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Variation in Microbial Community Structure in Two Boreal Peatlands as Determined by Analysis of Phospholipid Fatty Acid Profiles

INGVAR SUNDH,[1]* MATS NILSSON,[2] AND PETER BORGÅ[3]†

Department of Microbiology[1] and Department of Chemistry,[3] SLU, S-750 07 Uppsala, and Department of Forest Ecology, SLU, S-901 83 Umeå,[2] Sweden

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Analyses of phospholipid fatty acids (PLFAs) were used to assess variation in community structure and total microbial biomass in two boreal peatlands in Sweden. The total PLFA concentration in peat ranged from 0.16 to 7.0 nmol g of wet peat^{-1} (median, 0.70 nmol g of wet peat^{-1}). Principal-component analysis of PLFA data revealed that the degree of depth-related variation in PLFA composition was high among peatland habitats, with general differences between wet sites, with water tables within a few centimeters of the moss surface, and dry sites, with water tables >10 cm below the moss surface. However, variation in PLFA composition over the growing season was negligible. In the principal-component analyses, most PLFAs were determined to be parts of clusters of covarying fatty acids, suggesting that they originated in the same functional groups of microorganisms. Major clusters were formed by monounsaturated (typical of gram-negative eubacteria), terminally branched (gram-positive or anaerobic gram-negative eubacteria), methyl-branched and branched unsaturated (sulfate-reducing bacteria and/or actinomycetes), ω8 monounsaturated (methane-oxidizing bacteria), and polyunsaturated (eucaryotes) PLFAs. Within the clusters, PLFAs had rather distinct concentration-depth distributions. For example, PLFAs from sulfate-reducing bacteria and/or actinomycetes and those from methane-oxidizing bacteria had maximum concentrations slightly below and at the average water table depth, respectively.

Much interest has recently been focused on the biogeochemistry of peatlands. The main reasons are that peat deposits are an important storage component in the global carbon budget and that microbial mineralization processes in peatlands result in the production of greenhouse gases (e.g., CH_4 and N_2O) that may be emitted to the atmosphere and have impacts on the global climate (7, 21). However, in terms of the occurrence and distribution of functional and/or taxonomic groups of microorganisms, peatlands have been investigated much less thoroughly than aerated terrestrial soils and marine and freshwater sediments. Activity measurements indicate the presence of diverse microbial communities including nitrogen fixers (23), denitrifiers (47), sulfate reducers (39), methane producers (43), and methane oxidizers (41). Although many species of microorganisms in peatlands have been isolated and characterized (3, 29, 32, 53), limited information about these organisms' quantitative contributions to the microbial biomass has been provided.

Analysis of the fatty acid moieties of phospholipids (PLFAs) is an established method for estimating microbial biomass and community structure in complex environmental samples (14, 46, 49). The method takes advantage of the fact that microorganisms differ in the composition of their PLFAs. The major strength of the method is that fatty acids in intact phospholipids are mainly derived from living biomass, since the polar group of phospholipids in dead organic matter is rapidly hydrolyzed (22, 51). The method does not take archaebacteria (e.g., methanogenic bacteria) into account, however, since they have ether instead of ester bonds in their polar membrane lipids.

In two earlier studies of PLFA patterns in boreal peatlands, sampling was either restricted to deep, permanently anaerobic peat, with the strongest emphasis put on relationships between PLFA patterns and the botanical composition of the peat (5), or restricted to surface peat down to 7.5 cm (26). In the present study, the PLFA composition was analyzed in surface samples down to ca. 1/2 m. This is the horizon of an oscillating water table in many mire environments and the depth interval within which microbial mineralization is most rapid (13, 37). Emphasis was placed on measuring variation in PLFA composition among mire habitats, with depth, and with time of season. Thirty-nine fatty acids from a total of 72 samples were quantified, generating a large data set. Principal-component analy-

TABLE 1. Water table levels and dominating higher plants at sampled mire sites

Site and mire	Water table depth (cm)[a]	Dominating plants
Stor-Åmyran		
Hollow	4	*Sphagnum majus*, *Eriophorum vaginatum*
Mud-bottom	2	*S. majus*, liverworts
Minerotrophic	12	*S. majus*, *Sphagnum balticum*, *Carex rostrata*, *Oxycoccus quadripetalus*
String	16	*Sphagnum fuscum*, *O. quadripetalus*, *Calluna vulgaris*, *Andromeda polifolia*
Hummock	29	*S. fuscum*, *E. vaginatum*, *Pinus silvestris*, *Ledum palustre*
Björnmyran		
Flark	−7	*Carex* spp., *Eriophorum angustifolium*, *Equisetum fluviatile*, *Utricularia intermedia*
String	10	*Sphagnum fallax*, *Sphagnum papillosum*, *C. rostrata*, *E. vaginatum*
Sloping area	3	Plants similar to those of the flark

[a] Values are averages of three measurements taken during 1991 (Stor-Åmyran) and of four measurements taken during 1992 (Björnmyran).

