Epidemiology of the fungus *Athelia arachnoidea* in epiphytic communities of broadleaved forests under strong anthropogenic impact

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Department of Environmental Sciences, Vytautas Magnus University, Vileikos 8, LT-44404 Kaunas 35, Lithuania The effect of the basidiomycete *Athelia arachnoidea* on epiphytic communities was studied in broadleaved forests within the zone of influence of a phosphorus fertiliser factory in central Lithuania. Lichen communities in 23 permanent quadrats were observed for five years. During this period, the fungus was observed in 10 quadrats and caused significant damage in part of them. *A. arachnoidea* influenced both species number and cover in the quadrats, although its effect on various species differed both by the type of fungus infection and the individual reaction of the lichen species. *Phlyctis argena* and *Lecidella elaeochroma* showed comparative tolerance to the infection, being able to regenerate and re-establish rapidly; *Melanelia fuliginosa* was more susceptible, but probably capable of rapid re-establishment; the fast-growing, sterile, sorediate *Biatora* species profited by the infection, rapidly occupying newly-created gaps.

Key words: epiphytic lichens, lichen communities, air pollution, lichenicolous fungi, basidiomycota, *Athelia arachnoidea*, Lithuania

INTRODUCTION

Little attention is paid to the influence of biotic factors when investigating the development of lichen communities, especially in studies of those under anthropogenic pressure. In general, the most frequently studied biotic factors in plant (including lichen) community development are: 1) interspecific competition, 2) longevity/senescence, and 3) predation/disease (Lawrey, 1991). A number of invertebrates and fungi feed on lichens, causing damage to a varying extent; for example, lichen communities are known to be destroyed by various grazers (Gerson, Seaward, 1977; Hayward, Grace, 1982; Baur et al., 1995), and mollusc grazing was also observed in our study area. Pathogenic lichenicolous fungi are also commonly found on lichens. It is generally known that pathogens have a large effect on plant communities since they control population size and dynamics, maintain genetic variability in populations, influence the evolution and maintenance of sexual reproduction, determine species distribution, and enhance species diversity in the community (Augspurger, 1989). It is possible that pathogens have a similar effect on lichen communities. Probably the most significant damage to lichens is induced by the basidiomycete fungus Athelia arachnoidea (Berk.) Jül. (Gilbert, 1966, 1988; Poelt, Jülich, 1969; Arvidsson, 1976; Diederich, 1986; Parmasto, 1998; Yurchenko, Golubkov, 2003). But only Gilbert (1988) studied its effect on lichen communities, investigating simplified epiphytic swards of *Lecanora conizaeoides-Desmococcus*. The epidemiology of this infection in more complex communities is unknown. *Athelia arachnoidea* on lichens is found to parasitize wide range of hosts mainly in human-impacted areas (Poelt, Jülich, 1969; Arvidsson, 1976; Parmasto, 1998; Yurchenko, Golubkov, 2003). In Lithuania, the fungus is common in settlements, on the edges of roads and fields, as well as in small, isolated stands of deciduous trees, but as a lichen pathogen it is very rare and inconspicuous in large forest areas outside of industrial influence.

During a five-year investigation of the state and development of epiphytic communities in broadleaved forests in the proximity of a phosphorus fertiliser factory in central Lithuania, the conspicuous effect of *A. arachnoidea* on lichens was recorded. Observations over a comparatively long period and the variability of affected communities allowed recording some features of the fungus infection.

MATERIALS AND METHODS

For our investigations, six permanent plots in small stands of *Fraxinus excelsior*-dominated broadleaved forests were chosen to study lichen community deve-

lopment. The plots were situated in an industrial region, at a varying distance (1.5 km to 16 km) from the phosphorous fertiliser plant "Lifosa" in Këdainiai, Central Lithuania. In each plot, four trees (Fraxinus excelsior) were selected on which four permanent quadrats (20×20 cm) were marked, giving 24 quadrats in total. As tree 6_1 was felled in the course of the study, only 23 quadrats were actually sampled. The plots were visited once a year (in the last week of September) when a graphic chart of the community in a quadrat was traced onto a clear polythene sheet with a fine-tipped waterproof pen. The image was supplemented with field notes. The chart was digitized, and a lichen area was calculated using a specially designed software programme. Bark pH was measured with a portable IQ-150 pH meter with a stainless steel probe.

