Introduction to Fungal Physiology

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, industry and human health. In relation to ecological aspects, the biogeochemical cycling of elements in Nature would not be possible without the participation of fungi as primary decomposers of organic material. Furthermore, the dynamics of fungal activities are central to the efficiency of forestry and agricultural operations, as mutualistic symbionts, pathogens and saprophytes, by mobilizing nutrients and affecting the physico-chemical environment.

- Fungal metabolism is responsible for detoxification of organic pollutants and for bioremediation of heavy metals in the environment.
- The production of many economically important industrial commodities relies on exploitation of yeast and fungal metabolism and these include such diverse products as whole foods, food additives, fermented beverages, antibiotics, pigments, pharmaceuticals, biofuels, industrial enzymes, vitamins, organic and fatty acids and sterols.
- In terms of human health، some yeasts and fungi represent major opportunistic life-threatening pathogens.
- 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 several fungal genomes، including that of *S. cerevisiae*, have been completely sequenced and the information gleaned from fungal genomics and proteomics is providing valuable insight into human genetics and heritable disorders.

Based on their lifestyle, fungi may be circumscribed by the following set of characteristics:

1. Nutrition. Heterotrophic (lacking photosynthesis،(feeding by absorption rather than ingestion).
2. Vegetative state. On or in the substratum، typically as a non-motile mycelium of hyphae showing internal protoplasmic streaming. (motile reproductive states may occur).
3. .Cell wall. Typically present, usually based on glucans and chitin, rarely on glucans and cellulose (Oomycota).
4. Nuclear status. Eukaryotic, uni- or multinucleate، the thallus being homo- or heterokaryotic، haploid, dikaryotic or diploid, the latter usually of short duration (but exceptions are known from several taxonomic groups).
5. Life cycle. Simple or, more usually, complex.
6. .Reproduction. The following reproductive events may occur: sexual (i.e. nuclear fusion and meiosis) and/or parasexual (i.e. involving nuclear fusion followed by gradual de-diploidization) and/or asexual (i.e. purely mitotic nuclear division).
7. Propagules. These are typically microscopically small spores produced in high numbers.

8. Sporocarps. Microscopic or macroscopic and showing characteristic shapes but only limited tissue differentiation.
9. .Habitat. Ubiquitous in terrestrial and freshwater habitats, less so in the marine environment.
10. Ecology. Important ecological roles as saprotrophs، mutualistic symbionts, parasites, or hyperparasites.
11. Distribution. Cosmopolitan.

❖ The fungal cell

Fungal cells are similar to cells of other eukaryotic organisms in being composed of a membrane-bound cytoplasm containing a variety of organelles and at least one nucleus. However, most fungal cells are distinctive in that they possess a cell wall of unique composition, certain peculiar organelles, and septa, between adjacent cells. Fungal groups differ in the extent to which these characteristics are present, and these differences have been useful in fungal taxonomy.

FUNGAL CELL WALLS

Fungal cell walls are composed principally of polysaccharides with relatively small amounts of proteins, lipids, and inorganic ions. The polysaccharides occur in two major types of structures: **cablelike microfibrils** and a less highly organized **matrix**. Microfibrils are the principal structural components of the wall and are composed of separate polysaccharide chains wound around each other forming a strong, coarse strand. Networks of these strands are embedded in the matrix, an aggregation of smaller polysaccharides as well as proteins and lipids, which appears amorphous and granular. Portions of the fungal cell wall thus resemble reinforced concrete with the microfibrils functioning as the steel rods and the matrix the surrounding cement. This organization may explain the mechanical rigidity and strength of the wall.

In fungi microfibrils are composed of chitin, cellulose, or noncellulosic glucan. Chitin is an unbranched polymer of β-1,4-inked N-acetylglucosamine units, and its presence in cell walls is one feature distinguishing fungi from higher plants. Chitin is found in several of the major fungal groups including the Ascomycetes, Basidiomycetes, Deuteromycetes, and Chytridiomycetes. Cellulose is an un-branched polymer of β-1,4-linked glucose units and is present in the Oomycetes, the Hyphochytridiomycetes, and a few species of the Ascomycetes. cellulose present in these groups is slightly different from that found in the walls of green plants; it is less crystalline when examined by X-ray diffraction. The term glucan is used to describe a wide variety of polysaccharides composed entirely of glucose units, regardless of the type and extent of branching. Because of their complexity the structure of most glucans is not completely known. In addition, there is evidence that some fungi possess microfibrils composed in part of polysaccharide linked to protein.

