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THE ECOPHYSIOLOGICAL CLASSIFICATION OF YEASTS

Review Article

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Yeasts play very important roles in the livelihoods of peoples and various industries. This review consolidates the research on the physiological parameters used for yeast identification. Physiological parameters include the internal and external factors affecting yeast growth. External factors are confined to environmental and nutritional conditions. Environmental or physical factors include temperature, pressure, light and radiation, physiochemical (water and pH) characteristics, oxygen levels, presence of toxic compounds, and biological interactions with other living organisms. Nutritional factors include macro- and micro-elements, growth co-factors, and other parameters (e.g., CO_2 and humidity). Internal factors are specific to each yeast strain including the genus, species, species variety, isolates, genetic characteristics, age of colony, source of isolation and different yeast parts. The ecophysiological classification of yeast has great importance in various fields of biotechnology. It paves the way to introduce the most appropriate yeast strain for production of fermented foods and beverages, food additives, biofuel, efficient pharmaceutical compounds, environmentally and friendly green biofuels, biocides, probiotics, enzymes, bioremediation, plant growth regulators and the like.

Keywords: Yeast, environmental, nutritional, and internal factors.

1. INTRODUCTION

Seven thousand years ago, many ancient civilizations, particularly in ancient Egypt, used yeasts in the preparation of bread and alcoholic beverages. Currently yeasts have been used in various industrial applications, such as in the production of fermented foods (bakery yeast and baking, alcoholic beverages, dairy and cheese, meats and fish, grains, and fruits and juice, etc.), food additives as flavoring agents, for animal feeding, pharmacology (insulin, hormones, vaccines, tissue plasmogen activators, anticoagulant, etc.), folk and modern medicine, environmental applications (biocontrol, green energy, biofuel, etc.), cosmetics and perfumes, and biological research and genetic engineering. Using yeast on an industrial scale in fermentation offers numerous advantages as it is weather independent, requires few and limited nutritional and environmental conditions, grows easily on inexpensive substrates particularly in agriculture and agro-industrial residues, and the fermentation periods is only a few days. Additionally, yeasts offer high yield, safety, stability, and solubility in water and alcohol with natural metabolites, and it is relatively easy to extract good quality products from the growth media. Yeasts have applications in numerous industries that use yeast biomass, extracellular products (in the growth media), enzymes, and biotransformation (adding precursors converted by yeast enzymes to new expensive and beneficial compounds). Moreover, yeasts may be used as pure culture or in association with other organisms such as yeast, bacteria, and mold. Growing yeast on natural foods, any non-beneficial natural substrates, or toxic materials increases the nutritional value of this food, while improving its flavor (taste and, aroma), and texture. Yeasts also provide numerous bioactive metabolites improving human health, and prevent numerous deadly diseases via its anti-microbial effect that inhibits the growth of pathogens and other undesirable microbes in foods [1-3].

Industrial yeast cells behave like a factory, producing numerous beneficial products including *S. cerevisiae*. It is easy to acquire extra-cellular products in the culture around the cell, while intra-cellular metabolites formed within the cell are obtained using the entire biomass of the yeast cell. Yeast growth is affected by external factors (physical or environmental and nutrition or chemical factors) and internal factors (specific to the yeast). These factors may be used as a tool in yeast identification and classification [3-8].

The main goal of this review is to investigate the factors influencing yeast growth and identify and classify yeast based on these growth factors.

2. REVIEW

2.1 Influence of External or Environmental Factors (Physical Factors) on Yeast Growth

The environmental factors that influence yeast growth include pressure, temperature, light and solar radiation, physicochemical factors (water activity "*a*w", and redox potential), oxygen availability, pH, presence of toxic compounds (yeastcide and yeaststatic) and the interactions between yeast and other living organisms. Each factor initiates a division of yeast into many categories. Any biological process in the yeast is comprised of three cardinal points the minimum, optimum, and maximum points [4-6].

2.1_a Temperature

Yeasts are classified into four categories based on temperature at which they grow:-

i) Mesophilic yeasts that grow at 20 - 35^{O}C [4,5,9].
ii) Thermotolerant yeasts that grow at 38 - 42°C [4,5,9].
iii) Thermophilic yeasts that grow at 38 - 45°C (it riches by 30% to 40% of saturated fatty acids) [4,5,9].
iv) Psychrophilic yeasts that grow in the range -1 to 20^{O}C "it riches by 90% unsaturated fatty acids and contains 55% linolenic acid, $C_{18:3}$" [4,5,9-11] (Table 1).

2.1_b Pressure

At sea level conditions, atmospheric pressure does not affect yeast growth. Parophilic yeasts are observed only in the deep sea at a depth of 2000 - 6500 m, where cells experience high hydrostatic pressure. The genera of parophilic yeast isolated from these depths include *Rhodotorula, Sporobolomyces,* and *Kluveromyces nonfermentans* [12-14]. High pressure exerts a destructive force on cell structures, and the viability of yeast decreases with increasing pressures above 100 MPa; yeast cells are destroyed between 200 and 300 MPa [15]. Interestingly, when yeast cells are exposed to mild stress (hydrogen peroxide, ethanol, or cold shock), higher resistance to pressure is induced [4]. The resistance to high hydrostatic pressure paraphilic yeast has potential applications in food preservation [16].

2.1_c Light and solar radiation

Strong sunlight and ultraviolet radiation are inactivator agents that have the potential to destroy yeast cells. However, for *Cryptococcus* and *Rhodotorula* (pigmented yeasts), sunlight is a stimulator as these genera require light. As such these genera are abundant on the surfaces of plant leaves in the fields and forests [4,12,17].

Table 1 Classification of yeasts according to preferred growth temperatures [4,5,9-11].

