Ampelomyces hyperparasites – occurrence and effect on the development of ascomata of *Erysiphales* species under conditions of anthropopressure

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Abstract

Fungi of the genus *Ampelomyces* are the major antagonists of *Erysiphales* fungi being a significant group of phytopathogens. The hyperparasites attack various developmental stages of powdery mildews. As a result the infested ascomata do not reach the stage of maturity, do not form appendages nor ascospores, which is linked with a reduction of the source of primary infections. Studies conducted so far have mainly been devoted to *Ampelomyces* fungi application in the biological control of powdery mildews on crops, whilst a few only have been focused on the ecology of these mycoparasites on *Erysiphales* fungi infecting plants, especially in the urban environment. The present study addresses the natural occurrence and effect of *Ampelomyces* fungi on the development of ascomata of powdery mildews species. The material was collected in 2005–2009 in several cities of the northeastern Poland. First time ever *Ampelomyces* spores are reported in mature ascomata of *Erysiphales* with fully developed appendages. This phenomenon has been observed in the case of two species, viz.: *Erysiphe flexuosa* on *Aesculus* spp. and *E. vanbruntiana* var. *sambuci-racemosae* on *Sambucus racemosa* and is presumably linked with improved implementation, propagation and probably better survival during winter months.

Keywords: *Ampelomyces*, hyperparasites, *Erysiphales*, powdery mildews, ascomata, urban environment

Introduction

Species of the genus *Ampelomyces* Ces. ex Schltdl. are wide-spread hyperparasites found on more than 65 *Erysiphales* species [1]. Their hyphae penetrate the vegetative mycelium as well as conidiophores and conidia of the host fungus, thus forming inside them the spore-forming structures, i.e. pycnidia [2]. Hyperparasites may also colonize ascogonia and antheridia as well as young, immature chasmothecia of powdery mildews, transforming them into their own reproductive structures. Infested ascomata do not reach the stage of maturity, do not form appendages nor ascospores, which is linked with the reduction of the source of primary infections [3–7].

The capability of hyperparasites to infest different *Erysiphales* species, to suppress their sporulation as well as to inhibit the formation and development of chasmothecia has contributed to the advance of research addressing mainly the aspect of the application of *Ampelomyces* fungi in the biological control of powdery mildews [1,8–11]. From the economic point of view, *Erysiphales* species constitute a significant group of phytopathogens of multiple fruit plants and crops. Of high interest to researchers world-wide is also the problem of the genetic diversity of fungi of the genus *Ampelomyces*, which is still little known and requires in-depth examinations [12–16].

World and Polish literature provides a lot of information about presence *Ampelomyces* fungi on different *Erysiphales* species in natural condition ([11,17–24]. Relatively few investigations were focused on the ecology of these hyperparasites and their natural occurrence on various *Erysiphales* species under urban condition [25–27]. Therefore, the Department of Mycology of University of Warmia and Mazury in Olsztyn began studies on the occurrence of fungi from the genus *Ampelomyces* and their impact on the development *Erysiphales* in urban environment [28–30]. Data is also lacking on the effect of *Ampelomyces* fungi on the development of fruiting bodies of different species of powdery mildews infecting non-farming plants [29]. Works addressing this issue are devoted almost exclusively to a dangerous pathogen of grapevine – *Erysiphe necator* (*Uncinula necator*) – [3,5,6,31].

An analysis of the colonization of *Erysiphales* ascomata by *Ampelomyces* as well as the effect of mycoparasites on their development seems to be crucial in understanding the role of such antagonists in the natural dynamics of a powdery mildew population in its natural environment.

The objective of the study was to evaluate the occurrence of fungi of the genus *Ampelomyces* and their effect on the development of ascomata of species of powdery mildews in the urban environment.

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Material and methods

The mycological research was conducted in 2005–2009 in several cities of the northeastern Poland: Olsztyn, Frombork, Giżycko, Mrągowo and Kętrzyn. The experimental material were leaves of plants infested with *Erysiphales* fungi. The material were collected from different places of cities (parks, gardens, street and community lawns) always in the second half of the vegetative season (August-October), when mature fruiting bodies were visible on white mycelium. Ten leaves with symptoms of infestation by powdery mildews, randomly collected from each host plant, served as one sample.

