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YEASTS IN PEATLANDS: A REVIEW OF RICHNESS AND ROLES IN PEAT DECOMPOSITION

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Abstract: The richness and ecological roles of yeasts in peatlands are largely unknown. This paper presents a review of the literature on yeasts in peatlands and also provides new data with species isolated from peatlands in Saskatchewan, Canada, and West Siberia, Russia. To date, 75 yeast taxa have been reported from peatlands, including 46 identified species and 29 isolates identified only to genus or not at all. This represents 5%–10% of known yeasts and about 10% of all peatland fungi. *Cryptococcus*, *Candida*, *Pichia*, and *Rhodotorula* are the most prevalent genera, accounting for 58% of known peatland yeast species. We obtained 34 isolates from western Canadian and West Siberian bog and fen peat, including 12 identified species and eight unidentified taxa. Identified taxa comprised mostly species of *Candida*, *Cryptococcus*, and *Rhodotorula*. Unidentified taxa were described based on physiology and morphology. Globally, more species have been reported from bogs than fens (41 vs. 13 taxa), and the species composition differs between the two peatland classes. The effect of depth within the acrotelm on yeast abundance and species composition varies among peatlands. Physiological profiling of the yeasts from our study showed that they can use (poly)saccharides (primarily D-glucose, maltotriose, n-acetyl glucosamine, trehalose, and sucrose), organic acids (primarily D-gluconic acid, fumaric acid, malic acid, and succinic acid), sugar alcohols (primarily D-arabitol, D-mannitol, and D-sorbitol), glycosides (primarily arbutin and salicin), and amino acids (primarily L-glutamic acid) as carbon and nitrogen sources. Based on these profiles, yeasts likely access simple polymers that leach from senesced and/or dead plant materials in peatlands and probably play important roles during the initial stages of organic matter decomposition.

Key Words: BioLog, bog, carbon, fen, functions, nitrogen, organic matter, Saskatchewan, West Siberia

INTRODUCTION

Bogs and fens are the dominant wetland classes globally (Gore 1983, National Wetlands Working Group 1988). They are particularly important to the global carbon (C) cycle (Gorham 1991, Roulet 2000), because they accumulate peat, a heterogeneous assemblage of partially decomposed plant materials (about 45%–50% C; Clymo 1983), on annual through millennial time scales. Peat chemistry varies with depth in a peatland and among different peatlands as a result of botanical composition and degree of decomposition (Clymo 1983, Turetsky et al. 2000, Andersen et al. 2006). Peat is decomposed predominantly by fungi in the oxygenated peat horizon (acrotelm) and by bacteria in the anoxic peat horizon (catotelm). The degradation of organic matter is often viewed as a process of facilitation, whereby species of a particular fungal community alter the substrate sufficiently to allow

other fungal species to become established and continue the degradation process (Lumley et al. 2001). Such a succession has been shown in various upland (Heilman-Clausen 2001, Lumley et al. 2001) and wetland plant species (Tokumasu 1994, Thormann et al. 2003, 2004). Competition and antagonism within fungal communities are also factors at each stage of decay. Consequently, different fungal communities are responsible for the degradation of the varying components of peat, largely as a result of the differing abilities of fungi to synthesize the enzymes required to degrade organic matter (Thormann et al. 2002).

An array of fungi has been isolated from peatlands over the past century, most of which are saprobic and mycelial in nature (reviews in Thormann 2006a, b, Thormann and Rice 2007). Despite the abundance of yeast cells in peat (Baker 1970, Polyakova et al. 2001), peatland yeasts have received little attention, with fewer than ten studies focusing on yeasts from peatlands and few studies of peatland fungi even attempting to identify them (Thornton 1956, Christensen and Whittingham 1965, Dickinson and Dooley 1967, Latter et al. 1967, Christensen and Cooke 1970, Nilsson et al. 1992, Robson et al. 2004). In this paper, we present a review of the literature on yeasts in peatlands and supplement the literature data with a new study of species isolated from peatlands in Saskatchewan, Canada, and the West Siberia Lowland, Russia.

Yeasts are a ubiquitous polyphyletic group of 700–1,500 recognized species of fungi with varying ascomycetous and basidiomycetous affinities (see Kurtzman and Fell 1998, Suh et al. 2005, Kurtzman and Fell 2006, Kurtzman and Piskur 2006). They are generally unicellular; however, some may form a simple, irregular mycelium. Yeasts have been isolated from nearly all plant surfaces and soils in virtually all geographic locations (e.g., Bab'eva and Chernov 1995, Kurtzman and Fell 2006, Kurtzman and Piskur 2006). Many yeasts are involved in the degradation of organic matter; however, their specific roles during decomposition processes *in situ* remain poorly understood. The paucity of detailed yeast information from peatlands is likely attributable to the challenges involved in traditional yeast identification, i.e., extensive physiological profiling via growth on a series of substrata to elucidate their ability to use them, along with often limited distinguishing morphological characters among species. Modern molecular techniques (e.g., Kurtzman 2006, Kurtzman and Fell 2006) likely represent the future of yeast identification from peatlands and will undoubtedly uncover many additional taxa; however, these techniques are not without limitations (Anderson and Cairney 2004, Hambleton and Sigler 2005), particularly in that the generated sequences often remain unidentified, and the taxonomic precision of the identifications is limited by the taxonomic accuracy and phylogenetic breadth of the reference databases. More importantly, these methods preclude further experimental investigation, particularly the description of novel taxa and the elucidation of functional roles, because associated living cultures and voucher specimens are absent (Hambleton and Sigler 2005). In order to explore also their functional roles, we have chosen to use culture-based techniques to identify peatland yeasts. This approach provides phenotypic information on yeast taxa and allows for an elucidation of their functions in ecosystems, since a living specimen exists. Moreover, cladistic analyses, following the application of molecular techniques on cultured specimens, can be employed to determine evolutionary relationships among described yeast taxa. Our goals in this paper are to 1) investigate the species richness of peatland yeasts and explore whether this diversity is greater than previously suggested and 2) elucidate the roles that peatland yeasts may play in organic matter decomposition.