* Corresponding author. Mailing address: Department of Microbiology, SLU, P.O. Box 7025, S-750 07 Uppsala, Sweden. Phone: 46 18 673210. Fax: 46 18 673392. E-mail: Ingvar.Sundh@mikrob.slu.se.

† Present address: Bioanalytical Chemistry, Pharmacia & Upjohn AB, S-751 82 Uppsala, Sweden.

TABLE 2. Relative amounts of chemical classes of PLFAs in peat from two boreal peatlands in Sweden

Chemical class	Relative amt (mol%)		
	Median	Upper quartile	Lower quartile
Straight chain, saturated	28	36	21
Straight chain, monounsaturated	36	41	27
Terminally branched	16	24	11
Polyunsaturated	4.1	13	2.6
Mid-chain branched	4.3	6.0	2.8
Branched monounsaturated	3.9	6.2	2.6

sis (PCA) was used to reduce the dimensionality, facilitating interpretation of the data.

MATERIALS AND METHODS

Mire and site descriptions. Mire habitats are described with terminology from Gore (20). Stor-Åmyran (63°44′N, 20°06′E) is an acid mixed mire with an area of ca. 1 km^2. A large amount of its ombrotrophic parts is characterized by wet, fairly flat hollows where the water table is within a few centimeters of the moss surface. In a few mud-bottoms, the peat mainly consists of *Sphagnum* litter covered by liverworts, giving them dark-brown to black surfaces. Hollows are separated by raised, drier areas, either strings of a few meters' width or hummocks covering larger areas. A small part of Stor-Åmyran is minerotrophic, thus receiving nutrients both from surface runoff and from direct deposition.

Björnmyran (64°20′N, 18°18′E) is a medium-rich tall-sedge fen with an area of ca. 2.5 km^2. A large part of its surface has well-developed string-flark patterns. Like mud-bottoms, flarks are comparatively wet, but the vegetation is richer, including several sedge species. Some characteristics of the sampled sites are given in Table 1. More detailed descriptions of the mires have been given previously (41, 42).

Peat collection and storage. Methods of sampling and storing samples have been described previously (40), so only a brief description follows. Stor-Åmyran was sampled at all five sites on 18 June, 18 July, and 11 September 1991 (15 peat profiles in total). Peat samples from Björnmyran were collected on 9 September 1992. Two profiles were taken from the flark, and one profile each was taken from the string and the sloping areas. Peat profiles to a depth of ca. 50 cm at Stor-Åmyran and to a depth of ca. 70 cm at Björnmyran were withdrawn with a peat auger. Four 5-cm intervals distributed over the profiles were put into separate plastic bags and brought to the laboratory. There, the samples were cut with scissors, manually mixed, and stored at −20°C until lipid extraction.

Preparation of FAMEs. The lipid extraction and preparation of fatty acid methyl esters (FAMEs) have been described previously (40). Briefly, the frozen peat samples were allowed to almost thaw at room temperature. They were then manually homogenized with a knife, and 2 g of each sample was transferred to a glass tube with a Teflon-lined screw cap. Total lipids were extracted by a modified Bligh and Dyer extraction procedure (18, 51). They were further fractionated by silicic acid chromatography (45). The phospholipid fraction was dried under a stream of nitrogen and stored at −20°C until methanolysis.

The methyl ester of nonadecanoic acid (19:0) was added as an internal standard immediately before the phospholipids were transesterified by mild alkaline methanolysis (11). The FAME preparations were stored dry at −20°C until gas chromatography-mass spectrometry (GC-MS).

Quantification and identification of PLFAs. FAMEs were analyzed by GC-MS with a Hewlett-Packard (Palo Alto, Calif.) 5890A gas chromatograph connected to an HP 5970B mass-selective detector (Hewlett-Packard). The mass-selective detector was set up for selected-ion monitoring according to procedures described by Borgå et al. (5). Identification of FAMEs was based on the presence of characteristic ions and on a comparison of retention times with FAME standards (Larodan, Malmö, Sweden) and with the retention times for compounds previously identified in our laboratory. Double-bond positions were confirmed after dimethyl disulfide derivatization of FAMEs followed by GC-MS (30). Quantification was carried out by calibration against standard solutions of FAMEs.

