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Yeasts

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General Consideration and Taxonomy

The association of yeasts with human society was probably initiated many thousands of years ago. Evidence for the production of fermented beverages by yeasts, mostly *Saccharomyces cerevisiae*, dates back as far as 7000 BC, which is documented by several archaeological sites in China, Iran, and Egypt. Ancient humans unwittingly utilized yeasts to produce either alcohol-containing beverages or carbon dioxide for leavening. These practices and their associated yeasts spread throughout the world, inducing a particular selection, that is, 'domestication,' in particular for some foods such as bread, beer, and wine. However, the deliberate addition and commercial use of yeasts started only at the end of the nineteenth century after isolation and identification by Pasteur. Today, many species of yeasts contribute to the production of a myriad of commodities other than bread, beer, and beverages. Food-grade yeasts are now used as sources of high-nutritional-value proteins, enzymes, and vitamins, and processing aids are derived from them. With respect to foods and health foods, yeasts are utilized as nutritional supplement, food additives, conditioners, and flavoring agents and as starter cultures for producing specific foods or for their probiotic activity. Antifungal activity is exhibited by some yeasts that can be considered as biocontrol agents of food spoilage. Unfortunately, there are some drawbacks to yeast activity too, because some can cause spoilage of many commodities and may lead to pathogenic infections in immunocompromised persons or lead to allergic reactions. Table 1 reports the main roles of yeasts in food production and in the health of consumers.

The name yeast derives from the German word 'gift,' which describes the foam formed during beer fermentation. Yeast can be also described using the French word 'levure,' which indicates the role of yeasts inducing bread dough to rise. Yeasts are eukaryotic microorganisms whose vegetative growth results predominantly from budding or fission and that do not form their sexual states within or upon a fruiting body. Yeasts have two valid names: the first referring to the sexual state (teleomorph) and the second one to the asexual state (anamorph). The rules of yeast taxonomy are established in the 'International Code of Nomenclature for algae, fungi, and plants,' which was adopted at the 18 as apex International Botanical Congress in Melbourne, Australia. The 5 as apex edition of 'The Yeasts: A Taxonomic Study' in 2011 describes 1500 yeast species; but this number is increasing. The difference between the number of described species and that of new species is due to the fact that some ecological niches are far from being completely investigated and to the presence of cryptic species, which still have not been carefully characterized. Yeast taxonomy is based on biochemistry and molecular biology and is rapidly evolving. Criteria for differentiating genera have focussed on spore and cell morphology, type of conidiogenesis, life cycles, biochemical features, type of coenzyme Q, and G+C content. However, DNA hybridization or reassociation contributes to the establishment of relationships among yeast species. Two species are considered conspecific if they share more than 70% of DNA sequence homology, but this method does not allow assessing phylogenetic relationships between yeasts. Recently, the application of rapid, easy, and reliable molecular techniques allowed describing new phylogenetic relationships. As a result, the number of separate species groups was reduced and the diversity within them was increased. The most diffused molecular methods used in the identification of yeast species are based on the variability of the ribosomal genes 5.8S, 18S, and 26S because they show a low intraspecific polymorphism and a high interspecific variability. The first marker used for separation of the hemiascomycetes from the filamentous ascomycetes was the 18S rRNA gene. Subsequently, the D1/D2 variable region of the 26S rRNA (600 bp) has been adopted to differentiate basidiomycetes, hemiascomycetes, and filamentous euascomycetes. The availability of whole-genome sequences of yeasts revolutionized the taxonomy leading to the description of new markers for yeast phylogeny. Traditionally, the main genera can be divided into two groups: ascomycetes and basidiomycetes. However, budding and fission ascomycetes can now also be differentiated from each other and from euascomycetes by molecular methods, with the only exception of genus *Eramascus* (which does not form budding cells). A similar approach is applied to separate basidiomycetes from mushrooms and from taxa forming fruiting bodies.

