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1

Introduction to Fungal Physiology

Graeme M. Walker and Nia A. White

1.1 Introduction

Fungal physiology refers to the nutrition, metabolism, growth, reproduction and death of fungal cells. It also generally relates to interaction of fungi with their biotic and abiotic environment, including cellular responses to stress. The physiology of fungal cells impacts significantly on the environment, industrial processes and human health. In relation to ecological aspects, the biogeochemical cycling of carbon in nature would not be possible without the participation of fungi acting as primary decomposers of organic material. Furthermore, in agricultural operations, fungi play important roles as mutualistic symbionts, pathogens and saprophytes, where they mobilize nutrients and affect the physico-chemical environment. Fungal metabolism is also responsible for the detoxification of organic pollutants and for bioremediating heavy metals in the environment. The production of many economically important industrial commodities relies on the exploitation of yeast and fungal metabolism, and these include such diverse products as whole foods, food additives, fermented beverages, antibiotics, probiotics, pigments, pharmaceuticals, biofuels, enzymes, vitamins, organic and fatty acids and sterols. In terms of human health, some yeasts and fungi represent major opportunistic life-threatening pathogens, whilst others are life-savers, as they provide antimicrobial and chemotherapeutic agents. In modern biotechnology, several yeast species are being exploited as ideal hosts for the expression of human therapeutic proteins following recombinant DNA technology. In addition to the direct industrial exploitation of yeasts and fungi, it is important to note that these organisms, most notably the yeast Saccharomyces cerevisiae, play increasingly significant roles as model eukaryotic cells in furthering our fundamental knowledge of biological and biomedical science. This is especially the case now that numerous fungal genomes have been completely sequenced, and the information gleaned from fungal genomics and proteomics is providing valuable insight into human genetics and heritable disorders. However, knowledge of cell physiology is essential if the functions of many of the currently unknown fungal genes are to be fully elucidated.

It is apparent, therefore, that fungi are important organisms for human society, health and well-being and that studies of fungal physiology are very pertinent to our understanding, control and exploitation of this group of microorganisms. This chapter describes some basic aspects of fungal cell physiology, focusing primarily on nutrition, growth and metabolism in unicellular yeasts

and filamentous fungi.

1.2 Morphology of Yeasts and Fungi

Most fungi are filamentous, many grow as unicellular yeasts and some primitive fungi, such as the chytridomycetes, grow as individual rounded cells or dichotomous branched chains of cells with root-like rhizoids for attachment to a nutrient resource. Here, we will consider the most common growth forms: the filamentous fungi and unicellular yeasts.

1.2.1 Filamentous Fungi

The gross morphologies of macrofungi and microfungi are very diverse (see Plate 1.1). For example, we can easily recognize a variety of mushrooms and toadstools, the sexual fruiting bodies of certain macrofungi (the higher fungi Asomycotina and Basidiomycotina and related forms), during a walk through pasture or woodland. Microfungi (the moulds) are also diverse and are often observed on decaying foods and detritus, whereas many, including the coloured rusts, smuts and mildews, are common plant pathogens. Closer inspection of these visible structures, however, reveals that all are composed of aggregated long, branching threads termed hyphae (singular: hypha), organized to support spores for reproduction and dissemination. The hyphae of these aerial structures extend and branch within the supporting substratum as a network, termed a mycelium, from which the apically growing hyphae seek out, exploit and translocate available nutrients. Apically growing hyphae usually have a relatively constant diameter ranging from 1 to 30 μm or more, depending on fungal species and growth conditions. Filamentous fungi may be cultivated within the laboratory on a variety of different liquid or solid media. On agar, the radially expanding colonial growth form of the fungal mycelium is most evident, extending from an inoculum, on, within and sometimes above the substrate, forming a near spherical three-dimensional colony. This radiating, circular pattern is also visible during the growth of fairy ring fungi in grassland and as ringworm infections of the skin.

