1. MEMBRANE STRUCTURE AND MEMBRANE TRANSPORT IN PLANTS CELL

The basic functional units of plants, as with all living organisms, is the cell. Indeed, the study of plant physiology is very much a study of the physiology of plant cells and how their coordinated activities are reflected in the physiology of the whole organism. In a similar fashion, the architecture of a plant reflects the number, morphology, and arrangement of its individual cells. Architecture and function are inseparable.

Fig. 1.1. The plant cell. (A) A scheme of plant cell.

Fig. 1.1. Continued. The plant cell. (B) A representative plant cell is shown in Figure 1.1. A cell is an aqueous solution of chemicals called protoplasm surrounded by a plasma membrane. The membrane and the protoplasm it contains are collectively referred to as a protoplast. A living plant cell comprises protoplast and cell wall. Of course, the protoplasm and all of the components that make up protoplasm have important roles to play in the life of a cell, but the plasma membrane is a particularly significant because it represents the boundary between the living and nonliving worlds. The plasma membrane is also selectively permeable, which means that it allows some material to pass through but not others. Thus, the plasma membrane not only physically limits the cell, it also controls the exchange of material and serves to maintain essential differences between the cell and its environment.

We see in Figure 1.1. membranes are a singularly prominent feature. Additional selectively permeable membranes are found throughout the protoplast where they form a variety of subcellular structures called organelles. One of these organelles, the nucleus, contains the genetic information and is the control centre of the cell. The balance of the protoplasm, excluding the nucleus but including others organelles, is called cytoplasm. Different organelles in the cytoplasm are the sites of cellular respiration (a mitochondrion), photosynthesis (chloroplast), protein synthesis (ribosome), and so forth.

1.1 Cell membranes

There are membranes surrounding either the protoplast or any of the organelles within the protoplasm in cell. The term is frequently used as a synonym for the plasma membrane. All cell membranes have essentially the same structure and their selective permeability...
controls the passage of molecules and ions within the cell, particularly into and out of organelles. This ensures that metabolic processes are segregated without preventing links between biochemical pathways.

1.1.1. Plasma membrane (plasmalemma)

Plasma membrane is the outer layer of the protoplasm below the cell wall. Like most cell membranes it is formed by the orderly orientation of protein and phospholipids molecules. Plasma membranes range from 7.5 nm to 10 nm in thickness and are composed of approximately 60% proteins and 40% phospholipids. Membranes of different species contain characteristics types of polar lipids in proportions that are probably genetically determined. Davson and Danielli, in 1935, proposed that membranes are made up of a central region consisting of phospholipids and an outer denser region composed of proteins (Figure 1.2.).

![Image](image.jpg)

Fig. 1.2. The model of biological membrane (after Davson et Danielli 1935, modified).

The phospholipids molecules were believed to be arranged in two rows with their hydrophilic polar heads towards the outer edges and their hydrophobic hydrocarbon tails in the centre.

Although it is still accepted that two rows of phospholipids molecules form the backbone of the membrane it is believed that globular proteins, rather than forming a distinct outer layer, actually penetrate the whole width of the membrane in places (see Figure 1.3.). Both the phospholipids molecules and the proteins are thought to be able to move laterally giving the membrane fluid properties. This hypothesis of membrane structure is termed the fluid-mosaic model.
Fig. 1.3. (A) The Fluid-Mosaic model of biological membrane (after Singer et Nicolson 1972, modified).

Fig. 1.3. (B) A general model for membrane structure. This model is known as the Fluid-Mosaic (from Voet et Voet 1990, reprinted from G. Hopkins: Introduction to Plant Physiology. John Wiley et Sons, New York, 1995.)
Membrane protein may be categorized as integral protein or peripheral protein, according to whether it is integrated into the bilayer or bound to the hydrophyllic surface (Fig. 1.3).

Plasma membrane is selectively permeable, controlling the passage of material into and out of the cell. The proteins of the membrane include enzymes and compounds of the active transport system. Water and nonpolar molecules that dissolve in the phospholipide layers pass readily through the membrane. The membrane is relatively impermeable to charged ions, which enter the cell by means of the active transport system. Permeability varies in different parts of the plant and at different stages of development. Time-lapse photography of living membranes reveals almost constant and it is probable that there is continual replenishment of membrane constituents.

