REVIEW

CHITINOLYTIC ENZYMES OF FUNGI IN THE GENUS *TALAROMYCES*: A BRIEF REVIEW

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Abstract

Chitinolytic enzymes catalyze the hydrolysis of chitin, the second polysaccharide in nature and the main component of the cell wall of fungi and the cuticle of arthropods. Besides a growing attention in medicine, environmental management, and the food industry, these enzymes are increasingly considered for applications in crop protection based on their active role in the control of fungal pathogens and insect pests. Although many fungal biocontrol agents are known to share this potential, species in the genus Talaromyces stand out for their widespread occurrence as components of the plant mycobiome, as both endophytes and rhizosphere associates. An overview of the current knowledge on chitin degrading enzymes of these fungi, their properties, and potential applications in biocontrol is offered in this paper.

Keywords: *chitin, endochitinase, chitobiosidase, β-N-acetylglucosaminidase, mycoparasitism, entomopathogens, plant protection*

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1. Introduction

In the last decades, the awareness that the necessary increase in crop production, to be achieved to cope with the faster growth rate of the human population, cannot anymore be pursued by increasing the chemical inputs in agriculture has prompted this sector to more scrupulously follow the principles of the integrated pest management (IPM), and to implement all forms of biological control of plant pests and parasites. Besides the traditional methods based on the introduction and the augmentation of populations of biocontrol agents, there is an increasing trend to more effectively exploit the biological properties of components of the plant microbiome, which can participate in defensive mutualism [1, 2].

Chitin, a linear β-(1,4) homopolymer of *N*-acetyl-D-glucosamine, is the second polysaccharide occurring in nature after cellulose. It makes up the cuticle of the exoskeleton of arthropods and the cell wall of fungi; moreover, it is a structural component of the pharynx and eggshells of nematodes [3]. Therefore, it represents a target to be considered in the IPM of these agents of plant adversities. In the first instance, this implication has led to crop management practices focused on selecting plant genotypes that overexpress chitinolytic enzymes (chitinases) [4, 5]. However, the recent affirmation of the concept of the plant holobiont has prompted to consider the more immediate and sound support by the plant-associated microbes to provide this function [6].

Among the wide range of fungal and bacterial species that have been described for their aptitude to perform chitin degradation *in vivo*, fungi of the genus *Talaromyces* stand out for their pervasive spread as both endophytic symbionts and rhizosphere associates [7, 8], as well as for their connotation as biocontrol agents of both insect pests and fungal pathogens [9]. The present paper offers an overview of the state of the art concerning research on chitin degrading enzymes of these fungi and their impact in crop protection.

2. *Talaromyces*, Plants and Defensive Mutualism

The genus *Talaromyces* (Eurotiomycetes, Eurotiales, Trichocomaceae) was introduced 70 years ago to classify the teleomorphs of *Penicillium* species that produce soft-walled cleistothecia covered with interwoven hyphae [10]. Following the new taxonomic schemes in mycology based on the concept ‘one fungus, one name’, it has been officially defined as a separate entity, also including *Penicillium* species previously ascribed to the subgenus *Biverticillium* [11]. Widely distributed across terrestrial and marine environments, these fungi are also diverse taxonomically, with as many as 203 species accepted in a recent revision [12]. However, this number is continuously increasing, following the diffusion of molecular methods for the identification of fungi and the exploration of novel geographical and ecological contexts. Accurate phylogenetic analyses demonstrated that the genus was polyphyletic within its original taxonomic boundaries; thus, a number of species have been moved to new genera, such as *Rasamsonia* (e.g., *R. emersonii*) and *Evansstolkia* (e.g., *E. leycettana*) [12, 13], which are not examined in this review.

Within this widespread occurrence and adaptability, *Talaromyces* spp. have been reported to form symbiotic relationships with other organisms. In the case of plants, the available data have pointed out a diffuse aptitude to endophytic colonisation, more or less reflecting the implementation of defensive mutualism [7]. This valuable role can be exerted through multiple effects on plant health, ranging from the improvement of nutrition and growth promotion [14–16], to the release of antibiotics and other bioactive secondary metabolites [17–19], to the production of enzymes affecting the colonisation or infection by pests and disease agents [20–22]. Particularly, the ability to exert

