Chitin and Chitin Biosynthesis in Filamentous Fungi

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Chitin, a major structural component of the fungal cell wall, synthesized via the activityof the enzyme chitin synthase (*chs*), has become a high-profifile target for investigating the effect on morphology, development and pathogenicity of filamentous fungi. Besides, disruption of chitin biosynthesis can modify the mycelial morphology of filamentous fungi and regulate the biosynthesis of the target metabolites during submerged fermentation. Thus, we summarize the classifification, structure and function of *chs* enzymes, the biosynthetic pathway of chitin of filamentous fungi.

chitin mycelia morphology filamentous fungi development

1. Structure and Function of Chitin

After cellulose, chitin is the second most abundant natural polysaccharide, occurring widely in the exoskeletons of insects, crustaceans, and mollusks; it is also an important structural polysaccharide in fungal cell walls [1][2][3]. Notably, the chitin content in the fungal cell wall differs according to the morphological phase, accounting for only 1–2% of yeast cell wall dry weight [4][5], but reaching up to 10–20% of the cell wall dry weight of filamentous fungi (*Aspergillus*) [6]. Moreover, the content of chitin in the hyphal walls of *Candida albicans* is three times higher than that of other yeasts [7], whereas, in *Paracoccidioides brasiliensis* and *Blastomyces dermatitidis*, it is 25–30% higher than that in the yeast phase [8]. Chitin is a linear copolymer of *N*-acetyl-d-glucosamine (GlcNAc) and d-glucosamine units, linked by a *β*-(1–4) glycosidic bond, although predominantly comprising GlcNAc units [2]. Chitin chains of more than 100 and 190 GlcNAc monomers in length have been reported in cell walls and bud scars, respectively [9][10]. In addition, crystalline structural determinations have revealed that chitin can exist in three different forms, namely, α-, β-, and γ-chitin, representing antiparallel, parallel, and alternated arrangements of polymer chains, respectively [11][12]. In fungi, α-chitin is the major structural form [13], and γ-chitin is mainly found in the beetle family *Lucanidae* [14].

Chitosan is an important chitin derivative, generated by removing the acetyl group of chitin, either via treatment with concentrated alkali or the activity of chitin deacetylases. Chitin and its derivatives (chitosan and glucosamine series) have important applications in medicine and in the chemical industry, and as functional foods. Chitin and chitosan are considered advantageous biocompatible materials that can be used to augment or replace any tissue, organ, or function of the body [15][16]. Moreover, owing to their notable biological activities, including antibacterial, antifungal, antitumor, immunoregulatory, antioxidant, and anti-inflammatory properties, chitosan oligosaccharides have gained widespread application in the treatment and prevention of multiple life-threatening diseases and

disorders, including cancer, heart disease, diabetes mellitus, and serious infections [17]. In addition, chitin and chitosan have a high absorptive capacity for wastewater pollutants, and thus have application potential in industrial wastewater treatment [18]. In filamentous fungi, chitin molecules form intrachain hydrogen bonds, facilitating assembly into fibrous microfibrils that form a basket-like scaffold surrounding cells. These fibrous microfibrils are characterized by considerable tensile strength, thereby maintaining cell wall integrity. As depicted in **Figure 1**, the cell wall comprises a twin-layer structure, the innermost layer of which is a relatively conserved structural skeletal layer (crosslinked chitin-glucan inner layer) comprising chitin and *β*-(1,3)-branched glucan, whereas the heterogeneous outer layer consists of other polysaccharides and glycoproteins [19][20]. The *β*-(1,3):*β*-(1,6)-branched glucan of the cell wall is bound to proteins or other polysaccharides, the composition of which may vary according to the fungal species, although it generally comprises highly mannosylated glycoproteins and mannoproteins. Chitin plays multiple roles in fungal species, including the maintenance of cell structural integrity, regulation of epithelial adhesion, the linkage between the cell wall and capsule, and antifungal resistance [21][22][23]. Accordingly, chitin is a key factor in maintaining normal cell growth and metabolism in filamentous fungi.