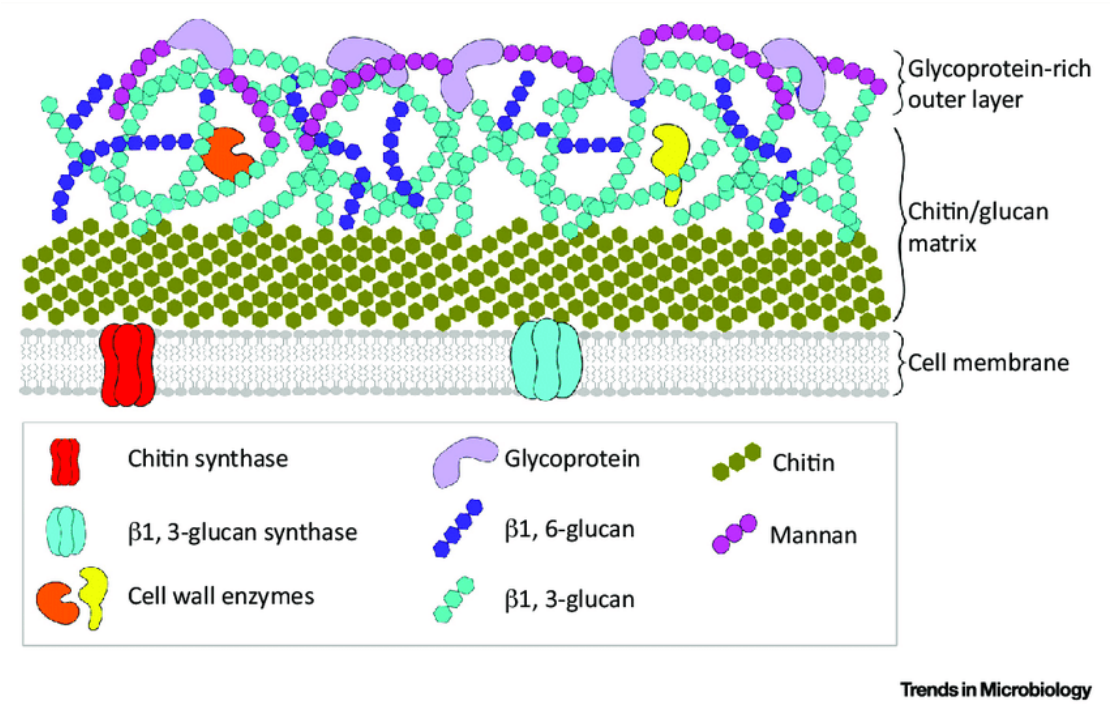
The carbohydrates present in the matrix vary considerably from one taxonomic group to another. The major matrix polysaccharides are chitin, cellulose, polymers of galactosamine, and noncellulosic glucans of various types including glycogen (a polymer of α-1,4-linked glucose), mannans (polymers of mannose), chitosan (polymers of glucosamine), and galactans (polymers of galactose). In addition, minor amounts of xylose, rhamnose, fucose, and uronic acids may be present.The arrangement of these monosaccharides in polymers and their roles in the architecture of the cell wall is not known.

The occurrence of microfibrils and matrix polysaccharides in fungal groups serves as one basis for fungal classification. (table 1). There is a fairly close relationship between classical fungal taxonomy based on morphology and a taxonomy based on the major wall polysaccharides. Thus, seemingly minor changes in the composition of the wall are correlated with rather striking morphological alterations and support the hypothesis that cell morphogenesis in fungi is controlled by patterns in cell wall differentiation.

Table 1: The major polymers found in different taxonomical groups of fungi together with the presence of perforate septa in these groups

Taxonomic grouping	Fibrillar polymers	Matrix polymers	Perforate septa present or absent
Oomycetes	β(1,3), β(1,6)-glucan cellulose	Glucan	Absent
Chytridomycetes	Chitin; glucan	Glucan	Absent
Zygomycetes	Chitin; chitosan	Polyglucuronic acid; glucuronomannoproteins	Absent
Basidiomycetes	Citin; β(1,3)-β(1,6) glucans	α(1,3)-glucan; xylomannoproteins	Present (mostly Dolipore)
Ascomycetes/ deuteromycetes	Citin; β(1,3)-β(1,6) glucans	α(1,3)-glucan; galactomannoproteins	Present (mostly simple with large central pore)

Proteins typically make up less than 10% of the cell wall matrix. Cell wall proteins function both as structural components and as enzymes. In the walls of *Saccharomyces cerevisiae* and *S. carlsbergenesis*, mannans are linked to protein via molecules of N-acetylglucosamine. Other glycoproteins present in der matophytes such as *Trichophyton*, *Aspergillus*, and *Microsporum* species occur on the outside of the wall and are responsible for the hypersensitive skin reactions of allergic humans and other animals. Numerous enzymes, particu larly hydrolases such as acid phosphatase, a-amylase, and protease have been located in the cell wall (fig.1). These enzymes may be important in hydrolyzing substrates in the environment to subunits that can be transported into the cell.



Figure(1): basic structure of the fungal cell wall

Lipids usually constitute less than 8% of the matrix, although *Blakeslea trispora* is reported to have a total lipid content of 30% . Wall lipids characteristically are composed of saturated rather than unsaturated fatty acids, and phospholipids are common. Small amounts of glycolipids and sphingosines have been identified in the walls of certain yeasts although the presence of glycolipids may be due to their being trapped in the wall in route from the cytoplasm into the medium . In *Candida tropicalis,* identified a mannan that is covalently linked to fatty acids. This mannan-fatty acid complex is found at the outer surface of the wall when the yeast is incubated on a medium containing n-alkanes as the carbon source but is absent when alkanes are replace with glucose. The hydrophobic portion of the mannan-fatty acid complex apparently is induced by the presence of hydrocarbons and serves as a medium in which the alkanes can dissolve, thus permitting their entry into the cell.

Cell walls also contain variable amounts of inorganic ions, which are usualy listed as "ash" following complete wall combustion. Usually the most abundant

element in ash is phosphorus, a component of phosphorylated sugars and phospholipids. Calcium and magnesium are often present in smaller amounts.