°C range	Yeast genus and species
	Mesophilic yeast 20-37°C
22-24	*Leucosporidium scotti*
20-35	*Candida lipolytica*
27-31	*Candida vini*
32–34	*Candida zeylanoides*
37	*Saccharomyces cerevisiae* industrial fermentation
30–35	*Saccharomyces bayanus*
32–37	*Debaryomyces hansenii*
37	*Pathogenic C. albicans* and other opportunistic pathogenic
35–37	*Pichia anomala*
33-37	*Yarrowia lipolytica*
30-37	*Kazachstania, Macrorhabdus, Cyniclomyces,* and *Malassezia* (Pathogenic yeast)
	Thermotolerant yeast 31-42°C
38-42	*Candida parapsilosis*, *Saccharomyces telluris*
31–39	*Metschnikowia pulcherrima*
35–37	*Pichia anomala*
33–40	*Yarrowia lipolytica, Db. hansenii*, and *P. membranifaciens*
	Thermophilic 40- up to 48°C
>40	*Klu. marxianus*, *P. polymorpha*, *Geo. capitatum*, *S. cerevisiae*, *Candida* & *Debaryomyces*
38–43	*Pichia guilliermondii*
43–46	*Candida glabrata*
42–46	*Candida albicans*
42–45	*Issatchenkia orientalis*
35-45	*Torulopsis bovina*, *Candida slooffli*
28-45	*Candida slooffli*
44-47	*Kluyveromyces marxianus*
up to 48	*Klu. marxianus* from fermented molasses
	Psychrophilic yeast -1 to 20°C
	Alteromonas, Aureobasidium, Candida, Capitatum, Cryptococcus, Cystofilobasidium, Dioszegia, Himalayans, Leucosporidium, Leucosporidiella, Lipomyces, Kluyeromyces, Mrakia, Naganishia, Rhodotorula Rhodosporidium; *Saccharomyces, Schwannomyces, Sporidiobolus, Sporobolomyces, Trichosporon*, and *Udeniomyces*.

2.1$_d$ Physicochemical factors

The physicochemical factors that influence yeast growth include *a*w, pH, and redox potential (Eh). Other factors are more chemical in nature, such as the acidity, and presence or absence of oxygen and nutrient availability. The most direct impacts on yeasts are exerted by inhibitory and anti-microbial compounds [4].

2.1d1 Water

Water is an essential requirement for the survival of yeasts, and needs to be available in free forms to dissolve nutrients and aid the uptake of nutrients, respectively. Water is also responsible for all biological processes that occur within the yeast cell. In food microbiology, the available water is known as the water activity (*a*w). Food spoilage yeasts have minimum *a*w values as 0.90–0.95 for growth. *Zygosaccharomyces rouxii* can grow at an *a*w as low of 0.62. Several other types of yeasts grow at a low *a*w in the presence of high concentrations of salt or sugar.

Yeasts can be divided into five groups according to aw: osmophilic, osmotolerant, halophilic, halotolerant, and xerophilic and xerotolerant [5,18-22] (Table 2). Xerotolerant yeasts do not have a general requirement for dry conditions or high osmotic pressure [23]. They can grow at *a*w values as low as 0.7; these species include *Zygosaccharomyces rouxii*, *Z. mellis,* and *Z. bisporus.* Some strains have a minimum *a*w of 0.76 for growth although the optimum value is above 0.95. Tokouka and Ishitani [24] observed that tolerance to a low *a*w depends on the type of *a*w-controlling solute, recommending that yeasts should be classified as salt-tolerant and sugar-tolerant. Some yeasts are capable of growing at *a*w as low as 0.62–0.65. However, Tokouka *et al.*, [25] could not detect yeast growth at *a*w of 0.70 or below. Of 140 freshly isolated strains, only four exhibited better growth at *a*w of 0.91 than at higher *a*w values. At *a*w values less than 0.70, yeast growth was inhibited and the slow death of cells occurred with a decimal reduction time of 57–445 hours at *a*w 0.625. Tokouka and Ishitani [24] observed that, of 35 yeast strains isolated from high sugar foods, one strain of *Zygosaccharomyces rouxii* had a minimum *a*w of 0.67 for growth (Table 2). The mechanisms adopted by yeasts in response to reduced *a*w (from increased osmotic pressure and salt stress) include the accumulation of a high concentration of polyols, such as glycerol, arabitol, and mannitol, the production of compatible solutes, and the active excretion sodium ions or their exchange for K+ ions. Extreme osmotic stress may exceed osmoregulatory capacity of cells, and cause a loss in cell viability [4].

Table 2 Minimum *a*w for yeast growth adjusted by different solutes, the effect of water yeast genus and species, and divided the yeast into categories according to osmotic stress and water.

Yeast species	Minimum *a*w for Growth Controlled by using				*a*w	MPa	*S. cerevisiae* Cell % Related to Control)	
	Glucose	Fructose	Sucrose	NaCl			Glycerol	PEG600
Candida lactiscondensi	0.79	0.78	0.79	0.92	0.9	-14.5	92	59
Candida versatilis	0.79	0.80	0.79	0.84	0.8	-30.8	65	58
Debaryomyces hansenii	0.84	0.86	0.81	0.84	0.7	-49.2	55	40
Hanseniaspora uvarum	0.90	0.93	0.90	0.95	0.6	-70.5	20	28
P. membranifaciens	0.90	0.92	0.90	0.94	0.5	−95.7	10	0
Rh. mucilaginosa	0.90	0.92	0.90	0.90				
S. cerevisiae	0.89	0.91	0.91	0.92				
Torulaspora delbrueckii	0.86	0.89	0.87	0.90				
Zyg. bisporus	0.85	0.85	0.79	0.95				
Zyg. rouxii	0.79	0.67	0.79	0.86				

