Cladosporium Entomopathogenicity

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The range of interactions between *Cladosporium*, a ubiquitous fungal genus, and insects, a class including about 60% of the animal species, is extremely diverse. Conventionally, *Cladosporium* species are not considered full-right representatives of the guild of entomopathogens, which is generally restricted to specialized fungi such as *Beauveria*, *Metarhizium* and *Lecanicillium/Akanthomyces*. However, like other fungi that are widely associated with crops such as *Trichoderma* and *Talaromyces*, the evidence is increasing that *Cladosporium* may also infect insects and cause epizootics in pest populations or promote plant defense reactions.

Keywords: interactions ; biocontrol ; *Cladosporium* ; insects ; fungi ; plant

1. Introduction

Fungi in the genus *Cladosporium* (Dothideomycetes, Cladosporiaceae) are ubiquitous and reported from any terrestrial and marine substrate, including all kinds of living organisms [1]. This is linked to their profuse sporulation, which allows the spread of conidia through atmospheric agents over long distances. Thus, the mere isolation of these fungi from plants and animals does not necessarily imply a symbiotic association. However, generality is not a rule, and in many cases, this pervasiveness subtends either occasional or more systematic biotic relationships that influence the fitness of the associated organisms in diverse ways [2][3][4].

Direct observations of the parasitic aptitude of insects are limited and essentially concern the case of *C. cladosporioides* on the sugarcane white wooly aphid (*Ceratovacuna lanigera*: Hemiptera, Aphididae); both light and electron microscopy at the host–parasite interface showed that nymphs and adults of the aphid were completely overgrown by the fungal mycelium, which penetrated and disrupted their powdery waxy coating [5].

However, circumstantial evidence of entomopathogenic aptitude in *Cladosporium* derives from several studies reporting on mortality induced by conidial suspensions administered at various concentrations and exposure times. In this regard, the available data concerning strains that proved to be effective against various targeted pests in experimental trials are summarized in **Table 1**.

Table 1. Reported effectiveness of conidial suspensions of *Cladosporium* in inducing mortality on insect pests.

Cladosporium Species	Source	Insect Targets	Country	Reference
C. cladosporioides	*Bemisia* sp.	*Bemisia* sp.	Egypt	[6]
	Brevicoryne brassicae	*B. brassicae*	Egypt	[7]
	Culex quinquefasciatus	*C. quinquefasciatus*	Iraq	[8]
	endophytic	*Duponchelia fovealis*	Brazil	[9]
	Kermes sp.	*Hemiberlesia pitysophila*	China	[10]
	Lycorma delicatula	*Tenebrio molitor*	USA	[11]
	Myzus persicae	*M. persicae*	Iraq	[12]
	Nilaparvata lugens	*Bemisia tabaci*	Bangladesh	[13]
	Pulvinaria aurantii	*Aphis fabae*	Iran	[14]
	Sitophilus oryzae	*Rhyzopertha dominica* *Sitophilus zeamais* *Trogoderma granarium*	Pakistan	[15]
	soil	*Metopolophium dirhodum*	Egypt	[16]
C. oxysporum	endophytic	*A. fabae*	Algeria	[17]
	endophytic	*Chilo partellus*	India	[18]
	Planococcus citri	*Pseudococcus longispinus* *Pulvinaria aethiopica* *Toxoptera citricida* *Trioza erytreae*	South Africa	[19]
	unknown	*Aphis craccivora*	India	[20]
C. sphaerospermum	endophytic	*D. fovealis*	Brazil	[9]
Cladosporium sp.	*Helicoverpa armigera*	*Aphis gossypii* *B. tabaci* *H. armigera*	Australia	[21]
	Spodoptera frugiperda	*S. frugiperda*	China	[22]
Cladosporium spp.	several species of sap-sucking Hemiptera	*A. craccivora* *A. gossypii* *B. tabaci*	Egypt	[23][24]
C. subuliforme	*Diaphorina citri*	*D. citri*	China	[25]
C. tenuissimum	*M. persicae*	*M. persicae*	Iraq	[12]
	Trachymela sloanei	*S. frugiperda*	China	[26]
C. uredinicola	*A. gossypii* *B. tabaci*	*A. gossypii* *B. tabaci*	Egypt	[27]
	Bemisia sp.	*Bemisia* sp.	Egypt	[6]
C. xanthocromaticum	*M. persicae*	*M. persicae*	Iraq	[12]

