Intracellular Mycoparasites in Action: Interactions Between Powdery Mildew Fungi and *Ampelomyces*

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Contents

Abstract

Pycnidial fungi of the genus *Ampelomyces* are widespread intracellular mycoparasites of powdery mildew fungi worldwide. Their pycnidia are produced in hyphae, conidiophores and immature ascomata of their mycohosts. Thus, they suppress both the asexual and the sexual reproduction of the invaded powdery mildew mycelia, and then destroy them completely. Conidia of *Ampelomyces* are released from the intracellular pycnidia by the rupture of the pycnidial wall; conidia then germinate on the host plant surfaces, penetrate the intact hyphae of powdery mildew mycelia found in their vicinity and invade them internally growing from cell to cell through the septal pores of the mycohost. The early stage of mycoparasitism is apparently biotrophic, but the invaded cytoplasm then begins to die and a necrotrophic interaction results. Toxin production has not been detected in *Ampelomyces*, so it might act directly by invasion and destruction of the

host cytoplasm. Experimental data showed that parasitized powdery mildew colonies can continue their growth, but their sporulation is stopped soon after *Ampelomyces* penetrated their mycelia. It is concluded that these mycoparasites represent a stress factor in the life cycle of their mycohosts but their role in the natural control of powdery mildew infections requires further investigations.

1. INTRODUCTION

Parasites, by definition, have a negative effect on host fitness because their activities represent a biotic stress for the host organisms (Jarosz and Davelos, 1995). Mycoparasites, that is, fungi that parasitize other fungi, are a diverse group of parasites which include fungi that absorb nutrients from their myco-hosts through haustoria, or other special interfaces between their cell walls and membranes, or invade the mycelia of the mycohosts internally, growing from cell to cell in the hyphae, spores, fruiting bodies and other structures of their mycohosts, and absorbing nutrients from there (Jeffries and Young, 1994). The structural and ultra-structural aspects of the diverse types of mycoparasitism are relatively well known (Jeffries and Young, 1994; Jeffries, 1997); however, mycoparasites are still a relatively less studied group of parasites from an ecological point of view (Hirsch and Braun, 1992; Cooke and Whipps, 1993; Jeffries, 1995, 1997; Kiss, 2001). Our knowledge on the role of mycoparasites in natural inter-fungal relationships is still very limited (Hirsch and Braun, 1992; Jeffries, 1995; Kiss, 1998). In a broader ecological context, in multi-trophic relationships, little is known about the interactions among parasitized fungi, their mycoparasites and a variety of organisms other than fungi (Hirsch and Braun, 1992; Kiss, 2001). In short, little is known about both the amount and the significance of the biotic stress caused by mycoparasites in their mycohosts under natural conditions. This is interesting to note because the use of a number of mycoparasites in the biological control of various plant pathogenic fungi is largely based on their supposed importance in the natural control phenomena (Cooke and Whipps, 1993).

The interactions between powdery mildew fungi, obligate biotrophic parasites of many plants, and their *Ampelomyces* mycoparasites, are one of the most evident cases of mycoparasitic relationships in nature, because this relationship is common worldwide and takes place exclusively on aerial plant surfaces, thus facilitating its direct observation (Kiss, 1998, 2004). Sometimes the natural occurrence of *Ampelomyces* mycoparasites in powdery mildew colonies is visible in the field even to the naked eye (Figure 1). Historically, pycnidial fungi, belonging to the genus *Ampelomyces*, were among the first mycoparasites to be studied in detail (De Bary, 1870) and also among the first fungi used as potential biocontrol agents of economically important plant pathogens (Yarwood, 1932). This paper reviews their mode of action in the mycohost mycelia and also the experimental data on the damage (the amount of stress) caused by them in the powdery mildew colonies.

Figure 1   Powdery mildew-infected *Lycium halimifolium,* a common solanaceous plant in eastern Europe and elsewhere. The brownish patches in the white powdery mildew colonies are masses of intracellular pycnidia of *Ampelomyces*. This is a common and an evident case of a tri-trophic relationship in the phyllosphere. **(See Colour Section)**

