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Microbial diversity in *Sphagnum* peatlands

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Introduction

Peat accumulates because the net production of organic matter exceeds its decomposition by microorganisms. Peatlands, and especially *Sphagnum*-dominated peatlands, were at one time erroneously believed to be devoid of microbial life. In reality, and despite the successful use of *Sphagnum* mosses as surgical dressings, diapers, or menstrual pads, *Sphagnum* mosses and peatlands in general are home to a high diversity of microorganisms. The numbers of published works on the subject are relatively low, probably because of the technical difficulties due to the abundance of organic matter particles that make direct observations challenging and the range and variability of water content of the substrate (Given and Dickinson, 1975; Gilbert et al., 2000b). The existing studies fall into two categories: the taxonomical approach and the functional approach.

In the taxonomical approach, the different groups of microorganisms (bacteria, protists, fungi, and micro-metazoa) are usually studied independently and the focus is usually on the taxonomy of the species restricted to peatlands. By contrast, little or no attention is given to abundance, biomass, and auto- and heterotrophic production. Recent studies of whole microbial communities, including all groups of microorganisms and measurements of abundance, biomass, and auto- and heterotrophic production, have demonstrated how microbial communities can be useful, first for the characterization of environmental conditions (Fisher et al., 1998) at the surface of peatlands, and second for assessing the effects of perturbations on these ecosystems (Gilbert, 1998a, b; Mitchell et al., 2003). In a long-term perspective (millennia), these studies are related to the use of microbial indicators such as testate amoebae for the reconstruction of past environmental conditions in paleoecological studies (Charman et al., 1999; Charman, 2001; Mitchell et al., 2001).

In the functional approach, the focus is on the role of microorganisms in the cycling of nutrients, mainly carbon and nitrogen, in the ecosystem. These processes remain poorly understood in peatlands, partly because of the lower funding for research in these ecosystems as compared to others more directly economically

relevant. Nevertheless, the important role of peatlands in the global carbon cycle, as carbon pools, sinks, and sources, and the increasing concern about the anthropogenic influence on the greenhouse effect, have resulted in a recent increase in the number of studies in microbial ecology (methanogenic and methanotrophic bacteria) and biogeochemistry of peatlands (Edwards et al., 1998). In a similar way, research on peatland restoration is now starting to include aspects of microbial ecology such as microbial density or respiration (Croft et al., 2001), or microbial community structure (Chapman et al., 2003).

Our goal in this review is to synthesize the existing knowledge on various aspects of microbial ecology in peatlands with a special focus on studies that include data on abundance and biomass. Thus, although bacterial and fungal communities are by far the most studied microbial groups in peat soils, this review focuses more on other microbial groups (auto- and heterotrophic protists and micro-metazoa). We also aim to demonstrate the interest of integrating these groups of microorganisms, and in particular testate amoeba, in studies of present or past perturbations of peatlands. Examples of some common testate amoebae are illustrated in Figure. 13.1, and a selection of microorganisms in living *Sphagnum* is illustrated in Figure. 13.2.

Microbial diversity in peatlands

Overview of the sampling, observation, and biomass estimation methods

Sampling and fixation

Because peatlands represent intermediate conditions between mineral soils and aquatic environments, the sampling and extraction methods for microorganisms depend on the kind of material sampled (peat, litter, or mosses) and the water content of the samples.

Peat samples are usually taken as cores, which are subsequently sliced (usually in 1–10-cm-thick slices) to analyze specific depths. Although peat coring is relatively easy–because of the absence of coarse mineral material, the local presence of woody remains can cause problems and the water saturation creates a suction effect that makes removing the cores difficult and creates risks of damaging them during extraction. In this case, the main risk is a compaction of the peat that makes it difficult to establish with confidence the exact depth of a given sample. Another risk in case of very decomposed peat is the upward or downward movement of material during coring that can cause microbiological contamination. To overcome these problems specific methodologies and equipments have been developed over the years. One such example is a double corer that allows the extraction of intact peat cores for the top 1–1.5 m of peat (Buttler et al., 1998).

Sampling in *Sphagnum* or other mosses can depend on the water content. In very wet conditions (bog pools or wet fens), it is possible to sample water by simply exerting a pressure on the moss surface. The advantage of this method is that it does not destroy the vegetation. However, this method is not optimal, because many microorganisms may remain attached to the mosses. A more reliable method is to

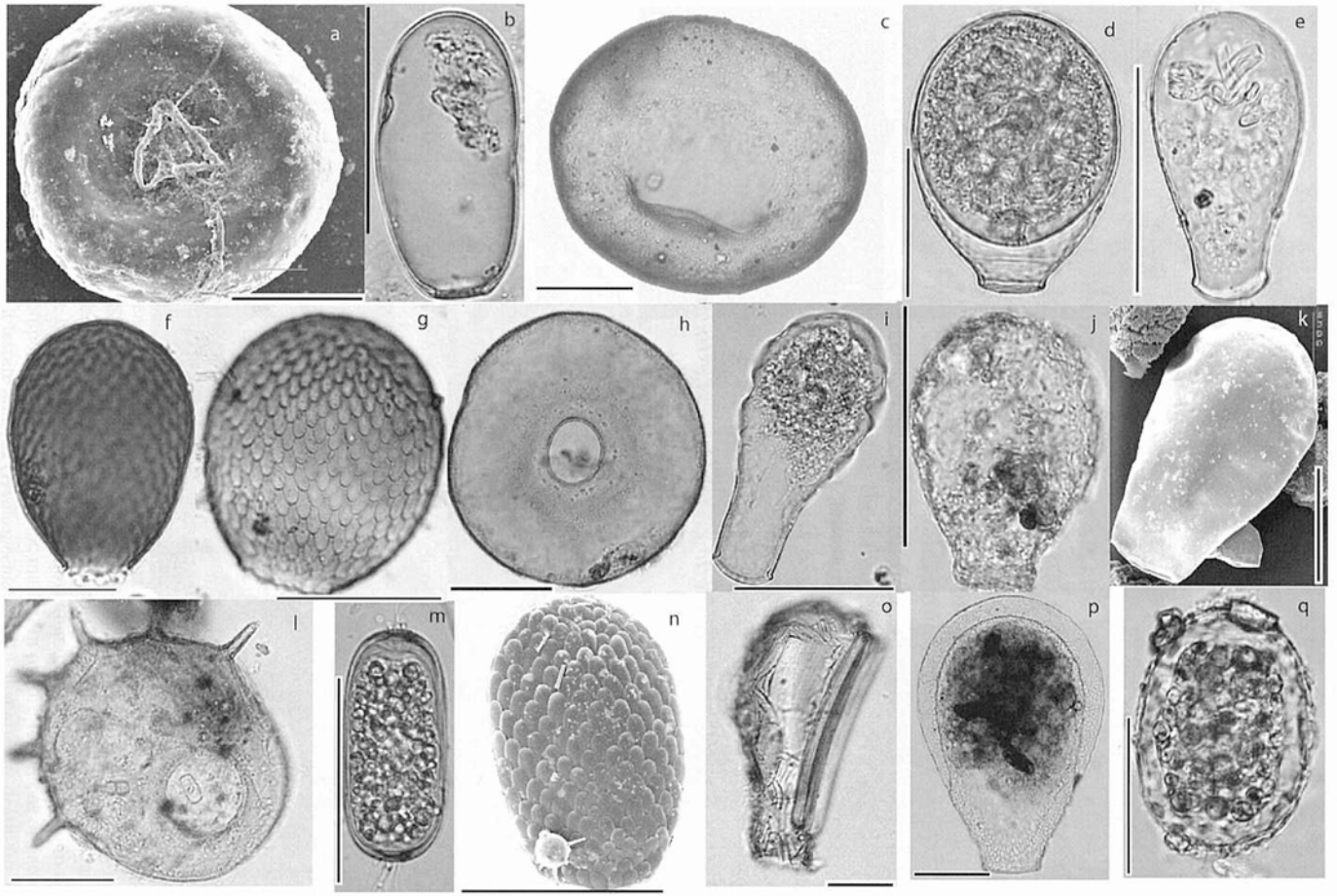
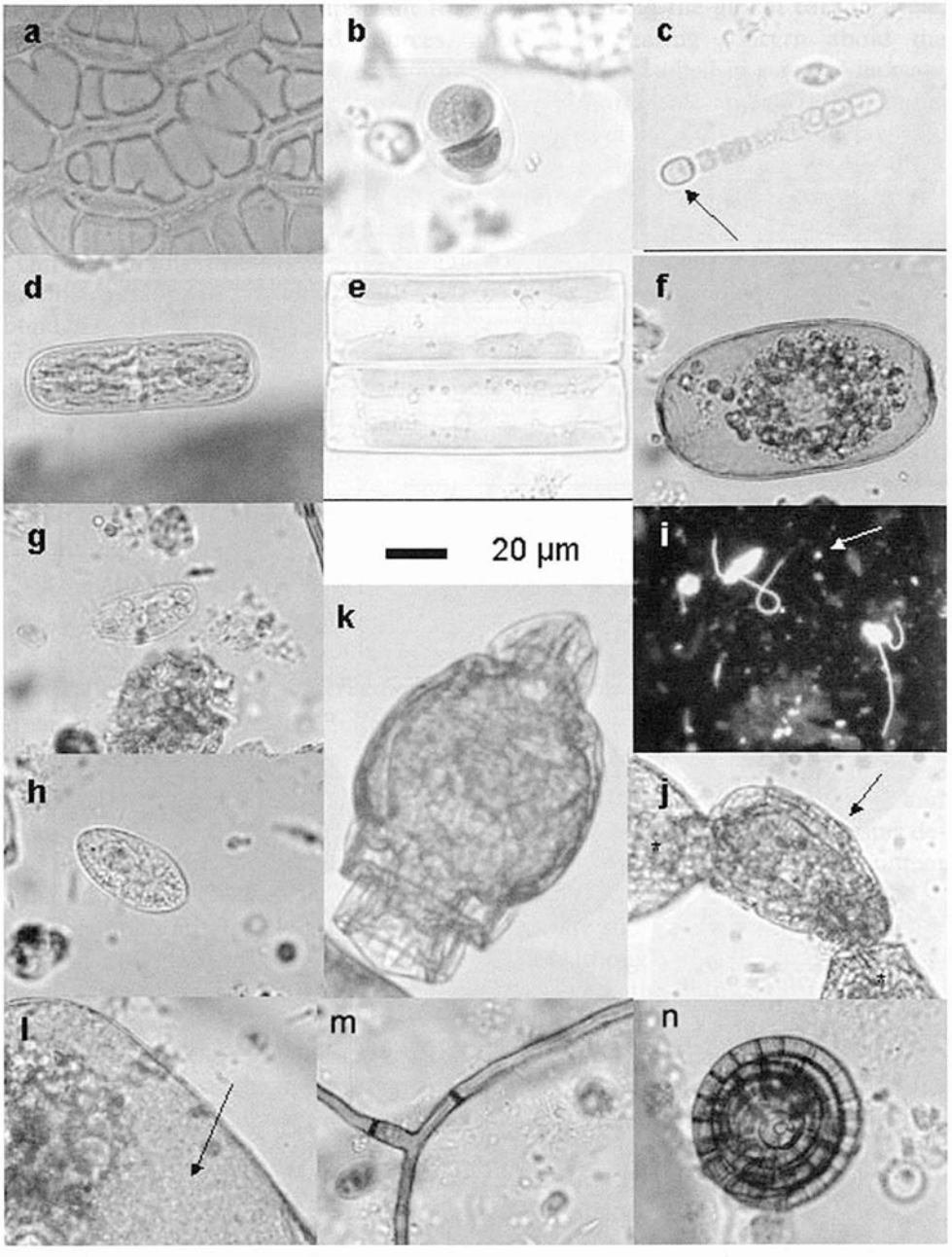


Figure 13.1. Examples of testate amoebae. (a) *Trigonopyxis arcula*. (b) *Hyalosphenia subflava*. (c) *Bullinularia indica*. (d) *Nebela tincta*. (e) *Nebela militaris*. (f) *Assulina muscorum*. (g) *Assulina seminulum*. (h) *Arcella arenaria*. (i) *Hyalosphenia elegans*. (j) *Physochila (Nebela) griseola*. (k) *Hyalosphenia papilio*. (l) *Centropyxis aculaeta*. (m) *Amphitrema flavum*. (n) *Placocista spinosa*. (o) *Difflugia bacillifera*. (p) *Nebela carinata*. (q) *Amphitrema wrightianum* (Scale bars indicate approximately 50 μm except for Figure f (*A. muscorum*) where scale is 20 μm.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sample the mosses and extract the microorganisms. One important aspect to keep in mind when preparing a sampling protocol is the spatial heterogeneity of microbial communities. Mitchell et al. (2000a), for example, demonstrated that a significant spatial heterogeneity existed in testate amoebae communities within a macroscopically homogeneous 40 × 60 cm surface of *Sphagnum magellanicum*. Spatial autocorrelation was significant up to a distance of about 15 cm and the structure of communities was significantly correlated to the almost flat micro-topography (maximum height difference within the surface: 6.6 cm). Therefore, although sampling a small number of mosses, or even only the capitulum (top 1 cm) of a *Sphagnum* moss may yield a sufficient number of microorganisms for community characterization, if the aim of the study is to characterize the general community structure of a study area, then it is preferable to sample a larger surface, or to pool several small samples from a given area.

