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Occurrence of fungal structures in bryophytes of the boreo-nemoral zone

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Abstract

A survey of arbuscular mycorrhizal structures in bryophyte species was conducted. In total, 43 bryophyte species belonging to 29 families were studied. A search was made for hyphae and vesicles resembling structures of arbuscular mycorrhizal (AM) fungi in bryophytes. AM fungal structures (arbuscules, vesicles, hyphal coils nonseptate intra and inter celular hyphae) were found only in epigeous hepatics. AM fungal structures were absent in 21 moss species and recorded in only four of the studied 21 hepatics species and one of the hornworts. Other fungal structures were also observed. Fungal structures were observed in bryophyte stem and leaf tissues, and in rhizoids. The AM association with bryophytes was observed to be symbiotic.

Key words: arbuscular mycorrhizal fungi, bryophyte, hepatics, moss, symbiosis.

Introduction

Bryophytes, which are classified into the divisions Marchantiophyta (liverworts), Anthocerotophyta (hornworts) and Bryophyta (mosses), are the oldest known land plants in the world (Zinsmeister, Mues,1987). Bryophytes play an important role in the dynamics of understory vegetation, nutrient cycling, soil structure and stability (Smith, Read 1997). The lack of vascular tissue in bryophytes species has led to a plethora of strategies in nutrient acquisition.

Arbuscular mycorrhizas, formed only by fungi in the division Glomeromycota (Goffinet 2009), are found in 85% of all plant families (Wang 2006). However, mycorrhizal fungus-bryophyte associations have also been reported, even in early studies on symbiotic associations (Rayner 1927; Kelley 1950; Gerdemann 1968; Harley 1969). Some liverworts and hornworts are known to form symbiotic relationships with arbuscular mycorrhizal (AM) fungi (Turnau et al. 1999; Schüβler 2000), which has been confirmed in studies using axenic cultures. Mycorrizal associations have been described between the fungus *Glomus epigeios* (G. versiforme), moss *Funaria hygrometrica* and companion plant *Asparagus* (Parke 1979), and between *Anthoceros punctatus* and *Glomus tenue* (Schüβler 2002), between *Glomus tenue* and *Pellia* sp. (Turnau et al. 1999). Read (2000) proposed that these fungal associations are ancient and important for the first plants to colonize land. Fosil evidence of Glomalen fungal structures associated with early bryophytes in Ordovician sediments that are 460 and 400 million years old support this contention (Redecker et al. 2000).

While the presence of AM structures in some bryophytes has been demonstrated, information on the overall occurrence and the level of colonization of mycorrizal associations in this group of plants is lacking. The aim of the present study was to determine the occurrence of AM structures in 43 bryophyte species collected from different natural habitats in Latvia.

Materials and methods

In July 2006 to 2011, bryophytes samples from 43 bryophyte species belonging to 29 families were collected in four areas from a variety of substrates and habitats (decayed wood, bark, agricultural soil, forest soil, meadows, bogs and sandstone). The areas and habitats considered were: forest groves and ravines of the Slitere National park N 57°37´48.5", E 22°17´38.7", agricultural soil and roof bryophytes in Iecava N 56°41'16", E 23°42'04", broad leaved forest in Kaltene N 57°28'00", E 22°54'00", and ruderal bryophytes from Salaspils N 56°51'40", E 24°20'58". In the study area, mean annual temperature is 5.7 °C and precipitation is about 400 to 600 mm.

Samples of the entire current year gametophyte were cleared in 10% KOH (20 min at 90 °C), acidified in lactic acid, and stained for 20 min with 0.5% cotton blue. A total of 30 1-cm-long fragments were mounted on slides in glycerol and examined with Olympus BX41 compound microscope at 100 to 400 × magnification. The presence of the following AM fungal structures was recorded: arbuscules, vesicles, hyphal coils and intra- and intercelluar hyphae. Colonization level was measured according to Trouvelot et al. (1986).

Bryophyte tissues with observed AM fungi were

cultivated in trap cultures together with the host plant *Plantago lanceolata* for two months (Oehl 2003). Seeds of *P. lanceolata* were surface-sterilized [15 min with a 10% sodium hypochlorite solution (w/v)]. The AM fungal inoculum consisted of pieces of 1-cm-long thallus of *Conocephalum salebrosum* containing fungal hyphae. The inocula were placed in 27 × 17 × 20 cm (length × width × height) pots containing a sterilized substrate (1 h at 120 °C) composed of sand:vermiculite (3 : 1, v/v). Each pot then received a transplant consisting in three *P. lanceolata* plants per pot. The plants were grown in a glasshouse for 2 months. Plants were watered from below by distilled water.