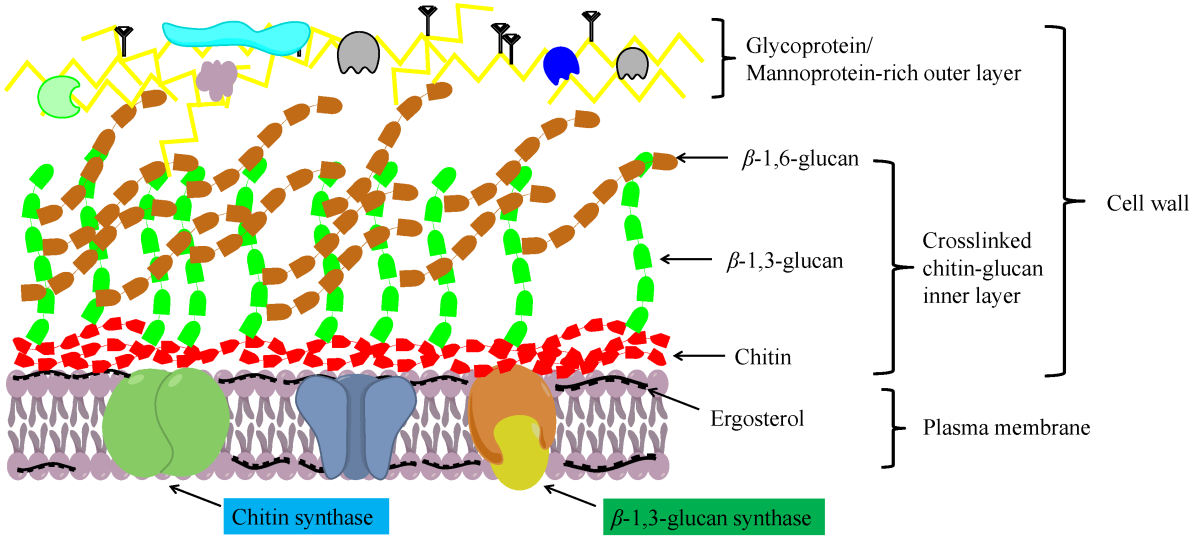

Figure 1. A schematic diagram showing the structure of the fungal cell wall.

2. The Chitin Biosynthetic Pathway

In fungi, chitin is synthesized via a highly complex biosynthetic pathway involving a multifarious series of biochemical and physiological processes [24]. As substrates, glucose or one of its storage compounds (glycogen or trehalose) undergoes bioconversion to a polymer of the amino sugar GlcNAc via a series of enzymatic reactions divided into three sets of sub-reactions [24]. In the first set of sub-reactions (**Figure 2**), the biosynthesis of GlcNAc-1P proceeds via three steps: the substrate, fructose-6-phosphate (fructose-6P), generated from glycolysis (or the Embden–Meyerhof–Parnas (EMP) pathway), and trehalose are mobilized by hydrolysis to glucose catalyzed by trehalase [EC:3.2.1.28], and glycogen is converted to glucose-1-P by glycogen phosphorylase [EC:2.4.1.1]. During this stage, glucokinase [EC:2.7.1.2] or hexokinase [EC:2.7.1.1], and glutamine-fructose 6-phosphate transaminase (isomerizing) [EC:2.6.1.16] are the rate-limiting enzymes. In addition, glucose-6P can be used for the biosynthesis

