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REVIEW

Physiological adaptations of yeasts living in cold environments and their potential applications

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Abstract Yeasts, widely distributed across the Earth, have successfully colonized cold environments despite their adverse conditions for life. Lower eukaryotes play important ecological roles, contributing to nutrient recycling and organic matter mineralization. Yeasts have developed physiological adaptations to optimize their metabolism in low-temperature environments, which affect the rates of biochemical reactions and membrane fluidity. Decreased saturation of fatty acids helps maintain membrane fluidity at low temperatures and the production of compounds that inhibit ice crystallization, such as antifreeze proteins, helps microorganisms survive at temperatures around the freezing point of water. Furthermore, the production of hydrolytic extracellular enzymes active at low temperatures allows consumption of available carbon sources. Beyond their ecological importance, interest in psychrophilic yeasts has increased because of their biotechnological potential and industrial uses. Long-chain polyunsaturated fatty acids have beneficial effects on human health, and antifreeze proteins are attractive for food industries to maintain texture in food preserved at low temperatures. Furthermore, extracellular cold-active enzymes display unusual substrate specificities with higher catalytic efficiency at low temperatures than their mesophilic counterparts, making them attractive for industrial processes requiring high enzymatic activity at low temperatures. In this minireview, we describe the physiological adaptations of several psychrophilic yeasts and their possible biotechnological applications.

Keywords Psychrophilic/psychrotolerant yeasts · Polyunsaturated fatty acids · Cold-adapted extracellular enzymes · Antifreeze proteins

Introduction

Microorganisms inhabiting extreme environments meet a variety of stressful and changing environmental conditions that challenge their optimal development. To successfully proliferate under these extreme conditions, microorganisms have evolved several immediate responses and long-term adaptation mechanisms. A large proportion of our planet (>80 %) experiences temperatures below 5 °C, including areas such as deep oceans, glaciers, and polar regions, and microorganisms that colonize these environments play important ecological roles (Russell 1990; Margesin et al. 2007).

At present, these microorganisms are referred to as psychrophilic or psychrotolerant (also cold-tolerant or psychrotrophic), differing in that psychrophiles grow faster at 15 °C or below and are unable to grow above 20 °C (Margesin et al. 2007). To overcome the challenges of low temperatures that affect the rates of biochemical reactions and the viscosity of their aqueous environment, these microorganisms have adapted their cellular processes to cold; furthermore, they synthesize cryoprotectant compounds such as trehalose and antifreeze proteins (D'Amico et al. 2006; Margesin et al. 2007; Rossi et al. 2009).

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Despite the suggestion that yeasts may be better adapted to low temperatures than bacteria (Shivaji and Prasad 2009), many studies have focused on bacteria; however, the number of reports describing the isolation of yeasts from cold environments is increasing (Guffogg et al. 2004; Gilichinsky et al. 2005; Russell 2006; de Garcia et al. 2007; Turchetti et al. 2008; Branda et al. 2010; Pathan et al. 2010; Thomas-Hall et al. 2010; Turchetti et al. 2011; Carrasco et al. 2012; de Garcia et al. 2012; Zhang et al. 2012; Singh et al. 2013). Considering that yeasts provide the benefits of single-cell fermentations and there are a large number of genetic tools to study and manipulate them, psychrophilic and psychrotolerant yeasts have attracted the attention of scientists for their potential application in various industries. In this minireview, we discuss three major "cold-loving" microorganism adaptations, focusing on yeasts, and their possible applications.

Membrane fluidity

Membranes compartmentalize biochemical reactions within the cell, forming a system that needs to keep its dynamism in changing environments for proper function. The well-established fluid mosaic model of the cell membrane (Singer and Nicolson 1972) describes the membrane as a liquid-crystalline lipid bilayer with embedded proteins. This structure is one of the primary cell protection barriers that separates the contents of the cytoplasm from the extracellular environment. Keeping the fluidity of the membrane is essential for its proper function, and organisms restructure their membrane lipid composition in response to environmental changes to keep lipids in a lamellar crystalline phase (Gunde-Cimerman et al. 2014). By modulating lipid composition it is possible to counteract the decrease in membrane fluidity and to adapt to low temperatures. Among the most common changes across different microbial phylogenetic groups to modulate fluidity are to decrease the saturation of fatty acids (FA) and to decrease the average length of FA chains (Russell 2008). In addition to FAs, sterols are essential structural and regulatory lipids in eukaryotic cell membranes that affect their fluidity, with ergosterol being the principal sterol in yeasts. Sterols intercalate across the FA chains, generally stabilizing and strengthening the membrane lipid bilayer (Russell 2008) and having a condensing effect if lipids are in a liquid crystalline state or a liquefying effect if they are in a gel state (Gunde-Cimerman et al. 2014). Even though the sterol composition does not typically change with temperature, a decrease in the relative proportion of sterols/phospholipids is an important feature that increases membrane fluidity in eukaryotic microorganisms at lower temperatures (Russell 2008).