STUDY AREA

The study area (Këdainiai district) is situated in Central Lithuania where the climate is subcontinental, with average temperatures of 17.5 °C in July and 6.0 °C in January, and annual precipitation of 500–550 mm; the prevailing winds are W, SW and NW (Kaušyla, 1981). Broadleaved forests prevail in the region, with *Fraxinus*-dominated stands as a significant component (Navasaitis et al., 2003). The Këdainiai district is under a strong anthropogenic pressure: only 26.2% of land is occupied by forests and waters, whereas the rest is industrial, urban or agricultural land.

According to available air monitoring data, SO_2 concentrations currently range from 5 to 15 μ g/m³ in the Këdainiai city and NO_2 levels range from 5 to 30 μ g/m³ (Lietuvos valstybinio oro monitoringo matavimø duomenys, 2004: http://aaa.am.lt/VI/artic-le.php3?article_id=441). Precipitation acidity in the region is close to the Lithuanian average, at present ca. pH 5 (Juknys et al., 2002). The bark of the phorophytes studied had a pH ranging from 5.12 to 6.34 in 2000 and from 5.31 to 6.38 in 2003.

RESULTS AND DISCUSSION

Epiphytic communities recorded in the quadrats varied considerably, ranging from simplified communities consisting solely of epiphytic algae in the 2nd plot to species-rich communities of lichens (up to 12 species per quadrat) and bryophytes in the 5th and 6th plots.

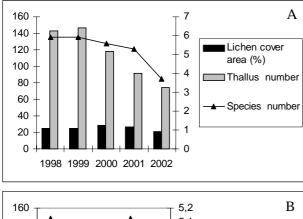
During the period 1998–2002, *A. arachnoidea* was noted in 5 out of 6 permanent plots and in 10 quadrats out of the total 23 (Table). In addition, some quadrats (*e.g.*, 4_2) showed signs of recent infection in 1998, possibly from the previous year. It is noteworthy that although the fungus was not recorded in the quadrats of Plot 1, it was present on other trees

in the plot. Thus, the fungus was effectively present in all study plots, and it can be hypothesised that over a longer time-span, all quadrats might eventually be influenced by *A. arachnoidea*.

The damage caused to the lichens or algae in the communities varied in different quadrats, ranging from devastating to rather insignificant. The fungus influenced both lichen cover and species richness. Regardless of whether A. arachnoidea was very aggressive or not, the total cover of all lichens in a quadrat reached its greatest extent at the beginning or at the peak of fungus infection and decreased afterwards. The same pattern was observed with species richness (Motiejûnaitë, Jucevièienë, 2003). General observations indicated that in the quadrats where A. arachnoidea did not appear during the study period, the initial average species numbers and lichen cover were higher than in fungus-affected quadrats (Fig. 1), although these decreased later. All three characteristics, species richness, cover area and abundance (thallus numbers) fluctuated in the affected quadrats during the study period. In unaffected quadrats, only the cover area tended to fluctuate, meanwhile species richness and thallus numbers steadily decreased. However, not all changes in species number, cover and abundance were attributable so-

Table. Presence of Athelia arachnoidea in quadrats during the study period

Quadrats	Athelia arachnoidea (area of infestations, % of the quadrat)				
	1998	1999	2000	2001	2002
1_1	-	-	_	-	-
1_2	_	_	_	_	-
1_3	_	_	_	_	-
1_4	_	_	_	_	-
2_1	1	85	85	24	24
2_2	-	-	-	-	-
2_3	-	-	-	-	-
2_4	2	2	3	-	-
3_1	7	19	5	-	-
3_2	-	-	5	-	-
3_3	-	-	1	4	-
3_4	-	-	-	-	-
4_1	-	-	-	-	-
4_2	-	-	-	-	-
4_3	20	77	-	-	-
4_4	-	3	-	-	-
5_1	-	-	-	-	1
5_2	-	-	9	32	11
5_3	-	-	-	-	_
5_4	-	-	-	-	_
6_2	-	-	-	-	_
6_3	-	-	2	5	_
6_4	_	_	_	17	-