The question of extracting microorganisms from *Sphagnum* has not yet been studied in detail with the exception of testate amoebae (Hendon and Charman, 1997). Nevertheless, the microscopic observation of *Sphagnum* mosses reveals that some microorganisms are able to enter the large, hollow hyaline cells though the small pores (mostly 5–15 µm) that connect the inside of the cells with the surrounding environment. Although these spaces are clearly easily accessible to bacteria and small protists such as flagellates, even relatively large microorganisms such as testate amoebae, and micro-metazoans such as nematode and rotifers have been observed in these cells. Microorganisms living in these spaces benefit from the double advantage of a physical barrier against predators and a wet environment that allows them to remain active longer during periods of dry weather.

Figure 13.2. Microorganisms in living *Sphagnum* and their role. Living *Sphagnum* micro-ecosystem: (a) *Sphagnum* mosses dominate vast expanses of nutrient-poor peatlands. They produce organic matter and provide habitat for microorganims. Some cells, the hyalocysts, lose their content and retain water. Microorganisms can live either between the leaves or inside the hyalocysts. Microbial photosynthesis: (b, c) Cyanobacteria: in the green part of *Sphagnum* mosses, non-filamentous cyanobacteria (b. *Choococcus* sp.) or filamentous cyanobacteria (c. *Anabanena* sp) use the sunlight to produce organic matter. Some species also fix atmospheric nitrogen in specialized cells, the heterocysts (see arrow, picture c). (d, e) Autotrophic protists : green algae (d. *Penium* sp.) and diatoms (e. *Eunotia* sp.) are two of the most important groups of microalgae in peatlands. (f, g) Mixotrophic protists: in *Sphagnum*, many protozoa are mixotrophic. Some testate amoebae (f. *Amphitrema flavum*) and ciliates (g. *Uronema* sp.) contain symbiotic algae. This symbiosis probably gives these protozoa a trophic advantage and helps them meet their nutritional requirements in nutrient-poor habitats. Microbial food chains: (h–j) Hetrotrophic protists: microbial food webs are complex. Many flagellates (i. heterotrophic flagellates observed in epifluorescence microscopy after a primuline coloration) and ciliates (g, h. *Uronema* sp. 1 and 2) prey on bacteria (see arrow in picture i1) or algae. Testate amoebae have a very broad range of prey. Some species are able to catch very large preys such as rotifera, ciliates, and even nematodes (j. two individuals of the species *Nebela collaris* (stars) are eating a rotifera, see arrow). (k) Small-size metazoa: Rotifera (k. Bdelloïda) and Nematoda, most of which are believed to be predators of bacteria, represent a minor proportion of the relative microbial biomass. Decomposition: (l) Hetrotrophic bacteria: bacteria are the most abundant microbial group in *Sphagnum* and play a major role in the decomposition of labile organic matter. In picture 1, millions of bacteria (grey points, see arrow) are degrading a testate amoeba (*Hyalosphenia papilio*), just after its death. (m, n) Fungi: fungi degrade the more resistant organic matter (cellulosic) (m. fungi hyphae). Many fungal spores are also found in *Sphagnum* (n. conidia of *Helicoons* sp.).

The fixation and preservation of peatland microorganisms is not different from that of other environments (glutaraldehyde, formaldehyde) (Fisher et al., 1998; Gilbert et al., 1998a, b), but, for *Sphagnum* moss samples, the water content (about 95%) must be taken into consideration, as it will cause a dilution of the fixing solution.

Observation and counting

The enumeration of microorganisms in peatlands can be done using several methods. None of these methods is specific to peatlands but we present them briefly here.

Culture methods for bacteria and fungi on gels were mainly used in the early studies of peat microbiology. These methods underestimate the abundance and diversity of microorganisms in soils and water by 90–99% because the culture conditions have little in common with the conditions of the natural environment (Given and Dickinson, 1975). This problem is likely to be even more acute in acidic peatlands because of the unique combination of environmental conditions (low nutrient, pH, temperature, redox state). For this reason, the direct counting method is considered to be the most reliable method for estimating microorganism densities. Bacteria are enumerated under epifluorescence microscopy after being stained by a fluorochrome, usually DAPI (Porter and Feig, 1980). In peat, the abundance of minute peat particles ($<2\,\mu m$) makes the counting more difficult by masking the bacteria and absorbing the fluorochrome. Thus, higher concentrations of fluorochrome are needed as well as the assistance of an image analysis system capable of accumulating the light signal over several tenths of a second. Picocyanobacteria (with diameter $<2\,\mu m$) can also be enumerated using epifluorescence microscopy using their autofluorescence property. Heterotrophic flagellates and other small size protists can be counted using fluorochromes such as primulin (Caron, 1983). Larger organisms, such as cyanobacteria ($>2\,\mu m$), protists, and micro-metazoa, are most commonly analyzed using the Utermölh's (1958) method that consists in placing a volume of water containing microorganisms in a plankton chamber slide, letting them settle, and counting them using an inverted microscope. This method allows the enumeration of organisms and the estimation of biovolumes, which can then be converted to biomass. However, this method does not allow identifying all of the microorganisms at the species level, which takes some additional preparation. In addition, the Uthermöl method is time-consuming despite the help of image-analyzing systems. The observation of fungal hyphae and spores using this method is not difficult but it seems that it is very difficult to extract fungi from *Sphagnum* mosses or from the peat in which they grow. Thus, direct methods certainly underestimate the biomass of fungi by an unknown proportion. For autotrophic microorganisms, epifluorescence can also be used with plankton chambers, but it is usually not possible to identify the algae to the species level; for this, $1000 \times$ magnification and special preparations are usually required. Testate amoebae are unusual among peatland microorganisms in that they build a shell (called 'test') that is very resistant to physical and chemical degradation. For this reason, and the relative ease of identification based on the test morphology, testate amoebae are the best-studied group

of protists in peatlands. Testate amoebae are usually studied using a standard upright microscope. Phase contrast microscopy is useful for the observation of genera such as *Euglypha, Trinema*, and *Corythion,* which produce siliceous scales almost invisible under bright-field microscopy.

The analysis of microbial RNA or DNA allows assessment of the diversity of microorganisms, and to some extent their abundance in the environment. This and other molecular methods have the advantage of being faster than direct counts. Furthermore, they provide information on the genotypic diversity and not only the morphological diversity. This is especially important for bacteria, for which direct observation methods do not allow distinguishing the different species, as well as for some groups of protists, for which the taxonomy in insufficiently documented in peatlands so that only broad morphological groups can be distinguished using direct methods of observation. The coupling of direct observations and molecular techniques, such as the FISH method of fluorescence in situ hybridization should allow in future more precise enumeration of different groups of bacteria and minute, hyaline protists. Other techniques, such as those using the microbial fatty acids (phospholipid fatty acids, or PLFA) have been used in a few studies to describe the structure of microbial communities (Borga et al., 1994; Sundh et al., 1995; Sundh et al., 1997; Schmidt et al., 2000; Cole et al., 2002).

Biomass evaluation

Using direct methods, the abundance of microorganisms and the biomass of each species or morphological type can be determined. From the morphology and biometric measurements of cells or organisms it is possible to estimate relatively precisely their specific biovolume and then, by taking into account the relative abundance of each type and, by using conversion factors, to convert the biovolume into biomass. However, none of the conversion factors currently used were determined from peatland microorganisms; instead conversion factors from marine or freshwater environments or from soils are used (Gilbert et al., 1998a, b; Mitchell et al., 2003). The biomass of microorganisms can also be determined using the fumigation-extraction method for total microbial biomass and using the ergosterol extraction method (for fungi).

Individual groups: diversity, abundance, biomass

Prokaryotes

(1) Methanogenic bacteria constitute a very important functional group of microorganisms in deep peat as they represent one of the main potential sources of CH_4 emission to the atmosphere. Using a DNA amplification method, Hales et al. (1996) found the diversity of methanogenic bacteria from a peatland in northern England to be very limited. However, Edwards et al. (1998), Galand et al. (2002; 2003), and Sizova et al. (2003) have identified numerous strains of methanogenic bacteria, some of which were hitherto unknown in deep peat. It also appears that different species of

methanogens are sensitive to the heterogeneity of the environment as attested by both horizontal and vertical patterns. For example, in an *Eriophorum* lawn of a Finnish fen, Galand et al. (2002) observed that the upper waterlogged layers contained methanogens belonging to a previously unknown group of Archaea related to the Methanomicrobiales, which they named 'fen cluster', whereas the deeper layers contained hydrogenotrophs belonging to the Rice cluster I. Interestingly, but perhaps not surprisingly, Galand et al. (2003) also observed differences in the near-surface Archaea communities between micro-sites (hummock versus lawn), whereas those occurring deeper in the peat were less variable.

(2) Heterotrophic bacteria constitute the most abundant microbial group in peat. The most frequently encountered species in ombrotrophic peatlands belong to the genera *Bacillus*, *Pseudomonas, Achromobacter,* and *Arthrobacter* (Given and Dickinson, 1975). According to Greaves et al. (1973), the size of cells is generally between 0.3 and 1 μm.

Direct counting methods using fluorochromes coloration and epifluorescence microscopy (Hobbie et al., 1977) yield abundance and biomass estimates of heterotrophic bacteria in peat ranging from about 10^9 to 10^{10} bacteria per gram peat dry weight and from about 10^6 to 10^7 bacteria per milliliter of water extracted from *Sphagnum*. These numbers are 10^3–10^4 times higher than those resulting from culture methods (Table 13.1). At the surface, although the abundance of bacteria is globally positively correlated to temperature, a decrease in the abundance of bacteria and other microorganisms is common during the summer. This phenomenon is especially clear in drained peatlands where the summer drought is most marked (Gilbert, 1998; Potila and Sarjala, 2004). In the peat itself, the abundance of bacteria decreases with depth (Francez ,1991; Sundh et al., 1997) and seasonal variations are less pronounced (Sundh et al., 1997). Methanotrophic bacteria that live at the interface between the aerobic and anaerobic zone benefit directly from the production of methane by Archea in the deeper peat. Their abundance has been estimated to be between 1.0 and 4.3×10^4 cell mL^{-1} using the most probable number method in filtered pore water (Williams and Crawford, 1983), and between 0.1 and 51.0×10^6 cells g^{-1} of peat using fluorescent antibodies (Vecherskaya et al., 1993) and the phospholipids fatty acids method (Sundh et al., 1995).

(3) Cyanobacteria play an important role in peatlands because some species are able to fix atmospheric nitrogen and can thus enrich the ecosystem in this often-limiting nutrient (Basilier, 1980). The input of nitrogen due to these organisms is significant. It is estimated to be about equivalent to atmospheric wet and dry deposition (Hemond, 1983). Cyanobacteria can be divided into four orders. Three of them comprise filamentous forms. Among them, two orders (the Nostocales and the Stigonematales) produce heterocysts and are able to fix atomospheric nitrogen in oxic conditions (Anabaena). The fourth order, the Chroococcales, comprise unicellular (and in some case colonial forms) and non-heterocystic species (*Chlorococcus*). The dominant genera of Cyanobacteria in peatlands are *Anabaena*, *Aphanocapsa*, *Aphanothece*, *Chroococcus*, *Eucapsis,* and *Synechococcus* (Dell'Uomo, 1981; Lederer, 1995a,b). For practical reasons, cyanobacteria are usually enumerated simultaneously with microalgae. Abundance and biomass results are therefore presented further together with microalgae.

Table 13.1. Densities and biomasses of heterotrophic bacteria in *Sphagnum* peatlands.