The Yeast Cell and Its Organelles

Yeast cells possess ultrastructural features typical of other eukaryotic cells, with the presence of membrane-bound organelles (Figure 1). Often, the words 'yeast' and '*S. cerevisiae*' are used as synonyms. Saccharomyces means 'sugar fungus' in Greek. Yeast cells exhibit a great diversity with respect to cell

Table 1 Main activities of yeasts in food production and in the human health

Activity	*Yeast species*	*Effect*
Food and beverage fermentation	*Candida milleri*, *Debaryomyces hansenii*, *Galactomyces candidus*, *Hanseniaspora uvarum*, *Kluyveromyces marxianus*, *K. lactis*, *Schizosaccharomyces pombe*, *S. cerevisiae*, *Kazachstania exigua*, *Torulaspora delbrueckii*, *Zygosaccharomyces rouxii*, *Yarrowia lipolytica*	Fermentation, flavor and color development, rheology
Food additive production	*Lindnera jadinii*, *K. marxianus*, *S. cerevisiae*, *Y. lipolytica*, *Rhodotorula glutinis*, *Sporidiobolus salmonicolor*	Release of B vitamins, proteins, peptides, amino acids, minerals, antioxidants, aromas, colorants, glutamic acids, nucleotides, vanillin, citronellol, linalool, geraniol, decalactones, β-glucans
Probiotic	*Saccharomyces cerevisiae* var. *boulardii*	Effect on enteric bacterial pathogen, maintenance of epithelial barrier Integrity, anti-inflammatory effects, effects on immune response, trophic effects on intestinal mucosa, clinical effects on diarrheal diseases
Food spoilage	*Brettanomyces bruxellensis*, *Pichia kudriavzevii*, *C. parapsilosis*, *D. hansenii*, *H. uvarum*, *Pichia membranaefaciens*, *Rhodotorula mucilaginosa*, *Rhodosporidium toruloides*, *S. cerevisiae*, *S. pombe*, *Kazachstania exigua*, *Zygosaccharomyces bailii*, *Z. bisporus*, and *Z. rouxii*	Blown cans of soft drinks, cloudy refermented wine, pink or red slime dripping from refrigerated meat, white yeast colonies on food, tainted fruit juices, off-odors, and off-tastes
Allergenic	Different yeast species	Food intolerance, migraines, respiratory problems, chronic fatigue syndrome, dysfunctional gut syndrome, irritable bowel syndrome
Pathogenic	*Candida* spp., *Filobasidiella neoformans*, *P. kudriavzevii*, *W. anomalus*, *K. marxianus*, *S. cerevisiae*, and *Rhodotorula* spp.	Mucocutaneous, cutaneous, respiratory, central nervous, systemic, and organ infections

Nomenclature is in agreement with the yeasts: a taxonomic study (5 as apex edition).

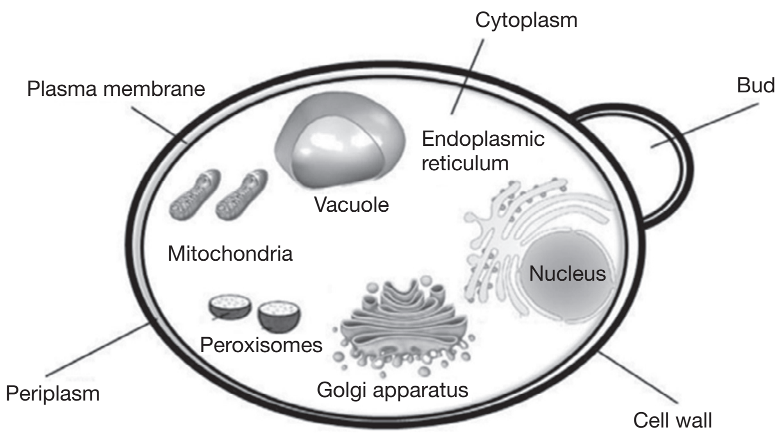

Figure 1 Yeast cell and its main organelles.

size, shape, and color. Cell size may be 2–3 μm in length up to 20–50 μm with a diameter of 1–10 μm. The yeast cell wall is a rigid structure about 100–200 nm thick and constituting about 25% of the total dry mass of the cell. The macromolecules that compose the wall are highly glycosylated glycoproteins (mannoproteins), two types of β-glucans, and chitin. The overall composition can vary considerably in relation with the growth conditions. The surface plasma membrane of yeast is a lipid bilayer, which harbors proteins serving as a cytoskeleton and enzymes for cell wall synthesis, signal transduction, and transport. The lipid components comprise mainly phospholipids and sterols (principally ergosterol and zymosterol). The periplasmic space is a region external to the plasma membrane (35–45 Å) that contains proteins unable to permeate the cell wall, such as invertase and phosphatase.