Yeast Categories	Water activity aw	Yeast species
1] Xerophilic	aw 0.85 dry loving yeasts	*Zyg. Bailii*
2] Xerotolerant	*a*w 0.62-0.65	*S. cerevisiae*, *Tsp. delbrueckii*, *Schizo. pombe*, *Zyg. rouxii*, *Zygo. mellis*, & *Zygo. Bisporus*
3] Halophilic	aw as 0.62 or 15–25% NaCl	*Zygosaccharomyces rouxii*
4] Halotolerant	1-5% NaCl salted, foods, pickles & olive	*Db. hansenii*, *C. versatilis*, *C. halonitratophila*, & *C. lactiscondensi*
5] Osmophilic	high sugar On Jam, Juice & fruits	*Saccharomyces cerevisiae*, *Zyg. rouxii*
6] Osmotolerant	Tolated to 5% salt or NaCl	*Zyg. rugosus*, *Z. rouxii*, *Torulopsis halonitatophila* , *S. mellis*, *S. cerevisiae*

Water Activity (*a*w) Water Potential (MPa**)** PEG: Polyethylene glycol

Table 3: The pH values and oxygen divided the yeast into the following categories

Effect of pH values on Yeasts Growth		
Category	pH	Yeast
Alkalotolerant	≥ 8	*Dekkera* (*Brettanomyces*), *Saccharo-mycodes*, & *Schizosaccharomyces*
Alkalophilic	≤ 10	Basidiomycetous *Rho. glutinis, Rho. mucilaginosa*, *Rho. minuta*, & *Cry. Laurentii*
Slightly acidic	4.5- 5.5	*Zygosaccharomyces rouxii*
Acidophilic	3-4	Most yeast genera
Strongly acidic	1.3-1.7	*Iss. orientalis, Dek. intermedia*, *P. membranifaciens, Kazach. Exiguous*

Effect of Oxygen on Yeasts Growth		
Class	Examples	Comments
1] Obligate fermentative	*Candida pintolopesii (S. telluris)*	Naturally occurring respiratory-deficient yeasts. Only ferment, even in the presence of O_2
2] Facultative fermentative Crabtree-positive	*S. cerevisiae*	Such yeasts predominantly ferment high-sugar-containing media in the presence of oxygen (respire-fermentation)
3] Crabtree-negative	*Candida utilis*	Do not form ethanol under aerobic conditions and cannot grow anaerobically
4] Non-fermentative or strictly aerobic	*Rhodotorula rubra & Cryptococcus*	Such yeasts do not produce ethanol, in either the presence or absence of oxygen

Table 4 Yeasts toxic agents or yeastcide includes chemical yeastcide and ethanol were effect on yeast growth

I] Chemical yeastcide inhibits yeast growth		
Compound	Act as	Yeastcide inhibiting the yeast growth
Captan & Dicholane	Yeastcide intracellular & cell-surface	Inhibiting agents with low fat solubility but face difficulty reaching the subcellular components inside the cell.
Aliphatic amine	Inactive the extracellular enzymes	Affecting the plasma membrane, stopping outer digestion & nutrient uptake
Polyphenols	Inhibit the pectolytic enzymes	Affecting the bioprocesses
Griseofulvin	Cell wall synthesis	Anti-yeast and anti-fungal antibiotic

II] Effect of ethanol on yeast growth and minimum inhibitory concentration	
Yeast	Ethanol % (v/v)
Candida utilis	6.1–6.5
Kluveromyces marxianus	8.6–9.4
Pichia anomala	10.0–10.9
Schizosaccharomyces pombe	11.8–12.5
Hanseniospora valbyensis	11.9–13.2
Saccharomyces cerevisiae	11.3–13.7

Note: a_w Values were adjusted to 300, 500, 600, 700, and 800 g L^{-1} final sugar concentrations were obtained by mixing 30% glucose and 70% fructose; temperature 25◦C; in presence of ethanol the pH decreased from 6 to 3.

Table 5 Natural yeastcide produced by other living organisms inhibiting yeast growth

Sources	Yeastcide or inhibiting compounds against yeast growth
Preservatives (foods natural agents)	acetate, lactate, some weak organic acids as benzoic and sorbic acids
Phytoalexins (plant & animal tissue)	develop in various parts of a wide range of plants in response to injury, microbial infection, or stress
Spices and herbs	Phenolic, aromatic compounds, essential oils of (allspice, cinnamon, clove, garlic, onion, oregano, savory, and thyme), volatile fatty acids, and oleoresins
Garlic	Ajoene,
Vegetable silage	Mustard oils or menthol
Coffee, cocoa beans, tea leaves, & kola nuts	Phenols hydroxycinnamic acids (caffeic, coumaric, and ferulic acids)
Soybeans	Glycinol
Bell peppers	Capidol
Potatoes	Phytotuberin

Table 6 Macroelements or non-metallic elements required for yeast growth includes