METHODS

Yeast Species Richness – Literature Review

In order to compile information about peatland yeasts, we reviewed reports from mycological and ecological journals, most prominently Mycologia, Mycotaxon, Mycologial Research, Canadian Journal of Botany, Fungi Canadensis, and New Phytologist, as well as Sylloge Fungorum (Saccardo 1882–1931, 1972) and the Index of Fungi (1920–present). Several Russian journals were also reviewed, e.g., Microbiology (Moscow), Ekologiya, and Izvestiya Akademii Nauk SSSR, Seriya Biologicheskie. A yeast record was defined as an individual unidentified taxon or one that was identified to genus and/or species in a peer-reviewed publication. Therefore, unpublished, mimeographed, and locally distributed reports, herbarium information, anecdotal references, and check lists were not included as record sources.

Study Sites

We isolated peatland yeasts from study sites located in peatland-rich regions of North America and Asia. The study sites were located in east-central Saskatchewan, Canada (two sites, one bog and one fen), and in the West Siberian Lowland, Russia (12 sites, eight bogs and four fens; Figure 1).

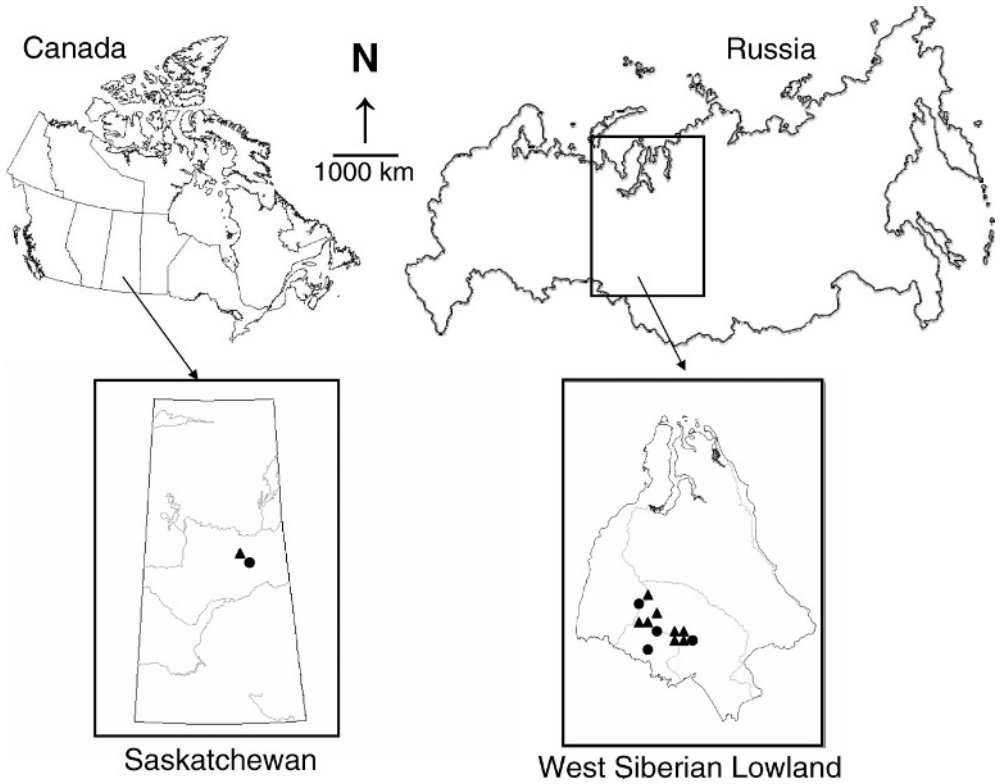

Figure 1. Location of the study sites in Saskatchewan, Canada, and in West Siberia, Russia. Triangles indicate bogs and circles indicate fens.

The Saskatchewan bog was dominated by *Picea mariana* (Mill.) BSP, ericaceous shrubs (primarily *Rhododendron groenlandicum* (Oeder) Kron & Judd and *Vaccinium vitis-idaea* L.), and the bryophytes *Hylocomium splendens* (Hedw.) BSG, *Pleurozium schreberi* (Brid.) Mitt., and *Sphagnum* spp. (primarily *Sphagnum fuscum* Klinggr.). The Saskatchewan fen was dominated by *Larix laricina* (Du Roi) K. Koch, *Betula pumila* L., *Salix* spp., *Andromeda polifolia* L., and the bryophytes *Aulacomnium palustre* (Hedw.) Schwaegr., *Campylium stellatum* (Hedw.) Lange & Jens., and *Tomenthypnum nitens* (Hedw.) Loeske. The climate of the Saskatchewan sites is characterized by cold, snowy winters and mild summers. The average annual precipitation is 467 mm, while the mean temperatures of the three coldest and three warmest months are −16.2°C (December–January–February) and 14.9°C (June–July–August), respectively (mean annual temperature of 0.4°C; data from the Waskesiu Lake weather station; Environment Canada 2004).

In the West Siberia Lowland, the eight bogs were dominated by *Pinus sylvestris* L., *Ledum palustre* L., *Chamaedaphne calyculata* L., and *Sphagnum* spp. (primarily *S. fuscum* and *S. angustifolium* (Russ.) C. Jens. in Tolf). The four fens were dominated by *Betula pubescens* Ehrh., *Carex* spp., *Menyanthes trifoliata* L., and a number of bryophytes, mainly *Calliergon* spp. and *S. angustifolium*. The climate of West Siberia is highly continental and characterized by cold, snowy winters and mild summers similar to those experienced at the Saskatchewan peatlands. The average annual precipitation is 433–541 mm, while the mean temperatures of the three coldest and three warmest months range from −16.7 to −19.6°C (December–January–February) and from 15.3–16.7 °C (June–July–August), respectively (the mean annual temperature ranges from −2.1 to 0.3°C; data from the Kanty-Mansisk, Aleksandrovskoe, Tobolsk, Kolpashev, and Tara weather stations in the West Siberia Lowland; Frey and Smith 2003).