Alternatively, the anti-insectan effect can be assessed through the addition of the fungi or their products to the laboratory diet. In this respect, when incorporated in the feed of larvae of the tobacco budworm (*Chloridea virescens*: Lepidoptera, Noctuidae), an isolate of *C. cladosporioides* was found to reduce larval and pupal weights by 56% and 7%, respectively; moreover, in preference tests, the caterpillars showed a marked tendency to avoid feed amended with the fungus [28]. Development of another noctuid moth, the tobacco cutworm (*Spodoptera litura*), was significantly prolonged when larvae were fed on a diet amended with ethyl acetate extract of *C. uredinicola* at concentrations of 1.25–2.00 μL g^{-1}; moreover, at 2.00 μL g^{-1}, a significantly higher number of adults emerged showing morphological deformities. At higher concentrations, significant reductions in adult emergence, longevity and reproductive potential were recorded. Finally, the toxicity of the ethyl acetate extract was further evidenced by a reduction in feed utilization by the larvae [29].

The ethyl acetate and methylene chloride extracts of a strain of *C. cladosporioides* were effective against nymphs and adults of the cotton aphid (*Aphis gossypii*: Hemiptera, Aphididae) [30][31]. Aphicidal effect was also displayed by formulations based on emulsions of culture filtrates of an endophytic strain of *C. oxysporum* endowed with proteolytic activity, which were more active than conidial suspensions against the black bean aphid (*Aphis fabae*: Hemiptera, Aphididae) [17]. In a subsequent experiment, formulations based on culture filtrates of this strain and two more endophytic isolates of *C. echinulatum* and *Cladosporium* sp. showed activity against the green peach aphid (*Myzus persicae*: Hemiptera, Aphididae), which increased at increasing concentrations. A significant reduction in the number of colonizing aphids and a relative increase in the number of winged adults were recorded. Moreover, the pretreatment of plants negatively influenced embryonic development, thus affecting fertility [32]. In the same study, consistent chitinolytic activity was determined in the culture filtrates of *Cladosporium* sp.; indeed, chitinases are considered a main factor in the bioactivity of fungal culture filtrates, as also documented for other strains of *Cladosporium* spp. [24], *C. cladosporioides* [12] [33], *C. tenuissimum* and *C. xanthocromaticum* [12].

Even more, the anti-insectan effects of culture filtrates may depend on the presence of toxic compounds (**Figure 1**). Fungi in the genus *Cladosporium* are known as prolific producers of bioactive secondary metabolites [34], some of which have been detected as possible determinants of detrimental effects on insects. This is the case of bassianolide, a cycloligomer depsipeptide identified as a product of a strain related to the *C. cladosporioides* s.c. [35]. The alkaloid 3-(4β-hydroxy-6-pyranonyl)-5-isopropylpyrrolidin-2-one was identified in the ethyl acetate extracts of another strain of *C. cladosporioides* displaying aphicidal activity [30]. Another alkaloid, hydroxyquinoline, was identified as the potentially active product in the extracts of a strain of *C. subuliforme* [25]. The novel compound citreoviridin A was extracted from an isolate of *C. herbarum* from a marine sponge and found to inhibit the growth of larvae of the cotton leafworm (*Spodoptera littoralis*: Lepidoptera, Noctuidae) [36]. Chlorogenic acid, purified from an endophytic isolate of *C. velox*, displayed insecticidal activity by inducing significant mortality in the larvae of *S. litura* or adversely prolonging their developmental period. This phenolic compound, previously known to cause gut toxicity in lepidopterans [37], was characterized as an α-glucosidase inhibitor, performing a non-competitive type of inhibition in vitro; it also inhibited the activity of α-glycosidases in the gut of the larvae [38][39].

