into high-quality papers. Therefore, the highest number of retrieved articles was 253 from the holistic database Scopus. On the other hand, WoS has 89 articles, as it also has wide-reaching coverage in this field. Additionally, ScienceDirect retrieved 38 articles, and PubMed retrieved 71. The differences in the number of articles from these databases were apparent because of their focus and selection of specific topics. However, these differences could yield a significant number of articles for the scoping review. By understanding these preference databases, this scoping review can serve as a guide for future researchers in choosing which resources are reliable for their topic.

2.2 Inclusion and Exclusion parameters

The inclusion criteria in this study were applied to capture the relevant literature in the databases (Table 1). It was essential to set the inclusion criteria to ensure that retrieved articles were helpful in

understanding carbohydrate interactions in plant pathology. To satisfy the inclusion criteria, the study must prioritize articles that experimentally investigate the influence of carbohydrates on plant pathology and the biochemical pathways of altered glycans. The only document types accepted in this study were articles with an experimental design and results. It was because the articles were original with in-depth experiments, and they provided significant insight into the topics. For credible data, all articles must present methodologies that include glycan profiling, lectin-binding, and molecular studies of plant-fungal interactions. These inclusion criteria allowed this scoping to include all types of plant species infected and the classification of carbohydrates. On top of that, all languages were allowed to review diverse research areas to eliminate potential bias arising from language restrictions. Studies were considered regardless of language; all included articles were published in English. Publication year was not restricted in the search strategy to ensure comprehensive coverage of the available literature.

The exclusion criteria for this study were duplicate and inaccessible articles. Review articles, conference abstracts, reports, and other forms of grey literature were also excluded. During article selection from databases, it was common to discover duplicate articles, as the same study was indexed in multiple databases, leading to redundant citations of the same work. Despite the duplicated articles seeming minor, they can affect the accuracy of literature reviews by unnecessarily inflating the number of resources. Therefore, it was essential to remove duplicate studies or the same study appearing in databases to produce accurate data for the scoping review. Meanwhile, the inaccessible articles could hinder the analysis of experimental details and results. Hence, the inclusion and exclusion parameters can indicate the availability of articles and the quality and relevance of studies. Title and abstract screening, followed by full-text assessment, were conducted independently by two authors based on inclusion and exclusion criteria. This independent screening process was performed to minimize selection bias and improve the reliability of study selection. Any inconsistencies between reviewers were resolved through discussion. When agreement could not be reached, a third author was consulted to make the final decision. A formal methodological quality assessment or risk-of-bias evaluation was not performed. This decision is consistent with the purpose of a scoping review, which aims to map the breadth, characteristics, and types of available evidence rather than to evaluate the effectiveness or methodological rigor of individual studies. The primary objective of this review was to identify research trends, study designs, and knowledge gaps related to carbohydrate interfaces in plant–fungal interactions. During the full-text assessment, 324 articles were excluded for the following reasons: not related to plant–fungal interactions (n = 70), no focus on carbohydrate or glycan components (n = 89), review or non-original articles (n = 124), and inaccessible full texts (n = 41). These exclusion reasons are presented in Figure 1.