Bryophyte nomenclature followed Hill et al. (2006) for mosses and Grolle and Long (2000) for liverworts.

Results

Among the examined 43 bryophyte species belonging to 28 families, AM fungal structures were found in five species (11.6 %; Table 1) and septate fungi on thallus or stem tissue surface in 13 species (30.2 %). The majority of species (25 species, 58.1 %) lacked fungal associations. Mycorrhizal symbiosis associations were not present in epiphytic and epixylic bryophytes. Only epigeic bryophytes were found to have mycorrhizal associations.

AM intercellular and intracellular hyphae were found only in gametophytes (Table 1): thallus tissues of Marchantiophyta (simple and complex thalloid species) and thallus of Anthocerotophyta, but were absent in Bryophyta stem and leaf tissues and in Machantiophyta (leafly species). Both AM hyphae and vesicles were observed in *Conocephalum salebrosum* (Fig. 1A) and *Fossombronia floevolata* (Fig. 1B, C). Arbuscules were found only in tissues of *Conocephalum salebrosum*. Fungal colonization may affect morphology of rhizoids, however, the rhizoids of *Conocephalum salebrosum* containing nonseptate hyphae (Fig. 1D) were unchanged. In contrast, swollen rhizoids of *Kurzia pauciflora* were observed to have septate fungal colonisation. The hyphal entry points into the bryophyte were rhizoids.

Fungal endophytes occurred in cell walls of *Cephalozia bicuspidata* (Fig. 1E) and stem tissues of *C. pleniceps*. Septate fungi possibly belonging to Ascomycetes or Basidiomycetes were observed growing on tissues of 13 bryophyte species (Table 1): *Aneura pinguis, Cephalozia bicuspidata, C. pleniceps, Homalia trichomanoides, Kurzia pauciflora, Trichocolea tomentella, Antitrichia curtipendula, Brachythecium rutabulum, Bryum argenteum, Ceratodon purpureus, Hylocomium splendens, Sphagnum magelanicum,* and *Syntrichia ruralis*.

The mean bryophyte colonization level by AM aseptate endophytes varied from 5 to 45% (Fig. 2) and by septate endophytes from 10 to 25%. The fungal colonization level of five Hepaticophyta species was 45% or less. In general, the colonization level in the studied bryophyte species ranged from low to average. Experiments with trap cultures failed to show symbiosis between fungi from bryophyte tissues and the host plant *Plantago lanceolata*.

Discussion

As expected, only epigeic bryophytes were found to have mycorrhizal associations. Two different types of endophytes were found in bryophyte tissues: those with septate hyphae and those with aseptate hyphae. Septate fungi belonged to several ascomycete or basidiomycetes species The morphology of liverwort–basidiomycete associations has been described by several authors (Kottke et al. 2003; Duckett et al. 2006; Davey 2006; Duckett, Ligrone 2008). *Cephalozia* species, according to the published data, are nonmycorrhizal, but grow together with ascomycetes. We found a mosaic of colonized (septate hyphae) and uncolonized cells in stem tissues of *Cephalozia* species (Fig. 1E). The thin leafed liverworts *Kurzia pauciflora, Trichocolea tomentella* were colonized with septate fungi. Mosses (Bryophyta) formed associations only with septate fungi. Rabatin (1980) reported the association of *G. tenuis* and unidentified „coarse" AM fungi in field-collected specimens of the *Pogonatum*. Our investigation of *Pogonatum urnigerum* did not show the presence any fungal endophytes in the gametophytes.

Aseptate fungi, representing AM fungi from the Glomaceae family, form symbiosis with bryophyte tissues (Pressel 2010). In the present investigation, the large complex thalloid liverwort *M. polymorpha* subsp. *ruderalis* was nonmycorrhizal. *Conocephalum salebrosum* and *C. conicum* were moderately mycorrhizal. *Blasia pusilla* and several *Riccia* species did not have fungal endophytes. The simple thalloid liwervorts *P. endiiviifolia* and *F. floevolata* were found to be mycorrhizal. Two simple thalloid liwervort species *A. pinguis* and *F. floevolata* often grow side by side in the same biotope, but AM hyphae were found only in thalli of *F. floevolata*. Intensity of the symbiosis was at a medium level. *Aneura pinguis* was nonmycorrhizal, but contained other septate endophytes.