The two monounsaturated PLFAs with the double bond in the ω8 position

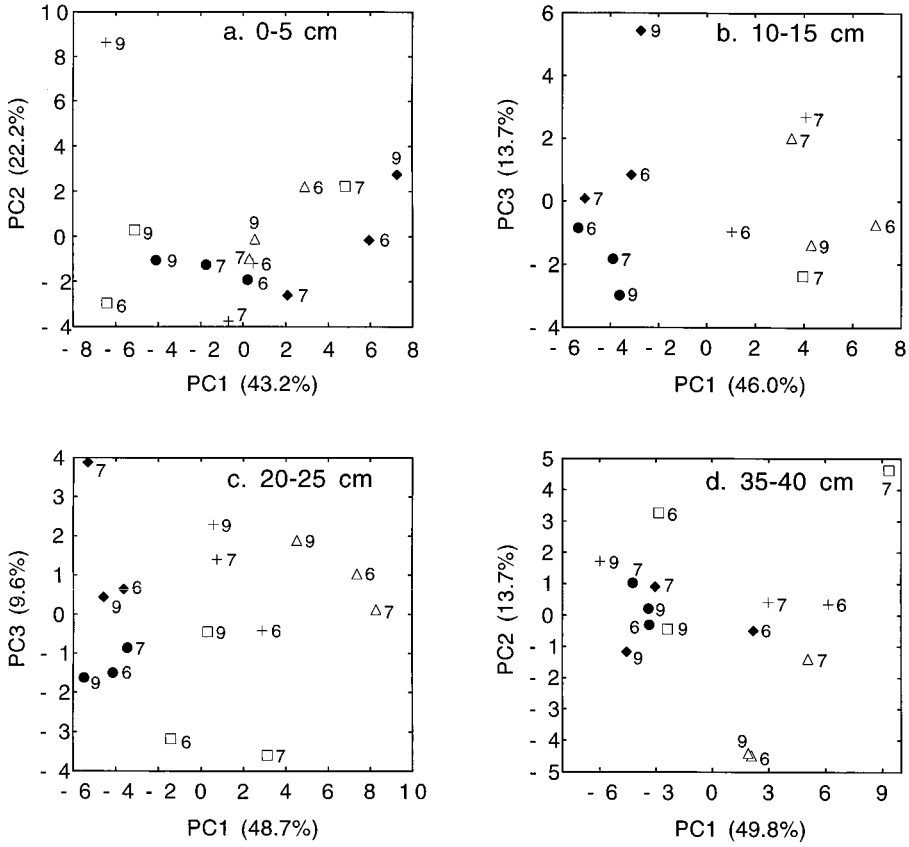

FIG. 1. PCA of PLFA compositions for samples from Stor-Åmyran, a Swedish boreal peatland. The analysis was performed separately for each depth of sampling. Samples were taken from hollow (●), mud-bottom (◆), string (✚), hummock (□), and minerotrophic (△) sites. The numerals 6, 7, and 9 designate samples taken in June, July, and September 1991, respectively. Numbers within parentheses show the variance explained by each component.

were quantified after dimethyl disulfide derivatization as described previously (30, 40).

PLFA nomenclature. Fatty acids are designated by the total number of carbon atoms, followed by a colon and the number of double bonds. Then an "ω" and a number show the position of the double bond relative to the aliphatic end of the chain, sometimes followed by a "c" or "t" for *cis* or *trans* configuration, respectively. The prefixes "i," "a," and "10Me" refer to methyl branching at the iso and anteiso positions and at the 10th carbon from the carboxyl group, respectively. Cyclopropane fatty acids have the prefix "cy."

PCAs. PCA is a multivariate statistical method used to reduce the dimensionality of data sets containing many interrelated variables while retaining as much as possible of the systematic variation in the original data set (24). In the analysis, the original variables are replaced by a few principal-component variables (PCs). The PCs are totally uncorrelated with each other and ordered so that PC1 contains most of the original variation and PC2 contains the second largest amounts, etc. The PCs were calculated from scaled and centered variables so that every PLFA has the same impact on each PC, independent of the total variance in that PLFA. To make the plots of the PCAs easily interpretable, we used sample-normalized values, i.e., the amount of each PLFA was divided by the total amount of PLFA in that particular sample. The number of statistically significant PCs was determined by cross validation (54).

By using PCA, the relationships between either specific peat samples or individual PLFAs can be evaluated by examining two-dimensional plots of the PCs. Samples with similar values for a PC would have a common pattern of PLFA composition as illustrated by that particular PC. This means that peat samples close together in PCA plots (e.g., Fig. 1) have similar PLFA compositions and hence similar organism compositions. Correspondingly, in the plots of individual PLFAs (see Fig. 2), clusters represent PLFAs which vary in their contributions among samples in a similar way.