Environment sampled	Type	Density	Biomass	Method	Reference
Sphagnum water	Aerobic	$5–140 \times 10^3$ cells mL^{-1}		Culture	Grolière (1977)
Sphagnum water	Aerobic	2.2×10^4 cells mL^{-1}		Culture	Francez (1991)
Sphagnum water	Total	7.3×10^6 cells mL^{-1}	0.5 μgC mL^{-1}	Fluorescence	Gilbert et al. (1998a)
Sphagnum water	Total	4.4×10^7 cells mL^{-1}	3.9 μgC mL^{-1}	Fluorescence	Gilbert et al. (1998a)
Sphagnum water	Total	$2.6–13.2 \times 10^7$ cells mL^{-1}		Fluorescence	Fisher et al. (1998)
Sphagnum	Total	$0.8–22 \times -10^6$ cells g^{-1}(DW)		Fluorescence	Mitchell (1999)
Sphagnum	Total		0.09–1.0 mgC g^{-1} (DW)	Fluorescence	Mitchell et al. (2003)
Mixed peat	Aerobic	0.2×10^6 cells g^{-1}(DW)		Culture	Gardiner (1975)
Peat (Review)	Aerobic	$0.03–5.5 \times 10^6$ cells g^{-1}(DW)		Culture	Given and Dickinson (1975)
Peat: 0–50 cm	Total	$2–11.9 \times 10^9$ cells g^{-1}(DW)		Fluorescence	Greaves et al. (1973)
Peat: 5–70 cm	Methanotrophic	$0.3\text{-}51 \times 10^6$ cells g^{-1}(DW)		Indirect	Sundh et al. (1995)
Peat: 5 cm	Aerobic	1.61×10^{10} cells g^{-1}(DW)	4.5 mgC g^{-1} (DW)	Culture	Clarholm and Rossswall (1980)
Peat: 5 cm	Aerobic	$0.08–90 \times 10^6$ cells g^{-1}(DW)		Culture	Hiroki and Watanabe (1996)
Peat: 5 cm	Cellulolytic	$2.7–0.87 \times 10^5$ cells g^{-1}(DW)		Culture	Hiroki and Watanabe (1996)
Peat: 15 cm	Aerobic	$4\text{-}6.3 \times 10^6$ cells g^{-1}(DW)		Culture	Croft et al. (2001)
Peat: 25 cm	Aerobic	2.1×10^4 cells mL^{-1}		Culture	Francez (1991)
Peat: 30 cm	Aerobic	3.5×10^6 cells g^{-1}(DW)		Culture	Waskman & Stevens (1929)
Peat: 32 cm	Aerobic	1.5×10^{10} cells m^{-2}	0.3 g m^{-2} (DW)	Culture	Martin et al. (1982)
Peat: 32 cm	Anaerobic	4×10^8 cells m^{-2}		Culture	Martin et al. (1982)
Peat: 50 cm	Aerobic	7×10^3 cells mL^{-1}		Culture	Francez (1991)
Peat: 80 cm	Aerobic	2×10^3 cells mL^{-1}		Culture	Francez (1991)

Note: DW, dry weight.

Fungi

Microscopic fungi, together with heterotrophic bacteria, are the main decomposers of organic matter in soils. This group includes a high diversity of forms, many of which grow as filaments. In northern peatlands the diversity estimates range from 22 to 55 species (Nilsson et al., 1992; Czeczuga, 1993; Thormann et al., 2001). The main genera encountered belong to the three higher groups of fungi: Zygomycota, Ascomycota, Basidiomycota, as well as to the imperfect fungi (Deuteromycota).

The abundance of viable fungi ranges between 10^5 and 10^6 units per gram of dry peat (Table 13.2). However, as for bacteria, this kind of enumeration provides little useful information because it does not correlate to the real fungal biomass. From the direct observation of filaments, which represent up to $12.4\,m\,g^{-1}$ dry peat, Collins et al. (1978) estimated this biomass at $1.4\,mg\,g^{-1}$ dry peat in the litter of a raised bog. Using direct counts of filaments and spores, Mitchell et al. (2003) estimated the fungal biomass to range between 0.1 and $0.2\,\mu gC\,g^{-1}$ *Sphagnum* dry weight at the surface of five different European *Sphagnum*-dominated peatlands, whereas Gilbert et al. (1998b) estimated it at $0.8\,\mu gC\,mL^{-1}$ in *Sphagnum* extraction water. As noted earlier, it seems likely that values obtained from *Sphagnum* water extraction underestimate the real fungal biomass substantially because most of the filaments are tightly bound to organic matter. The ratios among heterotrophic bacteria, yeasts, and fungi in the top 3 cms of peat and during spring was estimated to be 1:4:5 by Wynn-Williams (1982), whereas Golovchenko et al. (1994) estimated fungi to represent 80–99% of the total microbial biomass in peat. The relative higher importance of fungi as compared to heterotrophic bacteria in peatlands is likely due to their higher tolerance to acidity. In support of this, cellulose-degrading fungi were shown to be more abundant in peatlands than their bacterial counterparts (Hiroki and Watanabe, 1996).

Fungi respond to ecological gradients and experimental changes in environmental conditions. However, the addition of nitrogen or agricultural fertilizers, exposure to elevated atmospheric CO_2, and manipulations of solar ultraviolet light B (UVB) did not cause any significant change in fungal biomass (Gilbert et al., 1998a, b; Mitchell et al., 2003; Robson et al., 2004). But this lack of overall response may, however hide a species-specific response as attested by the response of fungi to the manipulation of solar UVB in a peatland in Tierra del Fuego (Robson et al., 2004) and the response of some micro-fungi to the nutrient content of plant litter (Thormann et al., 2003).

The respective role of fungi in litter decomposition in peatlands is still relatively poorly understood. Thormann et al. (2002) have found 55 species of fungi to be associated with *Sphagnum fuscum*. In a detailed study, they found nine of these to be able to degrade tannic acid and cellulose and generally concluded that fungi were able to degrade a wide variety of carbon substrates. These same authors (Thormann et al., 2003) further demonstrated the existence of a temporal succession of fungal communities during the decomposition of *Sphagnum fuscum* probably due to the changes in the biochemical characteristics of the substrate during the decomposition process.

Table 13.2. Densities and biomasses of fungi in *Sphagnum* peatlands.

Environment sampled	Type	Density	Biomass	Method	Reference
Sphagnum water	Hyphae		0.81 $\mu gC\,mL^{-1}$	Direct	Gilbert et al. (1998b)
Sphagnum	Hyphae	0.5–18.4 $\times 10^5$ ind. g^{-1}		Direct	Mitchell (1999)
Sphagnum	Total		0.03–0.4 mgC. g^{-1} (DW)	Direct	Mitchell et al. (2003)
Peat: surface	Total	10^5 ind. g^{-1} (FW)		Culture	Waskman and Stevens (1929)
Peat: surface	Total	2.5 $\times 10^5$ ind. g^{-1} (DW)		Culture	Gardiner (1975)
Peat: surface	Total	4.8 $\times 10^5$ ind g^{-1} (DW)		Culture	Francez (1991)
Peat: surface	Yeast	2.9 $\times 10^6$ ind. g^{-1} (DW)		Culture	Given and Dickinson (1975)
Peat: surface	Hyphae	160–320 m cm^{-3}		Direct	Given and Dickinson (1975)
Peat: surface	Total	2.7 $\times 10^3$ ind. mL^{-1}		Culture	Francez (1991)
Peat: 5 cm	Total	0.02–10 $\times 10^6$ ind. g^{-1} (DW)		Culture	Hiroki and Watanabe (1996)
Peat: 5 cm	Hyphae	1–12.4 m g^{-1} (DW)	0.4–5.2 mgC g^{-1} (DW)	Direct	Collins et al. (1978)
Peat: 5 cm	Cellulolytic	0.5–30 $\times 10^4$ ind. g^{-1} (DW)		Culture	Hiroki and Watanabe (1996)
Peat: 15 cm	Total	0.2–3.2 $\times 10^5$ cells g^{-1} (DW)		Culture	Croft et al. (2001)
Peat: 25 cm	Total	1.3 $\times 10^3$ ind. mL^{-1}		Culture	Francez (1991)
Peat: 50 cm	Total	0.2 $\times 10^3$ ind. mL^{-1}		Culture	Francez (1991)
Peat: 80 cm	Total	0.1 $\times 10^3$ ind. mL^{-1}		Culture	Francez (1991)

Note: DW, dry weight; FW, Fresh weight.

Microalgae

From a taxonomic standpoint, microalgae (autotrophic protists) and cyanobacteria are the best-studied groups of microorganisms in peatlands, together with testate amoebae. Autotrophic protists are highly polyphyletic and the organisms that are grouped under this name are spread across at least four of the eight major groups of eukaryotes (Baldauf, 2003). For example, green algae, such as Desmids, are related to higher plants, whereas diatoms are related to brown algae and euglenoids belong to yet another major group of eukaryotes and are related to the human parasites *Leishmania* and *Trypanosoma* (Baldauf, 2003). The only common characteristics of these different groups of organisms are that they are eukaryotes, contain chloroplasts, and are either unicellular or aggregated into colonies with no vascular tissue.

When all the different taxonomic groups are pooled together, microalgae are the most diverse group of microorganisms in peatlands although estimates vary considerably. Villeret (1955) identified 198 species of microalgae and cyanobacteria in peatlands of Brittany, whereas Cosandey (1964) found over 400 species in a Swiss peatland, Compère (1980) listed 248 species in peatlands of France and Belgium, and Mataloni (1999) observed 299 species in seven peatlands of Tierra del Fuego. However, Wutrich and Matthey (1978, 1980) identified 362 species of diatoms alone in a single peatland of the Jura Mountains of Switzerland, and estimate this group to represent 20 to 60% of the total diversity in peatland ponds. Mataloni cites several other earlier studies of microalgae in peatlands in which more information can be found (Mataloni and Tell, 1996; Mataloni, 1999). According to Dell'Uomo (1981), the 240 species identified in a small peaty lake in Italy were dominated by the green algae (46% of the species, 17% being desmids) and diatoms (27%), whereas euglenoids and cyanobacteria each represented 8%. Among the numerous green algae found in *Sphagnum*, desmids constitute the dominant group. The genera *Closterium*, *Staurastrum*, *Cosmarium*, *Micrasterias,* and *Mesotaenium* are thus frequently cited (Dell'Uomo, 1981; Dell'Uomo and Agostinelli, 1990; Dell'Uomo and Pellegrini, 1993a, b; Tomaszewicz, 1994; Gilbert, 1998a, b). Pennate diatoms are more abundant than centric forms in peatlands, the genera *Eunotia*, *Achnanthes*, *Cymbella*, *Frustulia*, *Gomphonema*, *Navicula, Nitzschia,* and *Pinnularia* being the most common (Dell'Uomo, 1981; Gilbert, 1998). Other groups of microalgae are less frequent, but genera, such as *Cryptomonas* (Cryptophyceae), *Euglena,* and *Trachelomonas* (Euglenophyceae) commonly occur.

Mataloni (1999) studied the spatial succession of microalgae along a hydrological gradient from open water in bog pools to emerged mosses 320 cm from the pool margin in seven peatlands of Tierra del Fuego. Along these transects, the diversity (genera and species richness) decreased. The relative frequency of all desmids decreased and they were replaced by species from other taxonomic groups that could tolerate the drier conditions, lower pH and higher conductivity (Mataloni, 1999). In the same study, Mataloni also observed that microalgal communities of bog pools differed in relation to the morphological and chemical characteristics of the pools. These observations confirm those of Kingston who noted a decrease in diversity from rich fen to poor fen and to bog hummocks (Kingston, 1982). In agreement with these studies, Poulícková et al. (2004) showed that the distribution of the diatom species

responded primarily to the water depth and pH in acidic mineral poor spring fens of the Carpathian Mountains.

Few data concerning the abundance of microalgae are available (Table 13.3). The abundance data range between 10^3 and 10^7 cell L^{-1}, depending on authors and sites, which corresponds to between 3 and 1041 μg L^{-1} of chlorophyll a and 3.8 mgC L^{-1} (Table 13.3). According to Gilbert (1998a, b), diatoms represent 34% of the total algal biomass, euglenoids 22%, and other microalgae (mostly green algae) 44% in *Sphagnum fallax*. The seasonal succession of microalgae is strongly influenced by climatic conditions. Duthie (1965) and Gilbert (1998a, b) have both clearly shown the existence of two peaks of development for microalgae, the first in spring and the second in fall.

Like other microorganisms, microalgae are susceptible to be passively transported by animals. For example, Wutrich and Matthey (1978) washed 12 snipes (*Gallinago gallinago* L.) caught near a Swiss lowland lake. They estimated the overall number of diatoms to exceed 3 million individuals, or about 250,000 per bird. A total of 119 species belonging to 29 genera were observed in these extracts. In a follow-up study, these same authors also estimated the potential for various aquatic insects to transport diatoms. From the analysis of 44 insects belonging to 11 species, they estimated the total number of diatoms to be 13,215 belonging to 24 species. Wind alone was estimated to bring 350,000 diatoms per square meter over a one-year period (Wuthrich and Matthey, 1980). Thus, significant numbers of microorganisms can be transported by migratory birds, insects, and wind (Wuthrich and Matthey, 1978, 1980).

Heterotrophic protists

Heterotrophic protists include here the three groups (heterotrophic flagellates, ciliates, and amoebae) that traditionally were commonly referred to as 'protozoa'. This name is no longer valid because the protozoa are not monophyletic (they do not share a common ancestor that would not be shared by other groups of protists).

(1) *Heterotrophic flagellates.* Detailed data on heterotrophic flagellates living in peatlands are very scarce. Different species of heterotrophic flagellates belonging to the genera *Chilomonas*, *Monosiga,* and *Monas* were observed by Henebry and Cairns (1984) on polyurethane supports immersed in peatlands water. Their abundance reached about 10^7 cell L^{-1} (Table 13.4).