Element	A privation	Conc.	Functions and corporate in synthesizes	Active form
Carbon	C	$>10^{-3}$	50% of yeast DW, structural element of fungal cells in combination with H_2, O_2, N_2 and energy source.	Organic compounds
Hydrogen	H_2	$>10^{-3}$	6-8% of DW, transmembrane proton motive force vital for yeast nutrition. Intracellular acidic pH (5-6) necessary for yeast metabolism.	Protons from acidic environments, H_2, water, and organic compounds
Oxygen	O_2	$>10^{-3}$	Substrate for respiratory and other mixed-function oxidative enzymes. Essential for ergosterol & unsaturated fatty acid synthesis.	Atmospheric O_2, organic compounds, & water
Nitrogen	N2	10^{-3}	A structural and functional element. Organic amino nitrogen synthesizes the proteins, enzymes, nucleic acid, vitamins, and nitrogenous 2ry metabolites	NH_4+ salts ($NaNO_3$, NH_4Cl, $Ca(NO_3)_2$, $Mg(NO_3)_2$ & KNO_3), urea, amino acids
Calcium	Ca	10^{-3} <M	A possible second messenger in signal transduction	Ca2+ salts
Sulfur	S	10^{-4}	Amino acids, vitamins, other sulfuric compounds	Sulphates, methionine, K_2SO_4
Potassium	K	10^{-3} 2-4mM	Enzyme activity, osmoregulation, carbohydrate metabolism, ionic balance.	KCl, K_2HPO_4
Phosphorus	Ph	10^{-3}	Nucleic acid (DNA, RNA), energy (ATP, ADP, AMP) & membranes	KH_2PO_4
Magnesium	Mg	10^{-3}, 2-4μM	Enzyme activity, ATP metabolism, cell and organelle structure	$MgCl_2$

Table 7 Microelements or non-metallic elements required for yeast growth includes

Element	**A privation**	**Conc.**	**Functions and corporate in synthesizes**	**Active form**
Iron	Fe	10^{-6} 1-3μM	Fe3+ is chelated by siderophore and released as Fe2+ within the cell. It is used in cytochromes, Apo-enzyme, pigments, and catalase enzyme. Effect on citric acid, some vitamins, and antibiotics.	$FeCl_3$, $FeSO_4$
Nickel	Ni	10^{-7} ~10μM	Urease activity	Ni2+ salts
Copper	Cu	$10^{-6 \text{ to } -7}$ 1.5μM	Enzyme activity like tyrosinase, redox pigments. Toxic at relatively high conc.	CuO &$CuSO_4$
Zinc	Zn	10^{-8} 4-8μM	Enzyme activity and nucleic acid synthesis. Toxic at high concentrations	$ZnCl_2$, $ZnSO_4$
Manganese	Mn	10^{-7} 2-4mM	Enzyme activity, for growth and sporulation, TCA cycle, and nucleic acid synthesize	$MnCL_2$, $MnSO_4$
Molybdenum	Mo	10^{-9} 1.5μM	Enzyme activity, nitrate metabolism & B_{12} synthesis	$NaMoO_4$
Cobalt Co	Co	10^{-9} 0.1μM	Cobalamin, coenzymes	

Table 8 Diversity of carbon sources for yeast growth

Carbon source	Uses as carbon and energy source
Hexose monosaccharides (Glucose, galactose)	In yeasts metabolism glucose acts as the main nucleus
D-fructose, D-mannose	If yeast does not ferment glucose, it can't ferment other sugars. If a yeast ferments glucose, it can also ferment fructose and mannose, but not necessarily galactose
Pentose monosaccharides (arabinose, xylose, xylulose, rhamnose)	*S. cerevisiae* can utilize xylulose but not xylose
Disaccharides (Maltose, sucrose, lactose, trehalose, melibiose, cellobiose, melezitose)	If yeast ferments maltose, it does not generally ferment lactose and vice versa. Melibiose utilization is used to distinguish ale and lager brewing yeasts. Yeasts utilize sucrose and other disaccharides
Trisaccharides (Raffinose, maltotriose)	Raffinose is only partially used by *S. cerevisiae*, but is completely used by other *S. carlsbergensis* & *S.kluyveri*
Oligosaccharides (Maltotetraose, maltodextrins)	*Debaryomyces occidentals* & *Lipomyces* are amylolytic can utilize it.
Polysaccharides (Starch, inulin, cellulose, hemicellulose, chitin, pectic substances)	Polysaccharide-fermenting yeasts are rare. Industrial processes must use mixed culture to hydrolyze the polysaccharides
Starch	*S. cerevisiae* is unable to hydrolyze starch and can't produce inulinase enzyme. But *Kluyveromyces* & *Saccharomycopsis diastaticus* are able to hydrolyze it by inulinase enzyme
Lower aliphatic alcohols (Methanol, ethanol)	*Pichia pastoris, Hansenula polymorpha* methylotrophic yeasts use them as respiratory substrates
Sugar alcohols (Glycerol, glucitol)	Can be respired by yeasts
Organic acids	Yeasts can utilize organic acids, but only a few can ferment them
Fatty acids (Oleate, palmitate)	Oleaginous yeasts can assimilate fatty acids
Hydrocarbons (n-alkanes)	Yeast and a few filamentous species can grow well on C_{12}-C_{18} n-alkanes
Aromatics (Phenol, cresol, quinol, resourcinol, catechol, benzoate)	Few yeasts can utilize these compounds. Several n-alkane utilizing yeasts use phenol as carbon source via the β-ketoa dipate pathway
Miscellaneous (Adenine, uric acid, butylamine, pentylamine, putrescine).	*Arxula adeninivorans* and *A.terestre* yeasts can utilize its compounds as a sole source of carbon and nitrogen.
Lignin	Lignin is rarely utilized by yeast as its directly gained net energy is little.
'Hard' keratin	Keratinophilic yeast

Table 9 Some vitamin required as co-factors for yeast growth

Vitamin	Conc. M	Enzyme activator	Active form
Thiamin (B_1)	$10^{-6 \text{ to } 9}$	Co-carboxylase	Thiamin pyrophosphate
Biotin (B_7)	$10^{-8 \text{ to } 10}$	Co-carboxylation's	Covalently bound to enzyme by carboxyl
Pyridoxine (B_6)	$10^{-5 \text{ to } 7}$	Co-transamination's	Pyridoxali-ph, pyridoxamine-ph
Riboflavin (B_2)	10^{-7}-10^{-5}	Co-dehydrogenases	Energy compound FMN, FAD
Nicotinic acid B_3	10^{-8}-10^{-7}	Co-dehydrogenases	NAD & NADP
P-Aminobenzoic acid	10^{-8}-10^{-6}	Co-one-C- transfers	Tetrahydro-folic acid
Pantothenic acid	10^{-7}	Co-2-C- transfers	Coenzyme A
Cyanocobalamin B_{12}	$10^{-6 \text{ to } 12}$	Co-methyl-transfers	Various cobalamin derivatives
Inositol	$10^{-5 \text{ to } 6}$	Membrane structure	Phospholipids