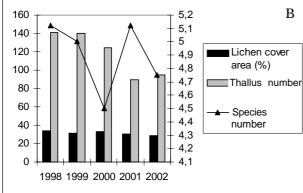


Fig. 1. Dynamics of epiphytic lichens in quadrats during the study period: a) quadrats devoid of *A. arachnoidea* presence; b) quadrats affected by *A. arachnoidea*

lely to *A. arachnoidea* infection. Loss of lichens was also caused by mollusc grazing and by sudden increases in illumination level (Motiejûnaitë, in press).

The individual response of different epiphyte species to infection was variable and difficult to interpret. Most easily discerned was a decrease in the quantity of epiphytic algae communities in the quadrats of Plot 2 (Motiejûnaitë, Jucevièienë, 2003). Generally, the infection process in these simplified communities was very similar to that described by Gilbert (1988).

With respect to lichens, *Lecidella elaeochroma* and *Phlyctis argena*, especially where they comprised a significant part of the community, demonstrated a steady although not very intensive growth reaching their peak together with the peak of *A. arachnoidea* infection or one year before the infection peak, decreasing afterwards and then displaying steady growth a year or two later. *Melanelia fuliginosa* reached its growth peak before infection and declined steadily afterwards. Meanwhile the cover of fast-growing species like *Bacidia*, *Bacidina* or a sterile unindentified species defined as "*Biatora*" sp. mainly decreased before the peak of infection and expanded quickly afterwards (for details, see Motiejûnaitë, Jucevièienë, 2003).

Although in some cases the damage induced by the fungus, both to the whole community and to its individual members, was quite spectacular (Fig. 2),

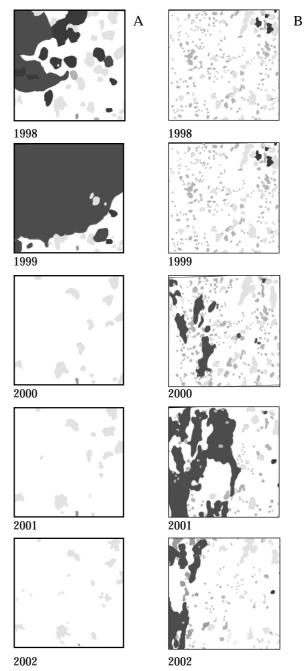
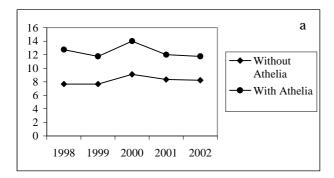


Fig. 2. Effect of *A. arachnoidea* (fungus infestations marked with dark colour) on study quadrats: a) quadrat 4_3; b) quadrat 5_2

the general developmental tendencies of individual species did not vary greatly between the parasite-affected quadrats and in those devoid of infection. For example, *Phlyctis argena* showed a very similar dynamics in thallus area and numbers in both quadrats devoid of the pathogen and those with infestations (Fig. 3), although notably the average thallus cover was higher in quadrats affected by the fungus. However, when the affected quadrats were divided into strongly and weakly infested, the trend was different (Fig. 4). Where *A. arachnoidea* was aggressive, both thallus numbers and cover were lower. The cover tended to decrease, but after a ste-



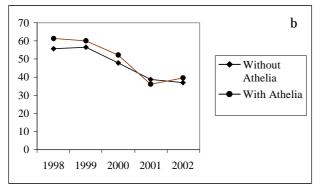
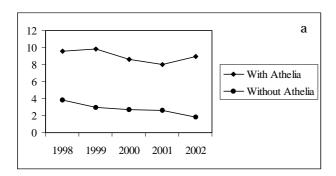


Fig. 3. Dynamics of *Phlyctis argena* in infested and non-infested quadrats: a) dynamics of thallus area; b) dynamics of thallus numbers