The yeast cytoplasm is an aqueous, slightly acidic colloidal fluid that contains proteins, glycogen, other soluble macromolecules and larger macromolecular entities such as ribosomes, proteasomes, and lipid particles. Many essential functions for cellular integrity are localized in the cytoplasm. The cytoskeleton of yeast cells comprises microtubules and microfilaments. In the center of the cell or slightly excentrically, the nuclear structure is located, which is surrounded by a double membrane that separates the nucleoplasm from the cytoplasm. The outer nuclear membrane is contiguous with the membrane of the endoplasmic reticulum.

The nucleolus within the nucleus is the specialized subnuclear compartment for ribosome synthesis. The nuclear chromosomes are in the nucleoplasm and packed into a chromatin structure; the genome sizes of yeasts are relatively constant and generally range from 10 to 15 Mb, whereas the number and sizes of the single chromosomes vary among species. Yeast cell contains different organelles surrounded by individual membranes, mostly the endoplasmic reticulum, the Golgi apparatus, and transport vesicles that are necessary for the manufacturing and trafficking of proteins, vacuoles, mitochondria, and microbodies. Structurally, the endoplasmic reticulum is a complex network of membranes, part of which is connected to the nucleus. The endoplasmic reticulum membrane forms a continuous sheet enclosing a single internal space called the endoplasmic reticulum lumen, separating it from the cytosol. It is involved in the selective transfer of secretory proteins between the endoplasmic reticulum and the Golgi apparatus. It also plays a key role in lipid and protein biosynthesis; in fact, it is the site of production of the transmembrane proteins and lipids for most of the cell's organelles (e.g., the endoplasmic reticulum itself, the Golgi apparatus, lysosomes, and endosomes). The Golgi apparatus is composed of stapled stacks of membranes called *cisternae*. Transport vesicles, received from the endoplasmic reticulum, are further processed and sorted for transport, for instance, releasing secretory proteins in the growth medium. Vacuoles are organelles involved in intracellular protein trafficking, receiving proteins from differing routes. In the vacuoles, there are degradative processes catalyzed by different hydrolases, such as phosphatases, phospholipases, lipases, nucleases, endopeptidases, aminopeptidases, and carboxypeptidases. Vacuoles also are involved in other physiological functions, such as the storage of amino acids, polyphosphates, and some metal cations (K^+, Mg^{2+}, and Ca^{2+}). Yeast mitochondria resemble the organelles found in higher eukaryotes, surrounded by an outer membrane and an inner membrane, the two of which embody an intermediate space that contains the mitochondrial matrix. If sufficient oxygen and carbon sources are supplied, few and large mitochondria carry out respiration and synthesis of ATP, whereas under anaerobic conditions, they reduce their size and activity. Other functions are the synthesis and desaturation of fatty acids, biosynthesis of ergosterol, adaptation to stress, mobilization of glycogen, and synthesis of enzymes. Microbodies (peroxisomes and glyoxysomes) consist of a proteinaceous matrix, surrounded by a single membrane that is involved in the primary metabolism of various carbon and organic nitrogen sources, such as ethanol, methanol, primary amines, *n*-alkanes, and fatty acids (oleic acid).

Metabolism

Yeasts are heterotrophic organisms in which the energy and carbon metabolism are interconnected and anabolism is coupled to catabolism. Yeasts preferentially metabolize sugars that are converted principally to ethanol and carbon dioxide, but they can utilize different carbon sources, such as amino and organic acids, polyols, alcohols, fatty acids, and other compounds, depending on the species. According to the process utilized to generate energy (respiration and/or fermentation), they can be classified as:

- nonfermentative yeasts with only a respiratory metabolism;
- obligate-fermentative yeasts, only capable of metabolizing glucose through alcoholic fermentation;
- facultative-fermentative yeasts, possessing either a fully respiratory or a fermentative metabolism or even both in a mixed metabolism depending on the growth conditions, the type and concentration of the carbon source, and/or oxygen availability.

