10.2478/v10067-010-0012-y

ANNALES
UNIVERSITATIS MARIAE CURIE-SKŁODOWSKA
LUBLIN – POLONIA

VOL. LXIV, 2 SECTIO C 2009

ANETA PTASZYŃSKA[1], WIESŁAW MUŁENKO[1], JAN ŻARNOWIEC[2]

[1]Department of Botany and Mycology, Institute of Biology, Maria Curie-Skłodowska University, Akademicka 19, 20-033 Lublin, Poland, e-mail: wieslaw.mulenko@poczta.umcs.lublin.pl
[2] Department of Ecology and Protection of Environment, Institute of Environmental Protection and Engineering, University of Bielsko-Biała, Willowa 2, 43–309 Bielsko-Biała, Poland

Bryophytes microniches inhabited by microfungi

Mikronisze zasiedlane przez briofilne grzyby mikroskopijne

SUMMARY

Traditionally treated bryophytes with 24,000 species noted in the world and among them 956 Polish species remain a largely unstudied reservoir of undescribed fungi species. About 400 obligate bryophilous fungi (mainly ascomycetes) have been described till now. The number is still very low, considering the fact that every year about 1,500 new fungi species are discovered. Therefore bryophytes deserve to arouse mycologists interest as a potentially rich source (reservoir) of undescribed species. In the manuscript we present a brief review of the current knowledge of bryophilous microfungi as well as a prospect for research conducted on these species, especially the endophytic ones.

STRESZCZENIE

Do tradycyjnie ujmowanych mszaków zaliczamy około 24 000 gatunków notowanych z całego świata, z czego 956 występuje w Polsce. Do tej pory opisano jedynie około 400 gatunków grzybów (głównie workowców) związanych obligatoryjnie z mszakami. Liczba zanotowanych taksonów grzybów briofilnych jest niewielka, zwłaszcza jeśli weźmiemy pod uwagę fakt, że co roku opisywanych jest około 1500 gatunków grzybów nowych dla nauki. Z tego powodu mszaki zasługują na szczególne zainteresowanie mykologów jako potencjalne bogate źródło (rezerwuar) nieodkrytych jeszcze gatunków. Niniejszy artykuł prezentuje obecny stan wiedzy dotyczący mikroskopijnych grzybów biofilnych oraz perspektywy badań nad tymi organizmami, zwłaszcza gatunkami endofitycznymi.

K e y w o r d s: cryptogamous plants, bryophilous microfungi, endophytes, ecology, taxonomy

INTRODUCTION

A majority of fungi (about 90%) are organisms connected with plants or detected on products made from plant materials, therefore almost all mycological research has been conducted on vascular plants, especially the domesticated ones (important from the economic point of view). Wild plants and among them spore plants have not been under consideration of very intensive investigations. Among lower plants, bryophytes are worthy of special attention. They consist of three divisions: the Anthocerotophyta (hornworts), Marchantiophyta (liverworts), and Bryophyta (mosses). The three groups were previously joined together as three classes of the division Bryophyta (Rajan 2000), but after detailed investigations which proved that the three units form a paraphyletic group, they are now placed in three separate divisions (Qiu et al. 2006, Troitsky et al. 2007). In the sense of evolution, Bryophyta are very old organisms which evolved independently from other plants. They are dispersed worldwide and play an important role in the environment, especially the long living structures (turfs, mats, cushions etc.) which they form.

Traditionally treated bryophytes consist of nearly 960 genera and 24,000 species (Rajan 2000); Polish taxa are represented by 91 families, 209 genera and 956 species (Klama 2003, 2006, Ochyra et al. 2003, Żarnowiec 2003). The gametophyte is a predominant plant body in the life cycle of Bryophyta. The sporophyte is a temporary generation dependent on the gametophyte. The gametophyte can be divided into two main categories: the thalloid and leafy (foliose) forms (Rajan 2000).

