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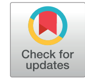
Forest soil yeasts: Decomposition potential and the utilization of carbon sources



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Fungi that inhabit forest topsoil can be distinguished into two morphological guilds: filamentous, multicellular fungi and predominantly unicellular yeasts. The nutritional mode of these two groups is expected to differ due to the dependence of yeasts on locally present nutrients. Here we explored the decomposition potential and carbon utilization profiles of dominant yeasts from the temperate forest topsoil. The results indicated that despite taxonomic heterogeneity, yeasts represent a fungal group with a specific nutritional strategy that is dissimilar from other tested fungi. While the efficient decomposition of hemicellulose, cellulose or chitin appeared to be restricted to only a few yeast taxa, carbon source utilization assays indicated that most yeasts could efficiently act as opportunists, utilizing the decomposition products generated by other microbes. Importantly, a large fraction of enzyme activity was associated with yeast cell surfaces indicating their adaptation to generate decomposition products so that they are readily available for intake.

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1. Introduction

The soil microbial community is a complex assemblage of prokaryotic and eukaryotic organisms, including archaea, bacteria, algae, protists and fungi. Each of these groups is more prominent in habitats that specifically favour their survival. For example, mineral soil layers are more suitable for unicellular organisms (bacteria, archaea and some yeasts) than for filamentous fungi, which primarily inhabit litter and coarse woody debris (Baldrian, 2017; Yurkov, 2017). A diversity of traits, both morphological and physiological, results in a more efficient distribution of microorganisms between microhabitats in the soil and adjacent substrates. Fungi living in soils can be divided into two functional groups, filamentous, multicellular fungi and predominantly unicellular yeasts. The hyphae of filamentous fungi allow them to bridge sites with unfavourable conditions or limited nutrients to access, translocate and utilize heterogeneously distributed resources. Filamentous growth enables fast, horizontal dispersal and is important for colonization of certain niches, e.g., decomposing bulky substrates (Boer et al., 2005). Functionally, yeasts can be considered to be especially adapted to thrive in liquid or semi-liquid media with high concentrations of easy-to-use nutrients (Lachance & Starmer, 1998). However, some yeast taxa are capable of forming a filamentous stage and are thus dimorphic during different stages of their life cycle. Whether or not the transition between filamentous and unicellular yeast growth has direct implications for the physiological adaptations and functions of soil fungi is unclear.

Substrate decomposition and carbon utilization by various groups of filamentous fungi that are considered to be primary decomposers of organic matter in temperate forest soil and litter have been frequently investigated (e.g., Martinez et al., 2005; Baldrian et al., 2011; Eichlerová et al., 2015). However, despite the evidence that yeasts represent an integral part of soil fungal communities (e.g., Yurkov et al., 2012; Yurkov et al., 2016b; Mašínová

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et al., 2017a), the role of unicellular fungi in the decomposition and mineralization of carbon in soils has received little attention. The majority of soil yeasts have been regarded as saprotrophs that contribute to C mineralization processes in the environment by utilizing various carbon compounds. In his review on soil yeasts, Botha (2006) noted that most are able to utilize the products of the enzymatic hydrolysis of lignocellulosic plant materials, such as L-arabinose, D-xylose, cellobiose and intermediates of lignin degradation, i.e., ferulic acid, 4-hydroxybenzoic acid and vanillic acid (e.g., Henderson, 1961; Sampaio, 1999; Slavikova and Vadkertiova, 2000; Mestre et al., 2011). On average, basidiomycetous yeasts have been reported to utilize a wider spectrum of carbon sources, including low-weight aromatic compounds, than ascomycetous yeasts, which have a copiotrophic lifestyle (Fonseca, 1992; Sampaio, 1999; Botha, 2006; Middelhoven, 2006).

Although yeasts have repeatedly been isolated from decaying plant material, these studies were limited to the description of novel species (e.g., Péter et al., 2003; Middelhoven, 2006; Kurtzman et al., 2011). Our knowledge of the functional relationships of yeasts with respect to wood decomposition is limited to a few studies that demonstrated either utilization of plant-derived compounds (e.g., Sampaio, 1999; Middelhoven, 2006) or community alteration in response to coarse woody debris (e.g., Yurkov et al., 2012). Basidiomycetous yeasts have been reported to be among the most numerous fungal operational taxonomic units (OTU, as a proxy for species) in culture-independent surveys (e.g., Bueé et al., 2009; Voříšková and Baldrian, 2013; Mašínová et al., 2017a). Yeasts assigned to the polyphyletic genera *Cryptococcus* and *Trichosporon* were demonstrated to obtain carbon from cellulose (Štursová et al., 2012), and the relative abundance of *Trichosporon* was also observed to increase during the decomposition of oak litter following the depletion of sugars (Voříšková and Baldrian, 2013). Notwithstanding the above evidence, the role of yeasts in the decomposition of recalcitrant biopolymers is often neglected in the literature. Yeasts are often considered to be organisms utilizing simple sugars resident to soils or associated only with nutrient-rich habitats.