The main nitrogen substrates used by yeasts during growth in food are inorganic ammonium compounds and free amino acids. Decarboxylation of amino acids leads to the production of amines, whereas metabolism of arginine and citrulline gives urea, precursor of the potential carcinogen ethyl carbamate. Whereas yeasts produce organic acids, with succinic and acetic acids being the main acids produced during sugar fermentation, some yeast species can use acetic and lactic acids and weak monocarboxylic acids under starvation conditions. Consumption of organic acids by yeasts may thus create conditions favorable for certain spoilage microorganisms. In cheese, lactate catabolism by some species such as *Debaryomyces hansenii*, *Kluyveromyces lactis*, and *Kluyveromyces marxianus* induces an increase of pH at the cheese surface, having a key role during ripening.

Sulfates are utilized to produce volatile sulfur compounds such as hydrogen sulfide, sulfur dioxide, and at lesser amounts mercaptans, thioesters, and other organic sulfites. Yeasts also show proteolytic and lipolytic activities depending on the species and strain.

Yeasts in Fermented Food and Beverages

Yeasts are undoubtedly one of the most important groups of microorganisms that are exploited for the elaboration of fermented foods. Fermentation is one of the oldest and most economical methods of producing and preserving food, providing also a natural way to reduce the volume of the material to be transported, to destroy undesirable components, to enhance the nutritive value and appearance of the food, to reduce the energy required for cooking, and to make a safer product. In these processes, mixed cultures of yeasts, bacteria, and fungi are active, participating either in parallel or in a sequential manner with a changing dominant microbiota during the course of the fermentation. Some yeast species are included in starter cultures for the production of specific types of fermented foods like cheese, bread, sourdoughs, fermented meats, and fermented vegetable products. Common fermenting yeasts, often selected as starter cultures, belong to the *Saccharomyces* genus, which results in alcoholic fermentation.

Yeasts in Dairy Products

Yeasts play an important role in flavor and texture development during the production of fermented milks, such as kefir and koumiss, and the ripening of cheese. They are used as secondary starter cultures to enhance the aroma or improve the growth of lactic acid bacteria or brevibacteria. The most important and dominant species, besides *S. cerevisiae*, are *D. hansenii*, *Yarrowia lipolytica*, *K. marxianus*, and *Galactomyces candidus*.

Yeasts in Fermented Meat Products

Studies on the presence and role of yeasts in fermented meat product are limited. The high salt concentration and the low water activity that are typical of fermented sausages favor the growth of *Debaryomyces* species, mostly *D. hansenii*, *Y. lipolytica*, and various *Candida* species, contributing to the development of color (by removing the oxygen) and flavor (by degrading peroxides and via lipolytic and proteolytic activities). Hydrolytic and oxidative changes carried out by yeasts during ripening produce the distinctive flavors of these products.

Fermentation of Cereal Products

Cereals, as a global staple food, are often fermented to improve shelf life and nutritional properties in comparison with the raw material. Fermented cereal products are produced from different cereal substrates and a number of them consist of a combination with legumes, thus improving the overall protein quality of the fermented product. Fermentation improves the nutritional value, sensory properties, and functional qualities. Besides the global importance of (sourdough) bread, a wide variety of different products come from Africa and Asia, as is the case for koko, banku, panjabi waries, papadams, jalebis, idli, dosa, dhokla, kishk, tarhana, ogi, kenkey, pozol, injera, and kisra. The microbiota responsible for the fermentation is in many cases indigenous and includes lactic acid bacteria, yeasts, and fungi. *Saccharomyces cerevisiae* strains are often found in the fermentation of various cereal products. Other yeast species frequently detected are *Kazachstania exigua*, *Candida milleri*, *Torulaspora delbrueckii*, and *Pichia* spp. The yeast species diversity in fermented cereal products, as well as their numbers, is affected by the degree of tolerance to the organic acids produced by the lactic acid bacteria.