Likewise on other plants, fungi have been detected on bryophytes as their pathogens, parasites, saprobes, endophytes and commensals (Davey 2006). Fungi can infect special body structures such as the protonema, thallus, rhizoids, leaves, cells, organelles or special body fragments, for example upper, intermediate or lower parts of the turfs. All the above-mentioned structures form niches (microniches), which are limited to a small place but they offer fungi all elements indispensable for living (Döbbeler 2002). Almost 400 species of bryophilous fungi have been described by now, but the number is low if we consider that there probably exist 1.5 million fungi species and each year about 1,500 new taxa are added by scientists. In some cases the fungus/plant ratio may exceed 5:1 (Hawksworth 1997, 2001); therefore, Bryophyta, plants that receive insufficient attention from mycologists, must be rich in the undescribed fungi species (Felix 1988, Davey & Currah 2006). One study revealed that 62 of 123 fungi detected on mosses were new and even a single moss genus *Dawsonia* yielded 21 Ascomycota new to science (Hawksworth 1997). Döbbeler found that up to 40 ascomycetes can be detected on particular moss genera and he estimated the number of obligate fungi on bryophytes as 2,000 species (Döbbeler 1997).

How unexploited this mycological research area is can be proved by the fact that by the year 2000 only four bryophilous ascomycetes had been known from the whole Africa (Hawksworth 2001). Generally, tropical forests are assumed to be richer in biodiversity than other geographical regions or habitats. Consequently, hornworts, liverworts and mosses which occur there must be rich in fungi.

But we should also remember that bryophytes are dispersed worldwide and can even inhabit polar regions. Such extremely diverse range of habitats and hence hosts for bryophilous fungi indicate that we can predict many new species to be found. But more emphasis should be put on the fact that divergent habitats require different techniques of fungi detections. Although some microfungi can be detected by a light microscope after e.g. staining with lactophenol cotton-blue, others must be cultured on special media as e.g.: PDA (potato dextrose agar), MEA (Malt Extract Agar Oxoid) or Sabouraud Dextrose Agar with the streptomycin and penicillin antibiotics. Moreover, the cultures should be kept at vast ranges of temperatures (from 2 to 45°C) to detect psychrophilic and thermophilic fungi as well. Especially endophytes, in many cases, can not be detected only by the use of the light microscope and must be cultured after thin cut sections. To avoid the culture contamination by the species found in air, dust and dirt, the thalloid, leaf or shoot surface sterilization must be very strict. To confirm that the isolated fungus is an endophyte, the studied structures of sterile tissues should be examined by scanning electron microscopy (Maheshwari 2006).

FUNGI DETECTED ON THALLOID BROPHYTES

Thalloid forms do not have organized leaves, roots, and stems as do the vascular plants. Their plant body (thallus) grows directly on the substratum and is anchored to the soil by rhizoids. On the dorsal thallus surface we can find various species of bryophilous ascomycetes genera such as *Bryoscyphus* on *Conocephalum*, *Marchantia* or *Reboulia* (Spooner 1984, Verkley et al. 1997) and *Lamprospora aneurae* on *Aneura pingius* (Benkert 1990). On the ventral side of the thallus, the following fungi can be observed: *Pseudonectria metzgeriae* on *Metzgeria furcata* (Döbbeler 1978) and *Didymella hepaticarum* immersed within the thallus on *Riccia* spp. (Döbbeler 1978) or *Didymosphaeria marchantiae* [according to Aptroot (1995) it is a synonyme of *Phaeodothis winteri* (Niessl) Aptroot] on *Marchantia polymorpha*, the latter was also observed on male and female receptacles (Racovitza 1959, Döbbeler 1978, Aptroot 1995).

FUNGI DETECTED ON LEAFY BRYOPHYTES

Leafy (foliose) forms have a central axis on which leaves can grow. The leaves (*phyllids*) are usually arranged in rows of two or three around the shoot and are generally one cell thick without the vascular tissue.