The hyphae of individual fungi may (theoretically) extend endlessly via apical growth, provided they are supported with appropriate nutrients and other environmental conditions. Eucarpic fungi, therefore, are spatially and temporally indeterminate organisms and, unlike animal, plant and other microbial individuals, have no predetermined maximum size or age. The mycelium is not, however, simply a homogeneously extending entity, but displays considerable developmental plasticity. Different interconnected regions of the fungal mycelium may grow, branch, anastomose (fuse), age, die, sporulate and display varying physiological and biochemical activities at different times or even simultaneously, depending on local micro-environmental conditions. Thus, colonies growing on relatively homogeneous media may be pigmented, exhibit different morphological sectors, produce aerial structures, grow as fast-effuse or slow-dense forms and even exhibit rhythmic growth (Plate 1.1). As well as reproductive structures and substrate mycelium, certain higher fungi, most notably the basidiomycetes, when growing within an environment where nutrients are distributed heterogeneously, can differentiate into long string-like structures called rhizomorphs or cords. These linear organs have evolved to rapidly explore for, connect and translocate water and nutrients between patches of resource (e.g. pieces of fallen timber on the forest floor or from tree root to tree root). Accordingly, many, particularly mature, rhizomorphs contain internal vessel hyphae which possess a wide diameter, forming a channel running along the organ. The peripheral hyphae are often closely packed and melanized for insulation.

Filamentous fungi and yeasts are simply different styles of fungal growth suitable for occupation of different habitats and produced by differing cell growth polarities. Many species termed dimorphic fungi can adopt either the hyphal or unicellular yeast forms according to environmental circumstances. For example, certain important human and animal pathogens exist as yeast forms mobilized in body fluids but are able to form hyphae or pseudohyphae for tissue invasion.

1.2.2 Yeasts

Yeasts are unicellular (mostly Ascomycete, Basidiomycete or Deuteromycete) fungi that divide asexually by budding or fission and whose individual cell size can vary widely from 2 to 3 μm to 20–50 μm in length and 1–10 μm in width. S. cerevisiae (commonly referred to as brewer's or baker's yeast), is generally ellipsoid in shape with a large diameter of 5–10 μm and a small diameter of 1–7 μm (Figure 1.1).

Figure 1.1 Scanning electron micrograph of a typical yeast cell. (×10 000). BS, bud scar; BirS, birth scar. (Reproduced with kind permission of Professor Masako Osumi, Japan Women's University, Tokyo.)

The morphology of agar-grown yeasts shows great diversity in terms of colour, texture and geometry (peripheries, contours) of giant colonies. Several yeasts are pigmented, and the following colours may be visualized in surface-grown colonies: cream (e.g. S. cerevisiae); white (e.g. Geotrichum candidum); black (e.g. Aureobasidium pullulans); pink (e.g. Phaffia rhodozyma); red (e.g. Rhodotorula rubra); orange (e.g. Rhodosporidium spp.); and yellow (e.g. Cryptococcus laurentii). The pigments of some yeasts have biotechnological uses, including astaxanthin from P. rhodozyma in aquacultural feed supplements for farmed salmon (that are unable to synthesize these natural pink compounds) (Table 1.1).

Table 1.1 Diversity of yeast cell shapes.

Cell shape	Description	Examples of yeast genera
Ellipsoid	Ovoid shaped cells	Saccharomyces
Cylindrical	Elongated cells with hemispherical ends	Schizosaccharomyces
Apiculate	Lemon shaped	Hanseniaspora, Saccharomycodes
Ogival	Elongated cell rounded at one end and pointed at other	Dekkera, Brettanomyces
Flask-shaped	Cells dividing by bud-fission	Pityrosporum
Miscellaneous shapes	Triangular	Trigonopsis
	Curved	Cryptococcus (e.g. Cryptococcus cereanus)
	Spherical	Debaryomyces
	Stalked	Sterigmatomyces
Pseudohyphal	Chains of budding yeast cells which have elongated without detachment	Candida (e.g. Candida albicans)
Hyphal	Branched or unbranched filamentous cells which form from germ tubes. Septa may be laid down by the continuously extending hyphal tip. Hyphae may give rise to blastospores	Candida albicans
Dimorphic	Yeasts that grow vegetatively in either yeast or filamentous (hyphal or pseudohyphal) form	Candida albicans