Fermented Beverages

As regards the fermented beverages produced by musts obtained from fruits (grape, cider, mixed tropical fruits, etc.), the natural fermentation is started by some non-*Saccharomyces* yeasts, such as species of *Hanseniaspora uvarum*, *Candida stellata*, *Wickerhamomyces anomalus*, *Metschnikowia pulcherrima*, and other yeasts. After 1 or 2 days, species of *Saccharomyces*, in particular *S. cerevisiae*, develop and dominate fermentation by forming high amounts of ethanol. During fermentation, many compounds are produced or metabolized by yeasts contributing to the aroma of beverages. However, during must fermentation, yeasts can produce off-flavors too, as is the case for *Brettanomyces*/*Dekkera* species that are reported to be involved in wine spoilage. Nowadays, selected starter cultures of *S. cerevisiae* are generally used to carry out must fermentation. In beer fermentation, two types of *Saccharomyces* yeasts are involved, that is, ale yeasts (top-fermenting yeasts, *S. cerevisiae*) and lager yeasts (bottom-fermenting yeasts, *S. pastorianus* (synonym *S. carlsbergensis*)). More than a thousand single different starter cultures of brewing yeasts have been described, varying in their technological properties, such as aroma production, rate and degree of attenuation, flocculation, oxygen requirement, and reproduction.

Cash Crops

Cocoa beans and coffee beans must undergo processes that involve the action of yeasts of various species of *Saccharomyces*, *Hanseniaspora*, *Kluyveromyces*, *Saccharomycopsis*, *Candida*, and *Pichia*. Cocoa beans have to be fermented to drain the pulp, stabilize the beans, and generate precursors for chocolate flavor, whereas coffee beans are mostly fermented to remove the pulp and the mucilaginous materials from the seeds.

Yeast for Health

Yeast as Probiotics and Nutraceuticals

The World Health Organization officially defined probiotics as "live microorganisms which, when administered in adequate amounts, confer a health benefit on the host." Most probiotic microorganisms are bacteria, usually including selected strains of certain genera of *Lactobacillus* spp. or *Bifidobacterium* spp. In recent years, the interest in using yeasts as probiotics increased, not only for human health but also to improve growth and health of animals and birds, in particular in aquaculture or with respect to industry cattle, pigs, and poultry.

Yeasts are able to face the stresses of the gastrointestinal tract, such as enzymes, bile salts, organic acids, and considerable variations of pH and temperature. The first species described as an effective biotherapeutic agent has been *S. cerevisiae* var. *boulardii*, isolated from lychee fruit in Indochina in the 1920s. This yeast is commonly used as a probiotic in different countries, as both a preventive agent and a therapeutic agent for diarrhea and other gastrointestinal disorders caused by the administration of antimicrobial agents. *S. boulardii* has many properties, such as survival transit capacity through the gastrointestinal tract, among other reasons because its temperature optimum is 37 °C, both *in vitro* and *in vivo*. Moreover, the species exerts inhibitory effects toward various enteric pathogens as its cell wall shows binding capacity to enterohemorrhagic *Escherichia coli* and *Salmonella enterica* serovar Typhimurium. Additionally, the yeast inhibits adherence of *Clostridium difficile*. Other probiotic beneficial effects on human health associated to the administration of *S. boulardii* include:

- maintenance of epithelial barrier integrity and permeability,
- restoration of the tight-junction structure,
- reduction of inflammation during bacterial infection by interference with host cell signaling pathways,
- stimulation of the host cell immunity in response to pathogenic infections,
- prevention of reaction to food antigens in particular when mucosal permeability is increased.

Other species, such as *D. hansenii*, *T. delbrueckii*, *K. lactis*, *K. marxianus*, and *Kazachstania lodderae*, have also shown tolerance to passage through the gastrointestinal tract and inhibition of enteropathogens. Recently, many researchers have focussed on the antioxidant ability and cholesterol assimilation of yeasts. Some reports indicated that *S. cerevisiae*, *K. lactis*, and *Pichia kudriavzevii* can remove cholesterol *in vitro*.