On the dorsal leaf surface of foliose hepatics we can observe e.g. various species of *Epibryon* on Jungermanniales (Racovitza 1959, Döbbeler 1978, 1985) or *Nectria egens* on *Leptolejeunea vitrea* (Corner 1935). On the ventral side, *Bryorella marginis* on *Bazzania spiralis* (Döbbeler 1982), *Epibryon deceptor* on *Radula flaccida* (Döbbeler 1998) can be found. Such fungi as *Epibryon intercellulare* on *Bazzania trilobata* and *Epibryon marsupidii* on *Marsupidium surculosum* are immersed in the leaves (Döbbeler 1979). Fungi (fungal stromata) can be also immersed in the stem of the leafy hepatics, e.g. *Bryorella semi-immersa* on Lophoziaceae (Döbbeler 1978).

On the mosses we can detect fungi in various microniches, e.g. on the stem of *Hypnum* sp. we can observe *Bryosphaeria quinqueseptata* (Döbbeler 1978), between the paraphylia of *Thuidium* spp. – *Epibryon diaphanum*, which is also observed on *Hylocomium* (Döbbeler 1979, 1985), the hyaline hair points of the

Grimmiaceae leaves are infected by *Bryochiton monascus* (Döbbeler 1978), *Hypobryon heterotropum* perforates the leaves of *Leucodon sciuroides* (Döbbeler 1983), and *Epibryon leucobryi* is immersed within the leaves of *Leucobryum* (Döbbeler 1978). Very interesting microniches are formed by the leaves of Polytrichales, which are typically 6 to 8 mm long and have lamellae that increase the productivity of photosynthesis. Between the lamellae, there are perfect conditions related to humidity, temperature and nutrient accessibility for fungi to leave, therefore we can observe a lot of fungi species there. Between the end-cells of the lamellae, there is immersed *Dawsophila polycarpa* (Döbbeler 1999, 2001), and between the leaf lamellae: *Bryorella compressa*, *B. pogonati-urnigeri*, *B. cryptocarpa*, *Dawsicola neglecta*, *Epibryon interlamellare*, *Gloeopeziza interlamellaris* and *Potriphila navicularis* (Racovitza 1959, Döbbeler 1978, 1981, 1985, 1986, 1987, 1996, 2001); on the abaxial leaf nerves there are *Potriphila neurogena* and *Rogellia nectrioidea* (Döbbeler 2001, 2002).

FUNGI CONNECTED WITH RHIZOIDS

Fungi can be found on rhizoids as well as on other parts of bryophyte body fragments. Also fungi that form mycorrhizal associations with vascular plants have been found to form similar cellular structures with bryophytes, but still, there is no experimental evidence for their physiological function. Therefore some scientists claim to term it mycorrhizal-like associations (Kottke & Nebel 2005) form by endophytic fungi. In 1985 Pocock & Duckett identified three different types of such mycorrhizal-like associations. In the first type, basidiomycete fungus creates associations with Aneuraceae and Jungermanniaceae that are similar to the orchid-type of mycorrhiza. In the second type, species that have swollen rhizoids from such families as: Calypogeiaceae, Cephaloziaceae and Lepidoziaceae are infected by endophytic fungi. The third one consists of species belonging to *Anthoceros*, *Marchantia*, *Fossombronia*, *Pellia*, *Pallavicina*, which are inhabited by endophytes that produce vesicles and arbuscules and are similar to the VA Mycorrhizal fungi (Pocock & Duckett 1985b, During & Tooren 1990). Also apothecia of *Lamprospora*, *Neottiella*, *Octospora* and apressoria of *Glomus* form associations with mosses' rhizoids (Benkert 1987, 1993, 1995, Warner 1984, Iqbal & Bareen 1990). Despite the fact that bryophytes are colonized by fungi that create mycorrhizal associations with higher plants, there is still no experimental evidence for the transfer of photoassimilates from plants to the fungus or nitrogen and phosphorus in the opposite direction (During & Tooren 1990). This is the reason why some scientists claim that interactions between bryophytes and mycorrhizal fungi are mainly saprobic or even mildly parasitic (Dowding 1959, Went & Stark 1968). But it should be emphasized that some research indicates this relationships stimulate plant growth and fungi spore productions (Fonseca & Berbara 2008). Moreover, bryophytes, in the absence of higher plant roots, also retain the infective ability of mycorrhizal fungi. Dead and senescent bryophyte body fragments can act as a fungal inoculum reservoir that is helpful in the process of mycorrhizal colonization of new roots in the spring (Rabatin 1980, Warner 1984, Iqbal & Bareen 1990). From the historical point of view, this is the pattern of mycorrhizal fungi and bryophytes co-evolution, because 'the symbiotic fungal associations of liverworts are the possible ancestor of mycorrhizae' (Nebel et al. 2004).