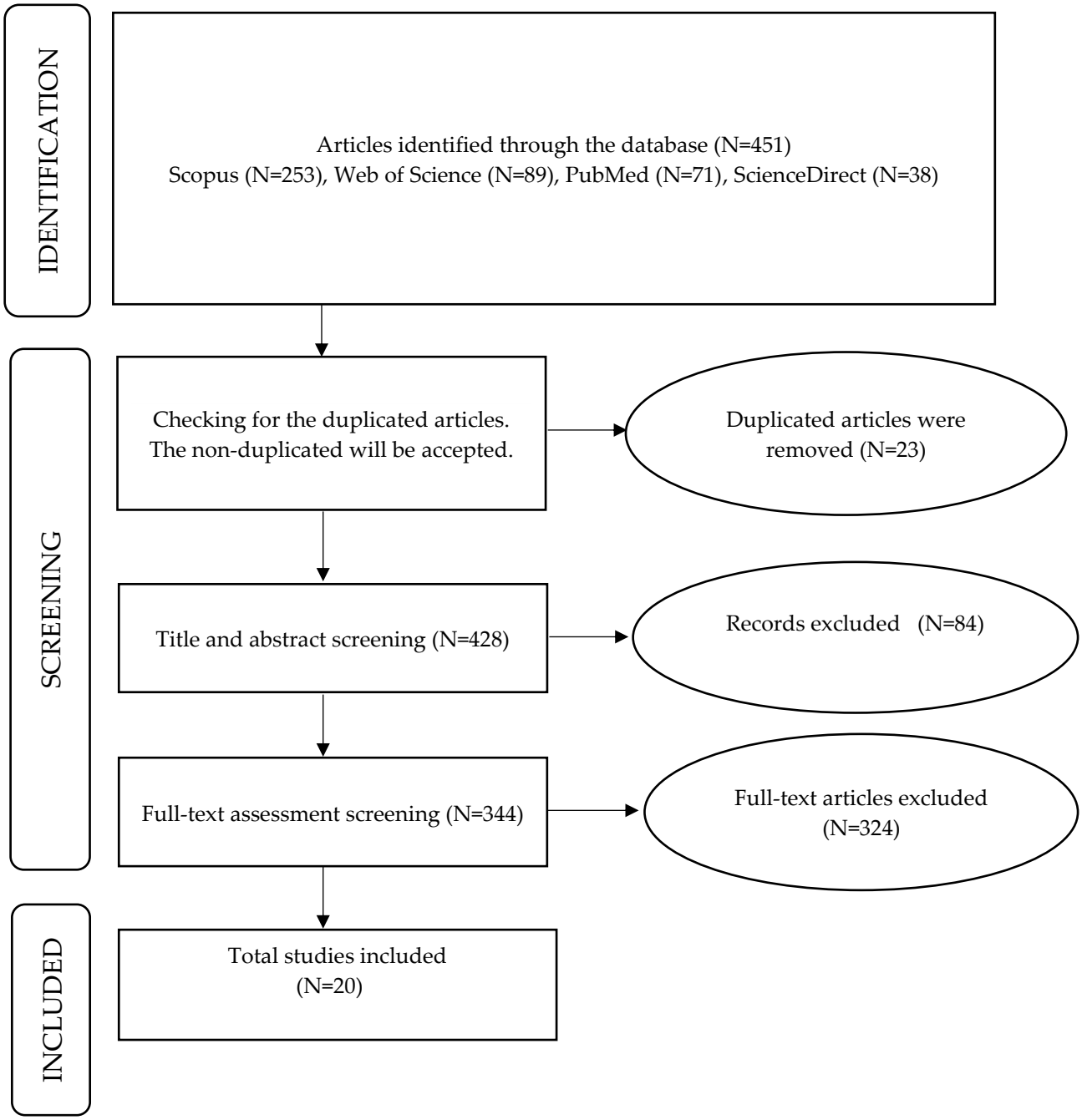


Figure 1. PRISMA flow diagram showing the study selection process. Articles were identified from Scopus, Web of Science (WoS), PubMed, and ScienceDirect. After duplicate removal, title and abstract screening, and full-text assessment, the remaining articles were assessed for eligibility. Reasons for full-text exclusion are described in Section 2.2.

Table 1. Overview of carbohydrate interactions with plants infected by pathogenic fungi.

Author(s)	Year	Country	Plant species	Fungal pathogen	Carbohydrate type	Study design	Key findings
[7]	2024	China	Kiwifruit (*Actinidia chinensis* 'Hongyang') Barley (*Hordeum vulgare*)	*Diaporthe eres* (causes kiwifruit postharvest rot *Blumeria graminis f. sp. hordei* (*Bgh*) (causes barley powdery mildew)	Callose Arabinoxylan Cellulose	A computer-based study of genomics using both short- and long-read sequencing, followed by CAZyme gene prediction and labeling.	Fungal pathogens degrade plant cell walls via cell wall-degrading enzymes (CWDEs), thereby weakening structural integrity and increasing susceptibility to infection.
[8]	2023	Germany	Maize (*Zea mays*)	*Ustilago maydis*	Chitin (chitobiose, chitotetraose)	Structural and functional analysis of Cpl1 employing X-ray crystallography, MST/HDX-MS, and fungal knockouts.	The Cpl1 protein from *Ustilago maydis* is critical for fungal virulence and interacts with the plant immune response, specifically inhibiting chitin-triggered immunity during maize infection.
[9]	2023	United States	Wheat and *Arabidopsis*	*Fusarium graminearum Colletotrichum higginsianum Sclerotinia sclerotiorum Botrytis cinerea*	*N*-glycans	Functional classification of the wheat TaPTL protein in *Arabidopsis* using heterologous production, fungal pathogen bioassays, and gene expression analysis.	GlcNAc plays an important part in the plant's defense against fungal infections, and the PFT protein in wheat helps detect this glycan, activating a resistance mechanism that inhibits the fungus's spread within the plant.