2. DETAILS OF THE MYCOPARASITIC INTERACTION

2.1 Life Cycle

Pycnidia of *Ampelomyces* are commonly found in the cells of the hyphae, conidiophores (Figures 2–3B) and immature ascomata (Figure 3C) of powdery mildew fungi worldwide (Falk *et al.*, 1995a, 1995b; Kiss *et al.*, 2004). Conidia are produced in these intracellular pycnidia and are unicellular, hyaline, mostly guttulate and are embedded in a mucilaginous matrix inside the pycnidia. In the presence of water, these matrices swell and conidia are released from intracellular pycnidia as a cirrhus by the rupture of the pycnidial wall (Figure 3C). In approximately 10–20 h, under conditions of high humidity, conidia germinates and the emerging hyphae of the mycoparasites can then penetrate the hyphae and conidia (Figures 3D–4B) of powdery mildews in their vicinity. The concentration of *Ampelomyces* conidia on the leaves is an important factor as Gu and Ko (1997) showed experimentally that germination rapidly decreases above a concentration of 10^6 cfu ml^{-1} due to the production of a self inhibitor. After penetration, the hyphae of the mycoparasite continue their growth internally (Figure 4A–D) and produce their intracellular pycnidia after 5–8 days in the mycelia of their host fungi (Figures 2–3B and 4D(II)). A high relative humidity of the environment enhances the internal growth and sporulation of *Ampelomyces* (Jarvis and Slingsby, 1977; Philipp and Crüger, 1979).

Conidia can be dispersed within the plant canopy by rain-splash or water runoff from plant surfaces. *Ampelomyces* can also spread to long distances as
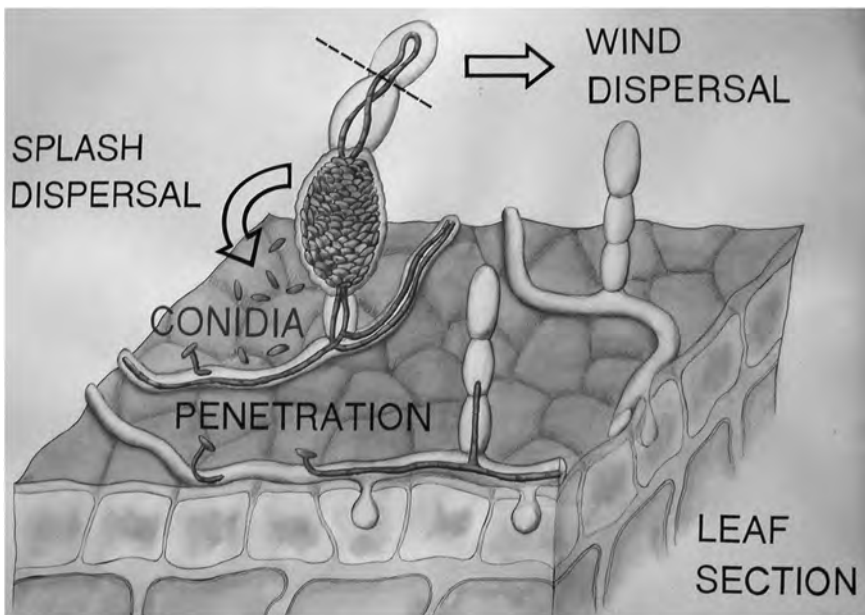