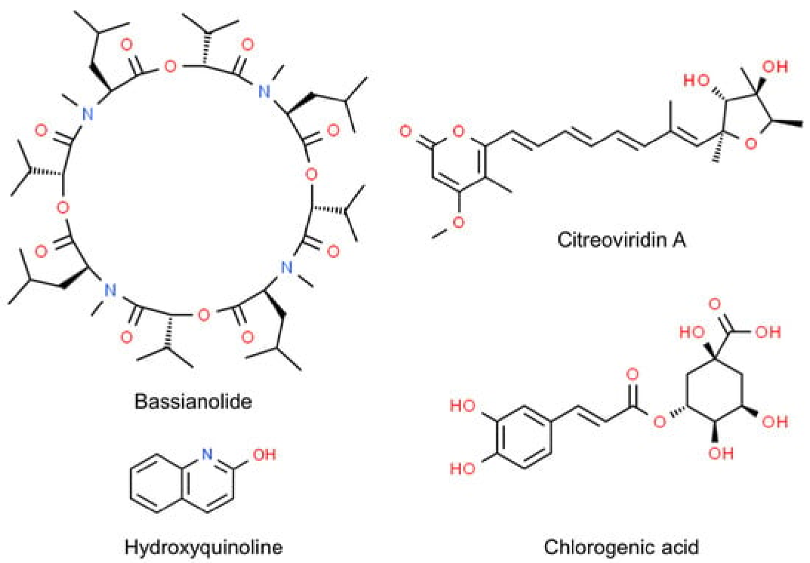

Figure 1. Chemical structure of *Cladosporium* secondary metabolites displaying anti-insectan effects.

The importance of secondary metabolites for entomopathogenic aptitude in *Cladosporium* has been further affirmed after a study carried out on strains associated with the Chinese white wax scale (*Ericerus pela*: Hemiptera, Coccidae). This insect is known to be infected by *Cladosporium* spp. related to *C. sphaerospermum* and *C. langeronii*, which kill the scales after dramatically altering their microbiome [40]. However, the scales were later found to also harbor a non-infective *Cladosporium*. Genome sequencing showed that the non-infective strain is related to *C. cladosporioides* and has a larger genome size than a pathogenic one, which is more related to *C. sphaerospermum*. Particularly, the former has specific genes involved in nutrition pathways that are absent in the pathogen. Conversely, the latter possesses genes participating in the biosynthetic pathways of mycotoxins, such as asperfuranone, emericellamide and fumagillin. These genes were not found in the non-pathogenic strain, which, on the other hand, presented genes associated with reduced virulence [3].

2. Interactions with Biocontrol Agents

Reports on the occurrence of an association with predatory and parasitoid insects introduce the question of whether the insecticidal properties of *Cladosporium* may also affect the performances of biocontrol agents employed in crop protection. Indeed, this association can be more than merely occasional, considering that *Cladosporium* were the most abundant fungi detected in the gut of the multicolored Asian lady beetle (*Harmonia axyridis*: Coleoptera, Coccinellidae) feeding on the pea aphid (*Acyrthosiphon pisum*: Hemiptera, Aphididae) [41]. Concerning this issue, a previously mentioned strain of *Cladosporium* sp. from *H. armigera* was found not to induce significant harmful effects on a panel of beneficial predatory insects, including the red and blue beetle (*Dicranolaius bellulus*: Coleoptera, Melyridae), the transverse ladybird (*Coccinella transversalis*: Coleoptera, Coccinellidae), the green lacewing (*Mallada signatus*: Neuroptera, Chrysopidae) and the damsel bug (*Nabis kinbergii*: Hemiptera, Nabidae) [21]. Conversely, laboratory assays carried out in Egypt showed that treatment with *C. uredinicola* affected the biocontrol of the silverleaf whitefly (*Bemisia tabaci*: Hemiptera, Aleyrodidae) by the eleven-spotted ladybird (*Coccinella undecimpunctata*: Coleoptera, Coccinellidae) and the parasitoid *Eretmocerus mundus* (Hymenoptera, Aphelinidae) in various ways. In fact, all larval stages of the coccinellid were sensitive to the fungus and tended to avoid feeding on the infected whiteflies. As for the parasitoid, although mortality of the exposed individuals was low, most females avoided laying eggs on treated nymphs; nevertheless, the combined use of *C. uredinicola* and *E. mundus* was found to synergistically increase the suppression of nymphs [42].