Saccharomycopsis fibuligera

Kluyveromyces marxianus

Malassezia furfur

Yarrowia lipolytica

Histoplasma capsulatum

1.3 Ultrastructure and Function of Fungal Cells

1.3.1 The Fungal Cell Surface

The cell envelope in yeasts and fungi is the peripheral structure that encases the cytoplasm and comprises the plasma membrane, the periplasm, the cell wall and additional extracellular structural components (such as fimbriae and capsules). The cell wall represents a dynamically forming exoskeleton that protects the fungal protoplast from the external environment and defines directional growth, cellular strength, shape and interactive properties. In filamentous fungi, cell-wall formation and organization is intimately bound to the process of apical growth. Thus, for example in Neurospora crassa, the wall is thin (approximately 50 nm) at the apex but becomes thicker (approximately 125 nm) at 250 μm behind the tip. The plasma membrane component of the fungal cell envelope is a phospholipid bilayer interspersed with globular proteins that dictates entry of nutrients and exit of metabolites and represents a selective barrier for their translocation. Ergosterol is the major sterol found in the membranes of fungi, in contrast to the cholesterol found in the membranes of animals and phytosterols in plants. This distinction is exploited during the use of certain antifungal agents used to treat some fungal infections, and can be used as an assay tool to quantify fungal growth. The periplasm, or periplasmic space, is the region external to the plasma membrane and internal to the cell wall. In yeast cells, it comprises secreted proteins (mannoproteins) and enzymes (such as invertase and acid phosphatase) that are unable to traverse the cell wall. In filamentous fungi, the cell membrane and wall may be intimately bound as hyphae and are often resistant to plasmolysis.

Fungal cell surface topological features can be visualized using scanning electron microscopy (SEM), and nanometre resolution is achieved using atomic force microscopy (AFM). The latter is beneficial, as it can be employed with unfixed, living cells and avoids potentially misleading artefacts that may arise when preparing cells for electron microscopy. Figure 1.1 shows SEM micrographs of a typical unicellular yeast cell envelope.

Ultrastructural analysis of fungal cell walls reveals a thick, complex fibrillar network. The cell walls of filamentous fungi are mainly composed of different polysaccharides according to taxonomic group. For example, they may contain either chitin, glucans, mannoproteins, chitosan, polyglucuronic acid or cellulose, together with smaller quantities of proteins and glycoproteins (Table 1.2). Generally, the semi-crystalline microfibrillar components are organized in a network mainly in the central cell wall region and are embedded within an amorphous matrix. Bonding occurs between certain components behind the extending hyphal tip, thereby strengthening the entire wall structure. There is evidence to suggest that the cell wall is a dynamic structure where considerable quantitative and qualitative differences occur not only between different fungal species, but also between different morphological forms of the same species and even in response to environmental stress. For example, a class of hydrophobic proteins called hydrophobins are localized within the aerial growth or appresoria (terminal swellings involved in infection) of certain fungi, whereas pigmented melanins are often found within some fungal cell walls to insulate against biotic and abiotic stresses.

Table 1.2 The major polymers found in different taxonomical groups of fungi, together with the presence of perforate septa in these groups

(adapted from Deacon (2005) and Carlile et al. (2001)).

The hyphae of higher fungi extend via tip growth followed by cross-wall formation or septation, whereas the lower fungi remain aseptate (except when segregating spores or in damaged colony regions). Septa may offer some structural support to hyphae. Significantly, septa serve to compartmentalize hyphae but are typically perforated, thereby permitting passage and

communication of cytoplasm or even protoplasm between compartments. However, septal pores can become blocked by Woronin bodies or other materials. This aids morphological and biochemical differentiation and serves to seal off stressed or damaged hyphae from undamaged colony regions. Again, different pore types are representative of different taxonomic groups and species (Table 1.2).

In yeasts, the cell-wall structure comprises polysaccharides (predominantly β-glucans for rigidity), proteins (mainly mannoproteins on the outermost layer for determining porosity), together with some lipid, chitin (e.g. in bud scar tissue) and inorganic phosphate material. Figure 1.2 shows the composition and structure of the S. cerevisiae cell wall. Hyphal cell walls generally contain fewer mannans than yeast cell forms, and such changes in composition are even observed during the transition from unicellular to mycelial growth of dimorphic fungi.

Figure 1.2 Cell envelope structure of the yeast S. cerevisiae (from Walker (1998). Permission obtained for First Edition).

Chitin is also found in yeast cell walls and is a major constituent of bud scars (Figure 1.3). These are remnants of previous budding events found on the surface of mother cells following birth of daughter cells (buds). The chitin-rich bud scars of yeast cells can be stained with fluorescent dyes (e.g. calcoflour white), and this can provide useful information regarding cellular age, since the number of scars represents the number of completed cell division cycles. Outside the cell wall in fungi, several extramural layers may exist, including fimbriae and capsules. Fungal fimbriae are long, protein-containing protrusions appearing from the cell wall of certain basidiomycetous and ascomycetous fungi that are involved in cell-cell conjugation. Capsules are extracellular polysaccharide-containing structures found in basidiomycetous fungi that are involved in stress protection. In Cryptococcus neoformans (the pathogenic yeast state of Filobasidiella neoformans) the capsule may determine virulence properties and evasion from macrophages. One extrahyphal substance, the polymer pullulan, is produced commercially from A. pullulans.