Not only does the wall composition vary among fungal taxonomic groups but differences are also seen in the walls of a single individual as it passes through its life cycle. We have seen that the dimorphic fungus *Mucor rouxii* can occur either as a filament or a unicell; the hyphal form produces spores. Glucans are the main structural components of spore walls, but chitosan predominates in the yeast and hyphal forms. Protein and melanin pigments are also higher in spore walls compared with walls of vegetative cells, but the phosphate content of spores is much lower. The architectural differences may be the key to understanding how the shape of the cell is determined.

PLASMA MEMBRANE

The plasma membrane regulates the passage of materials into and out of the cell

Because the membrane is selectively permeable it maintains the cell at a chemical composition much different from that of the external environment. Organelles and most macromolecules are effectively "trapped" within the membrane and are thus concentrated to the extent that the multitude of cellular reactions can take place at rates compatible with life. Indeed, life could not have evolved without this specific type of compartmentation. In those fungi that lack cell walls during a part of their life cycle, the plasma membrane also delimits the cell and gives some measure of physical as well as chemical protection from the environment.

Membrane Structure

The plasma membrane is composed mostly of lipid and protein in roughly equal amounts, in addition, small quantities of carbohydrates and occasionally even nucleic acids have been reported as being present.

The major lipids present in fungal membranes are phospholipids and sphingolip-

ids. These are polar molecules containing a hydrophilic "head'" and a long hydro- phobic "tail." Phosphatidylcholine and phosphatidylethanolamine are the most common phospholipids with phosphatidylserine and phosphatidylinositol present in smaller amounts. The fatty acid components present in phospholipids are roughly correlated with evolutionary relationships. In higher fungi the hydrocarbon tails tend to have an even number of carbons and are either saturated or monounsaturated: in lower fungi there are more odd-numbered fatty acids and most are polyunsaturated.

Sphingolipids are composed of one fatty acid, one polar head group, and the long-chain amino alcohol sphingosine or its derivative (Figure 2.9). This type of sphingolipid is also called a ceramide; if the polar group is a sugar the sphingolipid is a cerebroside. Although the structure of most fungal sphingolipids present in membranes has not been determined, ceramides and cerebrosides have been isolated from a wide variety of fungi. The term glycolipid is also used to denote lipid classes such as sphingolipids or phospholipids that contain a sugar moiety. Glycolipids composed of a carbohydrate linked to a fatty acid have been reported for several species, although it is uncertain whether they are membrane components or merely contaminants from the cytoplasm. Similarly, the reports of nonpolar lipids such as sterols and triglycerides in fungal membranes may be misleading due to the difficulty in isolating uncontaminated membrane fractions.

Experimental evidence suggests that phospholipids are arranged "back-to-back" in a bilayer (Fig. 2). On either surface of the bilayer are the hydrophilic heads؛ the hydrophobic tails are buried in the interior of the membrane away from the aqueous environment. The proteins are interspersed within the lipid bilayer. Some proteins are weakly bound and are easily removed by treatment with salts or chelating agents; these are termed peripheral proteins. Most, however, are integral proteins and are tightly bound. Membranes cleaved by freeze-fracturing in a plane parallel to the surface show these proteins forming a rough, pebblelike

array in the interior. Labeling studies indicate that surface proteins and lipids as well, tend to remain on the same surface but are able to move laterally. This observation has given rise to the "fluid mosaic" model of membrane structure in which proteins float upon a sea of lipids".