(2) *Ciliates.* Ciliates were studied quite extensively by Grolière (1974–1975, 1975, 1976, 1977). Among the identified genera, some are ubiquitous (*Paramecium*, *Cyclidium*, *Urotricha*, *Prorodon*, *Spirostomum*, *Nassula*, *Frontonia*, *Vorticella,* and *Spathidium*), whereas others, such as *Bryometopus* and *Climacostomum,* are specific to peatlands. Grolière (1974–1975, 1975) described many species found almost exclusively in *Sphagnum*. Measurements done on *Sphagnum* water extract yielded an estimated abundance ranging between 0 and 4.2×10^6 cells L^{-1} (Table 13.4). Overall abundance peaks were observed at the beginning and end of summer, but this general pattern masks the strong variability among species (Gilbert, 1998a, b; Grolière, 1977).

(3) *Naked amoebae and testate amoebae.* Both naked amoebae and testate amoebae occur in peatlands, but testate amoebae (also referred to as testaceans) have been

Table 13.3. Densities and biomasses of algae and cyanobacteria in *Sphagnum* peatlands.

Environment sampled	Type	Density	Biomass	Method	Reference
Pool water	Total		3–13 μgChl $a\,L^{-1}$	Direct	Henebry and Cairns (1984)
Pool water	Total		10–0^3 μgChl $a\,L^{-1}$	Direct	Schoenberg and Oliver (1988)
Pool water	Total	0.5–6.4 × 10^6 indiv. L^{-1}		Direct	Mataloni and Tell (1996)
Periphyton	Total		0.4–4 × 10^{-1} μgChl *a*. L^{-1}	Direct	Schoenberg and Oliver (1988)
Sphagnum water	Total	0.1–10 × 10^3 cells L^{-1}		Direct	Duthie (1965)
Sphagnum water	Total		79.6 μgChl $a\,L^{-1}$	Direct	Gilbert et al. (1998a)
Sphagnum water	Total		179 × 10^3 μgChl $a\,L^{-1}$	Direct	Gilbert et al. (1998a)
Sphagnum water	Chlorophyceae	0.1–7 × 10^3 cells L^{-1}		Direct	Duthie (1965)
Sphagnum water	Chrysophyceae	0–5 × 10^6 cells L^{-1}		Direct	Malatoni and Tell (1996)
Sphagnum water	Desmids	0.6–125 × 10^3 cells L^{-1}		Direct	Tomascewicz (1994)
Sphagnum water	Desmids	0.1–5 × 10^3 cells L^{-1}		Direct	Duthie (1965)
Sphagnum water	Diatoms	0.1 8 × 10^3 cells L^{-1}		Direct	Duthie (1965)
Sphagnum water	Diatoms	0–9 × 10^6 cells L^{-1}		Direct	Malatoni and Tell (1996)
Sphagnum water	Diatoms	0.2–4.4 × 10^7 cells L^{-1}	0.44 mgC L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum water	Dinophyceae	0–1.3 × 10^6 cells L^{-1}		Direct	Malatoni and Tell (1996)
Sphagnum water	Nanoalgae		10–53 μgChl $a\,L^{-1}$	Direct	Schoenberg and Oliver (1988)
Sphagnum	Microalgae		0.1–1.6 × 10^{-1} μgC g^{-1} (DW)	Direct	Mitchell et al. (2003)
Sphagnum	Microalgae	0.3–12 × 10^4 cells g^{-1}		Direct	Mitchell et al. (2003)
Sphagnum water	Cyanobacteria	0–2.8 × 10^6 cells L^{-1}		Direct	Malatoni and Tell (1996)
Sphagnum water	Cyanobacteria	0.2–22.4 × 10^7 cells L^{-1}	0.48 mgC L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum water	Cyanobacteria	4.5 × 10^7 cells L^{-1}	0.54 mgC L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum	Cyanobacteria		0.1–1.8 × 10^{-2} μgC g^{-1} (DW)	Direct	Mitchell et al. (2003)
Sphagnum	Cyanobacteria	0.6–64 × 10^3 cells g^{-1}		Direct	Mitchell et al. (2003)

Note: DW, dry weight.

Table 13.4. Densities and biomasses of protozoa and micrometazoa in *Sphagnum* peatlands.

Environment sampled	Type	Density	Biomass	Method	Reference
Sphagnum	Heterotrophic flagellates	$0–2.8 \times 10^4$ cells g^{-1} (DW)		Direct	Mitchell et al. (2003)
Sphagnum water	Heterotrophic flagellates	1.6×10^7 cells L^{-1}	0.14 mgC L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum	Ciliates	$0–0.7 \times 10^3$ cells g^{-1} (DW)		Direct	Mitchell et al. (2003)
Sphagnum water	Ciliates	$0–2.6 \times 10^6$ cells L^{-1}		Direct	Grolière (1977)
Sphagnum water	Ciliates	4.2×10^6 cells L^{-1}	1.01 mgC L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum	Testate amoeba	$0.8–4.6 \times 10^4$ shells g^{-1} (DW)		Direct	Warner (1987)
Sphagnum	Testate amoeba	$0.6–1.1 \times 10^3$ cells g^{-1} (DW)		Direct	Mitchell et al. (2003)
Sphagnum water	Testate amoeba	1.2×10^5 cells L^{-1}	0.94 mgC L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum	Testate amoeba	$0.13–23 \times 10^2$ shells cm^{-3}		Direct	Tolonen et al. (1992)
Sphagnum	Rotifera	$2.9–8.2 \times 10^4$ ind. m^{-2}	29–58 mgC. m^{-2} (FW)	Direct	Francez (1986)
Sphagnum	Rotifera	1–191 ind. g^{-1} (DW)		Direct	Mitchell et al. (2003)
Sphagnum water	Rotifera	5.3×10^4 ind. L^{-1}	0.27 mgC. L^{-1}	Direct	Gilbert et al. (1998a)
Sphagnum	Nematoda	$3.2–11.4 \times 10^4$ ind. m^{-2}	6–21 mgC. m^{-2} (FW)	Direct	Francez (1986)
Sphagnum	Nematoda	3–142 ind. g^{-1} (DW)		Direct	Mitchell et al. (2003)
Sphagnum water	Nematoda	3.2×10^4 ind. L^{-1}	0.02 mgC. L^{-1}	Direct	Gilbert et al. (1998)

Note: DW, dry weight.

much more intensively studied in the second part of the 20th century and many new studies have been published in recent years (Bonnet, 1958; Heal, 1964; Schönborn, 1965; Coûteaux, 1969; Meisterfeld, 1979; Beyens and Chardez, 1984; Warner, 1987; Tolonen et al., 1992; Charman, 1997; Woodland et al., 1998; Bobrov et al., 1999; Mitchell et al., 1999; Mitchell et al., 2000a,b; Booth, 2002; Gilbert et al., 2003). The most common species in *Sphagnum*-dominated peatlands of Europe and North America are listed in Table 13.5.

Like microalgae, testate amoebae are polyphyletic. They belong to at least two taxonomically distinct groups, the testate amoebae with filose pseudopodia (mostly the Euglyphida) and the Arcellinida, or testate amoebae with lobose pseudopodia (Meisterfeld, 2002a,b; Nikolaev et al., 2005). However, because of the key characteristics these two groups of organisms share (i.e., presence of a shell, size, generation time, and general feeding habits) they are usually studied together in ecological and paleoecological studies of peatlands.

Testate amoebae seem to be less affected by climatic variations than other microorganisms and are regularly present throughout the year, thanks in part to their ability to encyst during unfavorable periods. Their abundance is high and can reach 4.6×10^4 individuals (ind.) per gram dry weight of *Sphagnum* and 1.2×10^5 ind. L^{-1} (Table 13.5, Meisterfeld, 1977).

Several authors have studied the vertical micro-distribution of testate amoebae in *Sphagnum*. One of the main observations being that mixotrophic species such as *Hyalosphenia papilio*, *Heleopera sphagni*, and *Amphitrema* spp., (that contain symbiotic microalgae inside their cytoplasm) preferentially colonize the uppermost, photosynthetic part of the mosses, where their endo-symbionts can photosynthesize, whereas heterotrophic species are found at all depths but dominate the community in the lower part of the mosses (Heal, 1962; Schönborn, 1963; Meisterfeld, 1977; Mitchell and Gilbert, 2004). The composition of testate amoebae communities is primarily controlled by the moisture regime and to a lesser extent by pH (Warner and Chmielewski, 1992; Tolonen et al., 1994; Charman and Warner, 1997; Mitchell et al., 1999; Bobrov et al., 2002; Booth, 2002; Lamentowicz and Mitchell, 2005). In addition, Tolonen et al. (1992) found testate amoebae to be correlated to the trophic status and the concentration of mineral nutrients such as calcium. Finally, the relative importance, in terms of biomass, of testate amoebae in the microbial community as well as the broad range of organisms on which they feed (bacteria, fungi, protists, and micro-metazoa) suggest that they play a key role in the microbial food webs in peatlands (Gilbert et al., 1998a; Mitchell et al., 2003).

Micro-metazoa

(1) *Rotifers*. According to the classification of Sieburth et al. (1978), small metazoans can be considered as microorganisms when their size does not exceed 200 µm. This is the case for many rotifers, which are also considered as one of the component of microbial food webs (1993). Batut (1965), Francez (1981, 1987, 1988), and Bledzki and Ellison (2003) have established species lists for peatland rotifers. In terms of biomass, the Bdelloidea are dominant and mostly include species of the genera *Philodina* and *Habrotrocha*. In addition, many Monogononta species of the genera

Table 13.5. Most common testate amoebae taxa occurring in *Sphagnum* moss samples from peatlands of Europe and North America.

Taxon	Taxonomic group			Percentage occurrence[c]	Relative frequency			
	Arcellinida	Filosea[a]	Uncertain		Mean	Max	Median	SE
Assulina muscorum GREEFF		x		94.0	8.5	73.5	5.7	0.5
Nebela tincta (LEIDY)	x			72.6	10.8	86.1	3.5	0.9
Corythion dubium TARANEK		x		71.0	6.0	67.4	1.6	0.6
Assulina seminulum (EHRENBERG)		x		61.8	2.3	53.7	0.9	0.3
Hyalosphenia papilio LEIDY	x			59.6	8.6	91.4	1.7	0.9
Phryganella acropodia (HERTWIG & LESSER)		x		55.2	4.1	67.6	0.7	0.4
Nebela militaris PENARD	x			53.9	3.5	53.1	0.5	0.4
Hyalosphenia elegans LEIDY	x			51.1	7.6	77.6	0.7	0.7
Euglypha compressa (CARTER)		x		44.5	2.9	76.6	0.0	0.4
Amphitrema flavum ARCHER			x	42.9	4.9	66.9	0.0	0.6
Euglypha strigosa (EHRENBERG)		x		41.6	2.5	35.3	0.0	0.3
Euglypha laevis (EHRENBERG)		x		40.4	1.0	26.5	0.0	0.1
Bullinularia indica (PENARD)	x			39.7	1.0	46.5	0.0	0.2
Nebela tincta v. *major* DEFLANDRE	x			37.9	3.3	66.7	0.0	0.5
Euglypha ciliata EHRENBERG		x		37.2	1.7	46.9	0.0	0.2
Physochila griseola JUNG[b]	x			36.6	3.5	35.2	0.0	0.4
Heleopera sphagni (LEIDY)	x			35.6	3.3	65.4	0.0	0.5
Arcella arenaria GREFF[d]	x			33.8	1.2	26.1	0.0	0.2
Euglypha rotunda WAILES		x		31.2	0.9	21.0	0.0	0.1
Heleopera rosea PENARD	x			26.5	0.9	19.3	0.0	0.1
Heleopera petricola LEIDY	x			25.6	1.0	25.7	0.0	0.2
Trigonopyxis arcula (LEIDY)	x			25.6	1.2	31.8	0.0	0.2
Difflugia leidyi WAILES	x			25.2	1.8	36.9	0.0	0.3

Source: Compiled from the following: Kishaba and Mitchell, 2005; Mitchell and Gilbert, 2004; Mitchell et al., 1999, 2000a, b; Tolonen et al., 1992; Warner, 1987; and unpublished data.

[a] Testate amoebae with filose pseudopodia.

[b] Synonym: *Nebela griseola*.

[c] Calculated as 100 × number of samples in which the species was recorded/total number of samples.

[d] Includes *Arcella catinus*.

Lecane, *Colurella*, *Trichocerca,* and *Euchlanis* occur in peatlands. Francez (1981) identified 142 species in various peatlands of Auvergne (France). In addition, he observed that the abundance and average size of these organisms was higher in fens (8.2×10^4 ind. m^{-2}) than bogs (2.9×10^4 ind. m^{-2}) (Table 13.4). This trend is probably related to differences in moisture content and pH, both of which are lower in bogs than fens (Francez, 1987; Pejler and Berzins, 1993).