The degree of saturation in FAs is one of the most studied cold adaptation responses (Gunde-Cimerman et al. 2014). The proportion of unsaturated FAs in several psychrophilic yeasts can reach up to 50–90 % of the total FA composition (Shivaji and Prasad 2009). Unsaturated FAs include monounsaturated (MU) and polyunsaturated (PU) FAs, the latter containing more than one double bond at the aliphatic chain. Rossi et al. (2009) studied the FA composition of yeast strains representative of 12 species, which were classified as obligate psychrophiles and facultative psychrophiles (strains from cold habitats), and mesophiles (strains from temperate habitats), according to their origin and ability to grow at 4, 18 and 30 °C. In all the yeasts, only linear FAs were found at all the temperatures analyzed and about 97 % of these FAs had a chain length of 14–18 carbon atoms. Interestingly, the proportion of C18:1 and C18:2 FAs was significantly higher in both groups of psychrophiles than in the group of strains from temperate habitats when cultured at 4 °C, and the highest proportion of C18:3 was found in the obligate psychrophiles. Both psychrophilic groups displayed a higher proportion of PUFAs than the temperate group, which had a significantly higher content of MUFAs. Finally, the PUFA content in the facultative psychrophiles group decreased and the MUFA content increased as the growth temperature increased from 4–18 or 30 °C, a trend that was not observed among the strains from temperate habitats. In a similar study, the FA composition was analyzed in Antarctic and non-Antarctic yeasts, finding that in general, C18:2 and C18:3 were less represented in the non-Antarctic yeasts and absent in *Saccharomyces cerevisiae* (Bhuiyan et al. 2014). In agreement with these results, examples of high levels of PUFAs in psychrophilic yeasts (McMurrough and Rose 1973), yeasts isolated from Antarctic ecosystems (Thomas-Hall and Watson 2002; Thomas-Hall et al. 2002; Contreras et al. 2015) and Patagonian cold-adapted yeasts (Libkind et al. 2008) have been reported.

The production of C18 FAs could be required for introducing additional double bonds by Δ12 and Δ15 desaturases (Rossi et al. 2009). Among PUFAs, the n-6 (omega 6) and n-3 (omega 3) FA families are biologically relevant and essentials to mammals. Linoleic acid ($18{:}2\Delta^{9,12}$) and alpha-linolenic acid ($18{:}2\Delta^{9,12,15}$) are the precursors of the omega-6 and omega-3 families, respectively (Warude et al. 2006); therefore, these FAs and some of their elongation products, are essential nutrients for mammals (De Caterina 2011).

The demand for PUFAs is increasing (Warude et al. 2006), with fish oils being one of the most important sources; however, there are several concerns about fish oils. These include heavy metal pollution of marine ecosystems causing accumulation in fish (a hazard to human health), the undesirable fishy smell and taste that remain after

PUFA extraction from fish oils, and the complex mixture of FAs in fish oils that may have antagonistic effects (Abd El Razak et al. 2014). Microbial oils are attractive alternative sources of PUFAs (Ratledge 2004), and according to experimental evidence, psychrophilic microorganisms (including yeasts) may be promising sources of these metabolites.

Antifreeze proteins

Antifreeze proteins (AFPs) or ice-binding proteins (IBPs) were first discovered in Antarctic fishes (DeVries and Wohlschlag 1969), and later in bacteria, fungi, and plants (Duman and Mark 1993), microalga (Jung et al. 2014) and arthropods (Hawes et al. 2011). This kind of proteins have important functions in organisms that must tolerate freezing temperatures, as they lower the freezing point of a solution without affecting its melting point (thermal hysteresis, TH) and inhibits ice crystallization (Davies et al. 2002; Bang et al. 2013). In microorganisms that inhabit environments covered with ice, the secretion of IBPs probably helps in retention of a liquid environment surrounding the cells and maintains water channels necessary for nutrients fluxes, while still allowing the attachment of the microorganism to ice (i.e., to form biofilms) (Davies 2014). The mechanisms by which AFPs exert their effects may be variable because of the diversity of protein structures described as having this property (Sharp 2011; Davies 2014; Todde et al. 2015).