2.1$_e$ pH value

Yeasts have a pH range between 1.3 to 8 and this pH tolerance may be divided into five categories (Table 3). Yeasts tolerate acidic conditions better than alkaline conditions; however, alkali tolerance is widely varies among yeasts. The physiological basis of the effect of pH on yeast has not yet been completely understood. It is generally believed that the maintenance of a proton gradient across the plasma membrane against an intracellular pH of approximately 6.5 is vital for the critical metabolic process within the yeast cell [26-28].

2.1$_f$ Oxygen availability

Oxygen availability categorizes yeast into four respiration systems including obligate fermentative, facultative fermentative Crabtree-positive, Crabtree-negative and non-fermentative yeast (Table 3).

Facultative aerobic yeast grows in the presence of O_2. When O_2 is exhausted, the yeast, as *Saccharomyces,* lives anaerobically and uses alcohol fermentation. At high glucose concentrations, the yeast begins alcoholic fermentation even under aerobic conditions; this is known as the Crabtree effect [29]. Although fermentative yeasts are facultative anaerobic, under aerobic conditions, they switch to respiration under well-known metabolic regulation; this is known as Pasteur Effect. CO_2 is a metabolic product of various yeast respiration pathways. As it is easily soluble in water, CO_2 rarely accumulates in concentrations that are inhibitory to the growth of yeast. Often (depending on the pH), CO_2 forms bicarbonate ions that inhibit yeast growth [30-32]. Fruits, vegetables, and meat products are best preserved for extended periods under a controlled or modified atmosphere, with decreased oxygen and increased concentrations of CO_2 or N_2 [4].

2.1$_g$ Toxic compounds (yeastcide and yeaststatic)

All living cells produce numerous metabolites that are yeast inhibiting (yeaststatic) or yeast destructive (yeastcide). These metabolites include antibiotics, heavy metals affecting respiration, and enzyme inhibitors. Yeaststatic and yeastcide react with the essential constituents in yeast cells (such as cell wall, membrane, and ergosterol), preventing several physiological processes in yeast and ultimately impacting DNA synthesis causing mutation**.** Several yeastcide substances cause morphological abnormalities in yeast cells (Tables 4 and 5) [4-5,8,33-35].

Ethanol is the primary product in yeast alcoholic fermentation; it has toxic effects on various organisms that contain yeast and impacts the ethanol- producing strain itself. Some yeast species exhibits ethanol tolerance. Natural residents on grapes, such as the *Hanseniaspora* (*Kloeckera*) species, which aids the fermentation of grape juice, are relatively sensitive to ethanol, and dies at concentrations around 5%–8% (Tables 4 and 5) [8,35].

Most strains of the true wine yeast, *S. cerevisiae*, can tolerate 13%–15% ethanol, while some strains have a tolerance for 18% or higher. Specific by-products of alcoholic fermentation, such as, diacetyl, may also exert a toxic effect [36]. Tolerance to ethanol is influenced by other environmental factors, particularly temperature and pH [37,38]. Ethanol is considered to increase membrane permeability, thus affecting the internal pH [39].

The sensitivity of yeast to ethanol increases when the temperature ≥ to 30 °C and ≤ 10°C or below [40]. CO_2 another end product of alcoholic fermentation, also possesses antimicrobial activity. However, yeasts are much less sensitive to CO_2 than other microorganisms [31,32,41]. *Brettanomyces* species are the most tolerant and cause the spoilage of carbonated beverages. *C. intermedia*, *P. anomala*, and *Z. bailii* can also tolerate approximately 0.5 MPa pressure of dissolved CO_2**.** Selected strains of *S. cerevisiae* used in champagne production can ferment sugar under high CO_2 pressures [42].

2.1_h Interactions among environmental factors

Under natural conditions, the effects of different environmental factors do not occur independently. Rather they manifest together and simultaneously, mutually influencing the effect of each other [37]. These interactions are dynamic and change with time and space; the outcome of these interactions is difficult to predict when several factors are involved. The food industry is highly interested in the combination of physical and chemical factors to apply milder treatments and better retain the quality and stability of processed foods, without compromising safety [43]. The interactions among temperature, water aw, pH, salt, sugar, and preservatives have been studied in various combinations with different types of food. In this vast field, reference has only been made to some examples relating to the growth inhibition of spoilage yeasts [44,45]. The evaluation of interactions between two factors and the identification of the synergistic (mutually strengthening) combination is much easier. However, it is difficult to evaluate the interactions under several inhibitory factors. Extensive experiments and complex statistical methods, including predictive mathematical models, are required for such an evaluation [46,47].

2.2 Biological Factors

Biological factors imply the interaction between yeast species and other living organisms in natural ecosystems. For example, food and beverage yeasts are found together with other numerous organisms such as human, animal, bacteria, filamentous molds, higher plants; as such, these yeast species interacts with these organisms [4,5]. The interaction between yeasts and other living organisms may be classified into 10 interactions:

2.2_a Saprophytic yeast

Most yeast genera live as a saprophyte and feed only on dead organic matter for nutrients. They represent the strongest degrading organisms by producing numerous degradable enzymes and environmentally friendly [4,5].