mycoparasitism depends on the release of chitinolytic enzymes upon contact with the mycelium or sclerotia of susceptible plant pathogens, as previously documented for isolates of *T. pinophilus* against the polyphagous soil-borne pathogen *Rhizoctonia solani* (Figure 1). Hyphal coiling and penetration by *T. pinophilus* have also been observed on *Botrytis cinerea* [23]. However, mycoparasitism against important plant pathogens appears to represent a general aptitude in *Talaromyces*. In fact, microscopic evidence of this kind of lifestyle was also obtained for *T. flavus* towards *Verticillium dahliae* and *Agroathelia* (= *Sclerotium*) *rolfsii* [24, 25], for an unidentified strain (*Talaromyces* sp.) towards *Fusarium fujikuroi* and *Rhizopus oryzae* [26], as well as for a potato endophytic isolate of *T. muroii* towards *Alternaria alternata* [27].

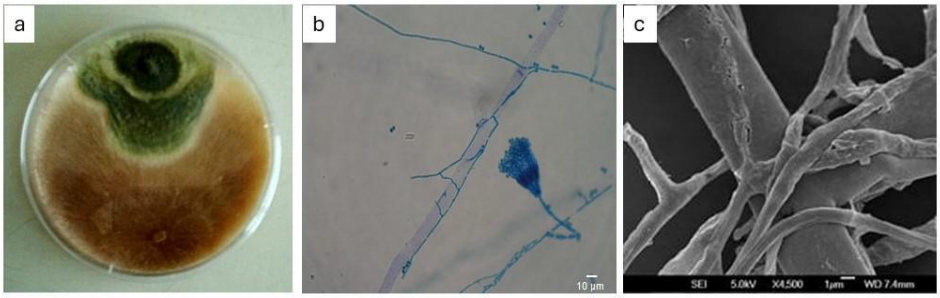

Figure 1. Mycoparasitism of *Talaromyces pinophilus* towards *Rhizoctonia solani*: (a) mycelial overgrowth in dual culture on potato dextrose agar; (b) the thin hyphae of *T. pinophilus* growing adpressed to those of *R. solani* (400×); (c) hyphal penetration after cell wall degradation as visualised by scanning electron microscopy.

Similar to other fungi used in biocontrol, such as *Trichoderma* [28], several studies have considered the direct antifungal effects of *Talaromyces* chitinolytic enzymes. Two such enzymes from the culture filtrate of a strain of *T. flavus* (CGMCC 3.4301) were found to degrade the cell walls of *Sclerotinia sclerotiorum*, *V. dahliae* and *R. solani*, and to inhibit spore germination and germ tube elongation of *A. alternata*, *Fusarium moniliforme* and *Magnaporthe grisea* [29]. Likewise, the purified chitinolytic enzymes of a strain of *T. funiculosus* (CBS 129594) inhibited the growth of *Aspergillus niger* and *Candida albicans* [30].

Indeed, there are several examples of how mycoparasitism by *Talaromyces* spp., either alone or in combination with other antagonistic properties, can be exploited for plant protection against fungal pathogens. Isolates of *T. funiculosus* (formerly *Penicillium funiculosum*) were reported to destroy sclerotia of *S. sclerotiorum* [31]. A strain of *T. purpureogenus* was employed as a biocontrol agent of *Fusarium oxysporum* f.sp. *momordicae* in the rhizosphere of bitter gourd (*Momordica charantia*) [32], while mycelial growth of *Ganoderma boninense*, the agent of basal stem rot of oil palm (*Elaeis guineensis*), was reduced by a strain of *T. apiculatus* [33]. Finally, effective bioformulations based on *T. flavus* were prepared against the agent of damping-off of sugar beet seedlings (*R. solani*) [34], as well as *Verticillium alboatrum* on potato [35].

Likewise, several studies have demonstrated the antagonistic aptitude of *Talaromyces* spp. against insects. A strain of *T. flavus* isolated from a mosquito breeding site in Mexico caused mortality in nymphs of the kissing bug (*Triatoma dimidiata*) [36]. Strains of *T. funiculosus* were able to kill larvae of mosquitoes (*Culex pipiens* and *Aedes aegypti*) [37], and to affect the vitality and oviposition of the leaf miner *Liriomyza sativae* on tomato [38]. Strains of *T. amestolkiae* were found to affect the survival of adults of the