of *β*-(1,3) glucan via three reactions catalyzed by the enzymes phosphoglucomutase [EC:5.4.2.2], UTP-glucose-1-phosphate uridylyltransferase [EC:2.7.7.9], and 1,3-*β*-glucan synthase [EC:2.4.1.34]. In the second set of sub-reactions, GlcNAc-1P is catalyzed to generate the activated molecule amino sugar UDP-*N*-acetylglucosamine (UDP-GlcNAc) via the action of UDP-*N*-acetylglucosamine pyrophosphorylase [EC:2.7.7.23], an essential enzyme for chitin synthesis. In the final set of sub-reactions, the enzyme *chs* [EC:2.4.1.16] catalyzes a polymerization reaction to synthesize chitin using the activated UDP-GlcNAc as a sugar donor. The first two sets of sub-reactions occur within the cell cytoplasm, while the third reaction occurs in the chitosome, located within the plasma membrane of cells in the hyphal tips and cell cross-walls of filamentous fungi [25]. In the chitin biosynthetic pathway, glutamine-fructose 6-phosphate transaminase [EC:2.6.1.16], UDP-*N*-acetylglucosamine pyrophosphorylase [EC:2.7.7.23], and *chs* [EC:2.4.1.16] serve as the rate-limiting enzymes that dictate the rate at which chitin is synthesized, and are highly regulated in cells. Among these enzymes, *chs* catalyzes the final reaction, which is specifically and directly associated with the biosynthesis of chitin, and accordingly, is acknowledged to be the key enzyme in chitin biosynthesis. As described in the Introduction section, *chs* plays a vital role in cell development and the mycelial morphology of filamentous fungi, thereby having a prominent role in the application of MEMFF.

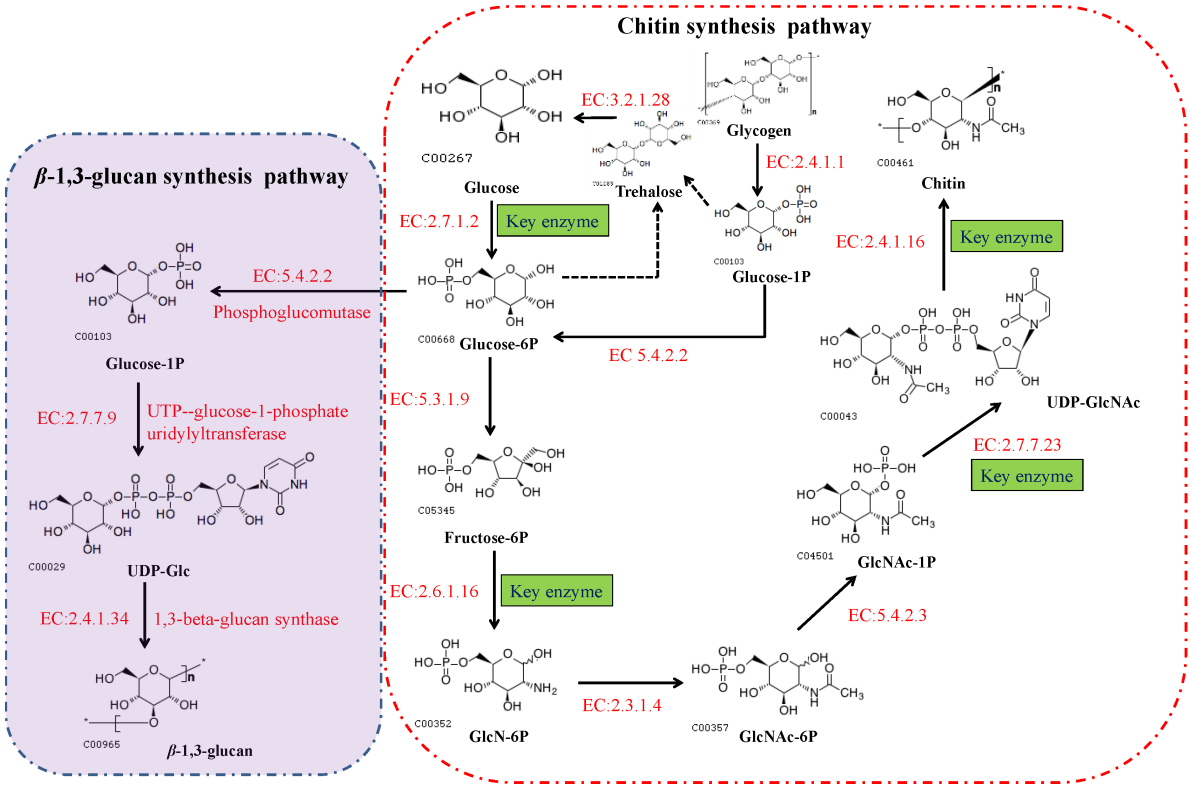

Figure 2. The biosynthetic pathways of chitin and *β*-(1,3) glucan in fungi. These pathways can also be viewed at the Kyoto Encyclopedia of Genes and Genomes website (https://www.kegg.jp/pathway/map00520, accessed on 11 September 2021).