Figure 1.3 Transmission electron microscopy of ultrathin sections of fungal cells reveals intracellular fine structure.

1.3.2 Subcellular Architecture and Organelle Function

Transmission electron microscopy of ultrathin sections of fungal cells reveals intracellular fine structure (Figures 1.2 and 1.4). Subcellular compartments (organelles) are bathed in an aqueous cytoplasm containing soluble proteins and other macromolecules, together with low-molecular weight metabolites. However, the hyphae of central (and therefore older) colony regions of filamentous fungi may become devoid of protoplasm and organelles, as protoplasmic components are driven forward or are recycled, to support the growth of actively growing hyphal tips. Cytoplasmic components additionally comprise microbodies, ribosomes, proteasomes, lipid particles and a cytoskeletal network. The latter confers structural stability to the fungal cytoplasm and consists of microtubules and microfilaments. The following membrane-bound organelles may be found in a typical fungal cell: nucleus: endoplasmic reticulum (ER), mitochondria, Golgi apparatus, secretory vesicles and vacuoles. Several of these organelles form extended membranous systems. For example, the ER is contiguous with the nuclear membrane and secretion of fungal proteins involves intermembrane trafficking in which the ER, Golgi apparatus, plasma membrane and vesicles all participate. The physiological function of the various fungal cell organelles is summarized in Table 1.3.

Figure 1.4 Electron micrograph of a typical yeast cell. (CW, cell wall; CM, cell membrane; CMI, cell membrane invagination; BS, bud scar; M, mitochondrion, N, nucleus; V, vacuole; ER, endoplasmic reticulum. (Reproduced with kind permission of Professor Masako Osumi, Japan Women's

University, Tokyo.)

Table 1.3 Functional components of an idealized fungal cell.

Organelle or cellular structure	Function
Cell envelope	Comprising: the plasma membrane, which acts as a selectively permeable barrier for transport of hydrophilic molecules in and out of fungal cells; the periplasm, containing proteins and enzymes unable to permeate the cell wall; the cell wall, which provides protection, shape and is involved in cell–cell interactions, signal reception and specialized enzyme activities; fimbriae involved in sexual conjugation; capsules to protect cells from dehydration and immune cell attack.
Nucleus	Relatively small. Containing chromosomes (DNA–protein complexes) that pass genetic information to daughter cells at cell division and the nucleolus, which is the site of ribosomal RNA transcription and processing.
Mitochondria	Site of respiratory metabolism under aerobic conditions and, under anaerobic conditions, for fatty acid, sterol and amino acid metabolism.
Endoplasmic reticulum	Ribosomes on the rough ER are the sites of protein biosynthesis.
Proteasome	Multi-subunit protease complexes involved in regulating protein turnover.
Golgi apparatus and vesicles	Secretory system for import (endocytosis) and export (exocytosis) of proteins.
Vacuole	Intracellular reservoir (amino acids, polyphosphate, metal ions); proteolysis; protein trafficking; control of cellular pH. In filamentous fungi, tubular vacuoles transport materials bidirectionally along hyphae.
Peroxisome	Oxidative utilization of specific carbon and nitrogen sources (contain catalase, oxidases). Glyoxysomes contain enzymes of the glyoxylate cycle.

The nucleus is the structure that defines the eukaryotic nature of fungal cells. It is bound by a double membrane and encases the chromosomes in a nucleoplasm. Most yeast and fungi are haploid, although some (e.g. S. cerevisiae) may alternate between haploidy and diploidy. Chromosomes comprise DNA–protein structures that replicate and segregate to newly divided cells or hyphal compartments at mitosis. This, of course, ensures that genetic material is passed onto daughter cells or septated compartments at cell division. Yeasts usually contain a single nucleus per cell. However, the hyphal compartments of filamentous fungi may contain one or more nuclei. Monokaryotic basidiomycetes possess one nucleus per compartment, whereas dikaryons or heterokaryons possess two or more genetically distinct haploid nuclei. The maintenance of multiple nuclei within individual hyphal compartments allows fungi to take advantage of both haploid and diploid lifestyles. This is discussed further in Chapter 2.

In filamentous fungi, a phase-dark near-spherical region, which also stains with iron haemotoxylin, is evident by light microscopy at the apex during hyphal tip growth. The region is termed the Spitzenkörper, the apical vesicle cluster or centre or apical body, and it consists of masses of small membrane-bound vesicles around a vesicle-free core with emergent microfilaments and microtubules. The Spitzenkörper contains differently sized vesicles derived from Golgi bodies, either large vesicles or microvesicles (chitosomes), with varying composition. It orientates to the side as the direction of tip growth changes, and disappears when growth ceases. This vesicle supply centre is involved in wall extension and, hence, tip growth, branching, clamp connection formation (in Basidiomycetes) and germ tube formation.