Laboratory analyses were conducted to verify the presence of *Ampelomyces* fungi on the mycelium of the *Erysiphales* species examined. Stereomicroscope (Olympus SZX9) and light microscope (Olympus BX51) used to observe the mycelium, chasmothecia of *Erysiphales* species and hyperparasites from the genus *Ampelomyces*. Camera XC 50 and analytical software Analysis were used for graphic processing (documentation, measurement).

Tab. 1 The list of *Erysiphales* species and host plants.

No.	*Erysiphales* species	Host plants	Samples with *Erysiphales* species	Samples with *Ampelomyces* species
1	*Erysiphe adunca* (Wallr.) Fr.	*Salix cinerea* L.	3*	0
2	*Erysiphe alphitoides* (Griffon et Maubl.) Braun & Takam.	*Quercus robur* L.	26 (2*)	1
3	*Erysiphe artemisiae* Grev.	*Artemisia vulgaris* L.	10	8 (80%)
4	*Erysiphe asperifoliorum* Grev.	*Symphytum officinale* L.	4	2
5	*Erysiphe berberidis* (DC.)	*Mahonia aquifolium* (Pursh) Nutt.	2*	2
		Berberis vulgaris L.	31*	23 (69%)
		Berberis thunbergii DC.	3*	0
6	*Erysiphe cichoracearum* DC.	*Sonchus arvensis* L.	6	5
		Helianthus tuberosus L.	14	8 (65%)
7	*Erysiphe convolvuli* DC.	*Convolvulus arvensis* L.	9	2
8	*Erysiphe depressa* (Wallr.) Link	*Arctium lappa* L.	2	1
9	*Erysiphe flexuosa* Peck. Braun & Takam.	*Aesculus* spp.	27 (24*)	22 (81%)
10	*Erysiphe galeopsidis* DC.	*Lamium album* L.	13	2
11	*Erysiphe hedwigii* (Lév.) Braun & Takam.	*Viburnum lantana* L.	3	0
12	*Erysiphe heraclei* DC.	*Pastinaca sativa* L. s.str.	3	0
		Heracleum sphondylium L.. s.str.	6	6 (83%)
13	*Erysiphe hypophylla* (Nevod.) Braun & Cunningt.	*Quercus robur*	23 (20*)	7
14	*Erysiphe magnicellulata* Braun	*Phlox* sp.	6	5
15	*Erysiphe palczewskii* Braun & Takam.	*Caragana arborescens* Lam.	25 (20*)	16 (68%)
16	*Erysiphe polygoni* DC.	*Polygonum aviculare* L.	17	6
17	*Erysiphe syringae* Schwein.	*Syringa vulgaris* L.	24 (19*)	4
18	*Erysiphe tortilis* (Wallr.) Link	*Cornus sanguinea* L.	2	0
19	*Erysiphe trifolii* Grev.	*Caragana arborescens*	1	0
		Astragalus glycyphyllos L.	2	0
		Trifolium campestre Schreb.	21	7
20	*Erysiphe urticae* (Waller.) Blumer	*Urtica dioica* L.	5	1
21	*Erysiphe vanbruntiana* var. *sambuci-racemosae* (Braun) Braun & Takam	*Sambucus racemosa* L.	31 (26*)	28 (90%)
22	*Phyllactinia fraxini* (DC.) Homma	*Fraxinus excelsior* L.	12 (9*)	6
23	*Golovinomyces sordidus* (L. Junell) Helluta	*Plantago major* L. s.str.	14	12 (85%)
24	*Phyllactinia guttata* (Wallr.) Lév.	*Betula pendula* Roth.	23 (21*)	3
		Corylus avellana L.	7*	0
		Fagus sylvatica L.	2*	0
25	*Podosphaera fusca* (Fr.) Braun & Shishkoff	*Taraxacum* spp.	21	16 (76%)
26	*Sawadaea bicornis* (Wallr.) Homma	*Acer campestre* L.	2*	0
		Acer ginnala Maxim.	2 (1*)	0
		Acer negundo L.	5*	0
27	*Sawadaea tulasnei* (Fuckel) Homma	*Acer ginnala*	11 (7*)	1
		Acer platanoides L.	29 (26*)	15
	The total number of samples		447	209 (47%)

The number of samples with powdery mildew infected and uninfected by fungi from the genus *Ampelomyces* in the years 2005–2009. Nos. 3, 5, 6, 9, 12, 15, 21, 23, 25 denote species of *Erysiphales* with the particiaption of *Ampelomyces* fungi >50% in samples. * Data from 2005–2006 years [30].