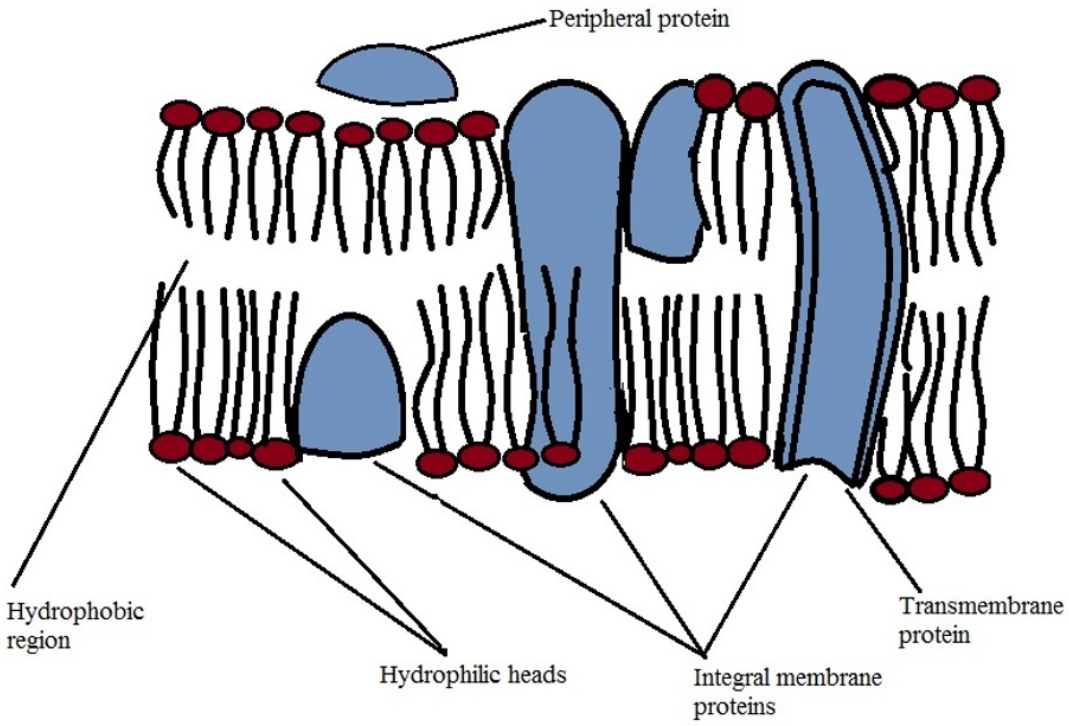


Figure 2: Model of a plasma membrane showing the arrangement of phospholipids and proteins in fungi.

The Movement of Materials Across Membranes

The lipoprotein structure of the plasma membrane makes it an effective barrier to the passage of most molecules. Those that can penetrate this barrier possess certain special attributes of size, shape, or solubility. These molecules enter the cell via one of three basic processes: **nonmediated diffusion**, **facilitated diffusion**, and **active transport**. These processes play a crucial role in fungal nutrition, and they have been studied extensively.

1. NONMEDIATED DIFFUSION

Certain molecules enter a cell by moving down an electrochemical gradient unassisted by other molecules. This is termed nonmediated diffusion and is a passive process, not involving the expenditure of metabolic energy. This process is characterized by having a transport rate directly proportional to the magnitude of the gradient. Once sufficient molecules have entered the cell so that the gradient no longer exists, diffusion ceases and the molecules across the membrane are said to being equilibrium.

It has been known for some time that lipids and lipid-soluble molecules diffuse readily across membranes. This is not surprising when we recall the high lipid content of membranes. Molecules that are lipid soluble can dissolve directly in the membrane lipids and move from one side to the other "in solution." Both CO_2 and O_2 are relatively lipid soluble and move across the membrane by diffusion.

2. FACILITATED DIFFUSION

Most fungal nutrients such as sugars, amino acids, and various ions penetrate the plasma membrane much faster than would be expected on the basis of their lipid solubility-they are simply too polar. Measurements indicate that transport is still passive, that is, transport occurs down an electrochemical gradient, but it is too rapid to be explained by nonmediated diffusion through the membrane lipids. In this case، polar molecules are "helped" across the membrane by specialized carrier proteins.This process is called facilitated diffusion; it is passive transport facilitated by a carrier.

Three principal criteria are used to determine if the movement of a particular nutrient is carrier-mediated. First, the rate of transport exhibits Michaelis-Menton saturation kinetics. This means that as the concentration of the molecule to be transported (called the substrate) increases, the rate of its uptake first increases linearly and then levels off at a certain maximum velocity, abbreviated V_{max} (Fig.3). Once the V_{max} plateau is reached, further addition of substrate change the uptake rate, and the system is said to be saturated with substrate. In nonmediated diffusion a plateau is not reached. The presence of saturation kinetics suggests that the substrate must first bind to another molecule (the

carrier) transport can take place. Saturation occurs when all the carriers are occupied by substrate; excess substrate molecules must then "wait their turn" until a car becomes available. A parameter that gives an indication of the affinity of a substrate for a particular carrier is the Michaelis constant, K_m, which can be obtained from graph like Figure 3a. The K_m, of a carrier-mediated process is that substrate concentration which yields a rate of uptake that is one-halt the maximum velocity. A high K_m value means that a relatively large amount of substrate is required before half the carriers are saturated; hence the carrier has a low affinity for the substrate A small K, value indicates a high affinity of the carrier for the substrate because half the carriers are saturated by a relatively low substrate concentration.

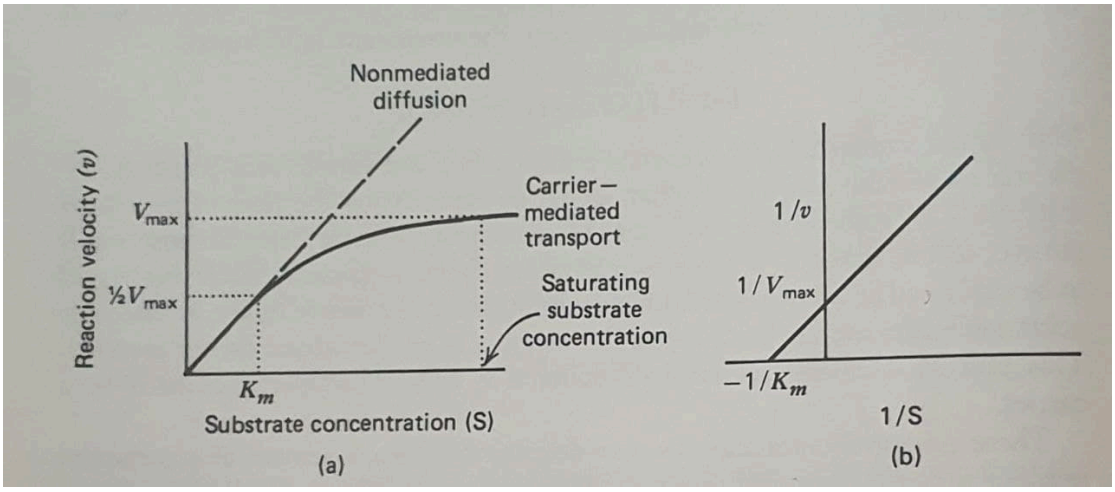


Figure3: kinetics of transports across membrane. (a) Transport via a carrier (—) becomes saturated at high substrate concentrations, but transport via nonmediated diffusion (-------) does not. (b) Data for carrier-mediated transport graphed in a double-reciprocal plot.