(2) *Nematodes.* Contrary to rotifers, nematodes are usually not included as an element of microbial food webs because their size is usually comprised between 0.2 and 1 mm and their feeding habits can be very varied. However, these organisms can be very abundant in *Sphagnum* and can have a significant impact in bacterial and fungal populations (Ingham et al., 1985). According to Wasilewska (1991) the relative abundance between bacterivorous and fungivorous nematodes on one side and phytophagous nematodes on the other is dependant on the moisture content of the environment. The abundance of nematodes is about 10^5 ind. m^{-2}, 1–200 µm g^{-1}, or 40 ind mL^{-1} (Table 13.4).

(3) *Other micro-metazoa.* Other microscopic metazoans occur in peatlands, but their abundance and biomass is limited and therefore they are unlikely to play a significant role in organic matter decomposition or microbial food webs. This is the case for gastrotrichs, a little known group of organisms of which 21 species have been described in a peatland complex of the north of Italy by Balsamo and Todaro (1993). Three other interesting groups of minute animals are the tardigrads (Tardigrada), also called water bears, the oribatid mites (Arachnida), and the flatworms (Platyhelminthes). In addition, *Sphagnum* mosses, when they are sufficiently humid, can harbor Harpacticoid copepods (Crustacea; Copepoda) and, in the wettest parts of peatlands, Cladocera (water fleas) (Francez, 1986). All these organisms are in most cases larger than 200 µm and are therefore not considered as microorganisms.

Total microbial biomass and relative importance of the different groups

Using the fumigation-extraction method, the total microbial biomass was estimated to represent 1.7–16 mgC g^{-1} dry weight of peat at the surface of peatlands. It decreases with depth to reach between 1.2 and 2.5 mgC g^{-1} peat dry weight (Table 13.6; Williams and Silcock, 1997; Brake et al., 1999; Baum et al., 2003). The microbial C:N ratio also decreases with depth, from 12.1 at the surface to 8.9 at 0.75 m (Francez et al., 2000). Total microbial biomass values estimated from direct counts are substantially lower than those obtained using the fumigation-extraction method, probably because of the underestimation of the fungal biomass.

The relative importance of different microbial groups, in terms of biomass has been estimated in July in a *Sphagnum fallax-Carex rostrata*-poor fen (Gilbert et al., 1998b). Heterotrophic bacteria represented 17% of the total microbial biomass, autotrophic microorganisms (algae and cyanobacteria) about 50%, heterotrophic protists 26%, fungi 2%, and rotifers 5%. In a study of five European peatlands, Mitchell et al. (2003) obtained the following proportions: bacteria 40–49%, fungi 15–36%, heterotrophic protists 6–32%, microalgae 1–22%, micro-metazoa (rotifers and nematodes) 5–9%, and cyanobacteria 0–4%. Overall it appears that the ratio of

Table 13.6. Total C, N, and P microbial biomasses in *Sphagnum* peatlands.

Environment sampled	Biomass	Method	Reference
Sphagnum	0.1–0.2 μgC g^{-1} (DW)	Direct	Mitchell et al. (2003)
Sphagnum water	12.9 μgC mL^{-1}	Direct	Gilbert (1998)
Peat: 0–10 cm	2–16 mgC g^{-1} (DW)	Fumigation-extraction	Potila and Sarjala (2004)
Peat: 0–10 cm	1.7–4.2 mgC g^{-1} (DW)	Fumigation-extraction	Francez et al. (2000)
Peat: 0–30 cm	1.2–3.2 mgC g^{-1} (DW)	Fumigation-extraction	Baum et al. (2003)
Peat: 0–50 cm	0.4–1.1 mgC g^{-1} (DW)	Fumigation-extraction	Brake et al. (1999)
Peat: 2–15 cm	5.2–9.1 mgC g^{-1} (DW)	Fumigation-extraction	Croft et al. (2001)
Peat: 75–100 cm	1.2–2.5 mgC g^{-1} (DW)	Fumigation-extraction	Francez et al. (2000)
Peat: 5–25 cm	20–250 mgC g^{-1}	Fumigation-extraction	Williams and Silcock (1997)
Peat: 0–10 cm	0.35 mgN g^{-1} (DW)	Fumigation-extraction	Francez et al. (2000)
Peat: 0–10 cm	0.3–0.6 mgN g^{-1} (DW)	Fumigation-extraction	Potila and Sarjala (2004)
Peat: 0–30 cm	0.1–0.5 mgN g^{-1} (DW)	Fumigation-extraction	Baum et al. (2003)
Peat: 20–170 cm	0.19–0.22 mgN g^{-1} (DW)	Fumigation-extraction	Francez et al. (2000)
Peat: 5–25 cm	25–60 mgN L^{-1}	Fumigation-extraction	Williams and Silcock (1997)
Peat: 0–30 cm	0.01–0.08 mgP g^{-1} (DW)	Fumigation-extraction	Baum et al. (2003)
Peat: 0–50 cm	0.004–0.043 mgP g^{-1} (DW)	Fumigation-extraction	Brake et al. (1999)

Note: DW, dry weight.

autotrophic photosynthetic microorganisms/heterotrophic microorganisms drops when the moisture content decreases (Gilbert, 1998; Mitchell et al., 2003).

Functional importance of microbial communities in peatlands

Heterotrophic activities: organic matter decomposition and nutrient cycling

Fungi and bacteria are the primary decomposers of complex organic molecules produced by plants. The fungi produce cellulolytic exoenzymes that are more efficient than those of bacteria and are generally responsible for most of the plant organic matter degradation (Davet, 1996), whereas bacteria occur preferentially in the vicinity of hyphae to benefit from the molecules of low molecular weight resulting from the activity of fungal exoenzymes (Clarholm, 1994). At the surface of peatlands, the two main sources of organic matter are the particulate organic matter resulting from the degradation of plant litter and the organic matter excreted by microorganisms. The two communities of decomposer microorganisms, bacteria and fungi, coexist and feed on this source of food.

Peatlands accumulate between 5 and 15% of the organic matter produced in a year (Clymo, 1983). This means that about 90% of the net primary production is lost, mainly through the respiration of organic matter by bacteria and fungi in the acrotelm. The total microbial respiration has been estimated at between 0.5 and 7.7 μgC g^{-1} h^{-1} (dry weight) at the surface and decreases with depth (Table 13.6). Inversely, the production of methane only takes place in the waterlogged peat where anoxic conditions prevail. Methane production can reach 0.2 μgC g^{-1} h^{-1} (dry weight) (Table 13.7). Other microbial activities, such as atmospheric nitrogen fixation and methane oxidation have been measured in a few cases (Table 13.7). The estimation of microbial respiration is essential for the establishment of the overall carbon budget of

Table 13.7. Microbial activities in *Sphagnum* peatlands.

Environment sampled	Activity	Variable measured	Method	Reference
Sphagnum water	0–2478 pmol L^{-1} h^{-1}	Microbial carbon incorporation	Leucine incorporation	Fisher et al. (1998)
Sphagnum water	0.7–6.1 μgC L^{-1} h^{-1}	Heterotrophic activity	Amino acid incorporation	Gilbert et al. (1998a)
Sphagnum water	1.8 μgC L^{-1} h^{-1}	Heterotrophic activity	Amino acid incorporation	Gilbert (1998)
Sphagnum water	5–261 μgC L^{-1} h^{-1}	Photosynthetic activity	^{14}C incorporation	Gilbert et al. (1998a)
Sphagnum water	0.2–45.8 μgC L^{-1} h^{-1}	Photosynthetic activity	^{14}C incorporation	Gilbert (1998)
Peat: 5–10 cm	9.9–23.5 μgC g^{-1} h^{-1} (DW)	Total CO_2 respiration	Peat incubation	Williams and Silcock (1997)
Peat: 10–25 cm	2.6–10.9 μgC g^{-1} h^{-1} (DW)	Total CO_2 respiration	Peat incubation	Williams and Silcock (1997)
Peat: 0–15 cm	3.8 μgC g^{-1} h^{-1} (DW)	Total CO_2 respiration	Peat incubation	Fisk and Schmidt (1996)
Peat: 0–50 cm	0.5–3.8 μgC g^{-1} h^{-1} (DW)	Total CO_2 respiration	Peat incubation	Brake et al. (1999)
Peat: 0–75 cm	5.8–7.7 μgC g^{-1}·h^{-1} (DW)	Total CO_2 respiration	*In situ fluxes*	Francez et al. (2000)
Peat: 15–30 cm	1.4 μgC g^{-1} h^{-1} (DW)	Total CO_2 respiration	Peat incubation	Fisk and Schmidt (1996)
Peat: 75–170 cm	1.1–2.1 μgC g^{-1} h^{-1} (DW)	Total CO_2 respiration	*In situ fluxes*	Francez et al. (2000)
Peat: 0–40 cm	0.3 μgC g^{-1} h^{-1} (DW)	Microbial CH_4 emission	Peat incubation	Krumholz et al. (1995)
Peat: 10–75 cm	0.2–0.4 10^{-3} μgC g^{-1} h^{-1} (DW)	Microbial CH_4 emission	*In situ fluxes*	Francez et al. (2000)
Peat: 75—170 cm	0.1–0.2 μgC g^{-1} h^{-1} (DW)	Microbial CH_4 emission	*In situ fluxes*	Francez et al. (2000)
Peat: 4–9 cm	7.5 μgC g^{-1} h^{-1} (DW)	Microbial CH_4 consumption	Peat incubation	Krumholz et al. (1995)
Peat: 0–20 cm	1.1–2.9 μgN g^{-1} h^{-1} (DW)	Microbial N_2 fixation	Peat incubation	Krumholz et al. (1995)

Note: DW, dry weight.

peatlands and the role they play as C sinks. In the perspective of peatland exploitation for horticulture and successive regeneration, Francez et al. (2000) have demonstrated that, during the restoration process, cutover peatlands can remain carbon sources for many years following the re-establishment of *Sphagnum* mosses.

Microorganisms play an especially important functional role at the surface of peatlands by recycling nutrients before they become incorporated in the peat. These processes are crucial for the functioning of peatlands which otherwise depend essentially from nutrient inputs through wet and dry deposition. Nitrogen, which is usually the limiting nutrient in peatlands except when they are subject to high N pollution levels (Aerts et al., 1992), is one of the main causes for inter-specific competition (Francez and Loiseau, 1999). *Sphagnum* mosses are especially efficient at retaining nutrients from precipitation in spring during the growth period (Clymo, 1963; Van Breemen, 1995), whereas microorganisms are especially efficient in keeping nutrients in summer (Li and Vitt, 1997). Moreover, microorganisms appear as a key group for nitrogen recycling in the acrotelm (Humphrey and Pluth, 1996; Croft et al., 2001; Potila and Sarjala, 2004), most of these microbial processes occurring in the first 10 cm of the peat (Francez and Loiseau, 1999).

Microbial primary production

The primary production from vascular plants and *Sphagnum* mosses has been much studied in peatlands. By contrast, microbial primary production has, to our knowledge hardly been studied at all. In a *Sphagnum fallax*-dominated peatland from the center of France, Gilbert (1998) estimated this production at about 3 $gC\,m^{-2}\,yr^{-1}$, or less than 1% of plant net primary production. Similarly, according to Thuillier (1998), the production of *Sphagnum* and vascular plants is 200 times greater than microbial primary production. Furthermore, microorganisms are quickly lysed after the death of the organisms, as attested by the fumigation-extraction experiments realized in peat. In these conditions, it seems justified to consider the necromass originating from photosynthetic microorganisms to be quantitatively negligible for peat accumulation processes.

The microbial loop

The microbial loop concept initially derived from studies of marine and lake ecosystems has been extended to soils and then to peatlands (Azam et al., 1983; Porter et al., 1985; Clarholm, 1994; Coleman, 1994; Gilbert et al., 1998a). In peatlands, the trophic chain based on photosynthetic assimilation by microalgae and cyanobacteria is relatively marginal. Instead, the main source of organic matter comes from the decomposition of *Sphagnum* mosses and vascular plants that grow on the peatland surface. Furthermore, in the microbial loop of aquatic ecosystems, bacteria constitute the essential link between organic matter and micro-zooplankton. In peatlands, it would appear logical to include the fungi in the microbial loop. Indeed, although

fungi and bacteria are two very different kinds of organisms, they both use dissolved organic matter and both fall prey to heterotrophic protists and micro-metazoa (Yeates and Foissner, 1995; Gilbert et al., 2000a, 2003).