2.2$_b$ Yeast competition or trophic interaction

Competition may be defined as the competition between yeast species and other organisms for food. The strong competitive activities (adaptation, digestion, up-take of nutrient, rapid growth, distribution, and flourishing) completely inhibit the growth of the other competing organisms. Yeast species that are successful competitors may be used in biological control. In wine fermentation, trophic yeast competes for the uptake and release of ethanol and organic acids during the decomposition of fruits, preventing the growth of undesirable bacteria [4,5].

2.2$_c$ Yeast antagonistic relationships

Yeast antagonizes and inhibits the growth of other living organisms by producing many metabolites that act as inhibitors.

Yeast and yeast antagonism: The production of ethanol by antagonistic *Saccharomyces* inhibits the growth of other yeast species that have a low alcohol tolerance. Some yeast species exert lethal effects on other yeast species via mycocins or destructive toxin production (polypeptides destroying bacteria and eukaryotes). A destructive toxin producer is widespread among yeasts; strains of the species that release the toxin are resistant to the toxin, while other species may be sensitive or neutral to the toxin [4].

The succession of yeast species during fermentation is governed by the competition for nutrients and tolerance to ethanol [4].

Yeast and filamentous mold antagonism: *Pichia guilliermondii, P. anomala*, and *Db. hansenii* yeasts inhibit molds from attacking fruits and grains, thereby controlling post-harvest fungal diseases by antagonism [4,49,50].

Yeast and bacteria antagonism: A common method of bacterial antagonism is pH alternation. Although some *Streptococci, Lactobacilli,* and *Candida* species can survive in a broad range of pH conditions, most are susceptible to an acidic pH. Thus, pH changes affect the microbial community structure by either promoting or inhibiting the growth of acid-sensitive organisms, as observed in the phyllosphere, human gut, or win and cheese production. For example, on the surface of the cheeses, yeast lactate metabolism and the production of alkaline metabolites such as ammonia cause de-acidification that favors the growth of less-acid-tolerant bacterial strains essential for cheese ripening. Co-inoculation with *S. cerevisiae* was found to significantly improve the viability of *Pseudomonas putida* in grape juice and a synthetic glucose-rich medium. This was attributed to yeast glucose metabolism, resulting in a reduced concentration of deleterious gluconic acid produced by bacteria under these nutrient conditions [4].

2.2$_d$ Yeast assisting relationships

Assisting relationship: Means that growth of an organism is enhanced by other microorganisms growing alongside. Different species breaks-down complex organic material polymers to provide food for another group of organisms that utilizes the simple products. This relationship is used as a mixed culture in industrial processes.

Assisting relationship between yeast and bacteria: *Candida albicans* enhances the biofilm formation by *Staphylococcus aureus* and its resistance to vancomycin antibiotics in human serum. The assisting interaction between yeast and bacteria plays an important role in determining the taste, quality, and safety of a wide range of fermented food products such as cheese, wine, tempeh, sourdough, soy sauce, and fermented tea [51].

Assisting relationship between mold and yeast: The growth of fungi hydrolyzes polysaccharides and produces simple sugars which improve the growth of yeast. The growth of *Botrytis cinerea* on grapes assists yeast growth by enabling growth on the surface of berries [52]. Some common soil fungi such as *Cladosporium*, *Aspergillus*, and *Penicillium* produce iron-containing siderophores as metabolic products enhancing the growth of *Db. mycophilus* yeast [53].

2.2$_e$ Synthesize for another yeast relationships

To synthesize for another relationship means that one species synthesizes a growth-substance in excess, so that another species can utilize it. For example *Chionosphaera* (basidiomycetous yeast) produces sexual spores when associated with *Cladosporium*. The *Cryptococcus laurentii* (antarctic yeast strain) produces an exopolysaccharide by bio-transforming different carbon sources (pentose's, hexoses, and oligosaccharides) into exopolysaccharides. It uses sucrose as the carbon source and forms the maximum biopolymer quantity of 6.4 g/L obtained at 40 g/L of sucrose, at 22°C over 96 -h of fermentation. The newly synthesized microbial carbohydrate include monosaccharide (arabinose, 61.1%; mannose, 15.0%; glucose, 12.0%; galactose, 5.9%; and rhamnose, 2.8%) and polymer molecules; 60% of these carbohydrates have a molecular mass of 4200 Da. The exopolysaccharide possesses good emulsifying and stabilizing properties in terms of oil/water emulsions. It also has a pronounced synergistic effect with other hydrocolloids such as xanthan, gum, guar gum, and alginate [54].

2.2$_f$ Mutualism or symbioses commensalism in yeasts

In mutualistic or symbiotic relationships, two organisms live in association with each other and both receive benefits.

Symbiosis with human and animal intestine (probiotic yeast species)

Probiotics yeasts offer beneficial effects on the growth, health and immune response of the host (human and animals) when ingested into the digestive system through the diet.

The beneficial effects of the probiotics yeast to the host include prevention of several diseases. It acts as anti-cholesterol agent, an immune-enhancers, a producer of glucans, vitamins, digestive enzymes, and folates, and is antifungal, antibacterial (prevents *Clostridium difficile* that causes diarrhea), anti-inflammatory, and anti-tumor. Probiotics yeast also generates anti-oxidant products based on the presence of oxidase and peroxidase enzyme, phenols and flavonoids, tripeptide γ-l-glutamyll- cystinylglycine and glutathione.