Reports describing AFPs from yeasts are far less common than reports involving other organisms. In one study looking at a freezeing-tolerant *Rhodotorula svalbardensis* sp. nov. isolated from Arctic cryoconite holes at Ny-Alesund, the presence of AFPs was suggested by the formation of hexagonal ice crystal structures in broth culture (Singh et al. 2014). High TH and inhibition of ice recrystallization properties were detected in culture filtrates of the psychrophilic yeast *Glaciozyma antarctica* and, according to genomic data, a cDNA encoding a probable 177-residue AFP was found. This cDNA was expressed in *Escherichia coli*, obtaining a recombinant protein with antifreeze properties (Hashim et al. 2013). The Arctic yeast *Leucosporidium* sp. secretes an IBP of about 26.8 kDa, whose deduced amino acid sequence has high identity with AFPs from fungi, diatoms and bacteria (Lee et al. 2010).

Considering their protective effect that prevents large ice formation and leakage of ions from the membranes, the obvious application of antifreeze proteins is as protecting agents in processes that involve the storage of different kinds of cells at low temperatures. The use of 0.4 and 0.8 mg/ml of the recombinant LeIBP (expressed in *Pichia* expression systems from *Leucosporidium* sp. AY30) together with 40 % glycerol, showed a cryoprotective effect on red blood cells (Lee et al. 2012) and successfully cryopreserved the marine diatom *Phaeodactylum tricornutum* (Koh et al. 2015). In food storage at low temperatures, AFPs contribute to preserve the food texture, reduce cellular damage, and minimize the loss of nutrients (Venketesh and Dayananda 2008).

Finally, the expression of an AFP from *Ixodes scapularis* in transgenic flies and mice, increased the *Staphylococcus aureus* infection resistance, raising a new potential application field for antifreeze proteins (Heisig et al. 2014).

Extracellular hydrolytic enzymes

As in all environments, yeast inhabiting cold regions must be able to assimilate different available carbon sources, contributing to nutrient recycling and organic matter mineralization. Psychrophiles and psychrotolerant organisms have developed the ability to degrade a wide range of polymeric substances by producing extracellular hydrolytic enzymes. These "cold-adapted" or "cold-active" enzymes have higher catalytic efficiencies than their mesophilic counterparts at temperatures below 20 °C and display unusual substrate specificities (Gerday et al. 2000), making them attractive for industrial processes requiring high enzymatic activity at low temperatures. In addition, because of their heat lability, the use of cold-adapted enzymes facilitates their specific inactivation by moderate heat treatment when required (Margesin and Feller 2010). Examples of the most used cold-adapted enzymes include—among others—amylases, cellulases, invertases, proteases and lipases, which are used in food, biofuel, and detergent industries (Buzzini et al. 2012; Burhan et al. 2014).

Proteases are applicable in the laundry, chemical, food and medical industries (Anwar and Saleemuddin 1998). However, studies characterizing cold-active extracellular proteases from psychropilic yeasts are rather scarce compared with those from bacteria or filamentous fungi. An alkaline protease was purified and characterized from the marine yeast *Aureobasidium pullulans*, which showed an optimal activity at pH 9.0 and 45 °C (Ma et al. 2007). A protease from the psychrophilic yeast *G. antarctica* was expressed in *Pichia pastoris*, and the recombinant enzyme was successfully secreted into the culture medium reaching a production of 28.3 U/ml and showing a maximum activity at 20 °C (Alias et al. 2014). The number of reports of protease activity, with no major enzyme purification or characterization, from yeasts inhabiting cold environments has increased. Protease activity was described in six unidentified yeasts isolated from alpine glacier cryoconite samples (Margesin et al. 2003); in psychrotolerant *Cr.*

gilvescens, *Leuconeurospora* sp., *Mrakia gelida* and *Wickemanomyces anomalus* isolated from subantarctic regions (Carrasco et al. 2012); in *Leucosporidiella* sp. and *L. creatinivora* isolated from Antarctic marine sponges (Vaca et al. 2013); in yeast belonging to *Leucosporidiella*, *Udeniomyces, Mrakia* and *Mrakiella* isolated from glacial ice of the Argentinian Patagonian Andes (de Garcia et al. 2012); and in *A. pullulans*, *Cryptococcus adeliensis*, *C. magnus*, *C. victoriae*, *Rhodotorula mucilaginosa* and *Rhodosporidium diobovatum* isolated from an oligotrophic lake in Argentinian Patagonia (Brandao et al. 2011). Specifically, casein degradation was described in yeasts identified as *Rhodotorula glacialis*, *Mrakia psychrophila* and *Cryptococcus gastricus*, which were isolated from sediments from small puddles in the vicinity of the Arctic Midre Lovénbreen glacier (Pathan et al. 2010).