Carrier-mediated transport is also highly specific. Each class of nutrients (e.g‹. sugars, amino acids, vitamins, and metal ions) has its own array of carrier proteins‹ and within each class there may be specific carriers for different stereochemical groups. For example, in *S. cerevisiae* there are two principal carrier systems for the facilitated diffusion of monosaccharides. **The first** carrier is specific tor monosaccharides having an equatorial hydroxyl group on carbons I and 4 when the sugar is

in the chair conformation. Sugars transported by this carrier include D-glucose, D- mannose, D-xylose, D-arabinose, D-lyxose, and L-glucose. The second carrier is specific for monosaccharides with an equatorial hydroxyl group on carbon 2 and an equatorial - CH,OH on carbon 5 in the chair conformation. This carrier transports D-glucose, D-galactose, D-fucose, L-rhamnose, D-ribose, L-arabinose, and L-xylose.

The third principal characteristic of carrier-mediated transport is that the uptake of a certain substrate can be inhibited by the addition of a similarly shaped molecule. For example, Rand and Tatum (1980) measured the rate of uptake by *Neurospora crassa* of different concentrations of ^{14}C-fructose with and without the presence of 20 mM sorbose. Fructose and sorbose thus compete for the same site on the carrier protein. This competitive inhibition is often observed in carrier-meditated uptake when two substrates of similar structure are present.

Many different models have been proposed to explain how facilitated diffusion might take place. The most satisfactory model at present proposes that the molecule to be taken up passes through a pore or channel in the center of certain transmembrane proteins. Consider the uptake of K^+ by facilitated diffusion (Fig. 4). The ion first binds to a portion of the protein that has the complementary shape (Fig. 4 a,b). This binding causes a conformational change in the protein that results in the K^+being carried through the protein interior to the inside (Fig. 4 ,c.) During this process, the shape of the binding site also changes so that the affinity of the protein for K^+ is reduced (Fig. 4,d). The K^+ is thus released into the cell، and protein changes back to its original shape (Fig. 4,e). Once of the attractive aspects of this model is that only a small portion of the protein actually moves. The hydrophobic parts of the protein remain in contact with the hydrophobic membrane lipids, and the hydrophilic ends of the protein at the inner and outer membrane surfaces remain stationary as well. However, the interior of the protein forms a hydrophilic channel to which the polar K^+ can easily bind and through which the ion can be transported without contacting the nonpolar hydrophobic groups. Transport by this mechanism is thus energetically quite feasible.

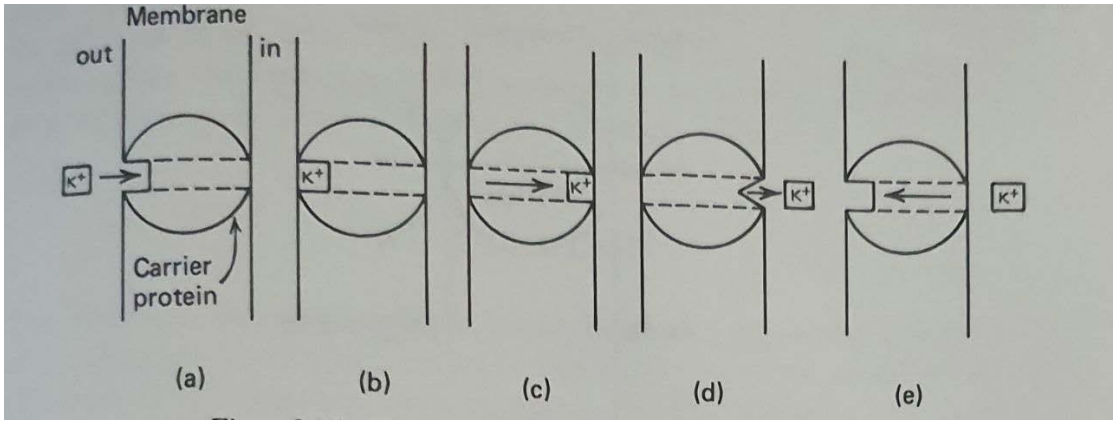


Figure 4: the pore model for the facilitated diffusion of K^+

3. ACTIVE TRANSPORT

In many cases, however, fungi are able to transport nutrients against an electrochemnical gradient. This uphill transport requires the use of metabolic energy, usually in the form of ATP, to actively "pump" molecules across the membrane. Because fungi possess these active transport systems they are able to scavenge nutrients present in small amounts in the environment by continuing to transport them into the cell even when their intracellular concentration exceeds their concentration in the environment.