Table 1. Overview of carbohydrate interactions with plants infected by pathogenic fungi. (continue)

Author(s)	Year	Country	Plant species	Fungal pathogen	Carbohydrate type	Study design	Key findings
[10]	2023	United States	Rice (*Oryza sativa*)	*Magnaporthe oryzae*	(1→3, 1→4)-β-glucans	Biochemical and structural characterisation of MoPMO4 by enzyme tests, X-ray crystallography, and substrate binding studies.	MoPMO4 promotes oxidative degradation of plant cell wall components and plays a functional role in the pathogenicity of *Magnaporthe oryzae*.
[11]	2022	United States	Maize (*Zea mays*)	*Fusarium graminearum, Fusarium proliferatum, and Fusarium verticillioides,*	*N*-glycans	Transgenic expression study testing a chimeric superlectin gene in maize callus against fungal pathogens and insect pests using growth-inhibition bioassays.	*N*-acetylglucosamine residues increase resistance *to Fusarium* fungi and insect pests, potentially enhancing sustainable pest management in maize cultivation.
[12]	2019	United Kingdom	*Arabidopsis thaliana*	*Serendipita indica Bipolaris sorokiniana Ustilago maydis Colletotrichum tofieldiae*	Chitin, β1-3 glucan, β1-6-glucan, Laminarin (β1-3-glucan with β1-6 linkages)	Biochemical and cytological characterization of FGB1 and WSC3 lectins using binding assays, microscopy, gene expression analysis, and fungal confrontation tests.	Root-associated fungi alter their cell walls to evade plant immune responses and facilitate successful colonization of plants.
[13]	2018	United States	Tomato (*Solanum lycopersicum*)	*Cladosporium fulvum*	Chitin, Chitohexose $(GlcNAc)_6$	Structural study of *Cladosporium fulvum* Avr4 effector using X-ray crystallography of Avr4-(GlcNAc)6 complex, mutagenesis, and chitin-binding assays.	CfAvr4 uses a CBM14 carbohydrate-binding module to bind chitin, protecting fungal cell walls from plant chitinases and promoting fungal infection while evading plant immunity.

Table 1. Overview of carbohydrate interactions with plants infected by pathogenic fungi. (continue)

Author(s)	Year	Country	Plant species	Fungal pathogen	Carbohydrate type	Study design	Key findings
[14]	2017	Czech Republic	Rice (*Oryza sativa*)	*Magnaporthe oryzae*	β-1,3-glucan	Mutant analysis and cell wall characterization study of rice blast (Gels) using microscopy, glycan analysis, and plant infection assays.	Alterations in β-1,3-glucan by gel proteins are essential for fungal cell wall integrity and pathogenicity.
[15]	2016	United States	Wheat (*Triticum aestivum*)	*Parastagonospora nodorum*	Chitin	Functional characterization of SnTox1 effector using protein expression, chitin binding assays, fungal transformation, and wheat infection/ plant defense assays.	The effector SnTox1 binds chitin, shielding the pathogen from attack by the plant's chitinases. This promotes infection and allows the pathogen to colonize the host effectively.
[16]	2015	United States	Rice (*Oryza sativa*)	*Magnaporthe oryzae*	*N*-glycans	Structural study of *Magnaporthe oryzae* CVNH-LysM protein using X-ray crystallography and NMR titration with chitin oligosaccharides (GlcNAc3-6).	The plant identifies the GlcNAc-containing oligosaccharides secreted from the fungal cell wall as pathogen-associated molecular patterns (PAMPs).
[17]	2014	China	Rice (*Oryza sativa*)	*Magnaporthe oryzae*	*N*-glycans	Genetic and functional study of *ALG3* mannosyltransferase mutants assessing *N*-glycosylation effects on Slp1 effector stability, chitin binding, and rice blast virulence.	*N*-glycosylation of the effector protein Slp1 is required for its chitin-binding activity, stability, and ability to suppress host immunity, all of which are critical for Magnaporthe oryzae pathogenicity during infection.