Figure 2 The life cycle of *Ampelomyces* mycoparasites in an asexually reproducing powdery mildew colony. The parasitism of immature ascomata is not represented in the figure. **(See Colour Section)**
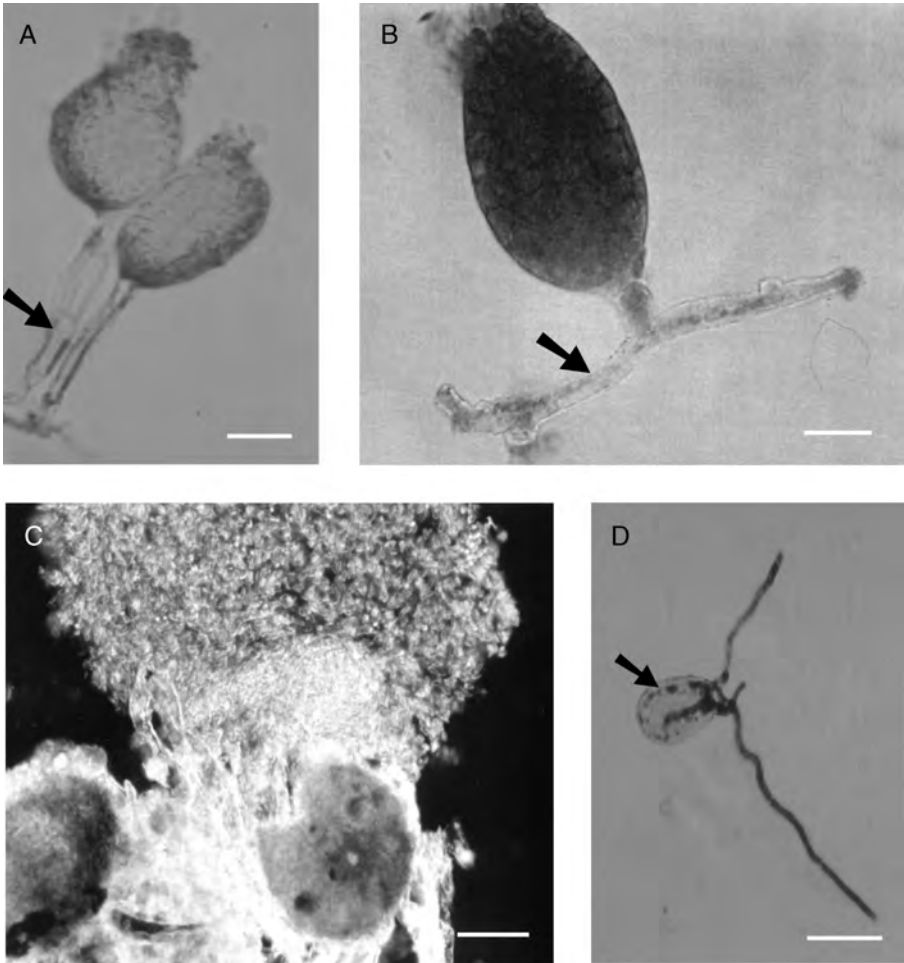
Figure 3 Aspects of the interactions between *Ampelomyces* mycoparasites and powdery mildew fungi. A: intracellular hyphae (arrow) and two pycnidia of *Ampelomyces*, slightly stained with cotton blue, and produced in the conidiophores of *Golovinomyces depressa* infecting *Arctium minus*. Bar equal 30 μm. B: a pycnidium of *ampelomyces* in the basal cell of a conidiophore of *G. orontii* infecting *Cucurbita pepo*. The arrow indicates an intracellular hypha. The *Ampelomyces* structures were stained with cotton blue. Bar equal 25 μm. C: conidia of *Ampelomyces* released from a parasitized ascoma of the apple powdery mildew fungus, *Podosphaera leucotricha*, after over-wintering in a bud on an apple tree. Bar equal 50 μm. D: intracellular hyphae of *Ampelomyces* (arrow), stained with cotton blue, emerging from a conidium of *E. syringae-japonicae* infecting *Ligustrum vulgare*, after placing powdery mildew conidia collected from the field on water agar for 24 h. Bar equal 20 μm. **(See Colour Section)**