tiger mosquito (*Aedes albopictus*) and the vinegar fly (*Drosophila melanogaster*) [39]. Strains of *T. verruculosus* caused mortality in Oriental tomato thrips (*Ceratothripoides claratris*), citriculus mealybugs (*Pseudococcus cryptus*) and silverleaf whiteflies (*Bemisia tabaci*) [40], as well as larvae of the Mediterranean flour moth (*Ephestia kuehniella*) [41]. Mortality was also induced by a strain of *T. pinophilus* in black bean aphids (*Aphis fabae*) and Russian wheat aphids (*Diuraphis noxia*) [42]. Development of the spotted wing drosophila (*Drosophila suzukii*) was impaired in terms of extension of the pupal stage and reduction of adult longevity by *T. minioluteus* found in the flies' laboratory diet [43]. A strain of *T. diversus* displayed insecticidal activity as assayed by both conidial suspension and culture filtrate against the cotton leafworm (*Spodoptera litura*) [44]. Finally, the use of a strain of *T. pinophilus* was effectively tested in the formulation of a bioinsecticide for controlling the coffee borer beetle (*Hypothenemus hampei*) [45].

It deserves to be mentioned that, besides essentially depending on the release of chitinases, the insecticidal effects of *Talaromyces* may derive from inhibitory effects on the insect's chitin-degrading enzymes. In this respect, phlegmacin B_1, a homodimeric dihydroanthracenone produced by a strain of unidentified species, was found to inhibit chitinase and β-*N*-acetylhexosaminidase of larvae of the Asian corn borer (*Ostrinia furnacalis*). This compound was predicted to bind to the active pockets of both kinds of enzymes. Moreover, it showed moderate inhibitory activities against other bacterial and insect chitinases [46].

3. Chitinolytic Enzymes in *Talaromyces*

Chitin-degrading enzymes belong to three families (18–20) of glycosyl hydrolases (GH) of different ancestral origin [47]. Those produced by fungi, which are involved in multiple functions, from cell wall remodelling to mycoparasitic interactions, belong to GH18 and GH20. With a molecular weight (MW) ranging from 27 to 200 kDa, GH18 chitinases are classified in three subgroups or subfamilies (A, B, and C); these enzymes display diversity in terms of amino acid sequences and structures at their carbohydrate-binding modules (CBMs), which enable stronger binding to insoluble substrates and increase processivity [48, 49]. Enzymes in subgroup A, with a MW of about 40–60 kDa, are exochitinases without CBMs, while members of subgroup B are endochitinases, with a size of 30–50 kDa and a species-dependent variable number of *C*-terminal CBMs. Finally, enzymes in subgroup C are larger in size (120–200 kDa), have *N*-terminal CBMs, and cleave the ends of chitin chains [48, 50]. From a functional point of view, subgroup A chitinases are mainly involved in species growth and development (autolysis); those in subgroup B are related to mycoparasitism and entomopathogenicity, while enzymes in subgroup C are involved in both self and non-self chitin degradation [48, 51].

Purified chitinolytic enzymes mostly show optimal activity at pH 4.0–7.0 and at temperatures between 20 and 40 °C. Depending on their amino acid sequences, three-dimensional structures and hydrolytic mechanisms of catalytic reactions, chitin-degrading enzymes can also be divided into five classes, which may act as endochitinases (EC 3.2.1.14) or exochitinases. The first cleaves at random sites inside the chitin chain to generate chitobiose, chitotriose and chitotetraose fragments. Exochitinases can be further divided into chitobiosidases (EC 3.2.1.29), which catalyse the progressive release of chitobiose from the non-reducing end of chitin, and β-(1,4)-*N*-acetylglucosaminidase (EC 3.2.1.52), which sequentially removes the *N*-acetylglucosamine units from the non-reducing end of the products generated in the course of chitin degradation [52]. Based on the characterisation of substrate specificity by molecular modelling, subgroups A and C are class V chitinolytic enzymes (fungal/bacterial), predicted to be exochitinases with a deep and narrow binding pocket,

while subgroup B corresponds to class III chitinolytic enzymes (fungal/plant), assumed to be endochitinases with a shallow and open binding groove [48]. However, results of a comprehensive study based on a large number of fungal genomes suggest that chitinolytic activity is variable even within subclades, making it problematic to predict their functionality [53].