Table 1. Overview of carbohydrate interactions with plants infected by pathogenic fungi. (continue)

Author(s)	Year	Country	Plant species	Fungal pathogen	Carbohydrate type	Study design	Key findings
[18]	2014	Australia	Canola (*Brassica napus)*	*Leptosphaeria maculans, Leptosphaeria biglobosa*	Pectin Xyloglucan Glucuronoarabinoxylan Chitin	Comparative genomics and dual RNA-seq transcriptomics study of canola-fungus interactions between Brassica napus and two Leptosphaeria species (*L. maculans* 'brassicae' and *L. biglobosa* 'canadensis').	The breakdown of pectin, xyloglucan, and glucuronoarabinoxylan is for cell wall penetration, while the plant recognizes chitin to trigger defense responses.
[19]	2014	Australia	Barley (*Hordeum vulgare*)	*Blumeria graminis f. sp. hordei (Bgh)*	Callose (1,3-glucan) Arabinoxylan Crystalline Cellulose	Histochemical and immunolocalization study analyzing polysaccharide (callose, arabinoxylan, cellulose) composition in penetrated versus non-penetrated papillae during barley powdery mildew infection.	The increased accumulation of callose, arabinoxylan, and cellulose in effective papillae enhances structural protection against *Blumeria graminis* f. sp. *hordei* in barley.
[20]	2012	Brazil	*Moringa oleifera* (seeds)	*Fusarium solani*	Chitin	Biochemical purification and characterization study of a chitin-binding protein from *Moringa oleifera* seeds using affinity chromatography, spectroscopy, and antifungal bioassays against phytopathogenic fungi.	A chitin-binding protein derived from *Moringa oleifera* seeds demonstrates antifungal properties and emphasizes the significance of carbohydrate recognition (chitin–protein interaction) in plant defense mechanisms.

Table 1. Overview of carbohydrate interactions with plants infected by pathogenic fungi. (continue)

Author(s)	Year	Country	Plant species	Fungal pathogen	Carbohydrate type	Study design	Key findings
[21]	2011	United States	Rice (*Oryza sativa*)	*Magnaporthe oryzae*	Mannose-based Glycans (CVNH Domain), Chitin-related Glycans (LysM Domain)	Structure-function analysis of *Magnaporthe oryzae* CVNH-LysM lectin using NMR spectroscopy, carbohydrate titration binding studies (GlcNAc oligomers), and live-cell imaging of appressorium localization.	*Magnaporthe oryzae* binds to mannose-based glycans via its CVNH domain and to chitin-related glycans via its LysM domain, with its presence in the appressorium suggesting a role in fungal invasion of rice.
[22]	2009	China	Canola (*Brassica napus)*	*Sclerotinia sclerotiorum*	β-1,3-glucans	Transcriptome microarray analysis comparing gene expression between resistant and susceptible *Brassica napus* cultivars following *Sclerotinia sclerotiorum* stem inoculation.	The fungal pathogen *S. sclerotiorum* utilized pectin-degrading pathways for infection, whereas the plant initiated phenylpropanoid metabolism to strengthen its structure.
[23]	2008	United States	Tomato *(Solanum lycopersicum)*	*Cladosporium fulvum*	Chitin	Characterization study of *Cladosporium fulvum* Ecp6 LysM effector using heterologous expression, chitin binding assays, RNA interference silencing, and tomato infection tests	The effector protein Ecp6 of *Cladosporium fulvum* binds to chitin, thus inhibiting host immune responses and increasing fungal virulence in tomatoes.
[24]	2007	Japan	*Arabidopsis thaliana*	*Alternaria brassicicola*	Chitin	Genetic and phenotypic characterization of Arabidopsis CERK1 mutants, demonstrating	Glycans stimulate plant defense responses through CERK1, which involves glycan-related