hyphal fragments in parasitized and detached powdery mildew conidia (Figures 2 and 3D) (Jarvis and Slingsby, 1977; Speer, 1978; Sundheim, 1982). When these parasitized air-borne conidia land close to any powdery mildew colony under humid conditions, the outgrowing hyphae of *Ampelomyces*
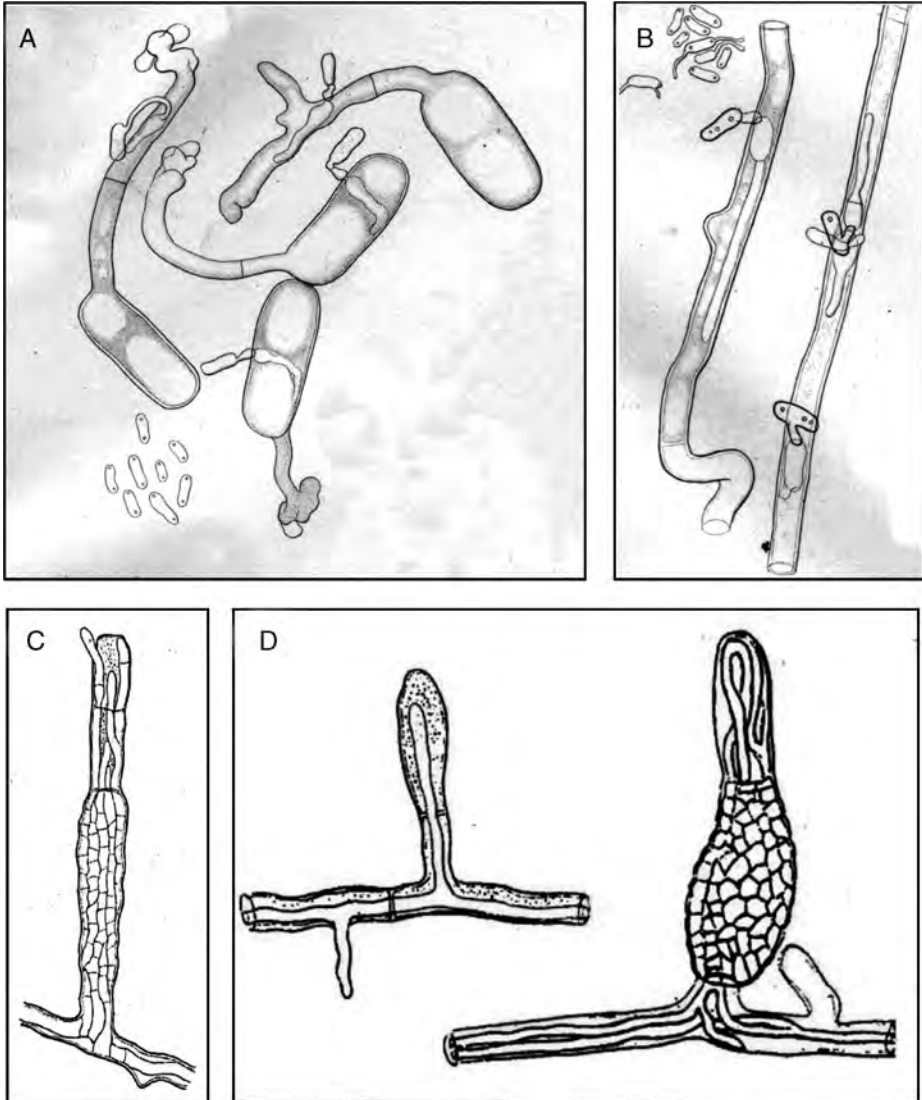
Figure 4 Drawings from De Bary (1870) showing the details of the interactions between *Ampelomyces* mycoparasites and powdery mildew fungi. A: Penetration of the germ tubes of *Ampelomyces* conidia into germinating conidia of *E. heraclei* infecting *Anthriscus silvestris*. B: Penetration of the germ tubes of *Ampelomyces* into the hyphae of *Neoerysiphe galeopsidis* infecting *Galeopsis tetrahit*. C: A young, immature pycnidium of *Ampelomyces* produced in the basal cell of a conidiophore of *N. galeopsidis* infecting *G. tetrahit*. The intracellular hyphae of *Ampelomyces* emerged from the cells of the conidiophore after keeping the parasitized powdery mildew mycelium in water for a few hours. D(I): An outgrowing *Ampelomyces* hypha from the same powdery mildew species after keeping the parasitized powdery mildew in water for a few hours. D(II): An *Ampelomyces* pycnidium in the basal cell of a conidiophore of the same powdery mildew species.

(Figure 3D) can penetrate their mycelia. Thus, *Ampelomyces* can be transported far from its original fungal host and can parasitize other powdery mildew species. After penetration, the hyphae of *Ampelomyces* invade the host mycelium internally (Figures 2 and 4A–D), and produce their pycnidia mostly in the conidiophores (Figures 2–3B and 4D(II)) and young, immature ascomata (Figure 3C) of powdery mildews. Occasionally, they also produce pycnidia in the invaded hyphal cells. The life cycle starts again when pycnidia are mature. The sexual stage is unknown in *Ampelomyces*.

Until recently, little was known about the over-wintering of *Ampelomyces*. De Bary (1870), Emmons (1930) and Yarwood (1939) found that the fungus can produce pycnidia saprophytically in the senescent or dead-plant tissues at the end of the season, and suggested that these structures served as over-wintering structures for *Ampelomyces* in the field. However, Falk *et al.* (1995a, 1995b) considered that saprophytic pycnidia produced in leaf debris were not significant for the over-winter survival of *Ampelomyces* in North American vineyards. They showed that pycnidia of *Ampelomyces* survived until the next season mainly in the parasitized ascomata produced on the bark of grapevine stocks. Similarly, Marboutie *et al.* (1995) found that pycnidia of *Ampelomyces* over-wintered in the parasitized ascomata of *Podosphaera pannosa* on the bark of peach trees. Conidia of *Ampelomyces* are probably rain dispersed from the parasitized ascomata in spring, and then germinate on the young leaves and, if powdery mildew colonies are present, penetrate their hyphae and invade their mycelia (Falk *et al.*, 1995a, 1995b).