1.4 Fungal Nutrition and Cellular Biosyntheses

1.4.1 Chemical Requirements for Growth

Yeasts and fungi have relatively simple nutritional needs and most species would be able to survive quite well in aerobic conditions if supplied with glucose, ammonium salts, inorganic ions and a few growth factors. Exceptions to this would include, for example, obligate symbionts such as the vesicular–arbuscular mycorrhizal (VAM) fungi which require growth of a plant partner for cultivation. Macronutrients, supplied at millimolar concentrations, comprise sources of carbon, nitrogen, oxygen, sulfur, phosphorus, potassium and magnesium; and micronutrients, supplied at micromolar concentrations, comprising trace elements like calcium, copper, iron, manganese and zinc, would be required for fungal cell growth (Table 1.4). Some fungi are oligotrophic, apparently growing with very limited nutrient supply, surviving by scavenging minute quantities of volatile organic compounds from the atmosphere.

Table 1.4 Elemental requirements of fungal cells.

Element Common sources Cellular functions

Carbon Sugars Structural element of fungal cells in combination with hydrogen, oxygen and nitrogen. Energy source

Hydrogen Protons from acidic environments Transmembrane proton motive force vital for fungal nutrition. Intracellular acidic pH (around 5–6) necessary for fungal metabolism

Oxygen Air, O2 Substrate for respiratory and other mixed-function oxidative enzymes. Essential for ergosterol and unsaturated fatty acid synthesis

Nitrogen NH4+ salts, urea, amino acids Structurally and functionally as organic amino nitrogen in proteins and enzymes

Phosphorus Phosphates Energy transduction, nucleic acid and membrane structure

Potassium K+ salts Ionic balance, enzyme activity

Magnesium Mg2+ salts Enzyme activity, cell and organelle structure

Sulfur Sulfates, methionine Sulfydryl amino acids and vitamins

Calcium Ca2+ salts Possible second messenger in signal transduction

Copper Cupric salts Redox pigments

Iron Ferric salts. Fe3+ is chelated by siderophores and released as Fe2+ within the cell Haem-proteins, cytochromes

Manganese Mn2+ salts Enzyme activity

Zinc Zn2+ salts Enzyme activity

Nickel Ni2+ salts Urease activity

Molybdenum Na2MoO4 Nitrate metabolism, vitamin B12

Being chemoorganotrophs, fungi need fixed forms of organic compounds for their carbon and energy supply. Sugars are widely utilized for fungal growth and can range from simple hexoses, like glucose, to polysaccharides, like starch and cellulose. Some fungi can occasionally utilize aromatic hydrocarbons (e.g. lignin by the white-rot fungi). Table 1.5 outlines the variety of carbon sources which can be utilized by yeasts and filamentous fungi for growth.

Table 1.5 Diversity of carbon sources for yeast and filamentous fungal growth

(adapted from Walker (1998)).

Carbon source Typical examples Comments

Hexose sugars D-Glucose, D-galactose, Glucose metabolized by majority of yeasts and filamentous fungi

D-Fructose, D-mannose If a yeast does not ferment glucose, it will not ferment other sugars. If a yeast ferments glucose, it will also ferment fructose and mannose, but not necessarily galactose

Pentose sugars L-Arabinose, D-xylose, D-xyulose, L-rhamnose Some fungi respire pentoses better than glucose. S. cerevisiae can utilize xylulose but not xylose

Disaccharides Maltose, sucrose, lactose, trehalose, melibiose, cellobiose, melezitose If

a yeast ferments maltose, it does not generally ferment lactose and vice versa. Melibiose utilization used to distinguish ale and lager brewing yeasts. Large number of yeasts utilize disaccharides. Few filamentous fungi (e.g. Rhizopus nigricans) cannot utilize sucrose

Trisaccharides Raffinose, maltotriose Raffinose only partially used by S. cerevisiae, but completely used by other Saccharomyces spp. (S. carlsbergensis, S. kluyveri)

Oligosaccharides Maltotetraose, maltodextrins Metabolized by amylolytic yeasts, not by brewing strains

Polysaccharides Starch, inulin, cellulose, hemicellulose, chitin, pectic substances Polysaccharide-fermenting yeasts are rare. Saccharomycopsis spp. and S. diastaticus can utilize soluble starch; Kluyveromyces spp. possess inulinase. Many filamentous fungi can utilize these depending on extracellular enzyme activity