3. Classification of Chitin Synthase

Based on amino acid sequence homology, the *chs* enzyme family can be grouped into seven classes (I to VII), with different fungal species expressing varying numbers of *chs* genes [26]. In 2019, researchers summarized three *chs* genes (classes I–III) in *Saccharomyces cerevisiae*, four in *Candida*, and six to ten in filamentous fungi [27]. Among the seven classes, *CHS* III, V, VI, and VII are found exclusively in filamentous fungi [28]. In the same year, in their review of fungal chitin synthesis and degradation, Yang and Zhang described the members of the seven classes of chitin synthase in different fungi [20]. However, since then, details of *chs* genes and their classification have not been furthered. We found differences in the number of *chs* genes in *Saccharomycotina*, although these are generally grouped into three classes (*CHS* I–III). For instance, there are six (as opposed to the originally reported three), five, and four *chs* genes in *S. cerevisiae* S288c, *Candida orthopsilosis* Co 90-125, and *Candida tropicalis* MYA-3404, respectively, whereas eight *chs* genes have been identified in *Sugiyamaella lignohabitans* CBS 10342. Except for those in goldfish (seven *chs* genes), there are generally few *chs* genes in animals, including Eutheria, Amphibia, and Euteleostomi. Notably, the number and classes of *chs* genes in fungal genera are distinctly higher than those in the species of Saccharomycotina and animals. For example, among species of Pezizomycotina, such as *Aspergillus fumigatus*, *Neurospora crassa*, *Cordyceps militaris*, and *Purpureocillium lilacinum*, *chs* genes are generally grouped into seven classes, with seven to nine genes in each. Moreover, certain hypothetical proteins are identified as *chs* enzymes in *Fusarium graminearum* and *Pestalotiopsis fici*, thereby indicating the potential occurrence of up to 10 types of *chs*. Strains of filamentous fungi in the genus *Monascus*, an important industrialized fermentative microorganism, are noted for their production of MSMs, including *Monascus* pigments and monacolin K. In our laboratory, we have sequenced the whole genomes of *M. purpureus* LQ-6 (accession number of PRJNA503091) and its mutant strain M183 (accession number of JAACNI000000000) based on the combined application of single-molecule real-time DNA sequencing and next-generation sequencing. Accordingly, we identified eight genes encoding *chs* enzymes, the classification of which appears to be complex. In addition, nine genes encoding *chs* enzymes (including three hypothetical proteins) have been identified in the genome of *M. purpureus* HQ1 (accession number of VIFY00000000), mainly classified as *CHS* I, II, III, V, and VII. The larger number of *chs* genes in filamentous fungi compared to Saccharomycotina reflects the greater complexity of hyphal development and polarized growth, as well as a higher cell wall chitin content.

Table 1. The members of the chitin synthase family in a section of diverse fungi. *chs*, represents the gene of chitin synthase; *CHS*, represents the class of the members of *chs* family. The genes encoding hypothetical proteins, but mostly like *chs*, are marked in red.

Organism	T-Number	The Members of Chitin Synthase						Number of Genes
Saccharomyces cerevisiae S288c	T00005	YBR023C, *chs* 3	YBR038W, *chs* 2	YNL192W, *chs* 1	YLR330W, *chs* 5	YJL099W, *chs* 6	YHR142W, no KO assigned | (RefSeq) *chs*7; *chs* 7p	6
Lodderomyces elongisporus NRRLYB-4239	T01116	LELG_05384, *chs* 2	LELG_05013, *chs* 1	LELG_02210, *chs* 2	LELG_00298, *chs* 3	LELG_00300, *chs* 3		5