Each infested leaf in a sample was observed under a stereo-microscope. Once hyperparasites were detected (symptoms of the presence of *Ampelomyces* fungi: change of mycelium color into brown, the presence of pycnidia on the mycelium), microscopic analyses were conducted for 10 young (yellow and orange pigmentation, lack of appendages) and 10 mature ascomata (brown pigmentation, branched appendages) collected at random from the surface of mycelium non-infested and infested by the hyperparasites. These analyses involved determinations of: (*i*) morphological features of mature ascomata (diameter, wall peridium pigmentation, the number and length of appendages); (*ii*) the development of asci with ascospores of mature ascomata (the presence of asci with ascospores; asci without ascospores; a lack of asci and ascospores); (*iii*) the presence of spores of *Ampelomyces* fungi in young and mature ascomata.

The fungi were identified by means of Braun's key [32]. The taxonomy and nomenclature were adopted after Braun and Takamatsu [33] and Braun et al. [34]. The host plants were identified using keys by Rutkowski [35]. The nomenclature was adopted after Mirek et al. [36].

Results

In total 447 samples were collected, including 27 of *Erysiphales* species. The presence of *Ampelomyces* fungi was detected on 23 (47%) analyzed species of powdery mildews. In the case of 10 species, the contribution of hyperparasites in the samples exceeded 50%. The greatest percentage of hyperparasites was observed on four host species: *Erysiphe vanbruntiana* var. *sambuci-racemosae* (90% samples with *Ampelomyces* fungi), *Erysiphe sordida* (85%), *Erysiphe flexuosa* (81%), and *Erysiphe heraclei* (83%; Tab. 1).

In the case of all powdery mildews investigated, the analysis of the presence of *Ampelomyces* species in ascomata demonstrated the hyperparasites to infest young fruiting bodies without developed appendages. In 25 analyzed species of *Erysiphales*, fungi from the genus *Ampelomyces* infested only young ascomata. In turn, in two species: *Erysiphe flexuosa* and *E. vanbruntiana* var. *sambuci-racemosae* the hyperparasites were observed in young and mature chasmothecia with fully developed appendages (Fig. 1, Fig. 2). In the case of *Erysiphe flexuosa*, *Ampelomyces* fungi infested mature ascomata in 50% of the samples, whereas in the case of *E. vanbruntiana* var. *sambuci-racemosae* in 79%.

In both analyzed species some differences were noted in the morphological characteristics of mature ascomata collected from the surface of mycelium non-infested and infested by fungi from the genus *Ampelomyces*. The diameter of mature ascomata is smaller, wall peridium pigmentation is paler and the number of appendages is smaller in the infested ascomata than the un-infested ones (Tab. 2).

On both surfaces, analyses demonstrated the prevalence of chasmothecia with fully-developed appendages (>80%). In contrast, differences were observed in the development of asci and ascospores in the ascomata. In the case of *E. flexuosa*, analyses showed 90% of ascomata with developed asci and ascospores on the surface of mycelium free of hyperparasites and 72% of these on the surface of mycelium colonized by *Ampelomyces* fungi. The latter mycelium was also characterized by 7% contribution of mature ascomata infested by the hyperparasites and 16% contribution of empty ascomata,
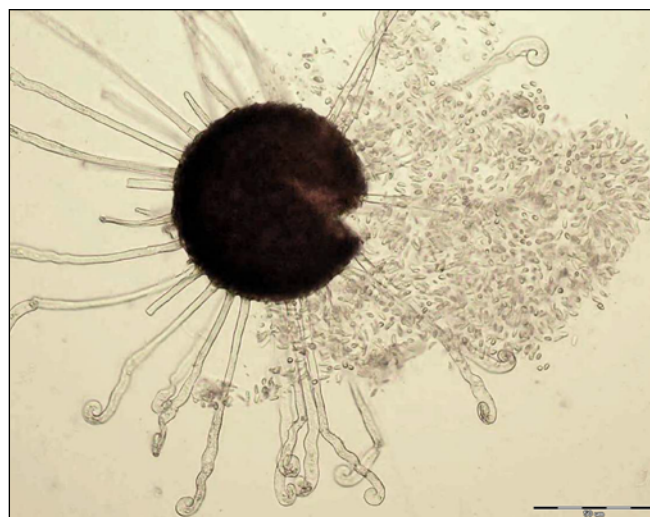