Active transport, like facilitated diffusion, is a carrier-mediated process and thus exhibits saturation kinetics, high specificity, and inhibition phenomena. Howeverٰ three principal characteristics make active transport unique. **First**, as we mentioned above, molecules are transported up an electrochemical gradient. But because both charge and concentration must be taken into consideration, it is often difficult to determine if such a gradient actually exists. **Second**, active transport is dependent on metabolic energy; it is not a passive process. Thus, transport can be inhibited by molecules or environmental conditions that affect the production of energy in the cell. For example, active transport is inhibited by anaerobicity, a condition that also reduces the cellular ATP supply. Fluoride, an inhibitor of glycolysis, also inhibits active transport. **Third**, active transport processes are unidirectional; a particular carrier can move its substrate in only one direction across the membrane. This is due to a decrease in affinity of the carrier for the substrate once the substrate has been transported.

In general, ATP hydrolysis drives active transport by powering a conformational change in the carrier protein. However, in the uptake of certain sugars, amino acids، and metal ions it has been found that ATP hydrolysis is linked only indirectly to substrate transport but is directly linked to the transport of hydrogen ions. A model illustrating this type of active transport is shown in Figure 5. ATP is thought to be hydrolyzed at the inner membrane surface via an ATPase that spans the membrane. The energy released in this hydrolysis is used to actively transport hydrogen ions from the cytoplasm into the environment. The pH of the medium thus drops do to the accumulation of hydrogen ions Another protein in the membrane has binding sites for both a hydrogen ion ad the substrate. When one of the accumulated hydrogen ion in the environment binds to this carrier it induced a conformational change that increases the affinity of the carrier for the substrate. Both the hydrogen ions and the substrate are then co-transports across the membrane down a hydrogen ion gradient. On the inside the hydrogen ion leaves the carrier, thus lowering its affinity for the substrate, and the substrate is released. The carrier then assumes its original conformation and is ready to bind an additional hydrogen ion and substrate molecule on the exterior membrane surface.

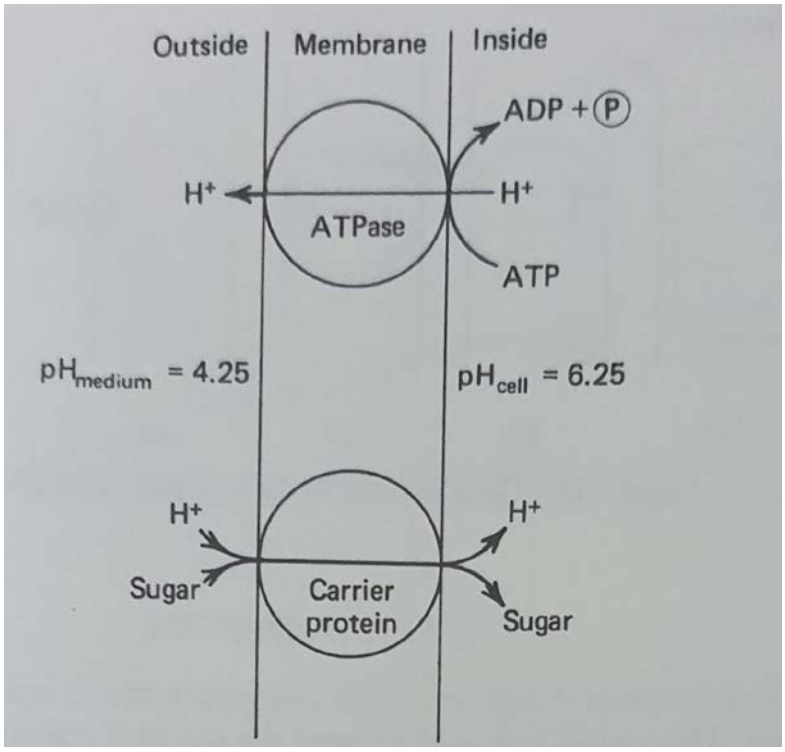


Figure 5: Active transport via ATP-induced hydrogen ion symport

By this two - step mechanism sugars and other substrates can be transported against t a gradient in substrate concentration because the - substrate-carrier complex is transported down a H^+ gradient. Hydrogen symport, as this type of active transport is called, can be inhibited by molecules such as 2,4-dinitrophenol and azide, which increase the permeability of the membrane to H^+ and thus destroy the hydrogen ion gradient

Still another variety of active transport involves the exchange of ions between the cytoplasm, the cell wall, and the incubation medium, For example, when potassium is taken up by *N. crassa* K^+ first binds to negatively charged groups (perhaps proteins or phosphates) in the cell wall, thus displacing other cations such as Na^+ that were previously bound there, This process does not depend on metabolic energy, but the extent of the ion exchange process depends on the pH of the medium, There is negligible exchange below pH 5.8, and exchange increases with increasing pH up to pH 9. This suggests that the cell wall constituents that bind cations are protonated at low pHs and thus have no affinity for cations, As the pH increases, these constituents become ionized and are thus effective ion exchangers, Following this exchange in the wall, K^+ binds to a carrier protein and is actively transported into the cell.

CYTOPLASM

The Cytoplasm, found immediately inside the plasma membrane, is a watery mass of dissolved solutes in which are embedded highly organized, membranous organelles such as mitochondria, Golgi apparatus, and microbodies as well as nonmemhranous structures such as ribosomes, microtubules, and microfilaments. Each organelle contains specialized enzymes which are compartmentalized within the organelle membrane and thus are separated from solutes in the amorphous portion of the cytoplasm. Compartmentation increases the efficiency of cellular metabolism by grouping together in one location the enzymes involved in a particular metabolic pathway. Also, the organelle membrane often serves as a surface area on which many of these reactions occur.