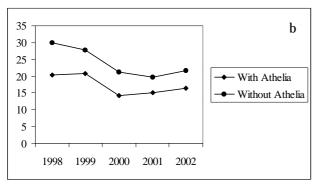
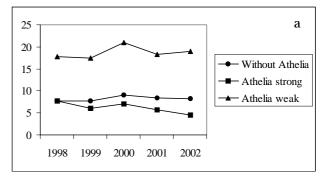


Fig. 5. Dynamics of *Lecidella elaeochroma* in infested and non-infested quadrats: a) dynamics of thallus area; b) dynamics of thallus numbers

ady decrease the thallus numbers started to increase, with small thalli invading post-infection gaps. In quadrats with weak infection, the thallus cover was larger, fluctuated towards an increase as thallus numbers steadily decreased until 2001, and then started to grow. This indicates development through



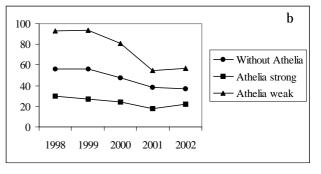
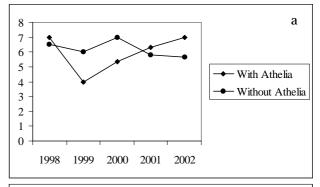


Fig. 4. Dynamics of *Phlyctis argena* in infested with aggressive, with non-aggressive *A. arachnoidea* and in non-infested quadrats: a) dynamics of thallus area; b) dynamics of thallus numbers



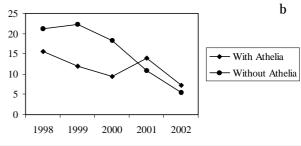
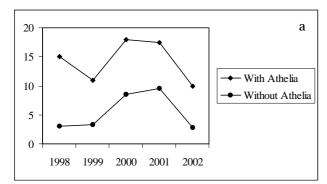


Fig. 6. Dynamics of *Melanelia fuliginosa* in infested and non-infested quadrats: a) dynamics of thallus area; b) dynamics of thallus numbers

the radial growth and merging of thalli. Similar tendencies were observed in quadrats devoid of infection. Other lichen species were not found in quadrats with both infection types on more than in one or two occasions, and hence it was only possible to compare their development in infected and non-infected communities.



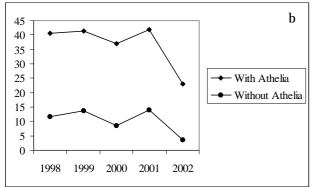


Fig. 7. Dynamics of *Biatora* sp. in infested and non-infested quadrats: a) dynamics of thallus area; b) dynamics of thallus numbers

Lecidella elaeochroma behaved similarly to *Phlyctis argena* with respect to thallus numbers in both groups of quadrats, but thallus cover tended to increase in the infested quadrats (Fig. 5). *Melanelia fuliginosa* behaved very differently (Fig. 6): in fungusaffected quadrats, both thallus cover and numbers fluctuated strongly, but in uninfected communities thallus cover increased more or less steadily whilst thallus numbers decreased, indicating thallus merging and radial growth. Moreover, in quadrats with aggressive *A. arachnoidea, M. fuliginosa* was totally eliminated, showing that this lichen is more susceptible to infection than other species, but possibly it can re-establish quickly, hence its common presence in the studied plots.

The fast-growing, sterile, sorediate *Biatora* species showed similar dynamics in both infested and non-infested quadrats (Fig. 7), but the species was more abundant in the infested quadrats and the fluctuation in thallus cover and numbers was great.

These four lichen species were the most common ones in the investigated quadrats: *P. argena* was recorded in 18 quadrats out of 23, and in 5 plots out of 6; *L. elaeochroma* in 13 quadrats and 5 plots; *Melanelia fuliginosa* in 9 quadrats and 4 plots; *Biatora* sp. in 8 quadrats and 5 plots. Their abundance suggests that all of them are relatively pollution-to-lerant. Regarding their tolerance to frequent stress (*e.g.*, infection), *Phlyctis argena* and *Lecidella elae-ochroma* can be characterised as stress-tolerant, whereas *Melanelia fuliginosa* is medium stress-tolerant,

but capable of rapid re-establishment. *Biatora* sp. can be regarded as a pioneer species rapidly invading post-infection areas. It also seems that *M. fuliginosa* and *Biatora* sp. are rather weak competitors, as both are scarce in species-rich communities. The fungus infection provides them with the necessary space to establish and grow.