Several studies have more in-depth characterised chitin-degrading enzymes and their properties in *Talaromyces*. Two chitinolytic enzymes from the previously mentioned strain CGMCC 3.4301 of *T. flavus* were purified to homogeneity by fractional ammonium sulphate precipitation, ion-exchange chromatography on DEAE-sepharose, and phenyl-sepharose hydrophobic interaction chromatography. The MWs of the two enzymes were estimated at 41 and 32 kDa, respectively, and their optimum pH values were determined at 4.0 and 5.0, respectively; the optimum temperature of both enzymes was 40 °C [29]. Another previously mentioned strain (CBS 129594 of *T. funiculosus*) was optimised to promote chitinolytic activity under solid-state fermentation of crustacean bio-wastes integrated with several substrates. The maximum enzyme yield (2.98 U/g substrate) was obtained after seven days of incubation at pH 6.5 with 1:2 crab shell chitin, supplemented with soybean meal, malt extract, yeast extract and cane and beet molasses. The enzyme was purified with a MW of 45 kDa and a specific activity of 9.32 U/mg; the highest activity was observed at pH 6.5 and 40 °C. Moreover, the purified enzyme was found to be activated by several cations (Ca^{2+}, Cu^{2+}, Mg^{2+}, Mn^{2+}, and Na^{+}) and inhibited in the presence of Hg^{2+} and Li^{+} at 10 mM, while Co^{2+} and Zn^{2+} had no effect [30]. The positive influence of sodium was confirmed in studies carried out with a halotolerant endophytic isolate of *T. stipitatus* from the root of the grey mangrove (*Avicennia marina*), which produced chitinolytic enzymes even in the presence of high NaCl concentration [54].

In a screening for chitin-degrading enzyme production by strains of *T. funiculosus, T. pinophilus, T. verruculosus* and *T. aculeatus*, the latter was selected as the best performer. The purified enzyme showed optimum activity at 50 °C and pH 5.5. Separation of isoenzymes was obtained through ion-exchange chromatography followed by gel filtration. Four major peaks corresponding to chitinolytic enzymes with MW of 82.7, 44.6, 28.2, and 26.9 kDa were observed after gel filtration chromatography, while three protein bands with MW of 82.6, 33.9, and 29.1 kDa were identified through SDS-PAGE [55]. This strain of *T. aculeatus* was again the best performer for endochitinase activity in a supplementary study, which comparatively included strains of *Beauveria bassiana* and *Trichoderma harzianum* [56].

Diversity in chitinolytic enzyme expression can also be observed within the same species. As determined in the culture filtrates of a pool of 12 *T. flavus* isolates, the specific activities of these enzymes varied up to 25-fold, with considerable differences among the isolates. Mycoparasitism and biological control were specifically linked to chitinolytic activity, and a mutant strain overproducing extracellular chitin-degrading enzymes showed a stronger activity against the target fungal pathogens [25].

In a recent study, production of chitinolytic enzymes was assessed in solid-state fermentation by two strains of *T. allahabadensis* and *T. funiculosus* isolated from dead black soldier flies (*Hermetia illucens*). The best carbon source was determined to be a powder of moulting mealworms, generating a maximum production of 46.8 and 55.07 U/g of chitinolytic enzymes for the two isolates, respectively. Besides *N*-acetylglucosamine and its dimer, oligosaccharides with a 4–6 degree of polymerisation were obtained, which can be relevant for applications in medicine and health products [57].

4. Genetics and Bioinformatics of *Talaromyces* Chitinolytic Enzymes

The number of chitinase genes varies among different groups of fungi. It has been conjectured that unicellular growth in yeasts is associated with a low number of chitinase gene copies, whereas filamentous growth, implying cell wall remodelling, is considered to require the combined action of several chitinolytic enzymes. This is particularly true in soil-borne ascomycetes performing antagonistic interactions against other fungi [58], as well as in fungi parasitising insects, such as *Metarhizium anisopliae*, which is reported to contain as many as 30 genes [59]. Fungi in the genus *Talaromyces* seem to stand out in this respect too, considering that an even higher number (53) has been recently determined in the genome annotation of strain DC2 (*Talaromyces* sp.), isolated as an endophyte of Madagascar periwinkle (*Cataranthus roseus*) [60]; moreover, GH18 chitinase genes were the most abundant genes annotated in the genome of strain Tp-2 of *T. albobiverticillius* [61].