Table 1. Overview of carbohydrate interactions with plants infected by pathogenic fungi. (continue)

Author(s)	Year	Country	Plant species	Fungal pathogen	Carbohydrate type	Study design	Key findings
[24]	2007	Japan	*Arabidopsis thaliana*	*Alternaria brassicicola*	Chitin	loss of chitin-induced defense responses, including ROS burst, MAPK activation, and gene expression.	signaling molecules and structural alterations in the plant's immune system.
[25]	2006	Netherlands	Tomato (*Solanum lycopersicum*)	*Cladosporium fulvum*	Chitin	Biochemical and protection assays demonstrate that the *Cladosporium fulvum* Avr4 chitin-binding lectin shields fungal cell walls from plant chitinase hydrolysis during tomato infection.	The protein Avr4 binds to chitin in the cell walls of fungi, preventing Cladosporium fulvum from being hydrolyzed by plant chitinase during infection.
[26]	2005	United States	Rice (*Oryza sativa*)	*Magnaporthe grisea*	Chitin	Whole-genome shotgun sequencing and comparative genomic analysis of *Magnaporthe grisea* strain 70-15 (40.3 Mb assembly).	The rice plant's response to fungal infection involves recognizing chitin-based glycans, which activate defense systems.

3. Results and Discussion

A trend over time was observed in the included studies spanning 2005 to 2024. In the earlier years (2005–2010), the studies focused on structural polysaccharides, particularly chitin, and their role in pathogen recognition and plant defense activation. Studies from 2011 onward have shown a progressive shift toward molecular and functional analysis and lectin-mediated glycan recognition mechanisms. More recent studies (2020–2024) increasingly employed advanced methods, such as genomics and glycoprotein analysis, with growing attention to protein-linked carbohydrates, including N-glycans, and their roles in fungal pathogenicity and immune interactions. The included studies were conducted across several regions, with the majority originating in the United States, China, and Europe. However, only a limited number of studies were identified from developing regions. This suggests a focus of research in countries with advanced research infrastructure and highlights potential geographic gaps in plant–fungal carbohydrate research. A descriptive analysis of the included studies showed that chitin and chitin-related glycans were the most frequently investigated carbohydrate types (n = 10), followed by *N*-glycans (n = 4) and β-glucans (n = 4). Rice (*Oryza sativa*) was the most commonly studied plant species (n = 6), while *Magnaporthe* spp. was the most frequently reported fungal pathogen (n = 6). This distribution indicates a research emphasis on major crop systems and economically important fungal diseases.

Table 2. Distribution of included studies by research focus

Category	Research focus	Number of studies(n)
Carbohydrate type	Chitin/ chitin-related glycans	10
	N-glycan/ protein *N*-glycosylation	4
	β-glucans (including laminarin)	4
	Plant cell wall polysaccharides (callose, arabinoxylan, cellulose, pectin, xyloglucan, glucuronoarabinoxylan)	2
	Mannose-based glycans	1
Plant species	Rice (*Oryza sativa*)	6
	Arabidopsis *(A. thaliana)*	3
	Tomato *(Solanum lycopersicum)*	3
	Maize *(Zea mays)*	2
	Wheat *(Triticum aestivum)*	2
	Barley *(Hordeum vulgare)*	2
	Canola *(Brassica napus)*	2
	Kiwifruit	1
	Moringa oleifera	1
Fungal pathogen	*Magnaporthe* spp.	6
	Cladosporium fulvum	3
	Fusarium spp.	3
	Blumeria graminis	2
	Ustilago maydis	2
	Sclerotinia sclerotiorum	2
	Other pathogens *(Alternaria, Parastagonospora, Serendipita, Diaporthe,* etc.*)*	5