A detailed study of the over-wintering of *Ampelomyces* on apple trees and 13 other woody and herbaceous host-plant species revealed that these mycoparasites can survive the winter in many different ways on the host-plant surfaces. Experiments carried out using detached mildew-infected leaves maintained *in vitro* demonstrated that the over-wintered pycnidia of *Ampelomyces* collected from the host plants in the spring, and produced in both the conidiophores and the immature ascomata (Figure 3C) of powdery mildews during the previous season, can initiate the life cycle of these mycoparasites (Szentiványi and Kiss, 2003). Conidia found in some of the over-wintered pycnidia and, in addition, cells of the pycnidial walls of empty pycnidia germinated in the spring and gave rise to new intracellular pycnidia of *Ampelomyces* when powdery mildew colonies were inoculated with them *in vitro*. Similar experiments showed that the thick-walled, brownish resting hyphae of *Ampelomyces*, described for the first time by De Bary (1870), could also serve as sources of primary inocula of *Ampelomyces* in the spring (Szentiványi and Kiss, 2003). So, this study demonstrated that the conidia, the pycnidial cells and the cells of the resting hyphae of *Ampelomyces* produced in the mycelia of powdery mildews during the previous season can initiate the life cycle of these mycoparasites in the spring.

2.1.1 De Bary's Pioneering Studies on *Ampelomyces*

In the 19th century, soon after *Ampelomyces quisqualis* was described succinctly as a pycnidial fungus associated with powdery mildew colonies covering grapevine leaves (Cesati, 1852), a number of mycologists (e.g., Mohl, 1852; Tulasne, 1856)

considered that its pycnidia are special-fruiting bodies of the powdery mildew fungi with which they were found (Figure 5). The first thorough study of *A. quisqualis* was carried out by De Bary (1870) who clearly recognized that this fungus is an intracellular parasite of the Erysiphales. He named it as *Cicinnobolus cesatii* and showed that its hyphae grow internally in the mycelia of powdery mildews from cell to cell through the septal pores (Figure 4A–D(I)), and produce their pycnidia in one or two cells of the hyphae, conidiophores (Figure 4D(II)), conidium initials and ascomata of their fungal hosts. Much later, Speer (1978) criticized De Bary's drawings as these do not show that the intrahyphal hyphae of *Ampelomyces* become narrower when they penetrate the septal pores and then thicken again in the next cell. However, this is clearly shown in some of De Bary's drawings (e.g., Figure 4A) that illustrate the penetration of the germinating conidia of *Ampelomyces* into germinating conidia of a powdery mildew fungus.

De Bary (1870) proved experimentally that the intracellular hyphae could grow out from the parasitized cells when placed in water for a few hours (Figure 4C and D(I)). In addition, De Bary (1870) carried out cross-inoculation experiments demonstrating that an *Ampelomyces* mycoparasite collected from a given powdery mildew species could also produce intracellular pycnidia in mycelia of other powdery mildew species. This was subsequently supported by many experiments (e.g., Philipp and Crüger, 1979; Sztejnberg *et al.*, 1989; Szentiványi and Kiss, 2003; Liang *et al.*, 2007).
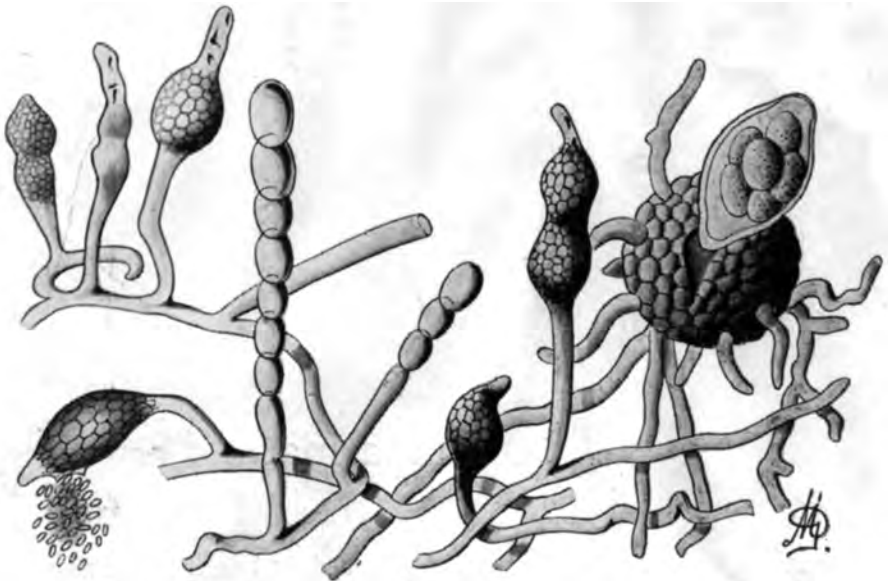
Figure 5 In the 19th century, some mycologists like Mohl (1852) and Tulasne (1856) thought that *Ampelomyces* pycnidia and conidia belong to the life cycle of the erysiphales. Thus, these were considered as special fruiting bodies of the powdery mildew fungi with which they were found. We show here one of Tulasne's drawings re-drawn by Moesz (1912).