The only representative from Anthocerota (*Anthoceros agrestis*) was found to have a low mycorrhizal intensity, which corresponds to published data (Lignore 1988; Kottke et al. 2003).

According to Lignore (2007), the hepatics *C. conicum* and *C. salebrosum* contain Glomeromycoetan endophytes, which were identified by molecular techniques. In the present study, AM structures (nonseptate hyphae, vesicles, arbuscules) were found in thalli of *C. conicum, C. salebrosum, F. floevolata* and *P. endiviifolia*, indicating functionally active mycorrhizal symbiosis. Functional structures always were present in the parenchymal tissue around the midrib in live tissues. Jakucs et al. (2003) suggest that the absence of arbuscules in mosses colonized by AM fungi may be due to seasonal fluxes in nutrient avaiability or the ephemeral

Table 1. Bryophyte species and fungal structures found

Bryophyte species	Glomeromycota		Ascomycota / Basidimoycota Septate hyphae on tissue surface	Ecological type / substrate
	Arbuscules / vesicles	Intracellular nonseptate hyphae / intracellular nonseptate hyphae		
Anthocerotophyta				
Anthoceros agrestis (Paton) Damsholt	–	+	–	Epigeic / clay
Marchantiophyta (Liverworts)				
Aneura pinguis (L.) Dum.	–	–	+	Epigeic / marsh
Blasia pusilla L.	–	–	–	Epigeic / clay
Cephalozia bicuspidata (L.) Dum.	–	–	+	Epigeic / swamp
Cephalozia pleniceps (Aust.) Lindb.	–	–	+	Epigeic / swamp
Conocephalum conicum (L. Dumort.)	–	+	–	Epigeic / clay
Conocephalum salebrosum Szweyk., Buczkowski & Odrzykoski	+	+	–	Epigeic / clay
Fossombronia floevolata Lindb.	+	+	–	Epigeic / clay
Frullania dilatata (L.) Dum.	–	–	–	Epiphytic / tree
Frullania fragilifolia (L.) Dum.	–	–	–	Epiphytic / tree
Homalia trichomanoides (Hedw.) B., S. et G.	–	–	+	Epiphytic / tree
Kurzia pauciflora (Dicks.) Grolle	–	–	+	Epigeic / swamp
Lophocolea heterophylla (Schrad.) Dum.	–	–	–	Epixylic / decaying trees
Marchantia polymorpha subsp. *ruderalis* L. emend. Burgeff	–	–	–	Epigeic / clay
Metzgeria furcata (L.) Dum	–	–	–	Epiphytic / tree
Mylia anomala (Hook.) S. Gray	–	–	–	Epigeic / swamp
Nowellia curvifolia (Dicks.) Mitt.	–	–	–	Epixylic / decaying trees
Pellia endiviifolia (Dicks.) Dum.	–	+	–	Epigeic / clay
Radula complanata (L.) Dum.	–	–	–	Epiphytic / tree
Riccia fluitans L. emend. Lorbeer	–	–	–	Epigeic / clay
Riccia glauca L.	–	–	–	Epigeic / clay
Riccardia palmata (Hedw.) Carruth.	–	–	–	Epixylic / decaying trees
Trichocolea tomentella (Ehrh.) Dum.	–	–	+	Epigeic / forest soil
Bryophyta (Mosses)				
Antitrichia curtipendula (Hedw.) Brid.	–	–	+	Epiphytic / tree
Atrichum tenellum (Röhl.) B. et S.	–	–	–	Epigeic / clay
Aulacomnium palustre (Hedw.) Schwaegr.	–	–	–	Epigeic / forest soil
Brachythecium rutabulum (Hedw.) B., S. et G.	–	–	+	Epiphytic / tree
Bryum argenteum Hedw.	–	–	+	Epigeic / soil
Ceratodon purpureus (Hedw.) Brid.	–	–	+	Epigeic / soil
Cinclidium stygium Sw.	–	–	–	Epigeic / marsh
Dicranum scoparium Hedw.	–	–	–	Epigeic / forest soil
Ditrichum flexicaule (Schwaegr.) Hampe	–	–	–	Epigeic / sandstone
Hylocomium splendens (Hedw.) B.,S. et G.	–	–	+	Epigeic / forest soil
Leucobryum glaucum (Hedw.) Ångstr.	–	–	–	Epigeic / forest soil
Neckera complanata (Hedw.) Hüb.	–	–	–	Epiphytic / tree
Plagiomnium cuspidatum Hedw.	–	–	–	Epigeic / forest soil
Pleurozium schreberi (Brid.) Mitt.	–	–	–	Epigeic / forest soil
Pogonatum urnigerum (Hedw.) P.Beauv.	–	–	–	Epigeic / clay
Sphagnum angustifolium (C.Jens. ex Russ.) C. Jens.	–	–	–	Epigeic / swamp
Sphagnum magelanicum Brid.	–	–	+	Epigeic / swamp
Syntrichia ruralis (Hedw.) Gaertn., Meyer et Scherb.	–	–	+	Epigeic / soil
Tetraphis pellucida Hedw.	–	–	–	Epixylic / decaying trees
Tortula lingulata Lindb.	–	–	–	Epigeic / sandstones