Yeasts can also produce nutraceuticals useful for the development of functional foods and for the protection from cardiovascular disease. The most important compounds seem to be the β-glucans, which act as bioactive polysaccharides, and bioactive peptides that inhibit angiotensin I-converting enzyme activity, reducing peripheral blood pressure and exerting antihypertensive effects *in vivo*. Only some yeast species, that is, *K. marxianus* and *S. cerevisiae*, have been shown to produce these compounds in fermented milks such as koumiss and kefir. Recent studies also indicate that some foodborne yeasts (especially *D. hansenii* and *S. cerevisiae*) are able to reduce the potential genotoxic risk due to mutagenic and genotoxic compounds. A recent study indicated that *S. cerevisiae* and *D. hansenii* show inhibitory activity against two model genotoxins, 4-nitroquinoline-1-oxide and *N*-methyl-*N*′-nitro-*N*-nitrosoguanidine. The antigenotoxic activity is probably due to the formation of a complex between genotoxins and thermolabile soluble cellular oligosaccharides (i.e., mannans and glucans). Nevertheless, a similar complex may also occur between the genotoxins and other compounds derived from yeast metabolism such as polyamines, mainly spermidine and spermine or the glutathione system.

These healthy effects appear to be promising features for the use of well-characterized yeasts as natural protective agents. In addition, yeast cells are also good sources of vitamins (thiamine, pantothenic acid, riboflavin, biotin, folic acid, B_6, and B_{12}), ergosterol, and coenzyme Q.

Antioxidants

In the past, yeasts and yeast extracts were used as a source of antioxidant compounds to be added to prevent oxidation of food products. Now, natural antioxidants, presumed to be safer for human, can also be used in nutraceutical applications as supplements. Natural antioxidants act by donating hydrogen protons to substrates, rendering them nonreactive to reactive oxygen species. This involves enzymes such as catalases, superoxide dismutases, glutathione (L-γ-glutamyl-L-cysteinylglycine), and NADP-dependent dehydrogenases. Several compounds involved in antioxidant actions are produced by yeasts and can be used to retard oxidative degeneration of fatty substances in food and to improve health and well-being in nutraceutical supplements. They consist of torularhodin, coenzyme Q, glutathione, hydroxymethyl and hydroxyethyl furanone (2H), tocotrienol, α-tocopherols, and other forms of tocopherols, riboflavin (vitamin B_2), and derived flavins. Several oxygenated carotenoids, selenium-enriched yeast cells, the wine component resveratrol, octacosanol, cell wall β-glucans, proteins produced in yeasts under oxidative stress, sulfur-containing amino acids, and cytochrome C are present at the end of fermentation in the products and/or in the yeast biomass.

Single-Cell Proteins

The use of yeasts for single-cell protein (SCP) production is convenient, resulting in nutritional supplements for animal feeds and human foods. In fact, yeast SCP is considered as a potential source of proteins, carbohydrates, fats, vitamins, minerals, and essential amino acids. SCP for human consumption should be free from nucleic acid as purine bases are metabolized to uric acid, a problem for some humans that do not possess the enzyme uricase. SCP production has been obtained by yeasts cultivated in mixtures of sugars and minerals, such as molasses, starch, cassava, whey products, brewing by-products, potato and cellulosic wastes, or other waste streams from agricultural and industrial processes. The yeasts are washed, thermolyzed and dried, and usually spray-dried into a powder. The production of value-added SCP from inexpensive substrates could beneficially contribute to the food supply. Whereas for human applications, *S. cerevisiae* (baker's and brewer's yeast) is the currently the organism of choice, animal feeds rely on *Lindnera jadinii*.

β-Glucans

β-Glucans have several beneficial properties and have found a variety of uses in human and in veterinary medicine, immunopotentiation, pharmaceutical, cosmetic and chemical industries, and food and feed production. Yeast is a good source of β-glucans that are present in the cell walls as branch-on-branch molecules containing linear (1,3)-β-glucosyl chains joined through (1,6)-linkages. Spray-dried yeast β-glucans are useful for food production, as food thickeners, replacers, dietary fibers, emulsifiers, and films. Furthermore, yeast glucans have important properties as water-holding, fat-binding, and oil-binding characteristics, as well as gelling properties. For these reasons, they can also be used in the production of sausages and meat products, mayonnaise, and other food products, such as dressings, frozen desserts, sauces, yogurts, and other fermented milks and soft doughs. They are safe for oral application and have a GRAS (generally recognized as safe) status.