Fermented foods are the primary sources of probiotic yeast particularly dairy products. **The most common probiotics yeast species includes** *Saccharomyces cerevisiae, S. cerevisiae* var. *boulardii, Candida albicans, C. humilis, C. parapsilosis, Debaryomyces hansenii, D. occidentalis, Geotrichum, Hanseniaspora, Isaatchenkia orientalis, Kloeckera lodderae, Kluyveromyces lactis, K. marxianus, Pichia kudriavzevii, Torulaspora, Rhodotorula,* *Wickerhamomyces*, *Williopsis* and *Yarrowia lipolytica*. Probiotic yeasts offer many advantages and have many shared characteristics; they are non-toxic to the host, can survives gastrointestinal transit, are highly concentrated in the product and have a long shelf-life. They are tolerant to stomach acidity and bile salts. The cell walls of probiotic yeast are highly adhesive to the intestinal mucosa and epithelial cells, and they are anti-biotic resistant, approximately 20 type of yeast are resistant to ampicillin (10–25 µgml^{-1}), chloramphenicol (30µgml^{-1}), erythromycin (5-15µgml^{-1}), penicillin (10 µgml^{-1}), streptomycin (25 µgml^{-1}), and tetracycline (30 µgml^{-1}). These types of yeast also produce digestive enzymes, secrete beneficial bioactive metabolites, act as immune-modulator, and are very safe without any pathogenic activity even when the host is immune-suppressed [55].

2.2$_g$ Meta-biotic relationships of yeast

The presence of specific organism is very important for the growth of another organism. For example *S. cervices* produces ethanol and *Acetobacter aceti* grows on this ethanol producing acetic acid (production of vinegar and glacial acetic acid).

$$\textit{Glucose} \xrightarrow{\textit{S. cervices}} \textit{ethanol} \xrightarrow{\textit{Acetobacter aceti}} \textit{Acetic acid}$$

Lactic acid bacteria growing on milk converts it to acidic substrate utilized by yeast which produces the flavoring compounds in the production of dairy products [4,5].

2.2$_h$ Parasitism relationships of yeasts

Parasitism occurs when one organism derives its food requirements from another living organism "host" causing harmful effects to the host [4,5,56].

Mold parasitism on yeast: Many myco-parasitic basidiomycetous fungi utilize yeasts as a nutrient sources of all the fungal groups [4,57].

Strictly human pathogenic yeasts: *Candida albicans*, *C. parapsilosis*, *Cry. neoformans*, and *Malassezia furfur* [58-60].

Yeast phytopathogen or parasites on higher plants: Yeasts are generally saprotrophic. They often develop intimate relationships with flowers, leaves, and fruits of plants; these relationships have been briefly summarized in the literature. *Nematospora coryli* and *Met. bicuspidata* yeasts act as plant pathogens.

Opportunistic or facultative spoilage yeasts: Yeast species are emerging due to the use of effective anti-bacterial treatments and immune-suppressive therapy; *S. cerevisiae* has been found in clinical infections. Several commensal yeasts may be isolated from the mouth, fingernails, and toenails of healthy hosts; a majority of them belong [1]. While many yeast species are saprophytic, they become pathogenic when the human host loses immunity, causing very serious diseases. Yeasts are saprophytic on fruits, vegetables, and uncooked and cooked foods. In wine-making, unwanted opportunistic yeasts are primarily *Candida, Kloeckera, Brettanomyces, Hansenula, Pichia*, and *S. bailii* which are also often observed in spoiled mayonnaise and salad dressings [61,62]. *Filobasidiella* (T) *neoformans* var. *neoformans* and *Filobasidiella neoformans* var. *bacillispora* or *Cryptococcus neoformans* (A) act as human pathogens [61,62].

2.2$_i$ Yeasts and bacteria relationships

Several known mutualistic and synergistic interactions exist in the association of yeasts and lactic acid bacteria, particularly in the fermented of food**.** Antagonism between bacteria and *Streptomyces* produces polyene anti-biotics such as nystatin and amphotericin B against Candidiasis (human pathogen)**.** Lactic acid bacteria produce hydrogen peroxide which has a lethal effect on yeasts**.** In wine, *S. cerevisiae* produces ethanol which prevents undesirable bacteria and other yeast species [4].

2.2$_j$ Yeast synergistic relationships of yeasts

In industrial processing, vitamins produced by yeasts and lactate produced by bacteria are mutually utilized in kefir grains (synergistic interaction) [4,47].

Lactobacilli bacteria ferments maltose in sour dough and produces glucose, fermented by yeasts [63].

In the fermentation of sauerkrauts and pickles, both fermentative and oxidative yeasts live together with lactic acid bacteria. The yeasts often form films on the surface of salt brine, on which the aerobic decomposition of lactic acid may facilitate spoilage [64].

In red wine, the malolactic fermentation by *Oenococcus* (*Leuconostoc*) *oenos* is facilitated by vitamins and amino acids produced by yeasts [65]. Oriental fermented foods, such as rice, soy, vegetables, and fish, consist of mixed communities of mold, yeast, lactic acid, and other bacteria that mutually interact [66].

In the ripening of sausages, cheeses, and other dairy products, yeasts develop interactive associations with bacteria [67].

2.3 Influence of Nutritional Factors on Yeast Growth

Yeast media or natural substrates are supplemented to the yeast through its principal nutritional requirements. Yeast growth is affected by several groups of nutrients that may be classified into the following [4,5,33-35] (Table 6-9):

1) Macro-elements: C, N_2, H_2, O_2, S, P, K, and Mg.

2) Micro-elements: Fe, Zn, Cu, Ca, Mn, Mo, Vn, Sc, Co, and Ga.

3) Growth co-factors: amino acids, vitamins, purines; pyrimidines, sterols, and others.

4) Other chemicals: CO_2 and H_2O (osmotic adjustment).