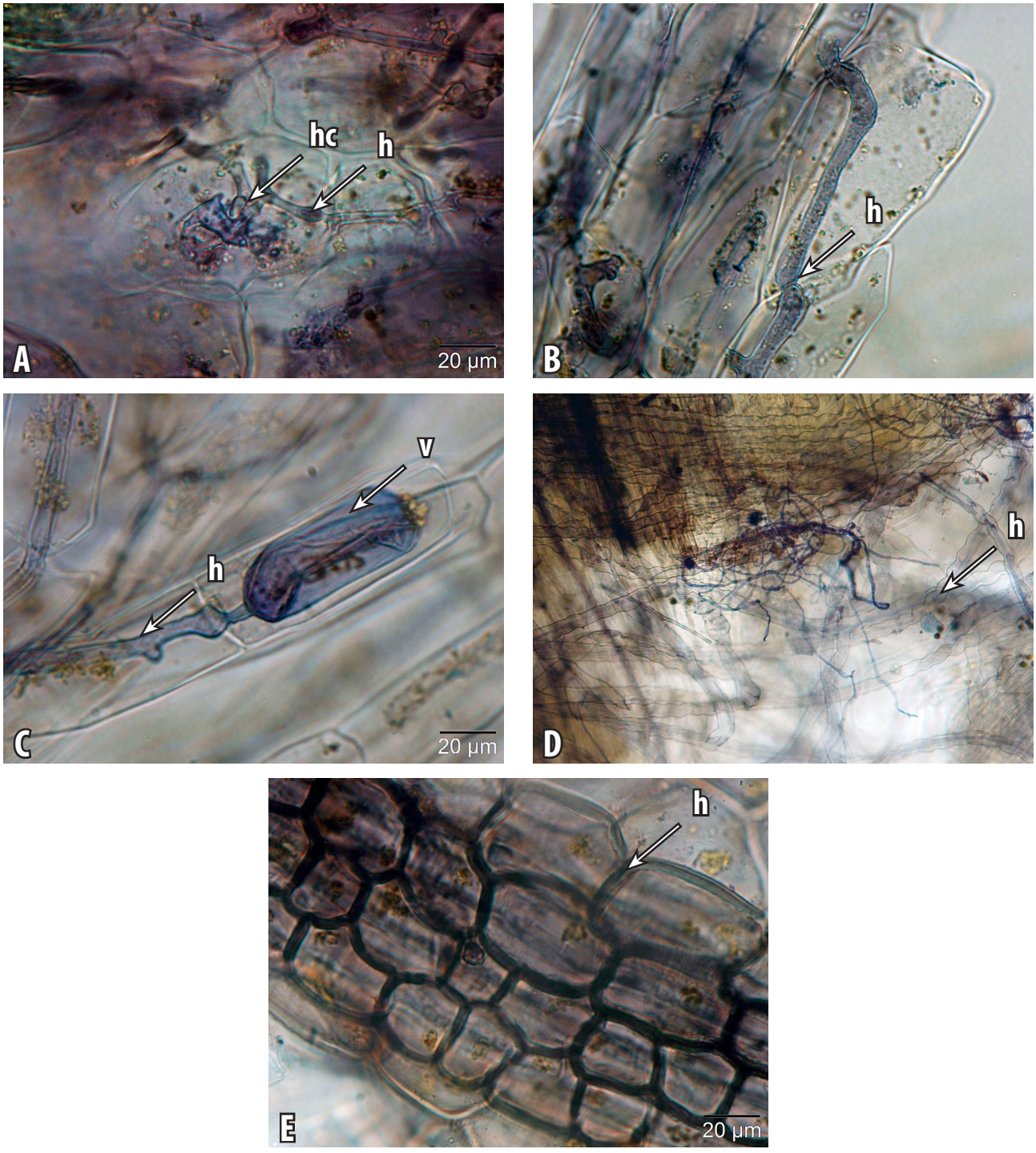

Fig. 1. *Conocephalum salebrosum* and AM-like fungi growing from cell to cell (A). AM in *Fossonmbronia floevolata* thallus with a penetration site of a fungal hypha (B). *Fossombronia floevolata* with AM fungal hypha and vesicle (C). Rhizoids of *Conocephalum salebrosum* with AM fungal hyphae (D). *Cephalozia bicuspidata* with fungal endophytes growing in cell walls (E). H, hyphae; HC, hyphal coils; V, vesicle.

nature af arbuscules. The observed hyphae passed directly through the cell walls of the liverworts. Rhizoids were the entrance points for fungal hyphae. We confirmed that the hyphae observed in this study belong to Glomeromycotan fungi. Most of the hepatics were non-mycorrhizal. In those that were mycorrhizal, the presence of arbuscules indicated functional symbiosis. These findings support the notion that the AM fungi-bryophyte associations are functional and species specific.

The occurrence of AM symbiosis in bryophytes may depend on defense systems such as allelopathy and fungicide activity (Pocock 1985). Several liwerwort

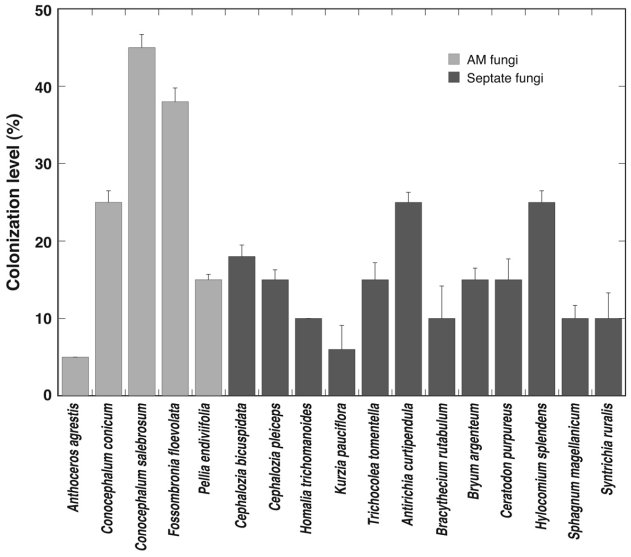

Fig. 2. Average bryophyte colonisation level by aseptate (AM) and septate fungal endophytes.

species (*Conocephalum conicum, Marchantia polymorpha*, *Plagiochila* sp., *Radula* sp.) show some antifungal activity and *Trichocolea tomentella* has mild antifungal activity. *Bryum argenteum* and *Ceratodon purpureus* have strong antifungal activity (Asakawa 2007; Singh 2007), imparted by cell walls containing polyphenolic-rich compounds that are either suitable as a substrate or toxic to the majority of microorganisms (Davey et al. 2006).