MICRONICHES INHABITED BY FUNGAL SAPROBES, PARASITES AND PATHOGENS

The relationships between fungi and bryophytes are difficult to categorize. Endophytes, which produce the intercellular mycelium and do not cause damage in host cells, can easily transform into parasites or saprobes when the environmental (microenvironmental) conditions change. According to Thormann et al. (2001) typical saprobes are among Zygomycota: *Mortierella alpina*, *M. elongata*, *M. horticola*, *Mucor hiemalis*, Ascomycota: *Sporormiella intermedia*, *Kernia retardata*, *Sordaria fimicola*, Basidiomycota: *Bjerkandera adusta* and anamorphic fungi: *Cladosporium herbarum*, *Aspergillus niger*, *Trichoderma aureoviride*, and *Botrytis cinerea*. A majority of saprobic fungi are cosmopolitan, but some of them may be host-specific and develop unique methods of degradation, like such fungi as *Oidiodendron maius*, *O. periconioides* and *Pochonia bulbillosa*, which have a distinct technique of degrading *Sphagnum fuscum* (Tsuneda et al. 2001, Rice et al. 2006). The overall decomposition of bryophyte cell walls is a very slow and difficult process because they contain substances (e.g. polyphenolic-rich compounds) that are toxic to most microorganisms (Asakawa 1990, Verhoeven & Liefveld 1997). Therefore, during the first stages of decomposition ascomycetes may dominate, but later they give way to basidiomycetes, which are able to synthesize enzymes decomposing complex carbohydrates (Deacon 1984). The succession of fungi can also be observed across a vertical section of turfs, mats and cushions. Bryophytes, unlike higher plants, wither from the bottom to the top, with apical fragments remaining alive and growing whilst the lower ones are decomposing. Therefore, in the upper parts of turfs, mats and cushions endophytes and pathogens dominate; in the intermediate layer we can observe the mix of endophytes, pathogens, parasites and saprobes and in the lower, where the processes of decomposition are the strongest, saprobes dominate.

Bryophyte pathogens can be detected by the black, brown or yellow necrotic and chlorotic spots that they cause. Such fungi as: *Bryoscyphus dicrani*

(Henderson 1972) or *Lizonia baldinii* (Döbbeler 2003) form small, necrotic spots on gametophyte. Others, such as: *Thyronectria hyperantarctica* and *Pythium ultimum* var. *ultimum* are the reason for the whole gametophyte death, which can be seen in the Arctic as huge 'fairy rings' (several meters in diameter) of dead mosses (Wilson 1951, Longton 1973, Fenton 1983).

CONCLUSIONS

Bryophytes create varieties of microniches that can be inhabited by fungi. In the life cycle of these plants gametophytes dominate. The sporophyte is a short living generation dependent on the haploid generation. Fungi are detected on all the structures or even on particular body fragments such as dorsal or ventral leaf surfaces, leaf axils, single leaf cells, stems, dorsal or ventral thallose surfaces, receptacles etc. Also upper, intermediate or lower parts of the turfs, mats and cushions have different fungi associations. Definitely bryophytes and fungi evolve together and develop unique adaptations. Sometimes the categorization of relationship types among fungi and bryophytes is difficult and it is not obvious if the particular fungus is an endophyte or parasite, because it changes in time. The interactions between bryophytes and fungi still remain poorly studied. Only few aspects were studied more carefully: the decomposition of bryophytes (focused on one genus: *Sphagnum*), for its importance in nutrient cycling in ecosystems and the biodiversity of bryophilous ascomycetes and basidiomycetes, which were investigated by Döbbeler (1997) and Kost (1988), respectively. Although the interactions between bryophytes and fungi are widespread in nature, they remain largely unstudied.