Organism	T-Number	The Members of Chitin Synthase										Number of Genes
Candida tropicalis MYA-3404	T01115	CAALFM_C113110CA, *chs* 3	CAALFM_C300710WA, *chs* 8	CAALFM_C702770WA, *chs* 1	CAALFM_CR09020CA, *chs* 2							4
Candida orthopsilosis Co 90-125	T02488	CORT_0A01870, *chs* 3	CORT_0D06430, chs 8	CORT_0G01660, *chs* 2	CORT_0H01960, *chs* 1	CORT_0H01970, *chs* 1						5
Sugiyamaella lignohabitans CBS 10342	T05270	AWJ20_11, *chs* 6	AWJ20_12, *chs* 3	AWJ20_13, *chs* 3	AWJ20_1163, *chs* 2	AWJ20_1500, *chs* 2	AWJ20_3769, *chs* 1	AWJ20_4861, *chs* 3	AWJ20_4948, *chs* 3			8
Xenopus laevis (African clawed frog)	T01010	108717413, *chs* 2	108716131, *chs* 2									2
Xenopus tropicalis (tropical clawed frog)	T01011	105947355, *chs* 2-like isoform X1										1
Carassius auratus (goldfish)	T07313	113057339 *CHS* 2-like	113061218 *CHS* 1-like	113061224 *CHS* 1-like	113061225 *CHS* 1-like	113061526 *CHS* 1	113061527 *CHS* 1-like	113113123 *CHS* 2-like				7
Pyricularia oryzae 70-15	T01027	MGG_09962, *chs* 4	MGG_06064, *chs* D	MGG_09551, *chs* 3	MGG_13013, *chs* 8	MGG_13014, *CHS* V	MGG_01802, *chs*1	MGG_04145, *chs* 2				7
Fusarium graminearum	T01038	FGSG_01272, *chs* 4	FGSG_01949, *chs* D	fgr:FGSG_12039, *chs* 6	fgr:FGSG_01964, hypothetical protein	fgr:FGSG_02483, *chs* 2	fgr:FGSG_10116, *chs* 1	fgr:FGSG_10327, *chs* 3	fgr:FGSG_10619, hypothetical protein	fgr:FGSG_03418, *chs* 1	fgr:FGSG_06550, hypothetical protein	10
Purpureocillium lilacinum	T05029	VFPFJ_00650, *chs* D	VFPFJ_00666, *chs* 6	VFPFJ_00667, *chs* 6	VFPFJ_03324, *chs* D	VFPFJ_04443, *chs* A	VFPFJ_08553, *chs* G	VFPFJ_08866, *chs* A	VFPFJ_11040, chs			8
Pestalotiopsis fici W106-1	T04924	PFICI_01118, *chs* 1	PFICI_01446, *chs* 4	PFICI_04362, hypothetical protein	PFICI_04363, hypothetical protein	PFICI_05017, *chs* D	PFICI_05238, *chs* 2	PFICI_06085, *chs* 3	PFICI_07201, *chs* 1	PFICI_12982, hypothetical protein	PFICI_13513, *chs* 1	10
Botrytis cinerea B05.10	T01072	BCIN_01g02520, *CHS* IIIb	BCIN_01g03790, *CHS* IV	BCIN_04g03120, *CHS* IIIa	BCIN_07g01300, *CHS* VII	BCIN_09g01210, *CHS* I	BCIN_12g01380, *CHS* II	BCIN_12g05360, *CHS* VI	BCIN_12g05370, *CHS* V			8
Aspergillus fumigatus Af293	T01017	AFUA_4G04180, *chs* B	AFUA_8G05630, *chs* F	AFUA_5G00760, *chs* C	AFUA_2G01870, *chs* A	AFUA_1G12600, *chs* D	AFUA_3G14420, *chs* G	AFUA_2G13430, *chs*	AFUA_2G13440, *chs* E			8
Aspergillus niger CBS	T01030	ANI_1_316024, chs	ANI_1_2332024, *chs*	ANI_1_1542034, *chs* C	ANI_1_684064, *chs* C	ANI_1_1986074, *chs* D	ANI_1_252084, *chs* D	ANI_1_498084, *chs* B	ANI_1_1214104, *chs* C	ANI_1_120124, *chs* A		9