The second level of the microbial loop includes the heterotrophic protists, which, in *Sphagnum* peatlands, are essentially the testate amoebae and the ciliates. Ciliates, and especially the smallest among them, are the main bacterivorous organisms at the surface of peatlands (Gilbert, 1998). By contrast the precise role of testate amoebae is harder to define. In soils, naked amoebae are responsible for the regulation of bacterial populations, owing to their ability to move in the interstitial volumes of the soil and because they are better adapted than filtering microorganisms to ingest bacteria forming biofilms on the surface of soil particles (Clarholm, 1981). At the surface of *Sphagnum* peatlands, the available pore space is much greater than in mineral soils and the bacteria are mostly associated with particulate organic matter in suspension in the water. The physical structure of the environment thus seems more favorable to the development of testate amoebae, which can easily move between the leaves of *Sphagnum*. Furthermore, these heterotrophic protists have an additional advantage over naked amoebae in that they benefit from the protection of a shell against predators. However, peatland testate amoebae do not appear to have exactly the same trophic role as naked amoebae in mineral soils. Indeed, the range of the types of food they ingest seems wider than that of naked amoebae, and reflects the full diversity of available prey in *Sphagnum*: heterotrophic bacteria, fungal hyphae and spores, microalgae, heterotrophic protists, small micro-metazoa (Gilbert et al., 2000a, 2003). This feeding behavior has been interpreted as a compensatory solution that does not allow them an optimal development (Coûteaux and Pussard, 1983). However, in case of food shortage, this behavior does provide testate amoebae an advantage over other predatory microorganisms. Finally, because they represent several trophic levels, testate amoebae constitute a key trophic link in the microbial communities of *Sphagnum* peatlands (Gilbert, 1998).

Transfer to higher trophic levels

The role of the meso- and macro-fauna in the trophic webs of peatlands has been little studied (Arndt, 1993). Depending on the water content of *Sphagnum* mosses, it is possible to observe many groups of organisms (oligochaeta, insect larvae and adults, crustaceans, mollusks, arachnids, and others) (Francez, 1984, 1986; Nowak and Pilipiuk, 1997). Recent studies in soils show that many detritivorous species live in the litter (Nieminen and Setälä, 1998). Furthermore, according to Bonkowski and Schaefer (1997), oligochaetes ingest naked amoebae in soils. Similarly, in peatlands it is likely that an important part of the energy and matter needed for the development of the meso- and macro-fauna come from the consumption of microorganisms, be it selective or fortuitous through the ingestion of bulk soil particles. Empty tests (shells) of testate amoebae found in the digestive tract of earthworms seems to attest of this (Gilbert, 1998). In the absence of specific studies on this subject, it is however difficult to reach definite conclusions on the significance of trophic interactions among meso- and macro-fauna and microorganism at the surface of peatlands.

Practical applications

Biomonitoring

Beyond their functional importance in the recycling of nutrients through the decomposition of organic matter, microorganisms are also a subject of interest for ecologists because of their value as bioindicators of the quality of natural, perturbed, or regenerating ecosystems. Heterotrophic protists, and especially the testate amoebae are well suited for such application (Buttler et al., 1996; Foissner, 1997, 1999; Jauhiainen, 2002; Laggoun-Défarge et al., 2004).

Sphagnum peatlands are fragile ecosystems whose functioning strongly depends on the maintenance of an appropriate level of moisture and low concentrations and inputs of nutrient. Any modification of hydrology or nutrient status will therefore have a strong impact on the structure and functioning of the ecosystem, and may, for example, cause the peatland to stop being a carbon sink and instead act as a carbon source. Perturbations may be caused by direct human impact through peat harvesting, drainage for forestry purposes, or fertilization for agriculture. But peatlands may also be affected indirectly by human activities, for example, through increases in nitrogen and sulfur deposition, atmospheric carbon dioxide concentrations, or global warming (Aerts et al., 1992; Jauhiainen et al., 1998; Lee, 1998; Berendse et al., 2001; Freeman et al., 2002, 2004; Mitchell et al., 2003). What can microorganisms tell us about these changes?

Drainage and nutrient inputs modify the structure and functioning of microbial communities in *Sphagnum*. The main effect on the functioning of the peatland ecosystem is an increase in rates of organic matter mineralization. For example, three years after the conversion of a peatland to agricultural land, the abundance of fungi decreased whereas that of bacteria and actinomycetes increased tenfold (Kuster, 1993). Furthermore, the addition of agricultural fertilizers (NPKCa and PKCa) to a *Sphagnum*-dominated peatland caused a strong increase in the relative abundance of heterotrophic bacteria, diatoms, and ciliates whereas testate amoebae and other microalgae decreased (Gilbert et al., 1998a). Similarly, controlled burning of the surface vegetation and litter with the aim of increasing plant productivity for fodder production caused an increase in the abundance of euglenes and diatoms (Kuster, 1993). Finally according to Francez (1991), mowing induced a decrease in the diversity of rotifers over the entire surface of a peatland.

A study on the impact of nitrogen addition on the surface of peatlands showed that the structure and functioning of microbial communities respond fast to perturbations (Gilbert et al., 1998b). Four months after the onset of the experiment, the addition of $5\,gN\,m^2$ caused the biomass of autotrophic microorganisms, chlorophyll a, and microbial primary production to increase strongly, whereas the biomass and activity of heterotrophic microorganisms increased less clearly. These observations suggest that, with increasing N deposition rates, *Sphagnum* mosses become less efficient in taking up N from precipitation, leaving a higher proportion of the input to be used by microorganisms and, deeper in the peat by vascular plants. This mechanism is in agreement with experimental evidence of a competitive shift in favor of vascular plants with higher N deposition rates (Berendse et al., 2001).

The ongoing increase in atmospheric CO_2 concentrations may also affect microbial communities indirectly through its effect on plants. In an in situ experimental study, Mitchell et al. (2003) found that the abundance and biomass of heterotrophic bacteria increased and the biomass of testate amoebae decreased under raised CO_2 levels. Whereas the effect on bacteria is likely due to increased production and release of labile organic compounds by plants, the reason for the decrease in testate amoebae is less straightforward. Interestingly, testate amoebae were also negatively affected by fertilization (Gilbert et al., 1998a, b) and experimentally reduced UVB (Searles et al., 2001) in peatlands, and the number of large heterotrophic protists decreased under elevated CO_2 in mineral soils (Treonis and Lussenhop, 1997). Thus, it appears that testate amoebae in general are systematically affected by experimental changes in their environment, but to date no satisfactory explanation has been proposed for these responses. Could it simply be that their central position in the microbial food webs makes them more likely to suffer from any changes in the structure of the microbial community? Conversely, the central position and higher number of links in the food web should ensure testate amoebae a higher resilience. So, the observed high responsiveness of testate amoebae to changes could be due merely to the higher number of studies on this group.

Paleoecology

The extent to which microorganisms can be useful for paleoecological studies depends on the preservation of recognizable body parts. Several groups of microorganisms can provide valuable information on past ecological conditions and especially diatoms, testate amoebae and fungal spores (Van Geel, 1978; Beyens, 1985; Tolonen, 1986; Campbell et al., 1997; Kuhry, 1997). Other groups such as chrysophyceans (Smol, 1990), copepods, cladocerans (Hann, 1990), and the rotifer genus *Habrotrocha* also occur in peat (Warner and Chengalath, 1988). However, in *Sphagnum* peatlands, of these three microbial groups the testate amoebae are most commonly used in paleoecological studies. Whereas the potential for using this group of organisms in paleoecology was recognized long ago (Harnisch, 1927), the development of quantitative numerical approaches (transfer functions) has made this tool much more valuable to paleoecologists (Tolonen, 1986; Beyens and Chardez, 1987; Warner, 1987; Charman, 2001). Transfer functions describe the relationship between species and an environmental parameter of interest (such as depth to water table) statistically and then apply this relationship to fossil assemblages to provide estimates of changes in the environmental parameter through time. Testate amoebae have several advantages that make them useful: they are diverse (usually about 10–30 species in a given sample, often over 100 species across an ecological gradient), numerous (1 cm^3 of peat is usually enough to extract a sufficient number of shells), and they allow quantitative inference of the moisture conditions and pH of the precise coring location. Thus they are now often used in parallel to pollen and spores, which provide information on the surrounding vegetation as well as the peatland in general. Through a combined, multiproxy approach, a sounder image of the history of a site can be achieved. Judging by the impressive number of recent publications

using testate amoebae in paleoecology, we expect this tool to become a standard component of the peatland paleoecologist's toolbox (Chiverrell, 2001; Booth and Jackson, 2003; Langdon et al., 2003; Mauquoy and Barber, 2002; Wilmshurst et al., 2002, 2003; Charman et al., 2004).

Open research questions

The complexity of micro-environmental conditions present in peatlands and the challenges associated with the proper sampling for microorganisms in this environment may, in part, explain the fact that microorganisms are still being much less studied than other components of the ecosystem. Very few studies have provided data on the abundance and diversity of various groups of microorganisms, despite the fact that most scientists agree that microorganisms play key roles in the functioning of ecosystems (nutrient cycling, methanogenesis, and others). When microorganisms are included in ecological studies of peatlands most often the methods used do not provide much detail (microbial biomass determined using the fumigation-extraction method), or only the result of their activity is measured (methane emissions, decomposition rates, carbon balance). Analyzing the structure of microbial communities by separating the major groups (heterotrophic bacteria, fungi, cyanobacteria, microalgae, different groups of heterotrophic protists, micro-metazoa) provides more information than total microbial biomass, but this approach to microbial community structure may still hide species–specific responses. The microbial world is clearly as complex, if not more so, than the macroscopic world. The size of these organisms and the spatial and temporal scale of environmental influences they respond to represent important challenges for ecologists. However, until we learn more about the microbial world we will not be able to achieve a full understanding of the functioning of peatland ecosystems. There is no a-priori reason to continue to study microbial communities with a black-box approach or not consider them at all. It is therefore fundamental to study the spatial and temporal changes in biomass for each of the microbial functional groups. This information should then be integrated in order to generate hypotheses about the functioning of the microbial loop that can be experimentally tested using field manipulative experiments or mesocosm studies.

Microorganisms respond fast to changes in their environment and therefore constitute early indicators of perturbations in peatlands and other ecosystems. This is especially interesting in the case of indirect perturbations such as long-distance nutrient or pollutant transport and deposition, which may be difficult to quantify owing to spatial and temporal variability in production, transport, and deposition. Furthermore, using microorganisms as bioindicators in seminatural or natural ecosystems could also be an alternative to measurements that are technologically more intensive, practically more difficult to set up in remote locations, and much more expensive. In such cases, a monitoring program can easily be established with point-time samplings of water, mosses, or soil samples, ideally combined to a paleoecological approach in order to compare the range of present changes with past ones.

In order for microorganisms to be more useful as a tool for ecologists and paleoecologists, and to better understand the functioning of peatland ecosystems, we

clearly need much more baseline data on the structure and functioning of microbial communities, their response to ecological gradients in different types of peatlands, in natural conditions and under a broad range of perturbations and subsequent recovery.

References

Aerts, R., Wallen, B., and Malmer, N., 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J. Ecol. 80, 131–140.

Arndt, H., 1993. Rotifers as predators on components of the microbial web (Bacteria, Heterotrophic Flagellates, Ciliates) – a review. Hydrobiologia 255, 231–246.

Azam, F., Fenchel, T., Field, J.G., et al., 1983. The ecological role of water column microbes in the sea. Mar. Ecol. Pro. Ser. 10, 257–263.

Baldauf, S.L., 2003. The deep roots of eukaryotes. Science 300, 1703–1706.

Balsamo, M. and Todaro, M.A., 1993. Gastrotrichi del Trentino: le viotte de Monte Bodone. Studi Trentini di Science Naturali. Acta Biol. 70, 9–22.

Basilier, K., 1980. Fixation and uptake of nitrogen in *Sphagnum* blue-green-algal associations. Oikos 34, 239–242.

Batut, J., 1965. Etude de la faune submicroscopique de quelques tourbières à *Sphagnum*. Hydrobiologia 25, 239–276.

Baum, C., Leinweber, P., and Schlichting, A., 2003. Effect of chemical conditions in re-wetted peats on temporal variation in microbial biomass and acid phosphatase activity within the growing season. Appl. Soil Ecol. 22, 167–174.

Berendse, F., Van Breemen, N., Rydin, H., et al., 2001. Raised atmospheric CO_2 levels and increased N deposition cause shifts in plant species composition and production in *Sphagnum* bogs. Glob. Change Biol. 7, 591–598.

Beyens, L., 1985. On the Subboreal climate of the Belgian Campine as deduced from diatom and testate amoeba analyses. Rev. Palaeobot. Palynol. 46, 9–31.

Beyens, L. and Chardez, D., 1984. Testate amoebae (Rhizopoda, Testaceae) from Southwest Ireland. Arch. Protistenkd. 128, 109–126.

Beyens, L. and Chardez, D., 1987. Evidence from testate amoebae for changes in some local hydrological conditions between c. 5000 BP and c. 3800 BP on Edgeøya (Svalbard). Polar Res. 5, 165–169.

Bledzki, L.A. and Ellison, M.A., 2003. Diversity of rotifers from northeastern USA bogs with new species records from North America and New England. Hydrobiologia 497 (1), 53–62.