RESULTS

PLFA concentrations. The average total PLFA concentration for all 72 samples was 1.0 nmol of PLFA g of wet peat^{-1}. A few surface samples with very high concentrations skewed the distribution, and the median was 0.70 nmol of PLFA g of wet peat^{-1}. Straight-chain saturated and straight-chain monounsaturated PLFAs made the highest median contributions, accounting for 36 and 28% of the total PLFAs, respectively (Table 2).

General differences among sites. In Fig. 1, PC1 and PC2 or PC3 for all individual PLFAs for all samples from Stor-Åmyran are plotted separately for the different depths. At the two intermediate depths (Fig. 1b and c), the wet sites (hollow and mud-bottom) were separated from the dry sites (string, hummock, and minerotrophic) along PC1. In addition, a clear separation between hollow and mud-bottom samples can be seen along PC3. No such separations were evident for the surface samples (Fig. 1a), and separations were much less pronounced for the deepest samples (Fig. 1d), showing that there were very small systematic differences in PLFA composition between sites at these depths. PC1 accounted for 43 to 50%, PC2 accounted for 14 to 22%, and PC3 accounted for 10 to 14% of the total variance in PLFA composition.

No systematic variation in PLFA composition due to time of sampling is evident in the results of the PCA (Fig. 1). This demonstrates that the degree of variation due to site and depth is much higher than the variation due to time of sampling (June, July, or September).

Covariation among PLFAs. The degree of covariation among PLFAs was also investigated by PCA. Analyses were made with the total data set as well as with subsets for specific mires, sites, and depths, etc. Patterns of PLFA clustering were similar irrespective of the data subset, but the separation of PLFAs was often stronger when data were restricted to one community (Fig. 2). Based on the PCA runs for all different data subsets, six major PLFA clusters could be identified (Table 3 and Fig. 2): straight-chain monounsaturated (cluster A), terminally branched saturated (cluster B), straight-chain ω8 monounsaturated (cluster C), mid-chain branched and terminally branched unsaturated (cluster D), straight-chain polyunsaturated (cluster E), and long, straight-chain saturated (cluster F)