ACKNOWLEDGEMENTS

The study was supported by the Polish Ministry of Education and Science (project No. N/N304/172436).

REFERENCES

1. Asakawa Y. 1990. Biologically active substances from bryophytes. [In:] Bryophyte Development: Physiology and Biochemistry. R. N. Chopra, S. C. Bhatla (eds), CRC Press – Ann Arbor: 259–287.
2. Aptroot A. 1995. Redisposition of some species excluded from *Didymosphaeria* (Ascomycotina). Nova Hedwigia 60: 325–379.
3. Aptroot A. 1995. A monograph of *Didymosphaeria*. Studies in Mycology 37: 1–140.

4. Benkert D. 1987. Beiträge zur Taxonomie der Gattung *Lamprospora* (Pezizales). Zeitschrift für Mykologie 53: 195–271.
5. Benkert D. 1990. Zwei neue Arten der Gattung *Lamprospora* (Pezizales, Ascomycetes). [Two new species of the genus *Lamprospora* (Pezizales, Ascomycetes)]. Feddes Repertorium 101: 631–637.
6. Benkert D. 1993. Bryoparasitic Pezizales: Ecology and systematics. [In:] Fungi of Europe: Investigation, Recording and Conservation. D. N. Pegler (ed.). Royal Botanic Gardens (Kew): 147–156.
7. Benkert D. 1995. Becherlinge als Moosparasiten. Boletus 19: 97–127.
8. Corner E. J. H. 1935. A *Nectria* parasitic on a liverwort: with further notes on *Neotiella crozalsiana*. Gardens Bulletin (Straits Settlements) 8: 135–144.
9. Davey M. L., Currah R. S. 2006. Interactions between mosses (Bryophyta) and fungi. Canadian Journal of Botany 84: 1509–1519.
10. Deacon J. W. 1984. Introduction to Modern Mycology. 2nd ed. Blackwell Scientific Publications, Oxford, UK.
11. Döbbeler P. 1978. Moosbewohnende Ascomyceten I. Die pyrenocarpen, den Gametophyten besiedelnden Arten. Mitteilungen der Botanischen Staatssammlung München 14: 1–360.
12. Döbbeler P. 1979. Moosbewohnende Ascomyceten III. Einige neue Arten der Gattungen *Nectria*, *Epibryon* und *Punctillum*. Mitteilungen der Botanischen Staatssammlung München 15: 193–221.
13. Döbbeler P. 1981. Moosbewohnende Ascomyceten V. Die auf *Dawsonia* vorkommenden Arten der Botanischen Staatssammlung München. Mitteilungen der Botanischen Staatssammlung München 17: 393–473.
14. Döbbeler P. 1982. Moosbewohnende Ascomyceten VI. Einige neue Pyrenomyceten. Mitteilungen der Botanischen Staatssammlung München 18: 341–358.
15. Döbbeler P. 1983. *Hypobryon* gen. nov. (Dothideales), eine bemerkenswerte Gattung bryophiler Pyrenomyceten. Nova Hedwigia 37: 1–17.
16. Döbbeler P. 1985. Moosbewohnende Ascomyceten VII. Neufunde einiger Arten der Gattung *Epibryon*. Mitteilungen der Botanischen Staatssammlung München 21: 757–773.
17. Döbbeler P. 1986. Ascomyceten auf Polytrichaceen. Sydowia 38: 41–64.
18. Döbbeler P. 1987. Ascomycetes growing on *Polytrichum sexangulare*. [In:] Arctic and Alpine Mycology II. G. A. Laursen, J. F. Ammirati, S. A. Redhead (eds). Environmental Science Research 34: 87–107.
19. Döbbeler P. 1996. *Potriphila navicularis* gen. et sp. nov. (Ostropales, Ascomycetes), ein bipolar verbreiteter Parasit von *Polytrichum alpinum*. Nova Hedwigia 62: 61–77.
20. Döbbeler P. 1997. Biodiversity of bryophilous ascomycetes. Biodiversity and Conservation 6: 721–738.
21. Döbbeler P. 1998. Ascomyceten auf der epiphyllen *Radula flaccid*a (Hepaticae). Nova Hedwigia 66: 325–373.
22. Döbbeler P. 1999. *Polytrichadelphus magellanicus* – a mycological Eldorado: five new ascomycetes on a single collection from Tierra del Fuego. [In:] Anonymous (ed.), Riclef-Grolle-Festschrift. Haussknechtia Beih. (Jena) 9: 79–96.
23. Döbbeler P. 2001. *Polytrichadelphus magellanicus* sensu lato (Musci) and its ascomycetes –different fungi on different hosts. Sendtnera 7: 35–45.
24. Döbbeler P. 2002. Microniches occupied by bryophilous ascomycetes. Nova Hedwigia 75: 275–306.
25. Döbbeler P. 2003. Ascomycetes on Dendroligotrichum (Musci). Nova Hedwigia 76: 1–44.