Peat Processing and Yeast Isolation

Peat samples were collected aseptically at each sampling plot at 5 and 25 cm depths in the Saskatchewan sites and at 0–10 and 10–20 cm depths in the Siberian sites, transferred to sterile containers, and transported in a cooler to the laboratory. All samples originated from the acrotelm in each site. A sub-sample of about 5 g (fresh-weight, randomly selected from each entire peat sample) was surface-sterilized for five min in H_2O_2 and washed three times with sterilized, distilled

water (sd-H_2O) to eliminate surface contaminants before being placed onto primary isolation media. Five segments (each about 2 mm^3, randomly selected from the sterilized 5 g-sub-samples) were transferred aseptically to each of nine plates of potato dextrose agar (PDA, 39.0 g Difco (Detroit, MI) potato dextrose agar, 1.0 L sd-H_2O) with or without amendments to isolate basidiomycetes selectively (Worrall 1991). Three plates were amended with Benlate (50% benomyl; B) and three plates were amended with a sterile stock solution containing Benlate, dichloran (2,6-dichloro-4-nitroaniline), and phenol in ethanol (5 mL L^{-1}; BDP). The remaining three plates received no additives. Therefore, there were three plates for each of the three isolation media (n = 3 per isolation medium, n = 9 per processed peat sample), and each plate contained five peat segments randomly selected from the sterilized sub-samples (n = 45 peat segments per peat sample). Oxytetracycline was added to the primary isolation medium to suppress bacterial growth. Plates were incubated in the dark at 22°C and examined daily for the first week, every other day for the following four weeks, and every five days for the following three months. Yeasts emerging from the peat segments were subcultured and maintained on malt extract agar (MEA, 15.0 g Difco malt extract, 20.0 g Difco agar, 1.0 L sd-H_2O). Representative cultures and slides were deposited at the Northern Forestry Centre Culture Collection.

Yeast Identification

Yeast isolates were identified using the BioLog Yeast MicroPlates. Yeasts were grown on yeast medium (YM, 20.0 g Difco agar, 3.0 g Difco Yeast Extract, 1.0 L sd-H_2O) in Petri plates for three weeks in the dark at 22°C. Yeast cells were transferred aseptically using sterile cotton swabs from the Petri plates into sd-H_2O in sterile glass screw-top test tubes (inoculum density 47 ± 2%, determined photometrically). The resulting suspension was transferred into a sterile pipette reservoir, and 100 μL were pipetted aseptically into each of the 96 wells of the BioLog Yeast MicroPlates. Each plate consisted of 27 unique substrata, 28 substrata that were tested for both oxidation (using tetrazolium violet as a calorimetric indicator of oxidation) and assimilation (scored turbidimetrically), 11 wells with two substrata to test for the co-utilization of various substrata with D-xylose, and two controls (empty wells). Plates were stored in plastic bags (to avoid desiccation) in the dark at 22°C. Absorbance at 590 nm was measured daily for seven days using a BioLog MicroStation 2. Identities were confirmed with published morphological and physiological information for each species. Yeast taxonomy followed Index Fungorum (CABI Science Databases 2007).

RESULTS AND DISCUSSION

Global Richness of Yeasts in Peatlands

We suspected that yeasts comprise a significant proportion of the peatland fungal community, which was supported by examination of the literature and by the results of our isolations. Fifty-eight yeast taxa had been reported previously from peatlands, of which 37 were identified to species, nine to genus, and 12 not at all. In our study of peatlands in Saskatchewan and West Siberia, we obtained 12 identified species and eight unidentified yeasts, bringing the total number of yeast taxa reported from peatlands to 75, including 46 species, nine genus-level reports, and 20 unidentified taxa (Table 1). This total (75 taxa) is the result of fewer than 20 studies, but still represents 5%–10% of known yeast species and about 10% of the fungal species isolated from peatlands (710 taxa in total, of which 601 are identified to species; Thormann and Rice 2007). Additional research combining molecular and culture-based techniques would undoubtedly increase this total. Among the identified species, ascomycetous and basidiomycetous yeasts are represented in similar proportions (23 and 22 species, respectively). Most yeast records originate from Asia (52 records, or 69%), with the remaining ones originating from northern Europe and the Americas (24 records, or 31%). This disparity is likely a reflection of the scarcity in peatland yeast research, with most studies having been conducted in Asia (Table 1).

Taxonomically, species of *Cryptococcus* predominate, with 10 identified species. Species of *Candida* (eight species), *Pichia* (five species), and *Rhodotorula* (four species) are also common (Table 1). *Cryptococcus* is a large basidiomycete genus with 261 species and varieties (CABI Science Databases 2007). Within the genus, fermentation (the degradation of complex polymers into simpler ones) of sugars is negative, assimilation (uptake) of nitrate is variable, and assimilation of inositol is positive. *Cryptococcus* species have been isolated from various organic substrates, soil, water, insects, and humans (Barnett et al. 1983). *Candida* is a large ascomycetous genus with 531 species and varieties (CABI Science Databases 2007). Within the genus *Candida*, fermentation, nitrate assimilation, and inositol assimilation may be present or absent. *Candida* is ubiquitous, with species occurring