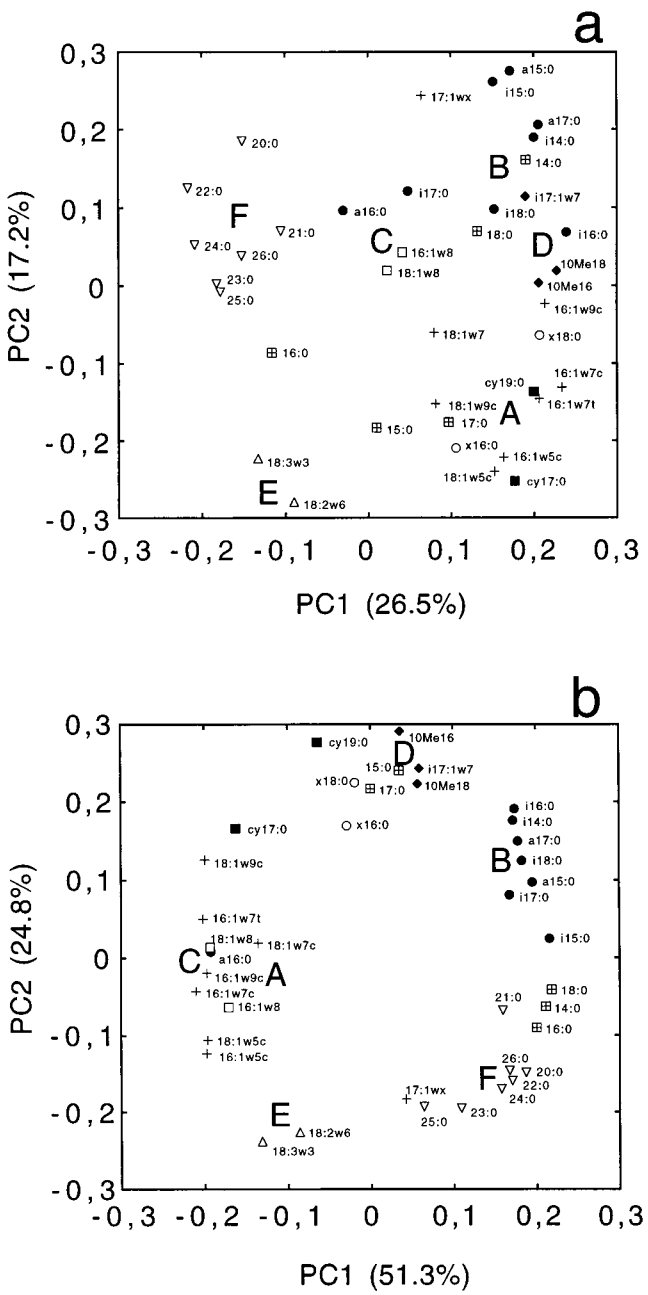

FIG. 2. PCAs of all quantified PLFAs. (a) All samples (n = 72); (b) Samples from the two flark profiles from Björnmyran (n = 8). The different groups of fatty acids shown are monounsaturated (✚), terminally branched saturated (●), ω8 monounsaturated (□), methyl branched and branched unsaturated (◆), polyunsaturated (△), saturated (C_{20} to C_{26}) (▽), unidentified, (○), cyclopropyl (■), and saturated (C_{15} to C_{19}) (⊞). Capital letters (A to F) designate major clusters (PLFAs of different clusters are shown in Table 3).

PLFAs. The fatty acids x16:0, x18:0 (x denotes substitution at an unknown position), a16:0, 17:1ωx, cy17:0, cy19:0, 14:0, 15:0, 16:0, 17:0, and 18:0 were not part of any major clusters. Their positions differed among PCA runs.

Depth distributions of PLFA concentrations. The total concentration of PLFAs decreased with depth in most profiles (Fig. 3a). Generally, the decrease was steeper for wet sites than dry ones. The depth distributions of the monounsaturated PLFAs of cluster A (Fig. 3b) were similar to the depth distri-

TABLE 3. Composition of PLFA clusters as determined by PCA

Cluster	Fatty acids	Organisms[a]
Monounsaturated, straight chain (A)	16:1ω9c, 16:1ω7c, 16:1ω7t, 16:1ω5c, 18:1ω9c, 18:1ω7c, 18:1ω7t	Eubacteria (mainly gram negative), eucaryotes[b]
Terminally branched, saturated (B)	i14:0, i15:0, a15:0, i16:0, i17:0, a17:0, i18:0	Eubacteria, mainly gram positive and anaerobic gram negative
Monounsaturated, straight chain, ω8 (C)	16:1ω8, 18:1ω8	Methane-oxidizing bacteria
Methyl branched and branched unsaturated (D)	10Me16:0, 10Me18:0, i17:1ω7	Sulfate-reducing bacteria, actinomycetes
Polyunsaturated, straight chain (E)	18:2ω6, 18:3ω3	Eucaryotes, particularly fungi; mosses; cyanobacteria
Long saturated, straight chain (F)	20:0, 21:0, 22:0, 23:0, 24:0, 25:0, 26:0	Higher plants, mosses, eucaryotes[b]

[a] The sources of data on PLFA composition of different organisms are references 8, 10, 12, 15, 27, 30, 46, 48, 49, and 52.
[b] Organisms in which these PLFAs make only a small contribution to their total PLFA content.

bution of the total PLFAs in wet environments but showed a less pronounced decrease with depth in the dry communities. The concentration of the polyunsaturated PLFAs of cluster E also consistently decreased with depth but in most cases decreased more steeply than the total concentration of PLFAs (Fig. 3c). The terminally branched PLFAs of cluster B, however, behaved differently and were the only PLFAs whose concentrations consistently increased with depth at most dry sites, while they slowly decreased or remained almost constant at wet sites (Fig. 3d). The two 10Me PLFAs and i17:1ω7 of cluster D showed a special pattern at the dry sites, often with a concentration peak at intermediate depths (Fig. 3e and f).

Although the concentrations of the long (C_{20} to C_{26}) saturated PLFAs (cluster F) were strongly correlated, these fatty acids failed to show consistent depth distribution patterns within wet or dry communities or within specific sites at Stor-Åmyran. The depth distributions of the two ω8 monounsaturated fatty acids of cluster C, which are considered biomarkers for methane-oxidizing bacteria, were similar to those of cluster D, each having its maximum concentration at an intermediate depth in the minerotrophic and string sites at Stor-Åmyran (40).

Relative amounts of PCA clusters. Clusters A, B, D, and E reflect the relative biomass contributions of gram-negative bacteria, gram-positive and/or anaerobic gram-negative bacteria, sulfate-reducing bacteria and/or actinomycetes, and eucaryotic microorganisms, respectively (Table 3). Even though there were general differences in PLFA composition between wet and dry sites, the relative amounts of the four clusters differed somewhat among the various wet sites. Generally, the terminally branched and the methyl-branched and branched unsaturated PLFAs occurred in the largest relative amounts at the mud-bottom (Fig. 4a) and in the smallest amounts in the hollow (Fig. 4c), whereas the opposite was true for the monounsaturated and polyunsaturated PLFAs. Among the dry sites, there was little variation both within and between the string and minerotrophic sites at Stor-Åmyran. Therefore, the averages for the different clusters for all six profiles from these two sites are shown as an example in Fig. 4d.