There are many enzymes which are not compartmentalized in organelles, and these along with a wide assortment of both large and small molecules

are found in the amorphous portion of the cytoplasm. The presence of these solutes, particularly proteins, gives the cytoplasm the capability of sol-gel transformations. Under certain conditions portions of the cytoplasm can be a semisolid (a gel) and under other conditions a liquid (a sol). Often the boundary between these two physical states within a single cell can be very sharp. For example, in the plasmodial stage of the slime mold *Physarum polycephalum*, cytoplasm in the gel state forms channels through which rivers of sol-state cytoplasm flow. After a few minutes these cytoplasmic states change so that channels become rivers and the rivers solidify to channels. Although their cytoplasmic functions are largely unknown, they may play a role in changing the physical state of the cytoplasm and the associated cytoplasmic streaming. It appears that as techniques improve the "amorphous" cytoplasm may be seen to have more structure than once imagined.

NUCLEUS

The fungal nucleus is a relatively large, membrane-bound structure that contains the cells genetic material. Nuclei vary widely in shape and size. They have been Observed squeezing through septal pores and are thus quite elastic. At a particular point their lite cycle, certain Ascomycetes and Basidiomycetes contain two genetically distinct nuclei and are said to be dikaryotic. The dikaryotic condition arises after two hyphae undergo cytoplasmic fusion (plasmogamy) without nuclear fusion (karyogamy). The nuclei in this binucleate cell then divide by mitosis, and the resulting dikaryotic hyphal strand can ramify throughout the medium, sometimes for extended periods of time, before the nuclei fuse.

The nucleus is surrounded by a double membrane called the nuclear envelope. The two membranes fuse at intervals, forming pores through which material can pass between the nucleus and cytoplasm. In yeast cells there may be as many as 400 Pores per nucleus, with the pores occupying almost 7% of the nuclear surface area.

Inside the nuclear envelope is the nucleoplasm, most of the time appearing amorphous and granular. The only clearly visible structure is the nucleolus, a densely staining spherical region containing large quantities of ribosomal RNA and other precursors for the synthesis of ribosomes.

The genetic material itself is largely invisible except when mitosis or meiosis is Occurring. The DNA and associated proteins form long thin threads of chromatin which condense when the nucleus begins to divide. Fungi exhibit considerable Fungi exhibit considerable variation in the behavior of their chromosomes during cell division.

THE ENDOMEMBRANE SYSTEM: ENDOPLASMIC RETICULUM، GOLGI, VESICLES, AND VACUOLES

Endoplasmic Reticulum

Fungal cells are criss-crossed by a system of narrow membrane-bound channels called the endoplasmic reticulum, or ER for short. The morphology and abundance of this membrane system varies with the physiological state of the cell and appears to be most abundant in cells that are rapidly growing. The ER undergoes continuous turnover; under certain conditions portions of the ER may break up into spherical microbodies which later coalesce and form new channels. Some of the ER is continuous with the nuclear membrane and may conduct material from the nucleus to the cytoplasm.

The ER may have ribosomes bound to its outer surface; it is then called rough ER, abbreviated RER. Ribosomes, whether attached to the ER or free in the cytoplasm, are the sites for the attachment of mRNA and the subsequent synthesis of proteins. Once synthesized, the proteins may be transported to the lumen of the ER, from which they migrate to different parts of the cell. Smooth ER lacks ribosomes and is the site f lipid synthesis. Vesicles containing the newly synthesized material may then form at the ER surface and be transported through the cell.

Golgi Apparatus

At certain locations in some cells portions of smooth ER are in close association with another membrane system called the Golgi apparatus. This structure is composed of a stack of flattened sacs with tubules and vesicles at the periphery. The flattened sacs are called cisternae, and a stack of cisternae makes up a dictyosome. Strictly speaking a Golgi apparatus is composed of several interconnected dictyosomes, but the term is also used to denote an isolated dictyosome. Macromolecules such

as lipids and proteins that have been synthesized elsewhere are transported to the dictyosomes, where they are chemically modified and packaged in a vesicle for transport through the cytoplasm. Precursors for the synthesis of additional plasma membrane and cell wall material are packaged in vesicles at the dictyosome and released at the cell surface. Hydrolytic enzymes are packaged in other vesicles that remain in the cell and function as lysosomes.

There is a functional continuum between the nuclear envelope, ER, dictyosomes‹ vesicles, and the plasma membrane (Fig. 6). The ER can be thought of as an extension of the nuclear envelope that ramifies throughout the cell. Near the Golgi apparatus portions of smooth ER form small vesicles that migrate toward a dictyosome and then coalesce to form cisternae on the dictyosome's proximal, or torming‹ face. These cisternae then migrate from the forming face to the opposite, or maturing, face where they give rise to vesicles. A steady-state is achieved between the formation of cisternae on one side of the dictyosome and their breakup on the other‹ so that the number of cisternae remains relatively constant. The vesicles thus produced may migrate to the plasma membrane, fuse with it, and release their contents to the outside; other vesicles apparently remain within the cell for some time. The Golgi apparatus 1s thus part of a complex endomembrane system composed of a variety of membrane-bound structures.