De Bary's pioneering work was the first detailed study of an inter-fungal parasitic relationship. Emmons (1930) subsequently published an extensive cytological study describing in detail the penetration, growth and sporulation of *Ampelomyces* in the ascomata of powdery mildews. The potential for biocontrol was realized around the same time and Yarwood (1932) reported the treatment of powdery mildew infected plants with a conidial suspension of *Ampelomyces*, thus carrying out the first biocontrol experiment against a plant pathogenic fungus.

2.1.2 Mode of Action of *Ampelomyces*

Some biocontrol fungi have more than one mechanism to antagonize their hosts (Jeffries and Young, 1994). *Trichoderma* spp., for example, produce antifungal compounds, act as mycoparasites, induce plant defence mechanisms and can stimulate plant growth (Howell, 2003; Harman *et al.*, 2004). In contrast, *Ampelomyces* acts directly by invasion and destruction of host cytoplasm. *Ampelomyces* kills the parasitized powdery mildew hyphae by causing a rapid degeneration of the cell contents (Hashioka and Nakai, 1980). Toxin production has not been detected in *Ampelomyces* (Beuther *et al.*, 1981) in contrast to other pycnidial mycoparasites, such as *Coniothyrium minitans* (Machida *et al.*, 2001; McQuilken *et al.*, 2002, 2003).

The presence of the mycohosts is recognized by *Ampelomyces*, and a water-soluble substance from powdery mildew conidia was shown to stimulate the germination of *Ampelomyces* conidia *in vitro* (Gu and Ko, 1997). Directed growth of germ-tubes of *Ampelomyces* towards powdery mildew hyphae has also been observed (Sundheim and Krekling, 1982). As with phytopathogenic fungi, penetration of the host cell wall is likely to involve both enzymatic and mechanical processes. Appressorium-like structures were reported at the point of penetration (Figure 4A) (De Bary, 1870; Sundheim and Krekling, 1982). Extracellular lytic enzymes have been identified in liquid cultures of *Ampelomyces*, which may play a role in the degradation of the powdery mildew hyphal walls during penetration (Philipp, 1985). Rotem *et al.* (1999) demonstrated that an exo-beta-1,3-glucanase is excreted both in culture and during mycoparasitism, and showed that culture filtrates of an *Ampelomyces* isolate could cause degradation of hyphal walls of the cucumber powdery mildew fungus in the absence of active mycelium.

3. MYCOPARASITISM AS A BIOTIC STRESS FOR THE PARASITIZED FUNGI

3.1 Direct Effects of Mycoparasitism: Impact on Growth and Sporulation of the Mycohosts

Ampelomyces mycoparasites suppress both the asexual and the sexual sporulation of the attacked powdery mildew mycelia by colonizing and destroying the conidiophores, and the immature ascomata, respectively. The early stage of mycoparasitism is apparently biotrophic, but the invaded cytoplasm then begins to die and a necrotrophic interaction results (Hashioka and Nakai, 1980; Sundheim and Krekling, 1982). Philipp *et al.* (1984) showed that the parasitized powdery

mildew colonies can continue their radial growth, but their sporulation stopped soon after *Ampelomyces* penetrated their mycelia. Similarly, Shishkoff and McGrath (2002) demonstrated that *Ampelomyces* could not stop the spread of powdery mildew colonies on detached leaves maintained *in vitro* but did reduce the amount of inoculum produced by each colony.

Microbial antagonists, which act through antibiosis against powdery mildews, such as *Pseudozyma* spp. or *Tilletiopsis* spp., can kill powdery mildew colonies rapidly, causing complete plasmolysis of their cells in 24–48 h (Bélanger and Labbé, 2002). As *Ampelomyces* acts against powdery mildews through mycoparasitism, without producing antifungal compounds, it destroys the invaded powdery mildew colonies only slowly, in 5–10 days, depending on the ambient temperature, relative humidity and other abiotic factors. During that period of time, some of the conidiophores of the invaded mycelium still produce fresh conidia, although these might contain intracellular hyphae of *Ampelomyces* (Figures 2, 3D, and 4C), and, thus, might contribute to the long-distance dispersal of the mycoparasites.