virtually everywhere, including air, soil, water, organic matter, humans and other mammals, insects, foods, fungi, and industrial effluent (Barnett et al. 1983). The teleomorphic ascomycete genus *Pichia* (it reproduces sexually) has 200 species and varieties (CABI Science Databases 2007). *Pichia* species are generally fermentation and nitrate assimilation negative. *Pichia* species have been isolated from organic matter, soil, water, foods, humans and other mammals, and insects (Barnett et al. 1983). All *Pichia* records from peatlands originate from Russia. The basidiomycete genus *Rhodotorula* has 130 species and varieties (CABI Science Databases 2007). *Rhodotorula* species do not ferment carbohydrates and produce urease enzyme. *Rhodotorula* species have been isolated from air, soil, water, organic matter, humans and other mammals, invertebrates, and foods (Barnett et al. 1983). Many species in the aforementioned genera are generalists, but several novel species have been described from peatlands (e.g., Golubev et al. 1981b), and some of the unidentified taxa likely represent novel species (Polyakova et al. 2001). It is probable that some of these species may have adapted as specialists in peatlands. One of the most interesting yeast species reported in multiple studies from bogs and fens in Canada and Russia is *Schizoblastosporion starkeyi-henricii*. This species is rare and of uncertain taxonomic affinity, and most, if not all, of the published reports of this species are from peatlands (Polyakova et al. 2001), suggesting that it is likely a peatland specialist.

Yeasts in Peatlands in Saskatchewan and West Siberia

We obtained 34 yeast isolates from peat samples from North America (Saskatchewan) and Asia (West Siberia). These included 14 ascomycetous yeasts (6 spp.), 11 basidiomycetous yeasts (5 spp.), and *Schizoblastosporion starkeyi-henricii* (Table 2). Most isolates belonged to the genera *Candida*, *Cryptococcus*, and *Rhodotorula* (20 isolates, 59% of all isolates), which coincides well with previous records of these genera (Table 1). *Cryptococcus albidus* var. *aerius* was the most frequently isolated yeast (five isolates, 16% of all isolates). Eight isolates could not be identified using the BioLog technique (Table 2), six from Saskatchewan and two from the West Siberia Lowland. Based on colony morphology and physiology, the eight unidentified isolates likely represent eight different species. Most of these were slow growing, produced terminal buds, and simple and elaborate pseudohyphae. Only two isolates, both from the Saskatchewan site, produced no pseudohyphae (yeast spp. 1 and 4). All of the unidentified isolates were ascomycetes (negative diazonium blue B test; Table 3). We did not attempt to name these eight isolates because of the likelihood of false identification. Future use of alternative methods, such as DNA sequencing, may result either in their identification or confirmation of their novelty.

Yeast Distribution by Peatland Class and by Depth

Yeast species richness and composition varies with peatland type and depth within the acrotelm. Of the 75 yeast taxa reported from peatlands (including our study), 41 were reported only from bogs, 13 only from fens, 12 from both bogs and fens, and the remaining nine from unspecified peatland classes (Table 1). These differences may reflect either more favorable conditions for yeasts in bogs than in fens or sampling bias. Evidence for the former is provided by the depth of the acrotelm in bogs vs. fens. Owing to the position of the water table, the acrotelm in bogs is generally substantially thicker than in fens, where water levels are much closer to the moss/peat surface, and the acrotelm is generally much thinner (e.g., Thormann and Bayley 1997). Since most yeasts are obligate aerobes, bogs would likely provide a more favourable environment for these organisms. Evidence for the latter is provided by comparing literature reports and our study. Among the previous literature reports of yeasts from peatlands, 37 taxa were reported exclusively from bogs, but only a single yeast species was reported exclusively from fens. Contrastingly, we observed the opposite trend in our study, with 15 yeast species recovered from fen peat, four from bog peat, and one species from both, even though we examined more bogs than fens (nine bogs vs. five fens). Hence, isolation protocols can significantly affect the species richness of yeasts from substrata or ecosystems. Conclusions regarding the distribution of yeast species among peatland classes are further complicated by differences in peatland classification and terminology. For example, Polyakova et al. (2001) included both oligotrophic and minerotrophic peatlands as bogs, while this study refers to them as bogs and fens, respectively. Ascomycetes were recovered more frequently than basidiomycetes from bogs and fens; however, basidiomycetes were more common when peatland type was unspecified, and species recovered from both bog and fen habitats tended to be basidiomycetes. Additional study of yeasts from both bogs and fens along with consistent classification of peatland types is required to determine whether these trends reflect real differences in the distribution of ascomycetous and basid-

Table 1. Yeast species from peatlands identified from the literature and from the present study.