Cold-active lipases may be used as additives in detergents for cold washing, baking, cheese manufacturing, and meat tenderizing; in environmental bioremediations and biotransformation; and in molecular biology (Joseph et al. 2008). The potential to remove milk fat BOD5 in activated sludge was described for the yeast *Mrakia blollopis*, isolated from an algal mat of sediments from the Naga-like lake in Skarvsnes in East Antarctica, and the degradation of milk fat in wastewater was performed by a lipase (Tsuji et al. 2013b). A novel cold-active lipase from *Candida albicans* with optimal activity at 15–25 °C and pH 5–6, was expressed in *P. pastoris* and displayed activity toward triacylglycerols such as olive oil and sunflower oil that increased in the presence of Zn^{2+} (Lan et al. 2011). A lipase enzyme from *Cryptococcus* sp. MLB-24 isolated from ice cores of the Arctic Midre Lovénbreen glacier at Svalbard, displayed the highest activity at 40 °C and pH 7.0 (Singh et al. 2013). Lipase activity has also been described in *Cr. gilvescens*, *Cr. victoriae*, *D. fristingensis*, *Leuconeurospora* sp., *Rh. larynges* and *W. anomalus* (Carrasco et al. 2012). Several yeasts and fungi isolates including *Cryptococcus victoriae*, *Trichosporon pullulans* and *Geomyces pannorum*, showed multiple enzymatic activities including lipase, cellulase and gelatinase, with higher activities at 4 and/or 20 °C (Loperena et al. 2012).

Cold-adapted chitinases have many potential applications, like processing chitin-rich wastes at low temperatures, or the biocontrol of phytopathogens in cold environments or microbial spoilage of refrigerated food. Chitinase activity was described in Antarctic yeast isolates *D. fristingensis, Leuconeurospora* sp., *Metschnikowia* sp., and *Sporidiobolus salmonicolor* (Carrasco et al. 2012). A cold-adapted chitinase from *G. antarctica* that exhibited optimum activity at 15 °C and pH 4.0 was expressed in *P. pastoris*, and its activity increased in presence of K^{+}, Mn^{2+} and Co^{2+} (Ramli et al. 2011).

Cellulose, the largest source of renewable energy on the planet, is hydrolyzed by cellulases (Kasana and Gulati 2011). These enzymes are useful in food production, environmental remediation, fuel production and the laundry industry (Kasana and Gulati 2011). Currently, most of the cellulases used in industry are produced by fungi and have an optimal temperature at 50 °C (Kádár et al. 2004). Cellulase activity has been described in yeasts *Cr. laurentii* and *Cr. nemorosus* (Gomes et al. 2015), *Tetracladium* (Abdullah 1989), in *Mrakia* species isolated from Arctic puddles (Pathan et al. 2010), in *Cr. victoriae*, *D. fristingensis, Leuconeurospora* sp., *M. blollopis* and *M. psychrophila*, isolated from sub-Antarctic region (Carrasco et al. 2012).

Amylases are comprised of three groups of enzymes: α-amylase, β-amylase and γ-amylase, which-despite structural and catalytic differences-all hydrolyze α-glucosidic bonds in starch (Vihinen and Mantsala 1989; Janeček and Ševčík 1999; Janeček et al. 2014). α- and β-amylases are important for alcoholic beverage production and as supplements to detergent during the generation of ethanol using raw material containing starch; γ-amylases are used in the food, pharmaceutical, and chemical industries (Gurung et al. 2013). Although there are limited data regarding amylase activity in yeasts, this activity has been described in *Cryptococcus* sp. (Iefuji et al. 1994), *M. blollopis* (Tsuji et al. 2013a), *R. svalbardensis* sp. nov (Singh et al. 2014), *Tetracladium setigerum* (Abdullah 1989) and species of *Cryptoccoccus*, *Leuconeurospora*, *Dioszegia*, and *Rhodotorula* (Carrasco et al. 2012). An amylase originally described in *Cr. flavus* (Wanderley et al. 2004), was successfully expressed in *S. cerevisiae*, obtaining a recombinant α-amylase with higher activity towards soluble starch (Galdino et al. 2011).