The sporulation rate of powdery mildew colonies depends on the inoculum density, physiological patterns of the host plant, abiotic factors and so on (Yarwood, 1957; Rouse *et al.*, 1984; Bushnell, 2002). When the sporulation and spread of these pathogens on the host-plant surfaces is intense, *Ampelomyces* mycoparasites can only slowly follow the spread of powdery mildew colonies. In these cases, they lag behind the spread of the disease, reducing its severity and limiting its negative effect on the infected plants to a certain extent. However, according to a mathematical model of the interactions between fungal parasites and their mycoparasites (Shaw, 1994; Shaw and Peters, 1994), mycoparasites might cause apparently random fluctuations in the abundance of their mycohosts from year to year, even in an absolutely constant environment. Thus, it is not obvious how environmental factors could be distinguished from intrinsic population instability in the field data on quantitative relationships between mycohosts and their mycoparasites.

In the field, *Ampelomyces* mycoparasites may not be observed on many plants until late in the growing season, long after powdery mildews have infected the aerial parts of their host plants (Gadoury and Pearson, 1988; Rankovic, 1997; Kiss, 1998). The situation is different for powdery mildew species that over-winter in buds, such as the apple powdery mildew fungus, *Podosphaera leucotricha*, and start their life cycles early in the season, because the mycoparasites might over-winter in the same buds, or on other parts of the host plant, in close vicinity of the primary powdery mildew inocula (Szentiványi and Kiss, 2003; Szentiványi *et al.*, 2005). However, even in these cases, the spread of the mycohosts in the spring is much more rapid after bud break than that of the over-wintered mycoparasites (Szentiványi and Kiss, 2003). Thus, powdery mildew epidemics usually reach damaging levels before their growth and sporulation are arrested by *Ampelomyces* in the field (Gadoury and Pearson, 1988; Falk *et al.*, 1995a, 1995b).

The phyllosphere is a much more dynamic environment than the rhizosphere as the leaves have a limited lifetime compared to roots (Fokkema and Schippers, 1986; Andrews 1990, 1992). Thus, both powdery mildews and *Ampelomyces* have

a shorter window of infection compared to the soil-borne plant pathogenic fungi and their mycoparasites (Kiss, 2001). The only powdery mildew structures that are exposed for a longer period of time to mycoparasitic attack are the over-wintering ascomata on the bark of woody crops such as grapevine. A part of the ascomata is destroyed by *Ampelomyces* every year in many powdery mildew species in the field (Emmons, 1930; Speer, 1978; Falk *et al.*, 1995a; Rankovic, 1997; Kiss, 1998; Füzi, 2003). However, biocontrol of grapevine mildew ascomata through mycoparasitism by *Ampelomyces* was not effective (Falk *et al.*, 1995a). From an ecological perspective, it looks like there are a number of biotic and abiotic factors that do not seem favourable for the activity of *Ampelomyces* against powdery mildew fungi in the field, yet the widespread, natural occurrence of these fungi would suggest otherwise.

3.2 Indirect Effects in a Tri-Trophic Relationship: Impact of Mycoparasitism on the Mildew-Infected Plants

The presence of *Ampelomyces* in the powdery mildew mycelium results in a reduction of the negative effects of the pathogenic fungus on the infected plant. Abo-Foul *et al.* (1996) showed that infected cucumber plants regained vigour after being treated with *Ampelomyces*, which killed the pathogen. Eight days after treatment with a conidial suspension of *Ampelomyces*, chlorophyll content and also CO_2-fixation in the infected cucumber leaves were almost the same as in uninfected controls. These results were supported by Romero *et al.* (2003), who found that a treatment with *Ampelomyces* significantly increased the chlorophyll content of detached and mildew-infected melon leaves maintained *in vitro*. We have also found that the chlorophyll content of powdery mildew-infected *Lycium* leaves collected from the field, and heavily parasitized by *Ampelomyces* (Figure 1), is significantly higher than that of the mildew-infected leaves on which the mycoparasites were not present (Kiss and Szentiványi, unpublished data). The relationship between host plants, powdery mildew fungi and *Ampelomyces* my-coparasites could be further studied as a model system for tri-trophic interactions in fungal and plant ecology (Kiss, 2001; Kiss *et al.*, 2004).