The reaction of other lichen species was difficult to interpret, as they were not common or abundant enough in the infected quadrats. Generally, it seems that there is no lichen species capable of fully resisting A. arachnoidea. However, parts of Phlyctis argena thalli often survived even the severest infection and were capable of regenerating, whereas post-infection remnants of Lecidella elaeochroma were less viable and regenerated slowly. Melanelia fuliginosa was killed in all cases and never regenerated. The reaction of lichens to the varying aggressiveness of the fungus was uneven: in some cases infection eliminated almost all members of the community, leaving only several remnants of P. argena thalli (e.g., in quadrat 4-3); in other cases several species were affected, but only parts of the thalli of all species present in the quadrat were eliminated, whilst the remaining ones successfully developed further (e.g., Lecidella elaeochroma, Buellia griseovirens, Phlyctis argena, Graphis scripta and Opegrapha rufescens in quadrat 6_4).

Lawrey (1991) stated that the species that are chemically well defended against predators/pathogens replace poorly defended species, but this hypothesis does not seem to fit the case of A. arachnoidea infection: for example, Buellia griseovirens and Phlyctis argena both contain the norstictic acid complex as secondary metabolites, the former containing additional substances as well. Nevertheless, P. argena appears to be the more infection-resistant species of the two. Moreover, as our study and reports of other authors (Poelt, Jülich, 1969; Arvidsson, 1976; Parmasto, 1998; Yurchenko, Golubkov, 2003) have shown, a range of lichens with very variable chemistry can be attacked and killed by the fungus. Most important in this case is the capability of the species to regenerate and/or re-establish more rapidly and successfully after infection; Arvidsson (1976) has already noted that frequently infested swards of Lecanora conizaeoides and Scoliciosporum chlorococcum re-establish rapidly. Therefore pioneer and other relatively fast-growing lichens seem to be better adapted to the conditions of frequent A. arachnoidea infection. A certain similarity can be observed in the post-infection reactions of forest trees, when strong competitors are removed by an aggressive pathogen and replaced by weaker competitors and early successional species (Dickman, 1992). The principal difference between infestations of trees and the infection of lichens by A. arachnoidea is the selectivity of the former (one or several closely related plant species are affected) and the universal effect of the latter (*A. arachnoidea* can kill all members of epiphytic communities, except bryophytes). Although Yurchenko and Golubkov (2003) reported *A. arachnoidea* infecting mosses as well, we have not observed such a phenomenon in our study. Our observations indicated mosses to benefit from the infection by rapidly occupying areas where lichens had been killed by the fungus.

In further comparing the effect of *A. arachnoidea* infection on lichens with plant pathogen infections, Arvidsson's (1976) statement that primordia and young thalli are most susceptible corroborate the fact that fungus-induced plant mortality is most important at the seed and seedling stage (Alexander, 1992). On the other hand, as observed by Motiejûnaitë and Jucevièienë (2003) and Yurchenko and Golubkov (2003), the problem is manifested not only in the destruction of diaspores but in the periodic destruction of adult thalli as well. Thus *A. arachnoidea*, like other plant pathogens, can alter age structure in lichen populations by killing large, older thalli and clearing space for numerous small young thalli arising from diaspores; it can also regulate population size.

"Monoculturisation" of epipytic communities probably facilitates attacks by the fungus, as postulated by Arvidsson (1976) and to some extent by Gilbert (1988). In our investigation, it was noticed that more aggressive infections were present only in the communities with a lower diversity of lichens, in plots situated closer to the emission source. However, the question of whether A. arachnoidea plays an instrumental role in simplifying lichen communities in polluted areas is a difficult one. The answer could be obtained by surveying lichen communities in relatively pristine areas before the start of operation of a major emission source. If the flush of A. arachnoidea coincides with a significant increase of pollution, then the fungus can be considered a native pathogen that encounters changing conditions and increases. Such pathogens are destructive when first introduced but, upon eliminating many susceptible species, become less damaging to the resulting community (Dickman, 1992). In the case of A. arachnoidea, it can then be hypothesised that after infection, epiphytic communities eventually reach a certain equilibrium and achieve the pattern seen in places frequently infested by the fungus. Thus, in accordance with our observations and those of Arvidsson (1976) and Gilbert (1988), it may be assumed that in more polluted areas, A. arachnoidea infections occur at a higher frequency than in less polluted places. However, it is more likely that the fungus is a secondary factor influencing the impoverishment of epiphytic communities in the polluted areas.