One of the most important enzymes in the food industry is phytase, as it is used as a supplement in feed to complement the digestive enzymes of animals and favor the liberation of inorganic phosphate from phytate (a major form of phosphorus in plant-based feeds). Furthermore, phytase is used to improve the nutritional value of cereal foods (Kumar et al. 2010). Cold-adapted phytases are appropriate to be used in aquaculture, because of their high catalytic activity at the animals' physiological temperature ranges. Although a phytase purified from a *R. mucilaginosa* strain isolated from Antarctic deep-sea sediment has optimal activity at 50 °C, it maintain 85 % of its activity at 37 °C and exhibited a higher activity than its mesophilic counterparts at 20–30 °C (Yu et al. 2015).

Concluding remarks

Despite the description of psychrophilic or psychrotolerant yeasts has been done for over one century, research in the field of cold-adapted yeasts is relatively young. As shown

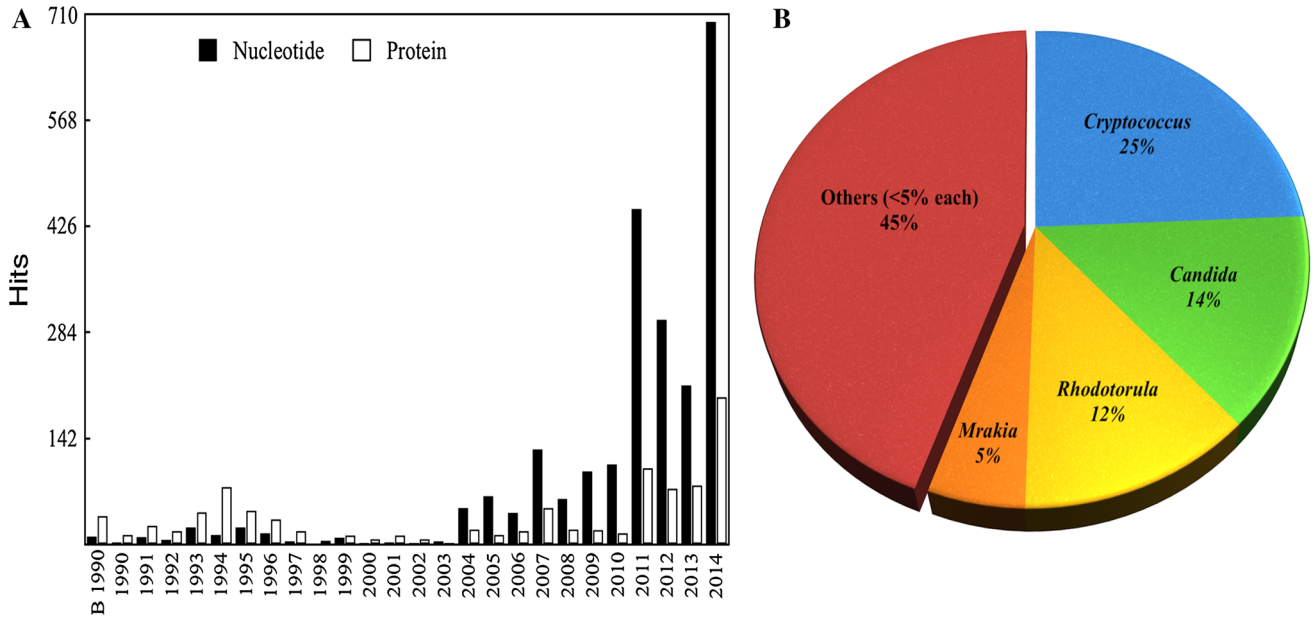

Fig. 1 Literature data revision related to cold-adapted yeasts. **A** Number of nucleotide and protein hits per year at NCBI related to cold-adapted yeasts using as search criteria: cold-adapted yeasts and then manually confirmed. **B** Percentage of yeast species isolated from cold environments, grouped by genus, described in literature. "Others" include 53 yeast genera where each one was less than a 5 % of the total number of yeast species (n = 240) gathered in our revision

in Fig. 1A, nucleotide and protein data related to cold-adapted yeasts had a pronounced rise in the last decade and in our literature revision it was observed that more than a half of the isolates belong to only four genera, from which *Cryptococcus* the most represented (Fig. 1B). Even though a great fraction of our planet is under cold conditions, little is known about cold-adapted yeasts that proliferate in these environments and the increasing scientific interest in the this kind of microorganisms is mainly due for their high biotechnological potential. Without doubts, information regarding cold-adapted yeasts will have a continuous increment especially with the development of new microbiological and molecular methodologies.

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