Yeast taxa	Peatland Type	Country	Reference
Ascomycota			
Candida catenulata Diddens & Lodder	Bog	Canada	1
Candida edax Van der Walt & E.E. Nel	Fen	Russia	1
Candida haemulonis (Uden & Kolip.) S.A. Mey. & Yarrow	Fen	Canada, Russia	1
Candida sake (Saito & M. Ota) Uden & H.R. Buckley *ex* S.A. Mey. & Ahearn	Bog	Russia	2
Candida valida (Leberle) Uden & H.R. Buckley *ex* S.A. Mey. & Ahearn	Bog	Russia	3
Candida vartiovaarae (Capr.) Uden & H.R. Buckley	Bog	Russia	3
Candida zeylanoides (Castell.) Langeron & Guerra	Fen	Canada	1
Candida spp.	Bog, fen	Ireland, Russia	2, 4, 5
Debaryomyces hansenii (Zopf) Lodder & Kreger	Bog, fen	Russia	2, 3, 5
Debaryomyces vanrijiae (Van der Walt & Tscheuschner) Abadie, Pignal & J.L. Jacob	Bog	Russia	3
Hanseniaspora uvarum (Niehaus) Shehata, Mrak & Phaff	Bog	Russia	2
Hansenula saturnus var. *saturnus* (Klöcker) anon. ined.	Bog	Russia	3
Metschnikowia pulcherrima Pitt & M.W. Mill.	Bog	Russia	2
Nadsonia elongata Konok.	Bog	Russia	3
Nakaseomyces delphensis (van der Walt & Tscheuschner) Kurtzman	Fen	Canada	1
Pichia capsulata (Wick.) Kurtzman	Bog	Russia	2
Pichia inositovora Golubev, Blagod., Suetin & R.S. Trots.	Bog	Russia	3, 6
Pichia jadinii (Sartory, A. Weill, R. Weill & J. Mey.) Kurtzman	Bog	Russia	2, 3
Pichia toletana (Socias, Ramirez & Peláez) Kreger	Bog	Russia	3
Pichia spp.	Bog	Russia	2
Saccharomyces kloeckerianus Van der Walt	Bog	Russia	3
Saccharomyces paradoxus Bach.-Raich.	Bog	Russia	2
Saccharomyces terrestris (V. Jensen) G.I. Naumov	Bog	Russia	3
Torula spp.	Bog, fen	Russia, UK	7, 8
Torulaspora sp.	Bog	Russia	2
Torulopsis sp.	Bog	Russia	3
Trichosporiella paludigena (Golubev & Blagod.) de Hoog, Rant.-Leht. & M.T. Sm.	Bog	Russia	2, 3, 6
Yarrowia lipolytica (Wick., Kurtzman & E.A. Herrm.) Van der Walt & Arx	Fen	Canada	1
Basidiomycota			
Bullera punicea (Komag. & Nakase) Nakase & M. Suzuki	Bog	Russia	2
Cryptococcus aerius (Saito) Nann.	Fen	Canada	1
Cryptococcus albidus (Saito) C.E. Skinner	Bog	Russia, USA	2, 3, 5, 9
Cryptococcus albidus var. *albidus* (Saito) C.E. Skinner	Bog, fen	Canada, Russia	1, 9
Cryptococcus gastricus Reiersöl & di Menna	Bog	Russia	3
Cryptococcus gilvescens Chernov & Babeva	Bog	Russia, USA	2
Cryptococcus hungaricus (Zsolt) Phaff & Fell	Bog	Russia	2
Cryptococcus laurentii (Kuff.) C.E. Skinner	Bog, fen	Russia	2, 3
Cryptococcus magnus (Lodder & Kreger) Baptist & Kurtzman	Unspecified	Russia	9
Cryptococcus podzolicus (Babeva & Reshetova) Golubev	Bog	Russia	3
Cryptococcus terreus di Menna	Bog	Russia	3
Cryptococcus terricolus T.A. Pedersen	Bog, fen	Russia	5
Cryptococcus sp.	Unspecified	Russia	2
Leucosporidium antarcticum Fell, Statzell, I.L. Hunter & Phaff	Bog	Russia	3
Mrakia frigida (Fell, Statzell, I.L. Hunter & Phaff) Y. Yamada & Komag.	Bog	Russia	2
Rhodotorula acheniorum (Buhagiar & J.A. Barnett) Rodr. Mir.	Fen	Canada, Russia	1
Rhodotorula aurantiaca (Saito) Lodder	Bog, fen	Canada, Russia	1, 2
Rhodotorula glutinis (Fresen.) F.C. Harrison	Bog	Russia	3
Rhodotorula mucilaginosa (A. Jörg.) F.C. Harrison	Bog	Russia, USA	2
Rhodotorula sp.	Unspecified	Russia	5
Rhodotorula sp. 1	Bog	Russia	2
Rhodotorula sp. 2	Bog	Russia	2

Table 1. Continued.

Yeast taxa	Peatland Type	Country	Reference
Sporidiobolus salmonicolor Fell & Tallman	Unspecified	Russia	9
Sporobolomyces roseus Kluyver & C.B. Niel	Bog	Russia	2
Trichosporon inkin (Oho) Carmo Souza & Uden	Fen	Russia	1
Trichosporon pullulans (Lindner) Diddens & Lodder	Unspecified	Russia	2, 9
Insertae Sedis			
Schizoblastosporion starkeyi-henricii Cif.	Bog, fen	Canada, Russia	1, 2
Unidentified taxa			
Yeast (brown)	Unspecified	Argentina	10
Yeast (white)	Unspecified	Argentina	10
Yeast (yellow)	Unspecified	Argentina	10
Yeast sp. 1	Bog	USA	11
Yeast sp. 1	Fen	Canada	1
Yeast sp. 2	Bog	USA	11
Yeast sp. 2	Fen	Canada	1
Yeast sp. 3	Fen	Canada	1
Yeast sp. 4	Fen	Canada	1
Yeast sp. 5	Bog	Canada	1
Yeast sp. 6	Bog	Canada	1
Yeast sp. 7	Bog	Russia	1
Yeast sp. 8	Fen	Russia	1
Yeast spp.	Bog	Canada	12
Yeast spp.	Bog	U.K.	13
Yeast spp.	Unspecified	U.K.	8
Yeast type A	Bog, fen	Sweden	14
Yeast type B	Bog, fen	Sweden	14
Yeast type C	Bog, fen	Sweden	14
Yeast type D	Bog, fen	Sweden	14

References: 1 = Thormann et al. (this study), 2 = Polyakova et al. (2001), 3 = Golubev et al. (1981b), 4 = Dickinson and Dooley (1967), 5 = Zvyagintsev et al. (1991), 6 = Golubev et al. (1981a), 7 = Golovchenko et al. (2002), 8 = Thornton (1956), 9 = Golubev (1986), 10 = Robson et al. (2004), 11 = Christensen and Whittingham (1965), 12 = Christensen and Cooke (1970), 13 = Latter et al. (1967), 14 = Nilsson et al. (1992).

iomycetous yeasts or are just a result of sampling limitations or bias. Future research is also necessary to determine whether individual taxa are adapted to specific peatland types; however, the relatively small number of species recovered from both bogs and fens suggests that most species are specialists.