The relative amount of the methyl-branched and branched unsaturated PLFAs was comparatively low (ca. 1%) in surface samples from the hollow and from the string and minerotrophic sites. In most other samples these PLFAs accounted for 5 to 10% of the total, and their relative contributions did not vary much with depth. In contrast to the other clusters, the relative amount of the polyunsaturated PLFAs was highest at the surface at all sites, in some cases reaching ca. 35% (Fig. 4).

The ratio of the amount of terminally branched PLFAs to that of monounsaturated PLFAs (the two clusters of common eubacterial PLFAs) increased with depth in all profiles. Thus, at the surface the terminally branched PLFAs made up a much smaller fraction of all PLFAs than did the monounsaturated PLFAs, whereas in some of the deepest samples they were the largest cluster (Fig. 4a).

DISCUSSION

The total PLFA concentrations in these peatlands differed considerably among both sites and depths. Concentrations were, however, of the same order of magnitude as those reported for other types of marine and freshwater lake sediments (16, 28, 38). Borgå et al. reported lower PLFA concentrations in peatlands similar to those that we sampled (5). Since total PLFA concentrations at our sites generally decreased with depth (Fig. 3a), this difference can probably be explained by the fact that Borgå et al. sampled at a greater depth.

No differences in PLFA composition were detected among the June, July, and September samples collected at Stor-Åmyran. This implies that the microbial community structure changes relatively little over the growing season in this type of peatland. Therefore, changes over the growing season in the in situ microbial activity in a discrete peat section are perhaps primarily determined not by changes in biomass but rather by changes in the prevailing environmental conditions (e.g., supply of oxygen and other electron acceptors, temperature, and organic and inorganic nutrients).

PLFA specificity. The clustering of PLFAs as revealed by the PCA demonstrates strong covariation in PLFA abundance. This is strong evidence that the PLFAs of a cluster originate in the same functional group of organisms or in perhaps the same family or genus. Still, the assignment of these clusters to specific microbial groups is not always straightforward. While the cluster of the two ω8 monounsaturated PLFAs could unequivocally be attributed to methane-oxidizing bacteria (31, 40), the other four clusters of microbial PLFAs (A, B, D, and E) could represent alternative microbial groups (Table 3).

One example of this is provided by the methyl-branched PLFAs 10Me16:0 and 10Me18:0, which may occur in both sulfate-reducing bacteria and actinomycetes (6, 34). In our samples, concentrations of these PLFAs were positively correlated ($r = 0.89$, excluding one outlier). In addition, they had rather distinct depth distributions, often with low surface concentrations and a maximum concentration at 10 to 20 cm in the dry communities (Fig. 3f). Known sulfate reducers containing 10Me16:0 do not contain considerable amounts of 10Me18:0 (11, 48). Conversely, many actinomycetes contain relatively large amounts of 10Me18:0, and some of these contain 10Me16:0 as well but in lower amounts (25). Therefore, the fact that concentrations of 10Me16:0 were higher than those of 10Me18:0 in this study (three to four times higher) suggests that the methyl-branched PLFAs came from sulfate-reducing bacteria