3.1 Functional role of carbohydrates in plant pathogen interactions

This study explored the roles of carbohydrates in plant–fungal interactions based on a summary of findings (Table 1). In this review, carbohydrates were classified according to their primary functional roles reported in each study. It is because a single carbohydrate can participate in multiple biological processes during infection, such as chitin, which appears across more than one functional theme depending on the

experimental context. Overall, the reported studies were organized into three functional themes: (i) structural roles in cell wall integrity and reinforcement, (ii) storage functions, and (iii) signaling and recognition roles in plant defense and pathogen interaction. Glycans are repetitive, often highly branched carbohydrate structures that are also added as post-translational modifications (PTMs) to proteins, resulting in glycoproteins [27-28]. Structural glycans were important for maintaining the structural integrity and mechanical support of plant and fungal cell walls [29]. The structural carbohydrates reported across the included studies include cellulose, chitin, callose, xyloglucan, pectin, arabinoxylan, β-glucans, and glucuronoarabinoxylan. Cellulose, the primary constituent of plant cell walls, is one of the most abundant biomolecules on Earth and consists of glucose units linked by β-1,4-glycosidic bonds [30]. Plants access cell wall integrity (CWI) through receptor-like kinases (RLKs) such as proteins THESEUS1 (THE1) and FERONIA (FER), which detect structural changes and regulate stress responses [31]. During fungal infection, such as that caused by Fusarium oxysporum, plants increase cellulose deposition to reinforce cell walls and restrict pathogen invasion [32]. Following cellulose, chitin is the second most abundant biopolymer and is composed of *N-acetylglucosamine* (GlcNAc) units linked by β(1→4) bonds [33]. Although chitin contributes structurally to fungal cell walls, it also has important roles in host recognition, as chitin-derived oligosaccharides function as pathogen-associated molecular patterns (PAMPs) that activate plant immune responses. Other plant structural polysaccharides, including callose, xyloglucan, and pectin, contribute to growth, development, and defense. Under pathogen stress, callose, a β-1,3-glucan, is rapidly attached at infection sites to form physical barriers against microbial penetration [34]. Xyloglucan regulates expansion, differentiation, and maintenance of final morphology in plant cell walls [35-36]. Pectin also contributes to defense by reinforcing the cell wall and triggering immune signaling pathways [37]. Similarly, arabinoxylan, β-glucans, and glucuronoarabinoxylan strengthen cell wall architecture and increase resistance to fungal enzymatic degradation [38]. In addition, β-glucans can function as PAMPs that activate plant immune responses [39].

In contrast, some carbohydrates serve storage functions. Laminarin, a β-glucan polysaccharide, is known for its role in energy storage and controlled release [40-41]. Derived from brown algae and considered non-toxic [42], laminarin has also been shown to induce pattern-triggered immunity (PTI) and systemic acquired resistance (SAR), leading to the upregulation of defense-related genes [43]. Signaling and recognition glycans represent another major functional theme. These include mannose-based glycans (CVNH domain-associated), *N*-glycosylated proteins, and chitin. Mannan oligosaccharides (MOS) act as danger-associated molecular patterns (DAMPs), activating MAPK signaling cascades, inducing defense gene expression, promoting phytoalexin accumulation, and strengthening physical barriers against pathogen invasion [44]. *N*-glycosylation, a post-translational modification, contributes to protein stability, stress responses, and plant development [45]. For example, GlcNAc-containing *N*-glycans have been shown to interact with wheat proteins during *Fusarium graminearum* infection, contributing to quantitative resistance and immune activation [46]. Plants also possess receptor-like kinases RLKs that recognize chitin oligosaccharides, with chitin elicitor receptor kinase 1 (CERK1) playing a central role in triggering defense responses [47]. Furthermore, chitinase, an enzyme that degrades chitin, is secreted by plant tissues and is upregulated during pathogen invasion to inhibit fungal growth [48]. Collectively, these findings highlight that carbohydrate-mediated interactions function through multiple, context-dependent mechanisms. The functional themes identified reflect the diverse roles reported across the studies (Table 1), highlighting that a single carbohydrate component can contribute to structural defense, immune signaling, and pathogen adaptation during different stages of plant–fungal interactions.