With the increasing accumulation of genomic sequence data for fungi in recent years, the number of identified *chs* genes in different species has reached approximately 200. However, most of these genes have yet to be fully characterized. Generally, *chs* enzymes are grouped into two divisions, division I (containing *CHS* I–III) and division II (containing *CHS* IV–VII) [29]. Among the members of the *chs* enzyme family (*CHS* I–VII), 6–10 *chs* genes identified in different fungi species encode proteins with discernable structural differences. As shown in **Figure 3**, there are obvious differences in the tertiary structures that distinguish the different classes of *chs* proteins. All *chs* members have multiple transmembrane domains (TMD); however, *CHS* IV–VII enzymes typically contain a cytochrome *b*5-like heme/steroid-binding domain (Cyt-*b*5), which is not found in classes I to III. Furthermore, *CHS* V and *CHS* VI proteins both have an *N*-terminal myosin motor domain (MMD) and a C-terminal chitin synthase domain (CSD) [30]. Although the structures of *CHS* V and *CHS* VI proteins are highly similar and difficult to differentiate, the MMD of *CHS* V proteins contains conserved ATP-binding motifs (ABM, including p-Loop, Switch I, and Switch II) absent in class VI chitin synthases [31]. In addition, *CHS* I–III proteins are characterized by hydrophobic C-terminal and hydrophilic N-terminal regions containing a catalytic domain. In our laboratory, the *chs* protein-encoding gene Monascus_05162, detected in the *M. purpureus* LQ-6 genome, was identified as a *CHS* VI class enzyme based on the tertiary structure of the protein and conserved domain analysis [32].

Organism	T-Number	The Members of Chitin Synthase									Number of Genes
513.88											
Aspergillus nidulans FGSC A4	T01016	AN1555.2, *CHS* V (*chs* D)	AN2523.2, *chs* B	AN4367.2, hypothetical protein	AN4566.2, hypothetical protein	AN6317.2, hypothetical protein	AN6318.2, hypothetical protein	AN7032.2, hypothetical protein			7
Neurospora crassa	T01034	NCU09324, *chs* 4	NCU04352, *chs* 5	NCU04350, *chs* 6	NCU05268, *chs* 6;	NCU05239, *chs* A	NCU03611, *chs* 1	NCU04251, *chs* 3			7
Penicillium digitatum Pd1	T04849	PDIP_79230, *chs* E	PDIP_62350, hypothetical protein	PDIP_46630, *chs* G	PDIP_26990, *chs* D	PDIP_24450, *chs* G	PDIP_15450, *chs* B	PDIP_07640, *chs* A	PDIP_03360, *chs* F		9
Coccidioides immitis RS	T01114	CIMG_05021, *CHS* V	CIMG_05598, *chs* C	CIMG_05647, *chs* G	CIMG_05022, *chs* 5	CIMG_08766, *chs* 4	CIMG_08655, *chs* 2	CIMG_06862, *CHS* VI			8
Monascus purpureus HQ1		TQB77221.1, *CHS* V	TQB75461.1, *CHS* III	TQB73913.1, *CHS* I	TQB72986.1, *CHS* VII	TQB70564.1, *CHS* II	TQB69157.1, *CHS* II	TQB73548.1, hypothetical protein	TQB73973.1, hypothetical protein	TQB73547.1, hypothetical protein	9
Monascus purpureus LQ-6		monascus_02563, *chs*2	monascus_02508, *chs*3	monascus_05,161 *chs* 4	monascus_05162, *chs* 6	monascus_02870, *chs* activator	monascus_02765, *chs* 5	monascus_02400, *chs* G	monascus_04382, *chs* A		8
Monascus purpureus M183		g872, *chs* 2	g920, *chs* F	g3077, *chs*E	g3078, *chs*	g2747, *chs* 3	g5275, *chs* 3	g4739, *chs* B	g5640, *chs* A		8

Figure 3. The structure and classification of members of the chitin synthase family.

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