Lower aliphatic alcohols Methanol, ethanol Respiratory substrates for many fungi. Several methylotrophic yeasts (e.g. Pichia pastoris, Hansenula polymorpha) have industrial potential

Sugar alcohols Glycerol, glucitol Can be respired by yeasts and a few fungi

Organic acids Acetate, citrate, lactate, malate, pyruvate, succinate Many yeasts can respire organic acids, but few can ferment them

Fatty acids Oleate, palmitate Several species of oleaginous yeasts can assimilate fatty acids as carbon and energy sources

Hydrocarbons n-Alkanes Many yeast and a few filamentous species grown well on C12-C18 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-ketoadipate pathway

Miscellaneous Adenine, uric acid, butylamine, pentylamine, putrescine Some mycelial fungi and yeasts, for example, Arxula adeninivorans and A. terestre can utilize such compounds as sole source of carbon and nitrogen

Lignin Can be decayed only by white-rot fungi (basidiomycotina). Little net energy gained directly, but makes available other polysaccharides such as cellulose and hemicellulose

'Hard' keratin Keratinophilic fungi

Fungi are non-diazotrophic (cannot fix nitrogen) and need to be supplied with nitrogenous compounds, either in inorganic form, such as ammonium salts, or in organic form, such as amino acids. Ammonium sulfate is a commonly used nitrogen source in fungal growth media, since it also provides a source of utilizable sulfur. Many fungi (but not the yeast S. cerevisiae) can also grow on nitrate and, if able to do so, may also utilize nitrite. Nitrate reductase followed by nitrite reductase are the enzymes responsible for converting nitrate to ammonia. Most fungi can assimilate amino acids, amines and amides as nitrogen sources. Most fungi (but not many yeasts) are also proteolytic and can hydrolyse proteins (via extracellularly secreted proteases) to liberate utilizable amino acids for growth. Urea utilization is common in fungi, and some basidiomycetous yeasts are classed as urease positive (able to utilize urea) whilst most ascomycetous yeasts are urease negative.

In terms of oxygen requirements, most fungi are aerobes and are often microaerophilic (preferring an oxygen tension below that of normal atmospheric). Although yeasts like S. cerevisiae are sometimes referred to as facultative anaerobes, they cannot actually grow in strictly anaerobic conditions unless supplied with certain fatty acids and sterols (which they cannot synthesize without molecular oxygen). In fact, there are thought to be very few yeast species that are obligately anaerobic. For aerobically respiring yeasts and fungi, oxygen is required as the terminal electron acceptor, where it is finally reduced to water in the electron-transport chain. Different fungal species respond to oxygen availability in diverse ways, and Table 1.6 categorizes fungi into different groups on this basis.

Table 1.6 Yeast and fungal metabolism based on responses to oxygen availability.

Mode of energy metabolism	Examples	Comments
Obligate fermentative	Yeasts: Candida pintolopesii (Saccharomyces telluris)	Naturally occurring respiratory-deficient yeasts. Only ferment, even in presence of oxygen
	Fungi: facultative and obligate anaerobes	No oxygen requirement for these fungi. Two categories exist with respect to the effects of air: facultative anaerobes (e.g. Aqualinderella and Blastocladia) and obligate anaerobes (e.g. Neocallimastix)
Facultatively fermentative		
Crabtree-positive	Saccharomyces cerevisiae	Such yeasts predominantly ferment high sugar-containing media in the presence of oxygen
Crabtree-negative	Candida utilis	Such yeasts do not form ethanol under aerobic conditions and cannot grow anaerobically
Non-fermentative	Yeasts: Rhodotorula rubra	Such yeasts do not produce ethanol, either in the presence or absence of oxygen
	Fungi: Phycomyces	Oxygen essential for such (obligately oxidative) fungi
Obligate aerobes	Gaemannomyces graminis (the take-all fungus)	The growth of these is markedly reduced if oxygen partial pressure falls below normal atmospheric

Adapted from Walker (1998), Deacon (2005) and Carlile et al. (2001).

Sulfur sources for fungal growth include sulfate, sulfite, thiosulfate, methionine and glutathione with inorganic sulfate and the sulfur amino acid methionine being effectively utilized. Virtually all yeasts can synthesize sulfur amino acids from sulfate, the most oxidized form of inorganic sulfur.