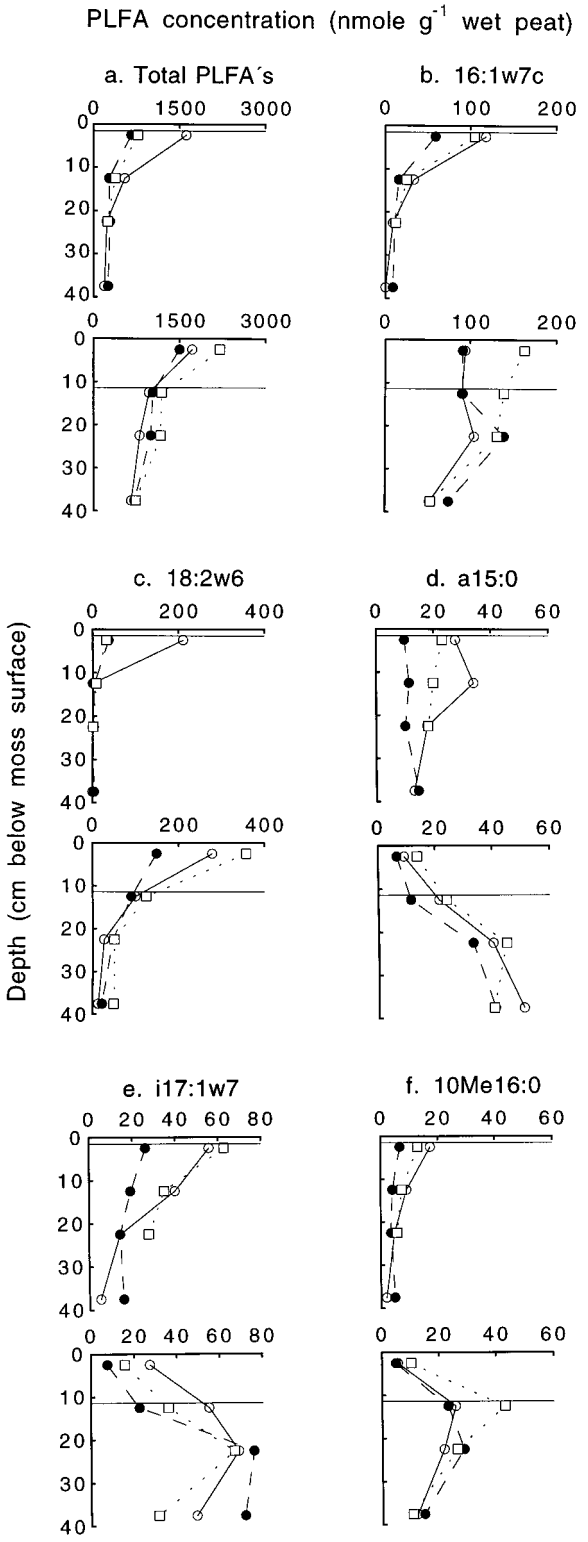

FIG. 3. Depth distributions of the total PLFAs (a) and of PLFAs representative of the different clusters (b to f) for a wet (mud-bottom [upper graphs]) and a dry (minerotrophic [lower graphs]) site at Stor-Åmyran. The horizontal lines show the average levels of the water table. Samples were collected in June (solid circles), July (open circles), and September (open squares).

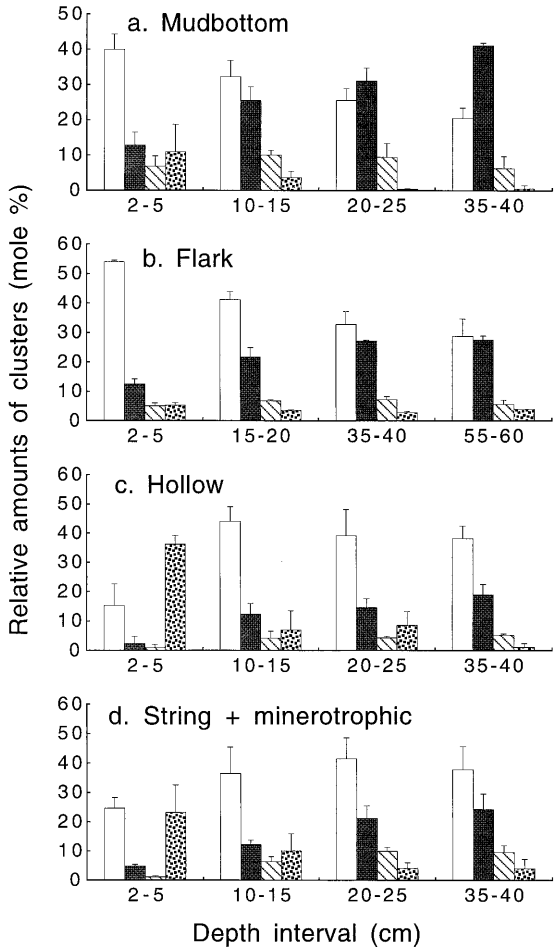

FIG. 4. Average relative amounts of PLFA clusters at different depths in four mire communities from Stor-Åmyran (n = 11) (a), Björnmyran (n = 8) (b), Stor-Åmyran (n = 12) (c), and Stor-Åmyran (n = 22) (d). □, cluster A (monounsaturated); ■, cluster B (terminally branched); ▨, cluster D (methyl branched and branched unsaturated); ▩, cluster E (polyunsaturated). Bars show standard deviations.

rather than from actinomycetes. Although this observation is inconsistent with data showing that sulfate-reducing bacteria containing 10Me16:0 do not contain 10Me18:0 (11, 48), the covariation of the 10Me PLFAs with another marker for sulfate-reducing bacteria, the branched unsaturated PLFA i17:1ω7 (Fig. 2), also indicates that the former PLFAs came mainly from sulfate-reducing bacteria. PLFA i17:1ω7 has been suggested as a marker of sulfate-reducing bacteria of the genus *Desulfovibrio* (44, 48). In desulfovibrios, both this PLFA and i15:0 are among the dominating fatty acids. The concentrations of these PLFAs showed a strong positive correlation (Fig. 5), suggesting that both i17:1ω7 and i15:0 originate in desulfovibrios.