Previous researchers have found some contradictory trends in yeast abundance: either the greatest abundance at the surface and decreasing abundance with increasing depth (Baker 1970), or greatest abundance in the middle and deeper horizons (Golubev et al. 1981a, Polyakova et al. 2001). Our results suggest that these seemingly contradictory observations could be explained by variation among peatlands. We found that yeast abundance, as indicated by number of isolates obtained, was substantially higher at 25 cm than at 5 cm depths in the Saskatchewan peatlands (15 vs. nine taxa), but was similar at both peat depths in the West Siberia peatlands (four vs. six taxa; Table 4). Differences in species composition with depth were also observed, with 14 of the 20 taxa recovered from either surface or deeper peat, but not both (Table 2). Only one species, *Candida zeylanoides*, was recovered from multiple depths in the same area of the same peatland (Table 2). Despite the observed differences in abundance and species composition with peat depth in the two peatlands, species richness was the same in both surface and deeper peat in both Siberia and Saskatchewan (13 taxa at each depth; Table 2). These results are consistent with the trends observed by Polyakova et al. (2001) in Russia, who found differences in abundance and species composition but not species richness with peat depth. Unfortunately, our present data are too limited for multivariate statistical analyses to investigate community differences by site, type, or depth; neither correspondence analysis nor non-metric multidimensional scaling yielded meaningful or stable results.

Roles of Yeasts in Peat Decomposition

Decomposition is a three-step process, which begins with leaching of soluble organic matter, is

Table 2. Yeasts isolated from peatlands in Saskatchewan, Canada, and West Siberia, Russia.

Yeast taxon	NOF No.	Peatland	Isolation information	
			Depth (cm)	Isolation Medium
Ascomycota				
Candida catenulata	2906	OBS, Saskatchewan	5	PDA + BDP
Candida edax	2907	Fen 4, Siberia, Russia	10–20	PDA + B
Candida haemulonis	2917	SF-N, Saskatchewan	25	PDA + BDP
		SF-N, Saskatchewan	25	PDA + BDP
	2918	Fen 4, Siberia, Russia	0–10	PDA + BDP
	2919	Fen 4, Siberia, Russia	0–10	PDA + BDP
	2920	Fen 4, Siberia, Russia	0–10	PDA + BDP
Candida zeylanoides	2914	SF-N, Saskatchewan	5	PDA + BDP
	2915	SF-N, Saskatchewan	25	PDA + RB
	2916	SF, Saskatchewan	25	PDA + B
Nakaseomyces delphensis	2908	SF-N, Saskatchewan	5	PDA + BDP
Yarrowia lipolytica	2910	SF-N, Saskatchewan	25	PDA + B
	2911	SF, Saskatchewan	5	PDA + BDP
Basidiomycota				
Cryptococcus aerius	2921	SF-N, Saskatchewan	25	PDA + BDP
	2922	SF-N, Saskatchewan	25	PDA + BDP
	2923	SF-N, Saskatchewan	25	PDA + B
	2924	SF-N, Saskatchewan	25	PDA + B
	2925	SF-N, Saskatchewan	25	PDA + RB
Cryptococcus albidus var. *albidus*	2928	OBS, Saskatchewan	5	PDA + BDP
	2929	Fen 3, Siberia, Russia	10–20	PDA + RB
Rhodotorula acheniorum	2912	SF-N, Saskatchewan	25	PDA + BDP
	2913	Fen 4, Siberia, Russia	0–10	PDA + B
Rhodotorula aurantiaca	2926	SF-N, Saskatchewan	5	PDA + BDP
	2927	Fen 3, Siberia, Russia	0–10	PDA + B
Trichosporon inkin	2933	Fen 3, Siberia, Russia	10–20	PDA + BDP
Insertae Sedis				
Schizoblastosporion starkeyi-henricii	2909	SF, Saskatchewan	25	PDA + RB
Unidentified taxa				
Yeast sp. 1	2931	SF, Saskatchewan	5	PDA + B
Yeast sp. 2	2937	SF, Saskatchewan	5	PDA + B
Yeast sp. 3	2932	SF, Saskatchewan	25	PDA + BDP
Yeast sp. 4	2935	SF, Saskatchewan	25	PDA + BDP
Yeast sp. 5	2936	OBS, Saskatchewan	5	PDA + B
Yeast sp. 6	2905	OBS, Saskatchewan	25	PDA + BDP
Yeast sp. 7	2938	Bog 2, Siberia, Russia	0–10	PDA + B
Yeast sp. 8	2934	Fen 4, Siberia, Russia	10–20	PDA + B

Note: OBS = Old Black Spruce, SF-N = Sedge Fen-North; PDA = potato dextrose agar, B = benomyl, RB= rose bengal, BDP = benomyl, dichloran, and phenol; NOF = Northern Forestry Centre Culture Collection.

followed by mass losses due to the assimilation of organic matter by microbial and animal communities, and is concluded with the loss of the physical structure and changes in the chemical constituents of the remaining organic matter (Brinson et al. 1981, Clymo 1983). Organic matter becomes structurally more complex as it decomposes, because simpler molecules are preferentially degraded during the early stages of decomposition. This progressive change in chemical constituents over the course of decomposition can result in a succession of fungi in decomposing organic matter, based on the ability of different fungi to synthesize various enzymes, and hence degrade organic substrata of different complexities. Deacon (1997) identified five behavioral groups of fungi involved in the degradation of organic matter. Weak pathogens and parasites (1) precede pioneer saprobes (2), which are followed by simple polymer degraders (3), and subsequently complex polymer degraders (4). Secondary saprobes (5) also occur during the latter

Table 3. Morphology and colony descriptions of 8 unknown yeast species from peatlands in Saskatchewan, Canada, and West Siberia, Russia.