Phosphorus is essential for biosynthesis of fungal nucleic acids, phospholipids, ATP and glycophosphates. Hence, the phosphate content of fungi is considerable (e.g. in yeast cells it accounts for around 3–5 % of dry weight; the major part of this is in the form of orthophosphate ($H_2PO_4^-$), which acts as a substrate and enzyme effector). The fungal vacuole can serve as a storage site for phosphate in the form of complexed inorganic polyphosphates (also referred to as volutin granules). Both nitrogen and phosphorus availability may be growth limiting in nature. Filamentous fungi have evolved a number of biochemical and morphological strategies allowing capture of often poorly available phosphorus within the natural environment. Plants exploit such efficiency during symbioses between their roots and certain mycorrhizal fungi. The major storage form of phosphorus in plants is phytic acid (myo-inositol hexa-dihydrogenphosphate), which is poorly utilized by monogastrics (e.g. humans, pigs, poultry), and fungal (and yeast) phytases have applications in reducing phytate content of foods and feeds.

Concerning requirements for minerals, potassium, magnesium and several trace elements are necessary for fungal growth. Potassium and magnesium are macroelements required in millimolar concentrations, primarily as enzyme cofactors, whereas other microelements (trace elements) are generally required in the micromolar range. These include Mn, Ca Fe, Zn, Cu, Ni, Co and Mo. Table 1.7 summarizes the main metals required for fungal growth. Toxic minerals (e.g. Ag, As, Ba, Cs, Cd, Hg, Li, Pb) adversely affect fungal growth generally at concentrations greater than 100 μM.

Table 1.7 Metals required for fungal growth and metabolic functions

(adapted from Walker (2004)).

Metal ion	Concentration supplied in growth mediuma	Main cellular functions
Macroelements		
K	2–4 mM	Osmoregulation, enzyme activity
Mg Mg	2–4 mM	Enzyme activity, cell division
Microelements		

Mn	2–4 μM	Enzyme cofactor
Ca	<μM	Second messenger, yeast flocculation
Cu	1.5 μM	Redox pigments
Fe	1–3 μM	Haem-proteins, cytochromes
Zn	4–8 μM	Enzyme activity, protein structure
Ni	□10 μM	Urease activity
Mo	1.5 μM	Nitrate metabolism, vitamin B12
Co	0.1 μM	Cobalamin, coenzymes

aFigures relate to yeast (S. cerevisiae) growth stimulation and are dependent on the species/strain and conditions of growth, but they would be generally applicable for fungal growth.

Fungal growth factors are organic compounds occasionally needed in very low concentrations for specific enzymatic or structural roles, but not as energy sources. These include vitamins (e.g. thiamine, biotin), purines, pyrimidines, nucleosides, nucleotides, amino acids, fatty acids and sterols. For fungi to have a growth factor requirement, this indicates that cells cannot synthesize the particular factor, resulting in the curtailment of growth without its provision in culture media. Some fungi (e.g. Aspergillus niger, Penicillium chrysogenum) have very simple nutritional needs and are able to synthesize their own growth factors from glucose.

Table 1.8 Principal ingredients of selected industrial media for yeasts and fungi.

1.4.2 Fungal Cultivation Media

Fungal nutritional requirements are important not only for successful cultivation in the laboratory, but also for the optimization of industrial fermentation processes. In the laboratory, it is relatively easy to grow yeasts and fungi on complex culture media such as malt extract or potato–dextrose agar or broth, which are both carbon rich and in the acidic pH range. Mushrooms are cultivated on various solid substrates, depending on provincial availability. Therefore, Agaricus bisporus (common button mushroom) is grown in the UK, USA and France on wheat straw; the padi-straw mushroom (Volvariella volvacea) is grown in South-east Asia on damp rice-straw and in Hong Kong on cotton waste; and in Japan, the shiitake mushroom (Lentinus edodes) is cultivated on fresh oak logs. In industry, media for fungal fermentation purposes need to be optimized with regard to the specific application and production process. For some industrial processes, growth media may already be relatively complete in a nutritional sense, such as malt wort or molasses for brewing or baker's yeast production respectively (Table 1.8). However, for other processes, supplementation of agriculturally derived substrates, like corn steep liquor, molasses or malt broth, with additional nutrients and growth factors may be necessary. For example, the following may constitute a suitable fermentation medium for penicillin production by Penicillium spp.: sucrose (3 g/L), corn steep liquor (100 g/L), KH_2PO_4 (1 g/L), $(NH_4)_2SO_4$ (12 g/L), $CaCl_2 \cdot 2H_2O$ (0.06 g/L), phenoxyacetic acid (5.7 g/L) – information from Jorgensen et al. (1995). However, other industrial processes, such as the growth of Fusarium graminarium for production of Quorn™ mycoprotein, require culture on a completely defined medium (see Chapter 5).