The PLFA 18:2ω6 is common in many species of fungi (27) and has been proposed for use as a biomarker for fungi in environmental samples. Frostegård and Bååth (17) found the concentrations of 18:2ω6 to be positively correlated with the concentrations of ergosterol (another fungal biomarker [46]) in a range of cultivated soils and forest soils, supporting the use of this PLFA as a biomarker for fungi. In another study, Nilsson and Rülcker (33) found that lengths of fluorescein diacetate-stained (metabolically active) fungal mycelium decreased with depth on several (but far from all) occasions in the string

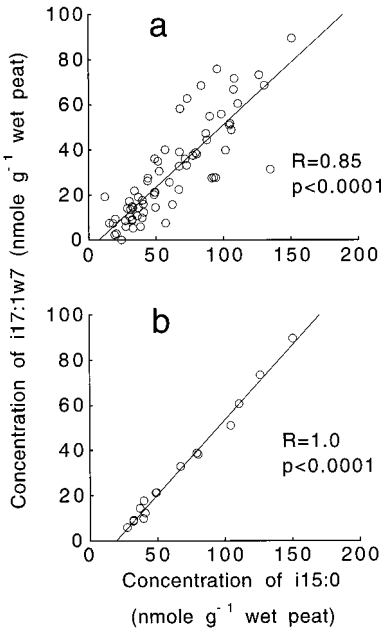

FIG. 5. Linear correlation between concentrations of the PLFAs i15:0 and i17:1ω7 in peat. (a) All samples (excluding two outliers, $n = 70$); (b) Björnmyran samples ($n = 16$).

and hollow environments at Stor-Åmyran that were analyzed for PLFAs. This decrease, however, was much less dramatic than the decrease in the 18:2ω6 concentration, particularly in the hollow. The main reason for the deviating patterns is probably that the large amounts of 18:2ω6 in our surface samples could have come from the top shoots of the *Sphagnum* mosses (10) or from cyanobacteria (27). This example illustrates that a certain PLFA may be a suitable microbial biomarker in one type of ecosystem but a less suitable one in others.

Distribution of aerobic and anaerobic eubacteria. The two groups of common eubacterial PLFAs (monounsaturated and terminally branched) overlap somewhat between gram-negative and gram-positive bacteria (27). Still, among the gram-negative bacteria, terminally branched PLFAs are more commonly found in anaerobes than in aerobes (52). In addition, field studies suggest that terminally branched PLFAs are markers of anaerobic bacteria in marine sediments (15, 35). Thus, in the peatland samples used in this study, the abundances of the monounsaturated PLFAs and of the terminally branched ones (Fig. 3b and d) most likely indicate the presence of aerobic and anaerobic eubacteria, respectively, rather than gram-negative and gram-positive bacteria. But this pattern is clearly not universal. For example, the terminally branched PLFAs are common in aerated mineral soils (2, 55), where high biomasses of anaerobic microorganisms are very unlikely to occur.

An important point when discussing the distributions of aerobic and anaerobic microorganisms is the level of the water table. Although it can be used to roughly delineate aerobic and anaerobic sections in the peat (4, 50), aerobic zones can occur below the water table as a result of oxygen transport by vascular plants to deep-lying roots (1). In addition, the presence of anaerobic microsites above the water table is highly probable. Consequently, both anaerobic and aerobic bacteria are likely to occur above as well as below the water table.

A distinct pattern at Stor-Åmyran was that the general difference in PLFA composition between wet and dry sites predominantly occurred at a depth of ca. 10 to 30 cm (Fig. 1). The lack of systematic variation within the surface samples could reflect the dominance of aerobic conditions at all sites. It may also be a result of the large relative amounts of the two polyunsaturated PLFAs, which may partly originate in the top shoots of the *Sphagnum* mosses. Small systematic differences between wet and dry sites at the greatest sampling depth, however, probably reflect the dominance of anaerobic conditions in all communities. In wet mire habitats, the intermediate depth interval is anaerobic on most occasions, whereas in dry environments it is subjected to fluctuations between predominantly anaerobic and aerobic conditions owing to oscillations in the level of the water table. Our PLFA data suggest that these conditions select for a special kind of microbial community. In this kind of environment, it will be a great advantage for microorganisms in the peat to be facultative or to be simply able to survive fluctuations between anaerobic and aerobic conditions. Indeed, obligately anaerobic organisms, such as sulfate reducers in sediments and some members of methanogenic communities in peat, survive exposure to oxygen (9, 19). Additionally, it has been shown that aerobic methane-oxidizing bacteria, which are common in this depth interval (40), can survive anaerobic conditions for extended periods (36).

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