The most important nutrients for yeasts are carbohydrates that serve as carbon and energy source. Yeasts can ferment only a few sugars, primarily hexoses and oligosaccharides. Yeasts can utilize aerobic the following carbon source includes hexose, pentose, alcohol, organic acid, and other carbon compounds (Table 8). Assimilation is the aerobic utilization of the substrate for yeast growth whereas yeast fermentation is defined as the anaerobic metabolism of carbohydrates to produce ethanol and CO_2. The differences in the fermentation and assimilation of carbon sources are important for the diagnostic characteristics in yeast taxonomy and identification. Mono- and oligosaccharides are widely utilized by yeasts, although the fermentation of galactose is limited to some species. Not all yeasts can metabolize certain disaccharides and trisaccharides (sucrose, maltose, lactose, or raffinose) as they lack the necessary hydrolytic enzymes. The utilization of pentose is also restricted among yeasts species, and the fermentation of xylose may be a potentially useful in the industrial production of ethanol from the hydrolysis products of plant hemicellulose. The ability of yeast to metabolize polysaccharides and complex carbohydrates is restricted to only a few species. The utilization of starch by yeast is of particular interest in the industrial production of yeast biomass (single-cell protein, SCP) from starchy agricultural wastes. *Debaryomyces occidentals* and *Lipomyces* species are among the few species that possess enzymes that may undergo various amylase activities. While *S. diastaticus* can hydrolyze starch, *S. cerevisiae* cannot [68]. Some yeast species possess pectinolytic and xylanolytic enzymes, although only a few species are known to have cellulolytic capabilities. Other potential carbon sources for yeasts are hydrocarbons; several species can grow on these compounds [69]. Both organic and inorganic nitrogen sources may also be utilized by yeast. Although very few species can hydrolyze proteins extracellularly, short peptides may be transported into the cell and utilized intracellularly. Amino acids, amines, urea, and inorganic ammonium salts are suitable nitrogen sources for almost all yeasts. However, nitrate utilization, is confined to certain yeast species or genera, and is a valuable diagnostic characteristic used for identification [70].

2.3_a Carbon and energy sources in yeast substrates

Yeast obtained their carbon sources from substrates include monosaccharides (hexose glucose, galactose, rhamnose and sorbose), pentoses (xylose, ribose, and arabinose), disaccharides (sucrose, maltose, cellobiose, trehalose, lactose, and melibiose), trisaccharides (raffinose and melezitose), polysaccharides (soluble starch and inulin), α-methyl-glucosides, salicins, arbutins (glycosides), sugar alcohols (erythritol, ribitol, D-mannitol, D-glucitol, inositol and glycerol), and organic acids (citric, lactic, succinic, and 2-ketogluconate) [71] (Table 8).

In addition to basic carbon and nitrogen sources, inorganic micro-elements and small amounts of complex organic growth compounds, mostly vitamins, may be required for the growth of yeasts [72]. These requirements are normally fulfilled adequately in natural substrates. The requirements for minerals and growth factors among yeasts vary widely (Tables 8 and 9).

2.3_b Yeast growth co-factors

Many species synthesize all the necessary vitamins for growth and propagate vigorously in vitamin-free media, whereas others require specific vitamins. The differences in vitamin utilization may be used for identification. Biotin appears to be the most commonly required vitamin among yeast species. Some species require niacin, thiamine, pantothenic acid, folic acid, riboflavin, or myoinositol. Certain yeasts are notable for their exacting properties. For example, *Schizosaccharomyces octosporus* strains grow poorly in synthetic media unless supplemented with adenine, whereas *Dekkera* and *Brettanomyces* require a high concentration of thiamine for growth [73] (Table 9).

2.4 Influence of Internal Factors on Yeast Growth

Yeast growth is affected by internal factors specific to each yeast. These factors include the yeast genus, species, isolates, parts (vegetative cells, buds, and sexual spores), genetic traits, age, and source of the yeast isolates [4,5].

Conflict of Interest

The authors declare no conflict of interest.

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التصنيف البيئى الفسيولوجى للخمائر

مقالة مرجعية

تأليف

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تلعب الخمائر أدوارا مهمة جدًا في حياة الشعوب والصناعات المختلفة**.** تركز هذة المقالة المرجعية على دور العوامل البيئية والفسيولوجية في تصنيف الخمائر. وتصنف هذة العوامل إلى عوامل داخلية وخارجية. إلعوامل الخارجية تشمل العوامل البيئية والتغذوية. تتضمن العوامل البيئية أو الفيزيائية درجات الحرارة والضغط والضوء والإشعاع والخصائص الفيزيوكيميائية **(**الماء ودرجة الحموضة**)** ومستويات الأكسجين ووجود المركبات السامة والعلاقات الاحيائية بين الخميرة والكائنات الحية الأخرى**.** أما العوامل الغذائية فيندرج تحتها العناصر الكبرى والصغرى والعوامل المساعدة للنمو والمعاملات الأخرى (مثل ثاني أكسيد الكربون والرطوبة**).** وبالنسبة للعوامل الداخلية فهى خاصة بكل سلالة من الخمائرعلى حدة بما في ذلك (الجنس والنوع ومصدرها والخصائص الوراثية وعمر المستعمرة ومصدر السلالة وأجزاء الخميرة المختلفة**).** يعتبر التصنيف البيئى الفسيولوجى للخمائر عظيم الاهمية فى المجالات المختلفة للتكنولوجيا الحيوية. انة يمهد الطريق لاختيار افضل سلالات الخمائر الامنة والنشطة جدا التى تستخدم فى انتاج المواد الغذائية والمشروبات المخمرة وتقدم المواد التى تضاف للاطعمة وانتاج مواد صيدلانية علاجية والوقود الحيولى الامن صديق البية والمبيدات الحيوية والبروبيوتك (الخمائرالنافعة المتكافلة فى أمعاء الانسان) والانزيمات والتخلص من المخلفات الضارة وانتاج منظمات النمو النباتية وما شابة ذلك.