1.4.3 Nutrient Uptake and Assimilation

Fungal cells utilize a diverse range of nutrients and employ equally diverse nutrient acquisition strategies. Fungi are nonmotile, saprophytic (and sometimes parasitic), chemo-organotrophic organisms. They exhibit dynamic interactions with their nutritional environment that may be exemplified by certain morphological changes depending on nutrient availability. For example, the filamentous mode of growth observed at the periphery of yeast colonies growing in agar is akin to

a foraging for nutrients as observed in certain eucarpic fungi. Metabolic dynamism is also evident in yeasts which, although not avid secretors of hydrolytic enzymes like higher fungi, are nevertheless able to secrete some enzymes to degrade polymers such as starch (as in amylolytic yeasts like Schwanniomyces occidentalis).

Several cellular envelope barriers to nutrient uptake by fungal cells exist, namely: the capsule, the cell wall, the periplasm and the cell membrane. Although not considered as a freely porous structures, fungal cell walls are relatively porous to molecules up to an average molecular mass of around 300 Da, and will generally retain molecules greater than around 700 Da. Typically, fungi absorb only small soluble nutrients, such as monosaccharides and amino acids.

The plasma membrane is the major selectively permeable barrier which dictates nutrient entry and metabolite exit from the fungal cell. Membrane transport mechanisms are important in fungal physiology, since they govern the rates at which cells metabolize, grow and divide. Fungi possess different modes of passive and active uptake at the plasma membrane: free diffusion, facilitated diffusion, diffusion channels and active transport (Table 1.9). Active transport of nutrients, such as sugars, amino acids, nitrate, ammonium, sulfate and phosphate, in filamentous fungi involves spatial separation of the ion pumps mostly behind the apex, whereas the symport proteins are active close to the tip. Thus, nutrient uptake occurs at the hyphal tip as it continuously drives into fresh resource, and the mitochondria localized behind the apex supply ATP to support the ion pump and generate proton motive force.

Table 1.9 Modes of nutrient transport in fungi.

Mode of nutrient transport	Description	Examples of nutrients transported
Free diffusion	Passive penetration of lipid-soluble solutes through the plasma membrane following the law of mass action from a high extracellular concentration to a lower intracellular concentration	Organic acids, short-chain alkanes and long-chain fatty acids by fungi and the export of lipophilic metabolites (e.g. ethanol) and gaseous compounds
Facilitated diffusion	Translocates solutes down a transmembrane concentration gradient in an enzyme (permease)-mediated manner. As with passive diffusion, nutrient translocation continues until the intracellular concentration equals that of the extracellular medium	In the yeast S. cerevisiae, glucose is transported in this manner
Diffusion channels	These operate as voltage-dependent ‘gates’ to transiently move certain nutrient ions down concentration gradients. They are normally closed at the negative membrane potential of resting yeast cells but are open when the membrane potential becomes positive	Ions such as potassium may be transported in this fashion
Active transport	The driving force is the membrane potential and the transmembrane electrochemical proton gradient generated by the plasma membrane H+-ATPase. The latter extrudes protons using the free energy of ATP hydrolysis that enables nutrients to either enter with influxed protons, as in ‘symport’ mechanisms, or against effluxed protons, as in ‘antiport’ mechanisms	Many nutrients (sugars, amino acids, ions)

1.4.4 Overview of Fungal Biosynthetic Pathways

Anabolic pathways are energy-consuming, reductive processes which lead to the biosynthesis of new cellular material and are mediated by dehydrogenase enzymes which predominantly use reduced NADP+ as the redox cofactor. NADPH is generated by the hexose monophosphate pathway (or Warburg–Dickens pathway) which accompanies glycolysis (see Section 1.5.1). In S. cerevisiae, up to 20 % of total glucose may be degraded via the hexose monophosphate pathway. This pathway generates cytosolic NADPH (following the dehydrogenation of glucose 6-phosphate using glucose 6-phosphate dehydrogenase and NADP+ as hydrogen acceptor) for biosynthetic reactions leading to the production of fatty acids, amino acids, sugar alcohols,

structural and storage polysaccharides and secondary metabolites. Besides generating NADPH, the hexose monophosphate pathway also produces ribose sugars for the synthesis of nucleic acids, RNA and DNA and for nucleotide coenzymes, NAD, NADP, FAD and FMN. This is summarized as follows:

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