While epiphytic and epixylic bryophytes lacked AM symbiosis, the epiphytes *Brachythecium rutabulum* and *Antitrichia curtipendula* and epixylic *Tetraphis pellucida* from Bryophyta did not have septate endophytes in stem tissues. However, septate and non septate endophytes were never found together in the same bryophyte. Some epigeic Bryophyta species from some habitats lacked AM, for example, single individuals of *C. conicum* and *P. endiviifolia*, in very wet habitats and *M. polymorpha* subsp. *ruderalis* in a nutrient-rich agricultural habitat. This is consistent with the idea that mycorrhzial associations depend on edaphic factors (Brundrett 1991).

Several authors have experimentally established arbuscular-mycorrhiza like symbiosis between fungi belonging to the order Glomales and bryophytes (Parke 1980; Schüβler 2000; Zhang 2007; Fonseca 2006). However, our experiments with trap cultures failed to show symbiosis between fungi from bryophyte and the host plant *Plantago lanceolata*. In the present study, it is likely that the time for symbiosis establishment was too short for roots colonization. Some members of the Glomeromycota are capable of producing spores very early three to four weeks after the primary root colonization, whereas others require more than six months to begin the process (Sieverding 1991; Velazquez et al. 2011).

However to further understand the physiology, anatomy, and etiology of these interactions, it is necessary to culture bryophytes and bryophylous fungi and create artificial axenic systems for study.

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