Olfactory experiments carried out in the laboratory indicated that the parasitoid wasp *Lysiphlebus fabarum* (Hymenoptera, Braconidae) can detect cues from aphids (*A. fabae*) infected by a pathogenic strain of *Cladosporium* sp. and avoid them; hence, the employment of this strain in the field could not affect the performance of the parasitoid, implying compatibility between these, and possibly more, biological control agents of aphids [14].

3. Plant-Mediated Interactions

In addition to arising after direct contact or ingestion of conidia, the entomopathogenic effects of *Cladosporium* can also be exerted in planta, as promoted by strains able to develop endophytically. Indeed, it is known that endophytic fungi may improve plant resistance to biotic adversities through various mechanisms, including general effects on fitness and growth promotion eventually exerted in synergistic relationships with other components of the plant microbiome [43][44]. The belief is gaining ground that these valuable properties could be exploited for improving yields while reducing the input of chemicals in crop management [45][46].

Cauliflower plants artificially infected with an endophytic strain of *C. uredinicola* did not show any disease symptoms, and the vigor of endophyte-infected plants also did not differ from untreated plants. Interestingly, larvae of *S. litura* feeding on leaves from treated plants were sluggish and underwent significantly higher mortality than the control. Most of the larvae died at the time of molting to the last instar, while the survivors took a significantly longer time to pupate and further suffered significantly higher mortality at the pupal stage. In the end, fewer adults emerged from larvae on endophyte-supplemented plants; some adults exhibited morphological deformities, such as crumpled and unequal wings, and survived for a very short time. Inhibitory effects were also observed on the reproductive potential and the hatchability of eggs. The life span of females that emerged from larvae fed on plants hosting *C. uredinicola* reduced significantly, while male longevity remained unaffected [47]. All these effects were assumed to depend on physiological changes induced by the endophyte. In fact, further studies disclosed cytotoxic effects on hemocytes of *S. litura* fed on endophyte-supplemented cauliflower plants, which showed changes in shape, extensive vacuolization and necrosis. Moreover, these abnormalities increased along with the feeding duration and ultimately resulted in adverse consequences on the fitness and survival of the insect [48].

However, it is quite intuitive to consider that plant-mediated relationships should be examined case by case, as the outcome of the interaction is not necessarily unfavorable to the insects. When inoculated in perennial thistle (*Cirsium arvense*), where it is known to develop endophytically, *C. cladosporioides* increased feeding of the thistle tortoise beetle (*Cassida rubiginosa*: Coleoptera, Chrysomelidae), while it had no effect on the cabbage moth (*Mamestra brassicae*: Lepidoptera, Noctuidae). Nevertheless, dual infection with *C. cladosporioides* and *Trichoderma viride* greatly reduced beetle feeding [49]. These findings indicate that the promoting effects of *C. cladosporioides*, as well as of other endophytes, depend on both the degree of specialization of the herbivore and the species assortment in the plant microbiome, which in turn may induce chemical changes in the host. Undoubtedly, these fungi deserve higher attention in the study of insect–plant interactions, considering that their endophytic occurrence could remarkably influence insect growth and even pest population dynamics.

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