Yeast isolate	Morphology and colony description
Yeast sp. 1	moist, cream colonies; slow growing; terminal budding; no filaments; DBB negative
Yeast sp. 2	moist, light-orange colonies; slow growing; terminal budding; simple and elaborate pseudohyphae; DBB negative
Yeast sp. 3	dry, cream colonies; slow growing; terminal budding; simple and elaborate pseudohyphae; DBB negative
Yeast sp. 4	dry, light-orange colonies; slow growing; terminal budding; no filaments; DBB negative
Yeast sp. 5	moist, cream colonies; fast growing; terminal budding; simple and elaborate pseudohyphae; DBB negative
Yeast sp. 6	dry, cream colonies; slow growing; lateral budding; simple and elaborate pseudohyphae; DBB negative
Yeast sp. 7	dry, cream colonies; slow growing; no budding observed; simple and elaborate pseudohyphae; DBB negative
Yeast sp. 8	dry, cream colonies; slow growing; terminal budding; simple pseudohyphae; DBB negative

Note: Growth rate was assessed at 22°C, DBB = diazonium blue B.

stages of decomposition, using metabolic by-products generated by polymer degrading fungi (Deacon 1997). Fungi from all five behavioral groups have been isolated from peatlands (e.g., Thormann et al. 2004); however, clear fungal succession patterns are not always observed (Thormann et al. 2003). In the only known study of yeast succession dynamics, Chernov (1985) documented a shift in fungal succession in decomposing plant matter in the Russian tundra. He observed yeast dominance during the early stages of decomposition (part of the pioneer saprobe community), but as readily soluble carbohydrates became limited, complex polymer-degrading filamentous fungi replaced the initial yeast community and continued the decomposition process. He also observed a second community of yeasts (part of the secondary saprobe community), which was unable to use complex polymers, but presumably used some of the metabolic by-products generated by filamentous fungi (Chernov 1985).

Although *in vitro* physiological profiles and assays do not document realized ecological niches of individual species or prove the functional diversity of an entire community, they indicate the potential functional diversity of the community (Dobranic and Zak 1999, Preston-Mafham et al. 2002, Fisk et al. 2003, Sobek and Zak 2003) and are a useful tool to elucidate the possible roles of individual species within a consortium (Hobbie et al. 2003, Rice and Currah 2005, Rice et al. 2006). All the yeasts isolated in our study have the ability to metabolize various simple and complex sugars, organic acids, sugar alcohols, glycosides, and amino acids. More specifically, saccharides like maltose, maltotriose, glucose, sucrose, trehalose, and galactose are used by many of the yeasts, as are various sugar alcohols, including arabitol, mannitol, sorbitol, glycerol, and maltitol (Tables 5, 6). Many of these carbohydrates are either storage products (e.g., mannitol) or metabolic compounds (e.g., glucose) and are most susceptible to leaching following senescence or death of a plant cell. In addition, the organic acids gluconic acid, fumaric acid, and malic acid were readily used by the 34 yeast isolates (Tables 5, 6). Several of these acids are intermediates in metabolic pathways in plant tissues and are also susceptible to leaching following cell death. As a group, these chemically simple carbohydrates occur in northern bog and fen surface peats in concentrations that can reach up to 100 mg g^{-1}, or about 10% of organic matter by mass (Williams et al. 1998, Turetsky et al. 2000). Consequently, the ability of yeasts to use these simple carbohydrates suggests their potential as active participants during the initial stages of peat decomposition, when these compounds are being rapidly metabolized. In contrast, complex polymers, such as cellulose and polyphenolic polymers, cannot be degraded by yeasts (Barnett et al. 1983, Chernov 1985), which generally precludes yeasts from the latter stages of decomposition except as secondary saprobes. Thus, we did not examine the ability of the yeasts in this study to degrade complex polymers.

Table 4. Distribution of the 34 yeast isolates in this study by peatland class and by depth from study sites in Saskatchewan, Canada, and West Siberia, Russia.

Peatland classes	Saskatchewan		West Siberia	
	5 cm	25 cm	0–10 cm	10–20 cm
Bogs	3	1	1	0
Fens	6	14	5	4

Table 5. Summary of physiological profiles of yeast species identified from peatlands in Saskatchewan, Canada, and West Siberia, Russia. Numbers in columns 3 and 4 indicate the number of identified yeasts able to use the specific carbon and nitrogen substrata.

	Substrata	Fermentation	Growth
Amino acids	L-Aspartic acid	3	No test
	L-Glutamic acid	11	18
	L-Proline	2	No test
Glycosides	Amygdalin	No test	1
	Arbutin	No test	7
	Salicin	1	8
Lipids	Tween 80	14	7
Organic acids	2-Keto-D-Gluconic acid	No test	1
	alpha-Ketoglutaric acid	No test	1
	Bromosuccinic acid	No test	1
	D-Gluconic acid	No test	19
	Formic acid	1	No test
	Fumaric acid	No test	18
	Malic acid	No test	18
	Methyl Succinate	1	0
	Succinic acid	19	No test
Saccharides	Adonitol	No test	3
	Arabinose	No test	3
	Cellobiose	1	9
	Dextrin	4	5
	D-Galactose	3	10
	D-Glucosamine	No test	5
	D-Glucose	7	14
	D-Melezitose	1	4
	D-Melibiose	1	6
	D-Psicose	16	1
	D-Raffinose	1	5
	D-Ribose	No test	6
	D-Xylose	No test	6
	Gentiobiose	1	9
	Inulin	2	0
	L-Rhamnose	No test	1
	L-Sorbose	1	1
	Maltose	2	13
	Maltotriose	4	14
	n-Acetyl-D-Glucosamine	18	19
	Palatinose	1	9
	Stachyose	1	2
	Sucrose	6	16
	Trehalose	5	17
	Turanose	1	10
Sugar alcohols	D-Arabitol	17	18
	D-Mannitol	19	21
	D-Sorbitol	19	17
	Glycerol	12	14
	i-Erythritol	No test	1
	Maltitol	No test	12
	Xylitol	1	5