Bobrov, A.A., Charman, D.J., and Warner, B.G., 1999. Ecology of testate amoebae (Protozoa: Rhizopoda) on peatlands in western Russia with special attention to niche separation in closely related taxa. Protist 150, 125–136.

Bobrov, A.A., Charman, D.J., and Warner, B.G., 2002. Ecology of testate amoebae from oligotrophic peatlands: specific features of polytypic and polymorphic species. Biol. Bull. Rus. Acad. Sci. 29, 605–617.

Bonkowski, M. and Schaefer, M., 1997. Interactions between earthworms and soil protozoa: A trophic component in the soil food web. Soil Biol. 29, 499–502.

Bonnet, L., 1958. Les thécamoebiens des Bouillouses. Bull. Soc. Hist. Nat. Toulouse 93, 529–543.

Booth, R.K., 2002. Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. J. Paleolimnol. 28, 329–348.

Booth, R.K. and Jackson, S.T., 2003. A high resolution record of late-Holocene moisture variability from a Michigan raised bog, USA. Holocene 13, 863–876.

Borga, P., Nilsson, M., and Tunlid, A., 1994. Bacterial communities in peat in relation to botanical composition as revealed by phospholipid fatty-acid analysis. Soil Biol. Biochem. 26, 841–848.

Brake, M., Höper, H., and Joergensen, R.G., 1999. Land use-induced changes in activity and biomass of microorganisms in raised bogs at different depths. Soil Biol. Biochem. 31, 1489–1497.

Buttler, A., Grosvernier, P., and Matthey, Y., 1998. A new sampler for extracting undisturbed surface peat cores for growth pot experiments. New Phytol. 140, 355–360.

Buttler, A., Warner, B.G., Grosvernier, P., and Matthey, Y., 1996. Vertical patterns of testate amoebae (Protozoa: Rhizopoda) and peat forming vegetation on cutover bogs in the Jura, Switzerland. New Phytol. 134, 371–382.

Campbell, D.R., Duthie, H.C., and Warner, B.G., 1997. Post-glacial development of a kettle-hole peatland in southern Ontario. Ecoscience 4, 404–418.

Caron, D.A., 1983. Technique for enumeration of heterotrophic and phototrophic nanoplankton, using epifluorescence microscopy and comparison with other procedures. Appl. Environ. Microbiol. 46, 491–498.

Chapman, S., Buttler, A., Francez, A.-J., et al., 2003. Commercial exploitation of peatlands and maintenance of biodiversity – a conflict between economy and ecology. Front. Ecol. Environ. 1, 525–532.

Charman, D.J., 1997. Modelling hydrological relationships of testate amoebae (Protozoa: Rhizopoda) on New Zealand peatlands. J. Roy. Soc. NZ 27, 465–483.

Charman, D.J., 2001. Biostratigraphic and palaeoenvironmental applications of testate amoebae. Quatern. Sci. Rev. 20, 1753–1764.

Charman, D.J., Brown, A.D., Hendon, D., and Karofeld, E., 2004. Testing the relationship between Holocene peatland palaeoclimate reconstructions and instrumental data at two European sites. Quatern. Sci. Rev. 23, 137–143.

Charman, D.J., Hendon, D., and Packman, S., 1999. Multiproxy surface wetness records from replicate cores on an ombrotrophic mire: implications for Holocene palaeoclimate records. Quatern. Sci. Rev. 14, 451–463.

Charman, D.J. and Warner, B.G., 1997. The ecology of testate amoebae (Protozoa: Rhizopoda) in oceanic peatlands in Newfoundland, Canada: Modelling hydrological relationships for palaeoenvironmental reconstruction. Ecoscience 4, 555–562.

Chiverrell, R.C., 2001. A proxy record of late Holocene climate change from May Moss, northeast England. J. Quat. Sci. 16, 9–29.

Clarholm, M., 1981. Protozoan grazing of bacteria in soil – impact and importance. Microb. Ecol. 7, 343–350.

Clarholm, M., 1994. The microbial loop in soil. In: Ritz, K., Dighton, J., and Giller, K.E. (Eds), Beyond the Biomass. Wiley, Chichester, pp. 221–230.

Clarholm, M. and Rosswall, T., 1980. Biomass and turnover of bacteria in a forest soil and a peat. Soil Biol. Biochem. 12, 49–57.

Clymo, R.S., 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. Ann. Bot. 27, 309–324.

Clymo, R.S., 1983. Peat. In: Gore, A.J.P. (Ed.), Mires: Swamp, Bog, Fen, and Moor. General Studies. Elsevier, Amsterdam, Vol. A, pp. 159–224.

Cole, L., Bardgett, R.D., Ineson, P., and Hobbs, P.J., 2002. Enchytraeid worm (Oligochaeta) influences on microbial community structure, nutrient dynamics and plant growth in blanket peat subjected to warming. Soil Biol. Biochem. 34, 83–92.

Coleman, D.C., 1994. The microbial loop concept as used in terrestrial soil ecology studies. Microb. Ecol. 28, 245–250.

Collins, V.G., D'Sylva, D.T., and Latter, P.M., 1978. Microbial populations in peat. In: Heal, O.W. and Perkins, D.F. (Eds), Production Ecology of British Moors and Montane Grasslands. Springer, Berlin, pp. 94–112.

Compère, P., 1980. Quelques algues de la région de Brûly (France, Ardennes; Belgique, Namur). Bull. Soc. Roy. Bot. Belg. 112, 151–165.

Cosandey, F., 1964. La tourbière des Tenasses sur Vevey. Matériaux pour le levé géobotanique de la Suisse 45, 1–320.

Coûteaux, M.-M., 1969. Thécamoebiens muscicoles de Gaume et de Moyenne-Belgique. Rev. Ecol. Biol. Sol. 6, 413–428.

Coûteaux, M.-M. and Pussard, M., 1983. Nature du régime alimentaire des protozoaires du sol. In: LeBrun, P., André, H.M., De Medts, A., et al. (Eds), New Trends in Soil Biology, Proceedings of the VIII. International Colloquium of Soil Biology, Louvain-la-Neuve (Belgium), pp: 179–195.

Croft, M., Rochefort, L., and Beauchamp, C.J., 2001. Vacuum-extraction of peatlands disturbs bacterial population and microbial biomass carbon. Appl. Soil Ecol. 18, 1–12.

Czeczuga, B., 1993. Aquatic fungi of the Gorbacz and Ostrowki Peatbogs. Acta Mycol. 28, 69–75.

Davet, P., 1996. Vie microbienne du sol et production végétale. Institut national de la Recherche Agronomique, INRA, Paris Cedex, pp. 383.
Dell'Uomo, A., 1981. Studio algologico del bacino torboso-palustre del Laghestel (Trento). Studi Trentini di Science Naturali. Acta Biol. 58, 169–230.
Dell'Uomo, A. and Agostinelli, A., 1990. Florula desmidiologica del trentino-alto Adige: le torbiere di nova Ponente e del Doss le Grave. Studi Trentini di Science Naturali 66, 83–111.
Dell'Uomo, A. and Pellegrini, E., 1993a. Desmids from a peat-bog in the Northern Apennines (Italy). Arch. Hydrobiol. /Suppl., Algological Studies 68, 27–38.
Dell'Uomo, A. and Pellegrini, E., 1993b. Desmids of a small peat-bog in the Lomasona Fen (Trento, Northern Italy). Cryptogam. Algol. 14, 191–198.
Duthie, H.C., 1965. A study of the distribution and periodicity of some algae in a bog pool. J. Ecol. 53, 343–359.
Edwards, C., Hales, B.A., Hall, G.H., et al., 1998. Microbiological processes in the terrestrial carbon cycle: methane cycling in peat. Atmos. Environ. 32, 3247–3255.
Fisher, M.M., Graham, J.M., and Graham, L.E., 1998. Bacterial abundance and activity across sites within two northern Wisconsin *Sphagnum* bogs. Microb. Ecol. 36, 259–269.
Fisk, M.C. and Schmidt, S.K., 1996. Microbial responses to nitrogen additions in alpine tundra soil. Soil Biol. Biochem. 28, 751–755.
Foissner, W., 1997. Protozoa as bioindicators in agroecosystems, with emphasis on farming practices, biocides, and biodiversity. Agric. Ecosyst. Environ. 62, 93–103.
Foissner, W., 1999. Soil protozoa as bioindicators: pros and cons, methods, diversity, representative examples. Agric. Ecosyst. Environ. 74, 95–112.
Francez, A.-J., 1981. Rotifères de quelques tourbières d'Auvergne. Ann. Stat. Biol. Besse-en-Chandesse 15, 276–287.
Francez, A.-J., 1984. Ecologie des peuplements de rotifères sessiles des lacs-tourbières d'Auvergne (France). Bull. Ecol. 15, 231–237.
Francez, A.-J., 1986. *Sphagnum* microfauna in two peatbogs of the French Massif Central. Suo 37, 1–6.
Francez, A.-J., 1987. Successions écologiques dans les tourbières: Le peuplement de rotifères du lac-tourbière de Chambedaze (Puy-de-Dôme, France). Bull. Ecol. 18, 31–38.
Francez, A.-J., 1988. Le peuplement de rotifères libres de deux lacs-tourbières du Puy-de-Dôme (France). Vie Milieu 38, 281–292.
Francez, A.-J., 1991. Production primaire et accumulation de matière organique dans les tourbières à sphaignes des monts du Forez. Influences des activités humaines sur leur fonctionnement et leur évolution. Ph.D Thesis, Univ. Pierre et Marie Curie, Paris 6., Paris, France, 397 pp.
Francez, A.-J., Gogo, S., and Josselin, N., 2000. Distribution of potential CO_2 and CH_4 productions, denitrification and microbial biomass C and N in the profile of a restored peatland in Brittany (France). Eur. J. Soil Biol. 36, 161–168.
Francez, A.-J. and Loiseau, P., 1999. The fate of mineral nitrogen in a fen with *Sphagnum fallax klinggr* and *Carex rostrata* stokes (Massif-central, France). Can. J. Bot.-Rev. Can. Bot. 77, 1136–1143.
Freeman, C., Fenner, N., Ostle, N.J., et al., 2004. Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. Nature 430, 195–198.
Freeman, C., Ostle, N., and Kang, H.J., 2002. An enzymatic 'latch' on a global carbon store. Nature 409, 149.
Galand, P.E., Fritze, H., and Yrjälä, K., 2003. Microsite-dependent changes in methanogenic populations in a boreal oligotrophic fen. Environ. Microbiol. 5, 1133–1143.
Galand, P.E., Saarnio, S., Fritze, H., and Yrjälä, K., 2002. Depth related diversity of methanogen Archea in Finnish oligotrophic fen. FEMS Microb. Ecol. 42, 441–449.
Gardiner, J.J., 1975. The influence of fertilisers upon microbial activity in peat. II-Calcium and nitrogen. Irish Forestry 32, 101–114.
Gilbert, D., 1998. Les communautés microbiennes à la surface des tourbières à sphaignes: structure, fonctionnement et impact des apports de fertilisants. Ph.D Thesis, Laboratoire de Biologie Comparée des Protistes, University Blaise Bascal (Clermont II), Clermont-Ferrand, France, 133pp.
Gilbert, D., Amblard, C., Bourdier, G., and Francez, A.-J., 1998a. The microbial loop at the surface of a peatland: structure, function, and impact of nutrient input. Microb. Ecol. 35, 83–93.