Allergenic or Pathogenic Yeasts

Viable populations of a diversity of yeast species present in fermented foods (dairy products, fermented and cured meats, fruits and fruit salads, table olives, and beer and wine) are unknowingly and inadvertently ingested. Unlike bacteria, viruses, and some filamentous fungi, yeasts are rarely associated with outbreaks of foodborne gastroenteritis or other foodborne infections or intoxications. However, an increase of yeast infections is reported, and some yeasts are now considered as opportunistic pathogens, such as *Candida albicans* and *Filobasidiella neoformans*, which can cause mucocutaneous, cutaneous, respiratory, central nervous, systemic, and organ infections. Moreover, other species that are frequently found in foods, such as *P. kudriavzevii*, *W. anomalus*, *K. marxianus*, *S. cerevisiae*, and various *Rhodotorula* species, can be potential pathogens. Even *S. cerevisiae*, intensively used in industrial processes, has been described as a pathogen in 1958. It displays low virulence against humans, but invasive *S. cerevisiae* infections have been increasingly common in recent decades, having been identified in blood cultures, including those from immunocompetent subjects. Therefore, vigilance on yeasts and foodborne diseases is required because there is a literature that connects yeast presence in foods to the onset of a broad range of allergic and hypersensitive reaction in humans. Indeed, yeasts may cause or contribute to food intolerances, migraines, respiratory problems, chronic fatigue syndrome, dysfunctional gut syndrome, and irritable bowel syndrome. Generally, these adverse reactions could be associated to the yeast cells themselves, yeast extracts, or associated metabolites such as sulfur dioxide, proteins, and biogenic amines. The latter, especially histamine, tyramine, phenylethylamine, putrescine, and cadaverine, are associated to headaches, hypotension, migraines, and digestive disturbances in humans. Although the quantity produced is not enough to create health concerns, yeasts can thus contribute to the accumulation of biogenic amines in fermented foods and beverages.

Yeasts Technological Features

Aromas

During fermentation, yeasts produce many aromas. For alcoholic beverages, this involves over 400 different chemical compounds, of which fusel alcohols, fatty acids, and their ester represent the main groups. In addition, carbonyl compounds, acetals, phenols, hydrocarbons, nitrogen compounds, sulfur compounds, lactones, sugars, and a variety of other unclassified compounds are present. Besides, yeasts also contribute to the aroma of bread, cheese and other dairy products, fermented meat, cocoa, vanilla, and fermented soy-derived foods.

Colors

The yeasts have been used as sources of a number of carotenoids for use as food colorants such as astaxanthin, β-carotene and γ-carotene, lycopene, lutein, torulene, torularhodin, and zeaxanthin. For instance, *Phaffia rhodozyma* and *Xanthophyllomyces dendrorhous* have been used in industrial-scale production of the carotenoid astaxanthin. This compound can be used for aquafeed as a colorant or as an immunostimulant in food or in poultry, fish, or mammalian feed. Other colorants produced by yeast fermentation are riboflavin and caramel colors produced from the processing of yeast extracts.

Flavors

Flavors produced by yeasts, such as yeast extract, autolysates, and dried preparations, are commonly used in the food industry as a source of savory accents (roasted, nutty, meaty, and other flavors). These flavors can originate from yeast metabolic products including alcohols, amino acids and derivatives, carbohydrates and glycosides, fatty acids and their esters, organic acids, lactones, and aldehydes. Among the yeast-derived products, yeast extract is often produced from spent brewer's yeast and provided as powders or pastes. Yeast extracts are flavor ingredients of which the quality is affected by the specific cell composition. Hydrolyzed edible proteins and peptides from yeasts, which are a good source of the essential amino acid L-lysine, are limited in sulfur-containing amino acids, such as cystine and methionine, which have to be added. Some extracts are also enriched in glutamic acid and nucleotides that function as strong flavor enhancers. Yeast-derived lecithin, inositol, glycerol, and glycolipids, recovered from the cell membrane lipid extracts or from fermentation broth, can be used as flavors in foodstuffs as emulsifiers and surfactants. Moreover, they show additional health benefits so they can also be used as food supplements.