3.2. Fungal infections and pathogenesis in plants

A wide range of plants have been studied in this scoping data, which revealed that most plants were critical to the agriculture sector, but pathogenic fungi had affected them. Fungal plant infections are known to cause severe crop diseases and are among the most prevalent, including symptoms of blight, canker, powdery mildew, rust, wilt, leaf spot, nd damping off [49]. The staple crops in this study were rice, wheat, soybean, and barley, alongside horticultural crops such as tomato, maize, and kiwi. The plentiful availability and cost-effectiveness of staple plant foods make them preferable in selecting raw materials to synthesize economically

viable food products [50]. Thus, the staple crops were widely studied, and the common fungi causing the diseases were Magnaporthe oryzae, Parastagonospora nodorum, and *Fusarium graminearum*. *Magnaporthe oryzae* is a fungus that causes rice blast disease, which can result in up to 30% loss in rice production [51]. This devastating fungus infects rice by attaching its spores to the leaf surface, forming an appressorium that exerts intense pressure to rupture the plant cuticle [52]. The most common symptoms caused by this fungus were seed degradation and damping-off during early growth, followed by brown stem lesions and tissue collapse in the later season [53]. Meanwhile, *Parastagonospora nodorum* is a necrotrophic fungal pathogen responsible for septoria nodorum blotch (SNB) in wheat (Triticum spp.), and it is predominantly spread through contaminated seeds, infested waste, and wind-borne sexual ascospores [54]. Then again, another catastrophic fungus, *Fusarium graminearum,* damages wheat by invading the plant surface, inhibiting immune responses through effector proteins, and producing toxins to promote colonization and induce tissue necrosis [55]. Figure 2 illustrates that fungal-*N* glycoproteins play a role in attachment to the host surface, induce plant defense signaling, and suppress immune detection.

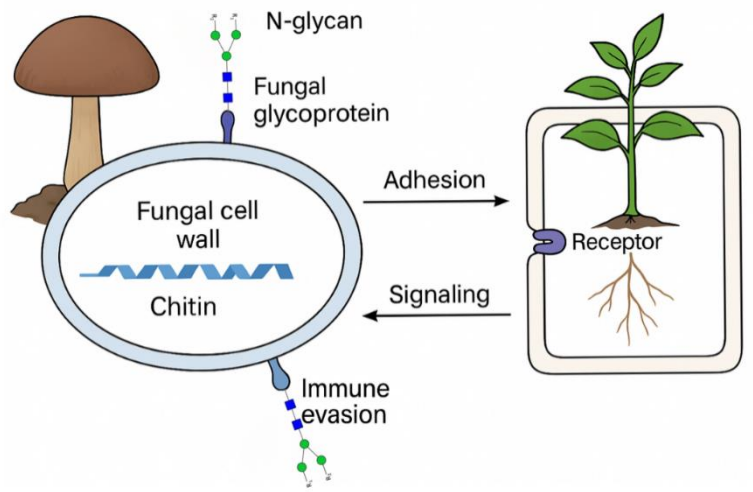


Figure 2. Fungal *N*-linked glycoproteins interact with plant receptors during infection. *N*-glycans enhanced immune evasion by secreting chitin to support the fungus-infected and manipulated the plant immune system.

The horticultural crops in this study were tomato, maize, and kiwi. The fungi mentioned in this study were *Cladosporium fulvum*, *Ustilago maydis,* and *Diaporthe eres*. *Cladosporium fulvum* infects tomatoes by penetrating leaf tissues, inducing a surge of reactive oxygen species (ROS), and modifying plant defense mechanisms. It influences plant hormone signaling by elevating salicylic acid (SA) and abscisic acid (ABA) while reducing jasmonic acid (JA) levels, ultimately altering gene expression and compromising the plant's resistance [56]. Corn smut is commonly caused by the fungus *Ustilago maydis*, which is characterized by tumor growth in the aerial portions of maize. This tumor arises from the de novo division of highly specialized bundle sheath cells followed by cell enlargement [57]. A study in China researched *Diaporthe eres*, as the causal agent of 'Hongyang' postharvest rot disease. This fungus harmed kiwifruit by releasing cell wall-degrading enzymes (CWDEs), including cellulase, β-galactosidase, polygalacturonase, and pectin methylesterases, which degrade plant cell wall polysaccharides, hence promoting fungal invasion and soft rot disease [7].