It has been shown that most organic matter decomposes at a negative exponential rate in peatlands, indicating relatively high mass losses during the early stages of decomposition, shortly after plant senescence or death (up to 10% in bogs and 30% in fens during the first 50 days; Thormann et al. 2001). These initial mass losses have been ascribed previously to various species of *Acremonium*, *Botrytis*, *Cladosporium*, *Mortierella*, *Mucor*, *Penicillium*, and *Verticillium*, which tend to predominate during the early stages of decomposition of peatland vascular and non-vascular plants (Thormann et al. 2003). Interestingly, yeasts are rarely considered important saprobes in peatlands. Nonetheless, based on our data and the abundance of yeast cells in peat (Baker 1970, Polyakova et al. 2001), yeasts may play significant roles during the first 50 days of decomposition. Along with zygomycetes, which also have a proclivity for sugars and simple polymers, yeasts may account for a large proportion of the total mass losses of peatland plants immediately following plant senescence or death. Although this suggestion is speculative, peatland yeasts may be important competitors for metabolic compounds and storage products that leach out of senesced and dead plant matter due to their mode of reproduction and ability to disperse rapidly in wet soils. It is not possible to isolate selectively any group of microorganism to assess their roles in any ecological process, such as decomposition. Consequently, the role of yeasts, a polyphyletic group of fungi, by themselves in the decomposition process of peat remains speculative. Clearly, there is a need to further examine the roles of yeasts in peatland C and N dynamics.

Physiological tests using the BioLog Yeast MicroPlates showed varying profiles for the eight unidentified isolates (Table 6). Yeast sp. 1 was the most limited in its ability to use any of the C and N substrata, metabolizing only glutamic acid, inulin, and Tween 80. The other seven isolates used more of the C and N substrata; however, while they generally grew on them, few substrata were actually metabolized and broken down. Of these, Tween 80 was most commonly metabolized by the isolates. Similar to the identified yeasts, these eight taxa are also most likely involved during the early stages of organic matter decomposition.

Using the BioLog method to identify our yeast isolates and assess their functional diversity has its limitations, since positive identifications are dependent on existing profiles in the BioLog data base; however, we are confident that our identifications are correct. Following the BioLog protocol, we confirmed the identity of each yeast isolate with published morphological and functional descrip-

Table 6. Physiological profiles of 8 unknown yeast species from peatlands in Saskatchewan, Canada, and West Siberia, Russia. G= growth on substrate, M = metabolism of substrate.

	Yeast species							
Substrata	1	2	3	4	5	6	7	8
Amino acid								
L-Glutamic acid	M					G		
Glycosides								
Arbutin		G		G				
Salicin		G		G		G, M		G
Lipid								
Tween 80	M	G		G, M		M	G, M	G, M
Saccharides								
Adonitol			G					
Cellobiose		G		G	G			G
Dextrin		G	G					G
D-Galactose		G	G	G	M			
D-Glucosamine		G	G	G				G
D-Glucose		G	G	G	G	G		G
D-Melezitose			G		G			
D-Melibiose		G			G			M
D-Raffinose		G		G				
D-Ribose			G					
D-Xylose			G					
Gentiobiose		G	G	G				G
Inulin	M	G	G				G	G, M
L-Sorbose						G		M
Maltose		G, M	G	G				G
Maltotriose			G	G	G			G
N-Acetyl-D-Glucosamine		G		G				G
Trehalose					G			G
Sugar alcohols								
D-Arabitol			G					
D-Mannitol			G			G		
D-Sorbitol			G					
Glycerol								G
i-Erythritol			G					
Maltitol		G	G					
Organic acids								
D-Gluconic acid				G				G
Fumaric acid			G	G				
L-Malic acid			G	G				
Methyl Succinate			G					
Succinic acid				G			M	
Combinations								
N-Acetyl-L-Glutamic acid + D-Xylose			G			G		
Dextrin + D-Xylose		G	G			G		G
D-Glucuronic acid + D-Xylose				G		G		
Guinic acid + D-Xylose						G		
D-Melibiose + D-Xylose					G			
Methyl Succinate + D-Xylose			G					
1,2-Propanediol + D-Xylose						G		

tions. We encountered some functional differences from published data for all yeast species in our study, which can be attributed to natural strain variation, sample preparation, and culturing conditions.

CONCLUSIONS

Yeasts have been largely under-represented in surveys of fungi in peatlands. The 75 yeast taxa reported to date from peatlands include 46 identified

species and 29 taxa identified to only genus or not at all. This number represents between 5%–10% of known yeast species as well as about 10% of fungi known from peatlands, thus, supporting our hypothesis that yeast richness in peatlands is higher than previously suggested. The paucity of studies on peatland yeasts further indicates that it is premature to suggest that they are taxonomically limited, even though only a few genera (*Cryptococcus*, *Candida*, *Pichia*, and *Rhodotorula*) represent over half of all known species of yeasts from these ecosystems. As a group, yeasts are involved in the degradation of mostly simple polymers, including sugars, alcohols, and amino acids, and they appear to play minor or no roles in the degradation of complex polymers, such as cellulose, pectin, and lignin and its derivatives. Hence, saprobic yeasts are likely restricted to roles as pioneer or secondary saprobes on senesced and dead plant matter, including peat, lending support to our hypothesis that they are involved in the early stages of peat decomposition. The relative abundance of yeast cells in peat suggests that they are potentially important, but generally underappreciated, players during the early stages of peat decomposition. Given that much of the mass losses of peat occur during these initial stages, it is plausible that significant mass losses of peat observed during these early stages of decomposition can be attributed in part to yeasts.

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