As observed earlier (Motiejûnaitë, Jucevièienë, 2003), *A. arachnoidea* displays a varying degree of aggressiveness and it seems that two (or maybe more) strains of the fungus invade epiphytic lichens. Al-

though highly damaging infections were more common in the plots closer to the emission source, less aggressive infestations were noted in all study plots and all community types. Notably, more damaging infections were usually caused by several merged lesions, possibly creating infestations of two or more genets. Small separate infestations caused less conspicuous damage. Although the morphology and biology of *A. arachnoidea* was described in detail by Yurchenko and Golubkov (2003), this merging phenomenon and variability of aggressiveness were not discussed.

In earlier papers, the distribution of A. arachnoidea was often attributed to high levels of SO_2 (Arvidsson, 1976; Gilbert, 1988) and was connected with a low bark pH, but it is evident that the fungus is equally vigorous in conditions of elevated nitrogen pollution, judging by the situation in our study area and by its preferences for nitrophilous hosts (see also Parmasto, 1998; Yurchenko, Golubkov, 2003).

CONCLUSIONS

- 1. *A. arachnoidea* infection affected both the diversity (species numbers) and structure (species abundance and cover area) of the epiphytic communities studied. All three characteristics fluctuated in the selected quadrats during the whole investigation period.
- 2. Individual response of different epiphytes to infection varied: the growth patterns of *Phlyctis argena* and *Lecidella elaaeochroma* did not differ significantly in the infested and non-infested communities, meanwhile *Melanelia fuliginosa* showed a strong negative reaction to the infection. Fast-growing lichen species benefited from the infection, rapidly occupying post-infection gaps.
- 3. Though *A. arachnoidea* infection in epiphytic community occurs more often in the localities under anthropogenic pressure, it is connected neither with specific pollutants nor with phorophyte bark pH.

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GRYBO *ATHELIA ARACHNOIDEA* EPIDEMIOLOGIJA LABAI ANTROPOGENIZUOTØ PLAÈIALAPIØ MIÐKØ EPIFITØ BENDRIJOSE

Santrauka

Vidurio Lietuvos plaèialapiø miðkuose, esanèiuose fosforo tràðø gamyklos poveikio zonoje, tirta papëdgrybio Athelia arachnoidea átaka epifitø bendrijoms. Penkerius metus buvo stebëtos epifitø bendrijos 23 pasirinktuose kvadratuose. Per visà tyrimo laikà grybas aptiktas 10 kvadratø ir kai kuriuose jø padarë nemabos balos. A. arachnoidea veikë tiek kerpiø rûðiø skaièiø, tiek padengimà, nors jo átaka skirtingoms kerpiø rûðims skyrësi ir dël infekcijos pobûdþio, ir dël individualios kerpiø reakcijos á jà: Phlyctis argena ir Lecidella elaeochroma palyginti gerai toleravo infekcijà, paþeisti jø gniuþulai gana greitai regeneravo bei ásikurdavo nauji, jauni gniubulai; Melanelia fuliginosa buvo jautresnë infekcijai, taėiau ji tikriausiai pasibymi sugebėjimu greitai ásikurti ið naujo, tuo tarpu greitai augantiems steriliems, sorediðkiems Biatora sp. gniuþulams grybo infekcija bendrijoje buvo naudinga, nes kerpë greitai ásikurdavo iðtuðtëjusiuose plotuose, kurie atsirasdavo grybui sunaikinus kitø rûðiø gniuþulus.

Raktaþodþiai: epifitinës kerpës, kerpiø bendrijos, oro tarða, kerpiø parazitai, papëdgrybiai, *Athelia arachnoidea,* Lietuva