The fungal GH18 gene family is thought to evolve primarily through adaptive selection schemes [58]. A recent phylogenetic analysis of 72 species belonging to the Ascomycota showed that the chitinase gene family size and enzyme types vary significantly with species evolution, especially in subgroups B and C. Gene expansion and contraction have occurred in most of the taxa, particularly in species in the Hypocreales (class Sordariomycetes). Subgroup B chitinolytic enzymes formed five clusters; their number in broad-spectrum mycoparasitic species appears to be higher than in obligate mycoparasites and saprotrophs. Moreover, a comparative genome analysis indicated that the relatively low number of subgroup B isoforms in *Trichoderma reesei* is likely a consequence of a lifestyle switch from mycoparasitic to saprotrophic [51]. The evidence that entomopathogenic fungi, such as *M. anisopliae* and *B. bassiana*, also possess a higher number of subgroup B chitinases than it would be expected from a random evolutionary process is indicative that both mycoparasites and entomopathogens have undergone selection for an increased employment of these enzymes [62–64]. However, phylogenetic assessments should be thoroughly verified and interpreted, also considering the evidence that the diversity of chitin-degrading enzymes in fungi has been partly shaped by horizontal gene transfer [53].

The above inferences are consistent with the multipurpose biocontrol potential of *Talaromyces*, whose phylogenetic relationships with other fungi were not examined in the study by Wang *et al.* [51]. Based on the availability of sequences of class III A2 chitinases in the National Center of Biotechnology Information (NCBI) online repository, we built an exploratory phylogenetic tree based on these sequences from several *Talaromyces* spp. and other species known as mycoparasites and/or entomopathogens (Figure 2). The separation of the former into two well-delimited clusters indicates a degree of genetic peculiarity and diversity in *Talaromyces*, underscoring the opportunity for more in-depth investigations of these fungi as a source of chitinolytic enzymes.

While a certain progress has been made in the characterisation of *Talaromyces* chitinase genes, data on their promoter motif architectures, transcription factor interactions, and post-translational modifications remain largely unknown [65]. However, gene expression regulatory mechanisms remain essential for optimising production of these enzymes in biotechnological applications [66].

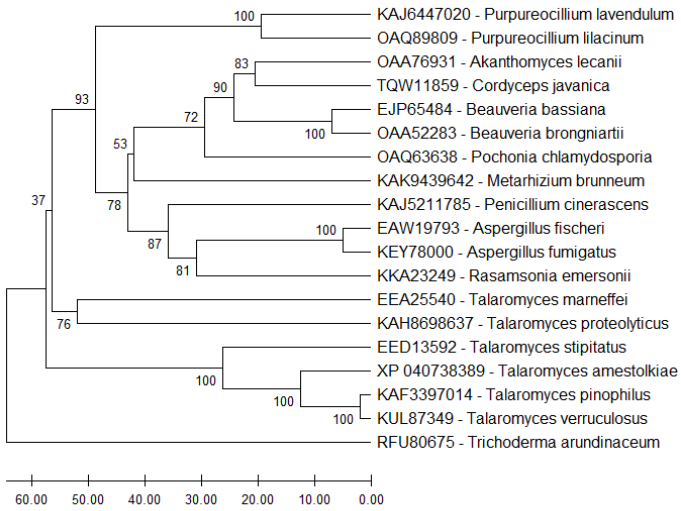

Figure 2. Phylogenetic tree of class III ChiA2 sequences from 19 mycoparasitic and entomopathogenic fungi built using the Unweighted Pair Group Method with Arithmetic mean (UPGMA) after alignment by ClustalW. Results of the bootstrap test (500 replicates) are shown next to the nodes. The evolutionary distances are in units of the number of amino acid differences per sequence. The analysis was conducted in the Molecular Evolutionary Genetics Analysis software ver. 12 (MEGA12) [67].

5. Biotechnological Applications

Recently, the amendment of soil with chitin substrates has become a common practice after several independent studies have shown that it triggers plant disease resistance and a suppressive effect on plant pathogens and nematodes, following a general increase in the abundance of chitinolytic microorganisms [68–70]. In this respect, *Talaromyces* spp. (*T. atroroseus* above all, but also other species such as *T. columbinus, T. flavus, T. radicus*, and *T. trachyspermus*) were found to be highly abundant in a crab shell soil compost produced in Newfoundland (Canada) [71]. This observation underscores the importance of these fungi as multipurpose plant-protection agents, and encourages the adoption of practices aiming to promote their presence and functions in the plant-associated mycobiome [8, 22, 72].

Besides the direct or indirect recruitment of *Talaromyces* in crop protection, chitinolytic enzymes produced by these fungi have raised interest in possible applications across various fields of biotechnology. Attempts to exploit the antifungal properties also concern the medical field, where chitinase from a strain of *T. varians* immobilised with UiO-66 nanoparticles displayed potent activity against *Candida auris* [73].