4. OTHER FUNGAL ANTAGONISTS OF POWDERY MILDEW FUNGI

A review of all known fungal antagonists of powdery mildews, including those found in the field and those tested as potential biocontrol agents of powdery mildew infections without any record of a natural antagonistic relationship, revealed that more than 40 fungal taxa could suppress the growth and sporulation of these plant pathogens (Kiss, 2003). This suggests that a high number of fungi, including mycoparasites and other antagonists, are associated with powdery mildew colonies in the field. These fungi use powdery mildew my-celia as nutrient sources and might exploit powdery mildew fungi for other purposes, as well. Very little is known about these interactions under natural conditions (Raghavendra Rao and Pavgi, 1978; Mathur and Mukerji, 1981;

Hijwegen and Buchenauer, 1984; Hirsch and Braun, 1992; Szentiványi *et al.*, 2006). Most antagonists of powdery mildews, other than *Ampelomyces*, were evaluated as potential biocontrol agents only (Bélanger and Labbé, 2002; Kiss, 2003; Kiss *et al.*, 2004;) without paying attention to their possible role in the natural control of powdery mildew infections.

4.1 Confusion of Ampelomyces with Other Pycnidial Mycoparasites of Powdery Mildews

Recent results suggested that a number of pycnidial fungi, other than *Ampelomyces*, could also parasitize powdery mildew colonies in the field. For example, Sullivan and White (2000) suggested the possibility that some pycnidial fungi isolated from powdery mildew colonies collected from the field, and characterized by a 3–4 mm radial growth/day in culture at room temperature, were confused with *Phoma glomerata* isolates. Sullivan and White (2000) found that such isolates, identified as 'fast-growing *Ampelomyces* isolates' in earlier works (e.g., Mhaskar and Rao, 1974; Rudakov, 1979; Kiss, 1997; Kiss and Nakasone, 1998), typically came from sessile pycnidia found on mildew-infected leaves, whilst the so-called 'slow-growing *Ampelomyces* isolates', with a radial growth rate of 0.1–1 mm day^{-1} in culture, came from intracellular pycnidia typical of the 'true' *Ampelomyces*. ITS1 sequence analysis showed that the 'fast-growing isolates' clustered in a clade typified by *Phoma* species, while the 'slow-growing isolates' were distinct (Sullivan and White, 2000). This study supported the earlier results obtained by Kiss and Nakasone (1998). It seems likely that the 'fast-growing *Ampelomyces* isolates' are, in fact, *Phoma* species, whilst the true *Ampelomyces* isolates are always slow growing in culture and always produce intracellular pycnidia in powdery mildew mycelia (Sullivan and White, 2000; Szentiványi *et al.*, 2005; Liang *et al.*, 2007). This suggests that a number of pycnidial fungi, confused with *Ampelomyces* in earlier works, are also natural mycoparasites of powdery mildews, although their mycoparasitic activity has not been characterized in detail yet.

5. CONCLUSIONS

The high number of known fungal antagonists of powdery mildews (for review see Kiss, 2003) suggests that these plant pathogens are often attacked and damaged by mycoparasites and other antagonists in the field. Among these, pycnidial fungi belonging to the genus *Ampelomyces* are the most widespread and the oldest known natural enemies of the Erysiphales (Kiss *et al.*, 2004). Many aspects of the interactions between powdery mildews and *Ampelomyces* are well known, similar to the interactions between some species of the Erysiphales and a few other powdery mildew antagonists, especially *Pseudozyma* spp. (Bélanger and Deacon, 1996; Avis *et al.*, 2000; Avis and Bélanger, 2001), *Tilletiopsis* spp. (e.g., Hoch and Provvidenti, 1979; Urquhart and Punja, 2002) and *Lecanicillium lecanii* (syn. *Verticillium lecanii*) (e.g., Askary *et al.*, 1997), which destroy the attacked

parts of powdery mildew mycelia much faster, through the production of hydrolytic enzymes and antifungal compounds. However, nothing is known about defence reactions of the powdery mildew mycelium against the attack of any of these antagonists. In some mycoparasitic interactions, papillae or other structural barriers are produced to stop the invaders (e.g., Vajna, 1985a, 1985b; Kiss, 2001); however, such structures have not been reported in powdery mildews so far. This would suggest that powdery mildews simply tolerate the biotic stress caused by mycoparasites and other antagonists; however, our knowledge on this aspect of inter-fungal parasitic relationships is, in general, too scarce to be able to formulate any general conclusions in this matter.

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