26. Dowding E. S. 1959. Ecology of *Endogone*. Transactions of the British Mycological Society 42: 449–457.
27. During H. J., van Tooren B. F. 1990. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society 104: 79–98.
28. Felix H. 1988. Fungi on bryophytes, a review. Botanica Helvetica 98: 239–269.
29. Fenton J. H. C. 1983. Concentric fungal rings in antarctic moss communities. Transactions of the British Mycological Society 80: 415–420.
30. Fonseca H. M. A. C.; Berbara R. L. L. 2008. Does *Lunularia cruciata* form symbiotic relationships with either *Glomus proliferum* or *G. intraradices*? Mycological Research 112: 1063–1068.
31. Hawksworth D. L. 1997. The fascination of fungi: exploring fungal diversity. Mycologist 11: 18–22.
32. Hawksworth D. L. 2001. The magnitude of fungal diversity: the 1.5 million species estimate revisited. Mycological Research 105: 1422–1432.
33. Henderson D. M. 1972. Fungi on Scottish bryophytes. Transactions and proceedings of the Botanical Society of Edinburgh 41: 385–391.
34. Iqbal S. H., Firdaus-e-Bareen 1990. Mycorrhizal associations in rock crevices: Vesicular arbuscular mycorrhizal infections in decaying aerial portions of *Adiantum capillus-veneris* L. induced by VA mycorrhizal bryophytes in rock crevices at Khanspur. Pakistan Journal of Forestry 40: 311–317.
35. Klama H. 2003. Różnorodność gatunkowa – wątrobowce i glewiki. [In:] Różnorodność biologiczna Polski. R. Andrzejewski, A. Weigle (eds). Narodowa Fundacja Ochrony Środowiska (Warszawa): 49–58.
36. Klama H. 2006. Systematic catalogue of Polish liverwort and hornwort taxa. [In:] An annotated checklist of Polish liverworts and hornworts. Biodiversity of Poland. Vol. 4. J. Szweykowski (ed.). W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków: 83–100.
37. Kottke I., Nebel M. 2005. The evolution of mycorrhiza-like associations in liverworts: an update. New Phytologist 167: 330–334.
38. Kost G. 1988. Interactions between Basidiomycetes and Bryophyta (Moss inhabiting Basidiomycetes III). Endocytobiosis and Cell Research 5: 287–308.
39. Longton R. E. 1973. The occurrence of radial infection patterns in colonies of polar bryophytes. British Antarctic Survey Bulletin 32: 41–49.
40. Maheshwari R. 2006. What is an endophytic fungus? Current Science 90: 1309.
41. Nebel M., Kreier H. P., Preußing M., Weiß M., Kottke I. 2004. Symbiotic fungal associations of liverworts are the possible ancestors of mycorrhizae. [In:] Frontiers in Basidiomycote Mycology. R. Agerer, M. Piepenbring, P. Blanz (eds). Eching, Germany, IHW Verlag: 339–360.
42. Ochyra R., Żarnowiec J., Bednarek-Ochyra H., 2003. Census Catalogue of Polish Mosses. Institute of Botany, Polish Academy of Science, Kraków, pp. 372.
43. Pocock K., Duckett J. G. 1985. Fungi in hepatics. Bryological Times 31: 2–3.
44. Prior P. V. 1966. A new fungal parasite of moss. Bryologist 69: 243–246.
45. Qiu Y. L., Li L., Wang B., Chen Z., Knoop V., Groth-Malonek M., Dombrovska O., Lee J., Kent L., Rest J., Estabrook G. F., Hendry T. A., Taylor D. W., Testa C. M., Ambros M., Crandall-Stotler B., Duff R. J., Stech M., Frey W., Quandt D., Davis Ch. C. 2006. The deepest divergences in land plants inferred from phylogenomic evidence. Proceedings of the National Academy of Sciences U.S.A. 103: 15511–15516.
46. Rabatin S. C. 1980. The occurrence of the vesicular-arbuscular mycorrhizal fungus *Glomus tenuis* with moss. Mycologia 72: 191–195.