Gilbert, D., Amblard, C., Bourdier, G., and Francez, A.J., 1998b. Short-term effect of nitrogen enrichment on the microbial communities of a peatland. Hydrobiologia 374, 111–119.
Gilbert, D., Amblard, C., Bourdier, G., et al., 2000a. Le régime alimentaire des thécamoebiens. Ann. Biol.-Paris. 39, 57–68.
Gilbert, D., Francez, A.-J., Amblard, C., and Bourdier, G., 2000b. Microbial communities at the surface of *Sphagnum* peatlands: good indicators of Human disturbances?. Bull. Ecol. 30, 45–52.
Gilbert, D., Mitchell, E.A.D., Amblard, C., et al., 2003. Population dynamics and food preferences of the testate amoeba *Nebela tincta major-bohemica-collaris* complex (Protozoa) in a *Sphagnum* Peatland. Acta Protozool. 42, 99–104.
Given, P.H. and Dickinson, C.H., 1975. Biochemistry and microbiology of peats. In: Paul, P.A. and Mc Laren, A.D. (Eds), Soil Biochemistry. Marcel Dekkets, New York, Vol. 3, pp. 123–212.
Golovchenko, A.V., Polyanskaya, L.M., Dobrovol'skaya, T.G., et al., 1994. The spatial distribution and structure of microbial complexes in bog forest Ecosystems. Eurasian Soil Sci. 26, 78–89.
Greaves, M.P., Weatley, R.E., Shepherd, H., and Knight, A.H., 1973. Relationship between microbial populations and adenosine triphosphate in a basin peat. Soil Biol. Biochem. 5, 685–687.
Grolière, C.A., 1974–1975. Etude de quelques ciliés hyménostomes des eaux acides de la région de Besse en Chandesse. Ann. Stat. Biol. Besse-en-Chandesse 9, 79–109.
Grolière, C.A., 1975. Descriptions de quleques ciliés hypotriches de tourbières a sphaignes et des étendues d'eau acides. Protistologica 11, 481–498.
Grolière, C.A., 1976. Ecology of *Sphagnum* Infusoria. J. Protozool. 23, A11.
Grolière, C.A., 1977. Contribution à l'étude de quelques ciliés des sphaignes: II-Dynamique des populations. Protistologica 13, 335–352.
Hales, B.A., Edwards, C., Ritchie, D.A., et al., 1996. Isolation and identification of methanogen-specific DNA from blanket bog peat by PCR amplification and sequence analysis. Appl. Environ. Microbiol. 62, 668–675.
Hann, B.J., 1990. Cladocera. In: Warner, B.G. (Ed.), Methods in Quaternary Ecology. Reprint series, Geoscience Canada, St. John's, Newfoundland, Vol. 5, pp. 81–91.
Harnisch, O., 1927. Einige Daten zur recenten und fossilen testaceen Rhizopodenfauna der Sphagnen. Arch. Hydrobiol. 18, 345–360.
Heal, O.W., 1962. The abundance and microdistribution of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum*. Oikos 13, 35–47.
Heal, O.W., 1964. Observations on the seasonal and spatial distribution of testaceans (Protozoa: Rhizopoda) in *Sphagnum*. J. Anim. Ecol. 33, 395–412.
Hemond, H.F., 1983. The nitrogen budget of Thoreau gog. Ecology 64, 99–109.
Hendon, D. and Charman, D.J., 1997. The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. Holocene 7, 199–205.
Henebry, M.S. and Cairns, J. Jr., 1984. Protozoan colonization rates and trophic status of some freshwater wetland lakes. J. Protozool. 31, 456–467.
Hiroki, M. and Watanabe, M.M., 1996. Microbial community and rate of cellulose decomposition in peat soils in a mire. Soil Sci. Plant Nutr. 42, 893–903.
Hobbie, J.E., Delay, R.J., and Jasper, S., 1977. Use of Nuclepore filters for counting bacteria by fluorescence microscopy. Appl. Environ. Microbiol. 33, 1225–1228.
Humphrey, W.D. and Pluth, D.J., 1996. Net nitrogen mineralization in natural and drained fen peatlands in Alberta, Canada. Soil Sci. Soc. Am. J. 60, 932–940.
Ingham, R.E., Trofymow, J.A., Ingham, E.R., and Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecol. Monogr. 55, 119–140.
Jauhiainen, J., Silvola, J., and Vasander, H., 1998. The effects of increased nitrogen deposition and CO_2 on *Sphagnum angustifolium* and *S. warnstorfii*. Annales Botanici Fennici 35, 247–256.
Jauhiainen, S., 2002. Testacean amoebae in different types of mire following drainage and subsequent restoration. Europ. J. Protistol. 38, 59–72.
Kingston, J.C., 1982. Association and distribution of common diatoms in surface samples from northern Minnesota peatlands. Nova Hedwigia. 73, 333–346.
Kishaba, K. and Mitchell, E.A.D., 2005. Changes in testate amoebae (Protists) communities in a small raised bog. A 40-year study. Acta Protozool. 44, 1–12.

Krumholz, L.R., Hollenback, J.L., Roskes, S.J., and Ringelberg, D.B., 1995. Methanogenesis and Methanotrophy within a *Sphagnum* Peatland. FEMS Microbiol. Ecol. 18, 215–224.

Kuhry, P., 1997. The palaeoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physico-chemical properties. Rev. Palaeobot. Palynol. 96, 183–224.

Kuster, E., 1993. The microbiology of peat. In: Heatwaite, A.L. and Gottlich, K.H. (Eds), Mires: Processes, Exploitation and Conservation. Wiley, Chichester, New York, pp. 311–324.

Laggoun-Défarge, F., Mitchell, E.A.D., Gilbert, D., et al., 2004. Biochemical characteristics of peat organic matter and distribution of testate amoebae in two naturally regenerating cutover *Sphagnum* peatlands of the Jura Mountains. In: Païvanen, J. (Ed.), Proceedings of the 12th International Peat Congress, Tampere, Finland, Vol. 1, pp. 383–384.

Lamentowicz, M. and Mitchell, E.A.D., 2005. The ecology of testate amoebae (Protists) in *Sphagnum* in north-west Poland in relation to peatland ecology. Microb. Ecol. 50, 48–63.

Langdon, P.G., Barber, K.E., and Hughes, P.D.M., 2003. A 7500-year peat-based palaeoclimatic reconstruction and evidence for an 1100-year cyclicity in bog surface wetness from Temple Hill Moss, Pentland Hills, southeast Scotland. Quatern. Sci. Rev. 22, 259–274.

Lederer, F., 1995a. A new species of *Cyanodictyon* (cyanoprokaryota, Chroococcales) from peat-bogs in the Sumava Mountains, Czech Republic. Preslia, Praha 67, 117–121.

Lederer, F., 1995b. Several little known cyanobacteria/cyanoprokaryota from peat-bogs in the Sumava Mountains. Czech Republic Algological Studies 79, 57–65.

Lee, J.A., 1998. Unintentional experiments with terrestrial ecosystems – ecological effects of sulfur and nitrogen pollutants. J. Ecol. 86, 1–12.

Li, Y.H. and Vitt, D.H., 1997. Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Ecoscience 4, 106–116.

Martin, N.J., Siwasin, J., and Holding, A.J., 1982. The bacterial population of a blanket peat. J. Appl. Bacteriol. 53, 35–48.

Mataloni, G., 1999. Ecological studies on algal communities from Tierra del Fuego peat bogs. Hydrobiologia 391, 157–171.

Mataloni, G. and Tell, G., 1996. Compartive analysis of the phytoplankton communities of a peat bog from Tierra del Fuego (Argentina). Hydrobiologia 325, 101–112.

Mauquoy, D. and Barber, K., 2002. Testing the sensitivity of the palaeoclimatic signal from ombrotrophic peat bogs in northern England and the Scottish Borders. Rev. Palaeobot. Palynol. 119, 219–240.

Meisterfeld, R., 1977. Die horizontale und vertikale Verteilung der Testaceen (Rhizopoda: Testacea) in *Sphagnum*. Arch. Hydrobiol. 79, 319–356.

Meisterfeld, R., 1979. Zur Systematik der Testaceen (Rhizopoda, Testacea) in Sphagnum. Eine REM-Untersuchung. Arch. Protistenkd. 121, 246–269.

Meisterfeld, R., 2002a. Order Arcellinida Kent, 1880. In: Lee, J.J., Leedale, G.F., and Bradbury, P. (Eds), The Illustrated Guide to the Protozoa. Society of Protozoologists, Lawrence, Kansas, USA, Vol. 2, pp. 827–860.

Meisterfeld, R., 2002b. Testate amoebae with filopodia. In: Lee, J.J., Leedale, G.F., and Bradbury, P. (Eds), The Illustrated Guide to the Protozoa. Society of Protozoologists, Lawrence, Kansas, USA, Vol. 2, pp. 1054–1084.

Mitchell, E.A.D., Borcard, D., Buttler, A.J., et al., 2000a. Horizontal distribution patterns of testate amoebae (Protozoa) in a *Sphagnum magellanicum* carpet. Microb. Ecol. 39, 290–300.

Mitchell, E.A.D., Buttler, A., Grosvernier, P., et al., 2000b. Relationships among testate amoebae (Protozoa), vegetation and water chemistry in five *Sphagnum*-dominated peatlands in Europe. New Phytol. 145, 95–106.

Mitchell, E.A.D., Buttler, A.J., Warner, B.G., and Gobat, J.M., 1999. Ecology of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum* peatlands in the Jura Mountains, Switzerland and France. Ecoscience 6, 565–576.

Mitchell, E.A.D. and Gilbert, D., 2004. Vertical micro-distribution and response to nitrogen deposition of testate amoebae in *Sphagnum*. J. Eukaryot. Microbiol. 51, 485–495.

Mitchell, E.A.D., Gilbert, D., Buttler, A., et al., 2003. Structure of microbial communities in *Sphagnum* peatlands and effect of atmospheric carbon dioxide enrichment. Microb. Ecol. 46, 187–199.

Mitchell, E.A.D., van der Knaap, W.O., van Leeuwen, J.F.N., et al., 2001. The palaeoecological history of the Praz-Rodet bog (Swiss Jura) based on pollen, plant macrofossils and testate amoebae (Protozoa). Holocene 11, 65–80.

Nieminen, J.K. and Setälä, H., 1998. Enclosing decomposer food web: implications for community structure and function. Biol. Fertil. Soils 26, 50–57.

Nikolaev, S.I., Mitchell, E.A.D., Petrov, N.B., et al., 2005. The testate lobose amoebae (order Arcellinida Kent, 1880) finally find their home within Amoebozoa. Protist 156, 191–202.

Nilsson, M., Baath, E., and Söderström, B., 1992. The microfungal communities of a mixed mire in northern Sweden. Can. J. Bot. 70, 272–276.

Nowak, E. and Pilipiuk, I., 1997. The influence of drainage on enchytraeids (Enchytraeidea, Oligochaeta) of fens in the Biebrza ice-marginal valley. Ekol. Pol.-Pol. J. Ecol. 45, 423–440.

Pejler, B. and Berzins, B., 1993. On the ecology of mire rotifers. Limnologica 23, 295–300.

Porter, K.G. and Feig, Y.S., 1980. The used of DAPI for identifying and counting aquatic microflora. Limnol. Oceanogr. 25, 943–948.

Porter, K.G., Sherr, E.B., Sherr, B.F., et al., 1985. Protozoa in planktonic food webs. J. Protozool. 32, 409–415.

Potila, H. and Sarjala, T., 2004. Seasonal fluctuation in microbial biomass and activity along a natural nitrogen gradient in a drained peatland. Soil Biol. Biochem. 36, 1047–1055.

Poulicková, A., Hájková, P., Krenková, P., and Hájek, M., 2004. Distribution of diatoms and bryophytes on linear transects through spring fens. Nova Hedwigia. 78, 411–424.

Robson, T.M., Pancotto, V.A., Ballaré, C.L., et al., 2004. Reduction of solar UV-B mediates changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community. Oecologia 140, 480–490.

Schmidt, I.K., Ruess, L., Baath, E., et al., 2000. Long-term manipulation of the microbes and microfauna of two subarctic heaths by addition of fungicide, bactericide, carbon and fertilizer. Soil Biol. Biochem. 32, 707–720.

Schoenberg, S.A. and Oliver, J.D., 1988. Temporal dynamics and spatial variation of algae in relation to hydrology and sediment characteristics in the Okefenokee Swamp, Georgia. Hydrobiol. 162, 123–134.

Schönborn, W., 1963. Die Stratigraphie lebender Testaceen im *Sphagnetum* der Hochmoore. Limnologica 1, 315–321.

Schönborn, W., 1965. Untersuchungen über die Zoochlorellen-Symbiose der Hochmoor-Testaceen. Limnologica 3, 173–176.

Searles, P.S., Kropp, B.R., Flint, S.D., and Caldwell, M.M., 2001. Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. New Phytol. 152, 213–221.

Sieburth, J.M., Smetacek, V., and Lenz, J., 1978. Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size-fractions. Limnol. Oceanogr. 23, 1256–1263.

Sizova, M.V., Panikov, N.F., Tourova, T.P., and Flanagan, P.W., 2003. Isolation and characterization of oligotrophic acido-tolerant methanogenic consortia from a *Sphagnum* peat bog. FEMS Microb. Ecol. 45, 301–315.

Smol, J.P., 1990. Freshwater algae. In: Warner, B.G. (Ed.), Methods in Quaternary Ecology. Reprint series, Geoscience Canada, St. John's, Newfoundland, Vol. 5, pp. 3–14.

Sundh, I., Borga, P., Nilsson, M., and Svensson, B.H., 1995. Estimation of cell numbers of methanotrophic bacteria in boreal peatlands based on analysis of specific phospholipid fatty acids. FEMS Microb. Ecol. 18, 103–112.

Sundh, I., Nilsson, M., and Borga, P., 1997. Variation in microbial community structure in two boreal peatlands as determined by analysis of phospholipid fatty acid profiles. Appl. Environ. Microb. 63, 1476–1482.

Thormann, M.N., Currah, R.S., and Bayley, S., 2003. Succession of microfungal assemblages in decomposing peatland plant. Plant Soil 250, 323–333.

Thormann, M.N., Currah, R.S., and Bayley, S.E., 2001. Microfungi isolated from *Sphagnum fuscum* from a southern boreal bog in Alberta, Canada. Bryologist 104, 548–559.

Thormann, M.N., Currah, R.S., and Bayley, S.E., 2002. The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. Can. J. Microbiol. 48, 204–211.