The aim of this study was to characterize the decomposition potential and the spectrum of carbon source utilization (metabolic fingerprints) by yeasts isolated from the topsoil of a temperate forest. Strains representing the 25 most prominent yeast species were selected based on their abundance in the analysis of environmental DNA (Mašínová et al., 2017a). We review common views on the role of yeasts in soil and challenge them using our experimental data to demonstrate that: (1) soil yeasts are able to utilize wide spectra of carbon sources, including mono- and oligosaccharides and some low-weight aromatic compounds, while their ability to decompose organic biopolymers, such as lignin, cellulose and hemicellulose, is frequently regarded as low; and (2) soil yeasts produce only a limited spectrum of extracellular enzymes, and the activity of these enzymes is lower than those in filamentous fungi. Additionally, we hypothesize that the adaptation to unicellular growth also affects the enzymatic capabilities of yeast. Because yeasts, being nonmotile and unable to move in space by filamentous growth or to overgrow nutrient patches as dense mycelial mats, they cannot translocate nutrients and can only assimilate those that are in their close proximity. To secure the products of substrate decomposition for their own cells, one of the relevant strategies would be to produce decomposition-related enzymes that are bound to their cell surface which guarantees the supply of decomposition products close to the cell surface. In this respect, yeasts are similar to bacteria that are also unicellular (de Boer et al., 2005). We thus hypothesize that a substantial portion of enzymatic activity may be associated with yeast cell walls to secure products of enzymatic decomposition for the enzyme-producing cell. This strategy is different from those of filamentous decomposers, such as wood decay fungi, which secrete most of the hydrolytic enzymes into the environment.

2. Materials and methods

2.1. Study site, sample collection and soil analysis

Samples were collected in the area of the Training Forest Enterprise Masaryk Forest Křtiny (Křtiny Forest). Křtiny Forest, located north of Brno, Czech Republic (16°15' E, 49°15 N), has a total area of 103 km^2 and is covered by a mixed temperate forest, with beech, oak and spruce as the most common tree species. Sampling for fungal DNA community analyses was performed at 80 sites during 2013 in a preceding study (Mašínová et al., 2017a). Soil and litter samples were collected in monoculture stands of *Fagus sylvatica*, *Quercus petraea* agg., and *Picea abies* as well as in mixed tree stands. At 18 of these sites (dominated by monocultures of *F. sylvatica*, *Q. petraea* agg., or *P. abies* [6 each]), samples were collected four times during a year. Litter samples were cut into approximately 0.25 cm^2 pieces, and soil was sieved through a 5-mm sieve and homogenized. Soil was freeze-dried and stored at −80 °C until DNA extraction. Physicochemical properties of the soils and litter were measured and published previously (Mašínová et al., 2017a).

The collection of soil and litter used to isolate yeast strains was performed at the 18 monoculture sites multiple times between October 2013 and April 2014. Fresh samples were transferred to the laboratory and maintained at 4 °C. Litter and soil samples were processed as described above. The isolation of yeasts was carried out within 48 h of sample collection.

2.2. Extraction and analysis of environmental DNA

Details of the DNA isolation from soil and litter samples, ITS2 amplification, sequencing and data analyses were described by Mašínová et al. (2017a). Briefly, total DNA was extracted in triplicate from 250 mg of soil using a modified Miller method (Ságová-Marečková et al., 2008) and a previously described protocol (Žifčáková et al., 2016). The PCR amplification of the fungal ITS2 region from DNA was performed using gITS7 and ITS4 barcoded primers (Ihrmark et al., 2012), with three PCR reactions per sample. The sequencing of the fungal amplicons was performed on an Illumina MiSeq. The sequencing data were processed using the SEED 1.2.1 pipeline (Větrovský and Baldrian, 2013). Pair-end reads were merged using fastq-join (Aronesty, 2013), and the ITS2 region was extracted using the ITS Extractor 1.0.8 (Nilsson et al., 2010) before processing. Chimeric sequences were detected using UCHIME within USEARCH 7.0.1090 (Edgar, 2013) and excluded from the subsequent analyses. For further analyses, datasets containing 10,000 randomly chosen sequences from each sample were used. For the 18 repeatedly sampled sites, a fungal community dataset for each site was created by averaging the four seasonal samplings to cover the seasonal variability of the community composition. OTUs were constructed at a 97% similarity level and yeast OTUs were further identified to the species level with a phylogenetic analysis (Mašínová et al., 2017a) using the UNITE version 7.1. dataset (Kõljalg et al., 2013).

2.3. Isolation of yeast strains

One gram of soil or litter was suspended in 5 mL of sterile, demineralized water, serially diluted and plated on yeast glucose agar (YG; Cooney and Emerson, 1964) supplemented with chloramphenicol (0.2 g L^{-1}). Plates were inoculated in triplicate and incubated at 4 °C for 14 d to prevent the rapid development of

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