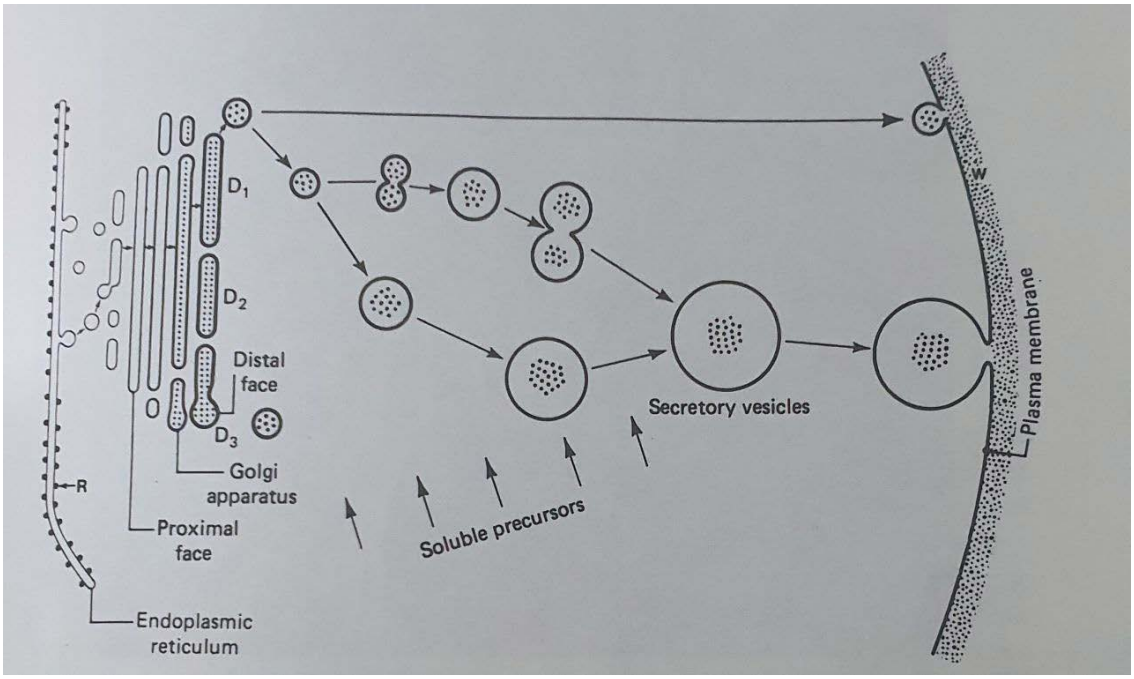


Figure 6: Relationship of the Golgi apparatus to other associated structure

Vacuoles

A vacuole is usually thought of as a large vesicle originating from smooth ER or a dictyosome just as other vesicles do. In addition, some vacuoles are formed at the plasma membrane as a result of pinocytosis or phagocytosis. In these processes، collectively called endocytosis, a portion of the plasma membrane surrounds a food particle (in phagocytosis) or some liquid (in pinocytosis). This membrane-enclosed material is then pinched off from the rest of the plasma membrane and enters the cytoplasm as a vacuole. In fungi, phagocytosis is common only in cells lacking cell walls, such as the amoeba stages of the slime molds. Pinocytosis is of more general occurrence.

Once in the cytoplasm, vacuoles may increase in size by fusing with other vacuoles. When phagocytotic vacuoles fuse with lysosomes the food particle is digested and its subunits released into the cytoplasm. Lysosomes can also digest other organelles such as mitochondria and ER and thus recycle their molecular building blocks back into the cell.

- ✓ Other functions of vacuoles???

MITOCHONDRIA

The mitochondria of fungi are basically similar in structure and function to those found in cells of plants and animals, Mitochondria are organelles that contain the enzymes involved in respiration, the degradation of fatty acids, and various other processes. All fungal cells possess at least one mitochondrion, but there is much structural variation not only among species but also during the life cycle of a single individual.

All mitochondria are composed of a cytoplasmic matrix surrounded by a double membrane. The outer membrane is smooth and resembles the plasma membrane، but the inner membrane is normally convoluted into a series of projections called cristae that may be either platelike or tubular. Platelike cristae are generally found in those fungi with chitinous cell walls (e.g., Chytridiomycetes، Zygomycetes, Ascomycetes, and Basidiomycetes). Tubular cristae occur in Myxomycetes and in fungi with cellulosic walls such as Oomycetes and Hyphocytridiomycete . Cristae provide an increased membrane surface area to which enzymes such as those associated with the respiratory electron transport chain are attached. Other enzyme systems are found in the matrix.

Mitochondria possess their own DNA, ribosomes, and protein-synthesizing machinery. The DNA and ribosomes in mitochondria are different from those found in the nucleus and cytoplasm of the parent cell and instead resemble those of bacteria. These and other observations suggest that mitochondria evolved from bacterial cells that were trapped inside a larger cell and were able to form a symbiotic relationship with this surrounding host.

- **Microbodies (peroxisomes and glyoxysomes)**
- **Woronine bodies**
- **Microtubules (cilia and flagella)**
- **Micerfilamenrs , Lomosomes, and Chitosomes**