3.3 Fungal virulence factors in plant infections

Environmental factors largely influence fungal infections, as plants grow in natural habitats and are cultivated in agricultural settings. However, most of the studies analyzed in this scoping review were conducted in standardized laboratory settings to ensure successful fungal inoculation and reproducibility. Regardless, the influence of environmental factors remains significant. The burden of plant diseases was mainly caused by soil, water, and air pollution from human activity, as well as changes innvironmental

conditions (Waheed et al. [58]). For example, rising temperatures can broaden the geographical distribution of fungal infections, thereby increasing disease prevalence and severity [58]. A study by Jabiri [59] found that ideal water potential plays a crucial role in the growth of pathogens such as *Phytopythium vexans*, with peak growth recorded at particular moisture levels. Within this research framework, *Magnaporthe oryzae*, the cause of rice blast, mainly occurs under light, humidity, and nutrient conditions that favor the production of spores [60]. Rising humidity increases the virulence of *Magnaporthe oryzae* by promoting conidial germination and appressorium development, both of which are essential for infection [61]. The intensity of rice blast disease is significantly influenced by temperature, with ideal conditions occurring between 24–30°C alongside elevated relative humidity, resulting in extensive outbreaks [62]. Rainfall is the most crucial environmental factor in predicting disease outbreaks because it promotes fungal growth and distribution [63]. Meanwhile, drought stress is a significant influence, as water-stressed plants have weakened immune responses, making it easier for *Fusarium* to spread infection [64]. In summary, drought conditions can facilitate fungal invasion of plants, while high humidity and excessive rainfall can promote fungal proliferation and aid spore dispersal.

3.4 Challenges and future directions

While this scoping review provides a comprehensive overview of carbohydrate interfaces in plant–fungal interactions, several potential sources of bias should be considered when interpreting the findings. First, although multiple major databases were searched, studies indexed in other databases may have been missed, potentially leading to publication bias. Second, most included studies were conducted under controlled laboratory conditions, which may limit the findings to natural field environments. Finally, variability in experimental approaches, plant species, fungal pathogens, and glycan analysis methods may influence the consistency and comparability of results. In addition, the knowledge gaps were identified through descriptive mapping of the included studies. This involved analyzing the frequency and distribution of carbohydrate types investigated, plant–fungal systems studied, and experimental approaches applied. Areas with limited representation, a lack of specific carbohydrate categories, or restricted methodological diversity were identified as potential research gaps.

3.5 Limitations of the study

Despite increasing interest in carbohydrate-mediated plant–fungal interactions, several challenges remain. First, current research is heavily focused on structural polysaccharides such as chitin, while protein-linked carbohydrates, particularly *N*- and *O*-glycans, remain underexplored. Second, many studies rely on controlled laboratory experiments, which do not fully reflect the complexity of field conditions. Third, technical limitations in glycan extraction and analytical methods continue to constrain comprehensive glycan profiling in plant–pathogen systems. In addition, the geographic distribution of studies indicates a concentration of research in countries with advanced research infrastructure, suggesting limited representation from developing regions. In future studies, researchers should prioritize functional and dynamic analyses of glycan modifications during infection, integrate advanced omics and glycomics approaches, and validate findings under field conditions. These efforts can support the development of glycan-based biomarkers for early disease detection and contribute to the breeding of disease-resistant crop varieties.

4. Conclusions

In conclusion, this scoping review provides a comprehensive mapping of current evidence on carbohydrate-mediated plant–fungal interactions and highlights key trends and research gaps in this field. The findings indicate that existing studies are largely focused on structural polysaccharides, particularly chitin, and their roles in pathogen recognition and plant defense. In contrast, protein-linked carbohydrates, especially *N*-glycans, remain limited, while studies specifically addressing *O*-glycans are largely absent. Most research has also focused on staple crops and laboratory-based experimental systems. These gaps suggest the need for greater emphasis on functional and dynamic analyses of glycan modifications during infection, broader representation of crops, and the application of advanced glycomic and molecular approaches. By identifying underexplored areas and synthesizing current knowledge, this review provides a foundation for

guiding future research toward the development of glycan-based diagnostic tools and disease-resistant crop strategies, contributing to improved plant health and sustainable agricultural production.

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