Glycosides play a valuable role in pharmacology due to their broad spectrum of biological and therapeutic properties. Fungal extracellular β-*N*-acetylhexosaminidases, which specifically cleave *N*-acetylglucosamine and *N*-acetylgalactosamine moieties from various substrates, are employed in the preparation of both natural and modified glycosides and oligosaccharides under mild conditions with good yields. The β-(1,4)-linked oligomers of *N*-acetylglucosamine with a degree of polymerisation ranging from 6 to 11, or chitooligomers, are also applicable in many industrial and pharmacological areas. β-*N*-acetylhexosaminidase from an extremophilic strain (CCF2686) of *T. flavus* (*Tf*Hex)

is remarkable for its synthetic potential and broad substrate specificity, enabling it to process carbohydrates with various functionalities. After having been sequenced and cloned, its production was improved in recombinant *Pichia pastoris*, where it retained the same biochemical and catalytic properties [74]. Computational studies disclosed its three-dimensional structure, revealing the structural features responsible for its higher substrate specificity [75]. Subsequently, it was engineered via site-directed mutagenesis, from which three efficiently transglycosylating variants were obtained displaying a suppressed hydrolytic activity. These mutant enzymes enabled the preparation of several natural and modified chitooligomers in sufficient amounts for complete spectral characterisation, which are available for potential biotechnological applications [76]. Further investigations revealed that the mutation of the Tyr470 residue to histidine greatly enhanced its transglycosylation capability. The mutant enzyme (Y470H) was tested with acceptors based on β-glycosides of uronic acid and *N*-acetylmuramic acid (AMA); a glycosylation product was isolated and characterised in low yield with the latter acceptor, representing the first example of enzymatic glycosylation of an AMA derivative [77]. Furthermore, seven glycosynthase-type variants of *Tf*Hex were designed bearing a mutation at the catalytic aspartate residue that stabilises the oxazoline reaction intermediate. Some variants lost most of their original hydrolytic activity towards *p*-nitrophenyl-2-acetamido-2-deoxy-β-D-glucopyranoside (*p*NP-β-GlcNAc) and were not active with 2-acetamido-2-deoxy-D-glucopyranosyl-α-fluoride as the proposed glycosynthase donor. Conversely, five mutant enzymes retained a strong transglycosylation activity towards *p*NP-β-GlcNAc, characterising them as valuable tools for the synthesis of chitooligosaccharides [78].

Talaromyces fungi have also been considered for biotransformation. A strain of *T. verruculosus* was used as the recipient of endo-β(1,4)-chitinase of *Thermothelomyces thermophilus* (= *Myceliophthora thermopila*) for its high secretory capacity, affording up to 60 g/L of extracellular protein in the culture medium; the recombinant CHIT strain stood out for high productivity of the target enzyme [79].

The interaction of chitinolytic enzymes with other exoenzymes concomitantly produced by biological control agents also deserves more in-depth assessments. In fact, fungi in the genus *Talaromyces* are also known and exploited in biotechnology for the production of other enzymes, such as mannanases [80], cellulases [81, 82], arabinofuranosidase [83], β-glucanases, xylanases, phytases, α-galactosidases, pectin lyases, polygalacturonases, dextranases and exo-inulinases [80], which may both integrate their biocontrol aptitude and boost plant resistance.

6. Conclusions

Chitinolytic microorganisms are at the forefront of crop protection. A key scope of future research should be a more in-depth understanding of the molecular mechanisms of production of chitin-degrading enzymes in plant-associated microbes, with the aim to improve their capacity to contrast all sorts of pests and disease agents. In this respect, *Talaromyces* spp. are particularly valuable with reference to their aptitude of being able to contrast both these kinds of plant adversities.

7. Acknowledgement

Luigi De Masi wishes to dedicate this review article to the beloved memory of his mother Carolina (17 December 1948 - 21 December 2025), who inspired his molecular biology studies and research activities on biodiversity and bioresources.

8. Author Contributions

Conceptualisation, R.N. and L.D.M.; writing—original draft preparation, R.N. and L.D.M.; writing—review and editing, R.N. and L.D.M.; supervision, R.N.; funding acquisition, R.N. and L.D.M. All authors have read and agreed to the published version of the manuscript.

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