Yeast Spoilage

Food and beverages spoilage by yeasts has been well documented in many recent reviews. Yeasts can cause defects in the final products, and problems with hygiene procedures appear upon failures in the decontamination procedure, leading to significant economic losses. Generally, yeast spoilage occurs in food products characterized by a retarded or inhibited bacterial growth, that is, without bacterial competition. Foods that are usually subjected to yeast spoilage are characterized by low pH, high sugar levels (e.g., more than 10%, w/v), high salt levels (more than 5% NaCl), and low levels of organic acids (e.g., sorbic, benzoic, and acetic). Fruits and derived products (juices, drinks, pulps, concentrates, and syrups), confectionery products, alcoholic beverages, carbonated beverages, vegetable salads with acid dressings, salt- and acid-based sauces, dairy products, and fermented or cured (salted) meat products represent the main candidates for yeast spoilage.

The main spoilage yeast species are *B. bruxellensis*, *P. kudriavzevii*, *Candida parapsilosis*, *D. hansenii*, *H. uvarum*, *Pichia membranaefaciens*, *Rhodotorula mucilaginosa*, *Rhodosporidium toruloides*, *S. cerevisiae*, *Schizosaccharomyces pombe*, *K. exigua*, *Zygosaccharomyces bailii*, *Z. bisporus*, and *Z. rouxii*. However, with the years, some other common food-contaminating yeasts have been described, such as *Y. lipolytica*, *Zygosaccharomyces lentus*, *Z. kombuchaensis*, *Candida wyomingensis*, *C. boidinii*, *Cryptococcus uzbekistanensis*, *Candida natalensis*, and *Pseudozyma antarctica*. The main alterations caused by yeasts in food include the alteration of physical and sensorial properties, discoloration, gas production, cloudiness, sedimentation or pellicle formation, and the formation of off-flavors. For instance, *D. bruxellensis* is responsible of serious economic losses in the wine industry because it produces volatile phenols (4-ethylguaiacol and 4-ethylphenol), which generate off-odors in wines. Exposure of beer to air will induce the growth of oxidative yeast genera such as *Pichia*, *Debaryomyces*, *Candida*, and *Hansenula*, which cause off-flavors and ferment residual dextrans in the beer.

Yeast as Biocontrol Agents

Several yeast species show a strong antagonistic activity against filamentous fungi. For this reason, they can be used for biocontrol of fungi that cause pre- and postharvest spoilage of fruits and vegetables, increasing food quality and hygienic safety. As such, they can the control the development of *Botrytis*, *Penicillium*, *Aspergillus*, and *Rhizopus* spp., reducing the need for chemical fungicides and, consequently, their potential oncogenic risks. The yeast species showing biocontrol capacity are mostly *M. pulcherrima*, *Candida sake*, *Sporobolomyces roseus*, *W. anomalus*, *Aureobasidium pullulans*, and various *Cryptococcus*. For commercial use, the main species diffused are *C. oleophila* and *Pseudozyma flocculosa*, which are registered as Aspire and Sporodex, respectively. The combination between *C. oleophila* and two bacterial strains is widely used as biocontrol agent of postharvest diseases of citrus and apple fruits. Yeast antagonistic activity is mainly related to the production of killer toxins, inhibitory proteins and peptides, lytic glucanases, and chitinases, which act against fungal cell wall. Moreover, they inhibit fungal development through nutrient competition and the production of toxic metabolites, such as ethanol, acetaldehyde, ethyl acetate, and fatty acids. The use of yeasts as biocontrol agents has several advantages because they are easy to cultivate, are characterized by a fast growth, and can be found in several ecological niches.

Conclusion

In summary, yeasts play an essential role in many food and beverage fermentations, conferring the required stability, safety, and sensory properties to the final product. Moreover, several beneficial health effects are clearly evident such as probiotic (prevention and treatment of intestinal diseases and immunomodulatory action), antigenotoxic, and antioxidant activities. Recent advances in molecular biology (DNA recombination, mutagenesis, etc.) can be applied to obtain specialized yeasts with new properties to improve human life.

See also: Cheese: Chemistry and Microbiology; Cheese: Composition and Health Effects; Fermented Foods: Use of Starter Cultures; Fermented Foods: Fermented Meat Products; Fermented Foods: Fermented Vegetables and Other Products; Fermented Foods: Composition and Health Effects; Fermented Foods: Fermented Milks; Food Additives: Classification, Uses and Regulation; Food Allergies; Foodborne Pathogens; Functional Foods; Probiotics; Spoilage: Yeast Spoilage of Food and Beverages; Wines: Wine Production.

Further Reading

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www.yeastgenome.org – Stanford University.