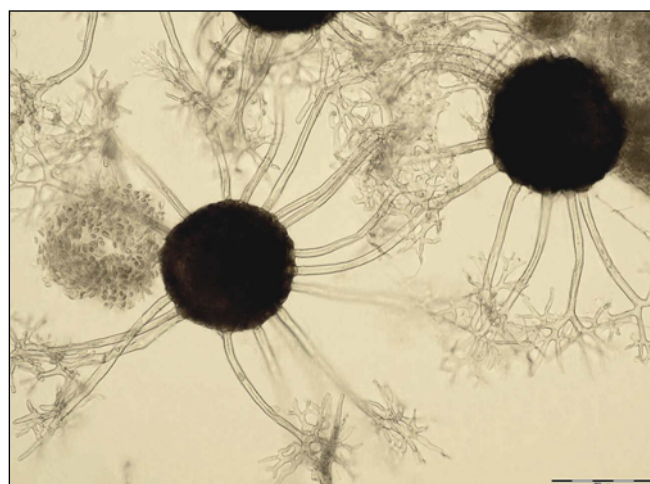**Fig. 1**   *Erysiphe flexuosa* – spores of *Ampelomyces* fungi in mature ascomata. Scale bar: 50 μm.

Fig. 2   *E. vanbruntiana* var. *sambuci-racemosae* – spores of *Ampelomyces* fungi in mature ascomata. Scale bar: 50 μm.

without any asci nor ascospores (Tab. 3). In the case of *E. vanbruntiana* var. *sambuci-racemosae*, the difference in the development of asci and ascospores turned out to be alike, i.e. 87% of the ascocarps containing asci and ascospores on the surface of mycelium without *Ampelomyces* fungi and as little as 60% of these on the surface of infested mycelium. In the latter, analyses showed additionally a very high percentage (38%) of *Ampelomyces* species in mature ascomata as well as 1% of empty chasmothecia (Tab. 3), which results in nearly 40% reduction of ascomata.

Discussion

Fungi of the genus *Ampelomyces* are considered to be major antagonists of *Erysiphales* species [11]. The range of their occurrence corresponds with the range of powdery mildews, which points to the ecological specialization of these hyperparasites. This has been confirmed in our study, where fungi of the genus *Ampelomyces* were noted on all investigated species, and with a high contribution in the samples (>50%).

Tab. 2 Morphological description of mature ascomata non-infested and infested by *Ampelomyces* fungi.

Morphological Features	EV		EF	
	A(−)	A(+)	A(−)	A(+)
Diameter (μm)	119–139 (–160)	(75–) 109 –119 (–139)	116–143	(68–) 99–116
Wall	brown	fawn brown	brown	fawn brown
Pigmentation	dark brown	brown	dark brown	brown
The number of appendages	18–27	(11–) 15–22	31–44	(7–) 13–31
Length of branched appendages (times as long as ascomata diameter)	1–1.5	1–1.5	0.5–1.5	0.5–1.5

A(−) – mature ascomata un-infested by *Ampelomyces* fungi; A(+) – mature ascomata infested by *Ampelomyces* fungi; EF – *Erysiphe flexuosa*; EV – *Erysiphe vanbruntina* var. *sambuci-racemosae*.