47. Racovitza A. 1959. Étude systematique et biologique des champignons des bryophiles. Memoires du Museum National d'Histoire Naturelle Botanique 10: 1–288.
48. Rajan S. S. 2000. Practical Manual of Bryophyta. Anmol Publications New Delhi, pp. 113.
49. Rice A. V., Tsuneda A., Currah R. S. 2006. *In vitro* decomposition of *Sphagnum* by some microfungi resembles white rot of wood. FEMS Microbiology Ecology 56: 372–382.
50. Spooner B. M. 1984. Ascomycetes. [In:] An Account of the Fungi of Arran, Gigha and Kintyre. P. M. Kirk, B. M. Spooner. (eds). Kew Bulletin 38: 503–597.
51. Thormann M. N., Currah R. S., Bayley S. E. 2001. Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. Bryologist 104: 548–559.
52. Troitsky A. V., Ignatov M. S., Bobrova V. K., Milyutina I. A. 2007. Contribution of genosystematics to current concepts of phylogeny and classification of bryophytes. Biochemistry (Moscow) 72: 1368–1376.
53. Tsuneda A., Thormann M. N. Currah R. S. 2001. Modes of cell wall degradation of *Sphagnum fuscum* by *Acremonium* cf. *curvulum* and *Oidiodendron maius*. Canadian Journal of Botany 79: 93–100.
54. Verhoeven J. T. A., Liefveld W. M. 1997. The ecological significance of organochemical compounds in *Sphagnum*. Acta Botanica Neerlandica 46: 117–130.
55. Verkley G. J. M, van der Aa H. A., de Cock G. W. 1997. *Bryoscyphus atromarginatus* spec. nov. (Leotiaceae), a new ascomycete parasitizing the thallus of *Marchantia polymorpha*. Persoonia 16: 383–387.
56. Warner A. 1984. Colonization of organic matter by vesicular-arbuscular mycorrhizal fungi. Transactions of the British Mycological Society 82: 352–354.
57. Went F. W., Stark N. 1968. Mycorrhiza. BioScience 18: 1035–1039.
58. Wilson J. W. 1951. Observations of concentric 'fairy rings' in arctic moss mat. Journal of Ecology 39: 407–416.
59. Żarnowiec J. 2003. Różnorodność gatunkowa – mchy. [In:] Różnorodność biologiczna Polski. R. Andrzejewski, A. Weigle (eds). Narodowa Fundacja Ochrony Środowiska, Warszawa: 59–65.