While infesting the host fungus, these hyperparasites colonize the mycelium, the conidial stages and young, yet immature fruiting bodies [3,5,17,25,32]. Ample investigations [5,31,37] have shown that *Ampelomyces* species are capable of infecting chasmothecia only at the early stage of their development, before the formation of appendages and development of walls. Young fruiting bodies are, obviously, susceptible to infections, whereas the mature ones are seemingly resistant. However, results of these investigations are only in part consistent with our findings. In the powdery mildews analyzed, the hyperparasites were very often detected only on the perfect stage and infested mainly young ascomata in various developmental stages – from white to orange ones with undeveloped appendages or at the early stages of development. They were transforming them into their own reproductive structures, yielding abundant production of conidial spores. In contrast, in the case of two species, *Erysiphe flexuosa* on *Aesculus* spp. and *E. vanbruntiana* var. *sambuci-racemosae* occurring on *Sambucus racemosa*, the presence of *Ampelomyces* fungi was additionally detected in mature ascomata with fully developed appendages, with an especially high percentage reaching 38% in *E. vanbruntiana* var. *sambuci-racemosae*. This is the first documented case of this phenomenon. The worldwide literature does not provide any information on the colonization of fully mature fruiting

Tab. 3 Percentage participation of mature ascomata with different degree of development of asci and ascospores from surface of mycelium non-infested and infested by *Ampelomyces* fungi.

The presences of asci, ascospores and spores of *Ampelomyces* fungi	EV		EF	
	S(−)	S(+)	S(−)	S(+)
ac(+) as(+) A(−)	87	60	90	72
ac(+) as(−) A(−)	11	1	7	5
ac(−) as(−) A(−)	2	1	3	16
ac(−) as(−) A(+)	0	38	0	7
	100%	100%	100%	100%

A – spores of *Ampelomyces* fungi; ac – asci; as – ascospores; S(−) – surface of mycelium non-infested by *Ampelomyces* fungi; S(+) – surface of mycelium infested by *Ampelomyces* fungi.

bodies by the hyperparasites. The presence of *Ampelomyces* fungi on apparently mature fruiting bodies of *Erysiphe necator* (*Uncinula necator*) was mentioned by Füzi [11]. This author described infested fruiting bodies as apparently mature due to the observed residual appendages and speculated on the terminated process of peridium formation before the infection with the hyperparasites.

Infested fruiting bodies may be recognized by their fawn, milk-brown color and smaller sizes [5,6]. Results of our study confirm these changes of the colonized mature ascomata both in *E. flexuosa* as well as in *E. vanbruntiana* var. *sambuci-racemosae*.

However the infested ascomata possessed well developed appendages (>80%), whose development was very often synchronized with the development of asci and ascospores. In our study, apart from conidia of the hyperparasites, no other residues of those structures were observed in the ascomata. Therefore, it remains unclear when the chasmothecia are being infected. Being endoparasites, *Ampelomyces* fungi colonize structures of the host-fungi from the inside. The infection of fruiting bodies proceeds through thin hyaline hyphae of the mycelium that penetrate into the male sexual cell and ascogonium as well as into young chasmothecia, thus inhibiting their development [5]. The presence of fully developed appendages probably indicates the infection of ascomata at the final stage of their development.

The colonization of mature fruiting bodies is, probably, a phenomenon pointing to the adaptation of *Ampelomyces* species to a better overwintering and dissemination. Falk et al. [4] report that the survivability of *Ampelomyces* fungi in young fruiting bodies reaches as little as 1–3%. Thus, it may, be speculated on a low effectiveness of these hyperparasites in their natural environments, which has been proved by annual epiphytoses induced by powdery mildews. The low survivability of *Ampelomyces* fungi is certainly due to the immature wall of ascomata which at this developmental stage are not capable of surviving low temperatures. This has been confirmed by Mmbaga [38], who reported that fruiting bodies with just partly developed walls are not capable of surviving the winter. Therefore, the stage of colonizing mature chasmothecia – that completed the process of peridium formation and possess well developed appendages – by the hyperparasites seems to be understandable. Probably it provides suitable conditions for the hyperparasites for a better overwintering and transmission in their environments. The improvement of the adaptation

strategy of *Ampelomyces* fungi may lead to changes in the dynamics of an *Erysiphales* population.

Thus, further researches of the occurrence of these hyperparasites of powdery mildews in their natural environment are advisable. They will enable recording the direction of those changes in a complicated system, viz. plant – parasite – hyperparasite.

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