1.1.2. Tonoplast

The membrane separating the cell vacuole from the protoplasm. It has the same structure as the plasma membrane and mediates between the protoplasm and the vacuolar sap. In newly formed cells, when division has ceased, vacuoles are formed from small detached parts of the endoplasmic reticulum. As fluid (cell sap) accumulates they enlarge and coalesce to form a single vacuole, pushing the protoplasm against the cell wall. The surface area of the wall is increased, by stretching and the formation of additional material, to accommodate the increased volume of the cell. The vacuolar sap is a solution of organic and inorganic compounds. These may include sugars, soluble polysaccharides, soluble proteins, amino acids, carboxylic acid, red, blue, and purple anthocyanins, and mineral salts. Starch grains, oil droplets, and crystals of various kinds may also be present. These constituents of the sap probably represent metabolic by-products and reserve food material.

1.2. Membrane transport

As our understanding of membrane structure has changed over the years, so have the models that attempt to interpret how solutes cross these membranes. There are, however, three fundamental concepts – simple diffusion, facilitated diffusion, and active transport – that have preserved, largely because they have proven particularly useful in categorizing and interpreting experimental observations. These three concepts now make up the basic language of transport across all membranes of all organisms. These three basic models of transport are interpreted schematically in Figure 1.4.
1.2.1. Simple diffusion

The rate, which molecules in solution diffuse from one region to another is a function of their concentration difference. Since the membrane barrier is primarily lipid in character, nonpolar solute molecules tend to pass through more rapidly. Thus, the permeability coefficient generally reflects the lipid solubility of diffusing molecules. Few solutes of biological importance are nonpolar and only three \((\text{O}_2, \text{CO}_2, \text{NH}_3)\) appear to traverse membranes by simple diffusion through the lipid bilayer. Water, in spite of its high polarity, also diffuses rapidly through lipid bilayers. This is apparently because water is a neutral molecule and has a very small molecular volume.

1.2.2. Facilitated diffusion

We know that natural membranes contain a large number of proteins, many of which function as transport proteins. Some of these transport proteins facilitate the diffusion of solutes, especially charged solutes or ions, into the cell by effectively overcoming the solubility problem. In facilitated diffusion is determined by the concentration gradient (for uncharged solute) or electrochemical gradient (for ions).

Transport by diffusion, whether simple or facilitated, is considered a **passive** process. Passive means that the transport process does not require a direct input of metabolic energy. The energy for transport by diffusion comes from the concentration or electrochemical gradient of the solute being transported. As a consequence, transport by diffusion does not lead to an accumulation of solute against an electrochemical gradient.
Two major classes of transport proteins are known: **carrier proteins** (also known as carriers, transporters) and **channel proteins** (see **Figure 1.5**.). Whereas a carrier may transport between $10^4$ to $10^5$ solute molecules per second, a channel may pass on the order of $10^8$ ions per second.

![transporter versus channel](image)

**Fig. 1.5. Mechanisms of passive membrane transport – transporter or channel (from Voet et Voet 1995)**

### 1.2.3. Active transport

There is the transport of substances, usually polar molecules or ions, across a membrane against a concentration gradient. Active transport is energy requiring and is mediated by specific **carriers proteins** or **translocases**, which selectively bind a substrate and transport it across the membrane.

By definition, active transport is tightly coupled to a metabolic energy source – usually, although not always, hydrolysis of ATP. In other words, active transport requires an input of energy and does not occur spontaneously. Unlike facilitated diffusion, active transport is unidirectional - either into or out of the cell – and is always mediated by carrier proteins. Most of carriers are highly specific for one or a limited number of ion species. Active transport serves to accumulate solutes in the cell when solute concentration in the environment is very low. When used to transport solute out of the cell, active transport serves to maintain a low internal solute concentration. Because active transport system move solutes against a concentration or electrochemical gradient, they are frequently referred to as **pumps**.

There are, however, three fundamental concepts of active transport: uniport, symport, and antiport (see **Figure 1.6**.).
biological membrane

\[ \text{ATPase proton pump} \]

\[ \text{uniport} \]

\[ \text{symport} \]

\[ \text{antiport} \]

Fig. 1.6. The scheme of active membrane transport systems (after Lüttge et al. 1983, modified).

1. **uniport system** – at the same time a single ion species is translocated by single carrier in one direction.

2. **symport system** – cotransport, where the two ions of opposite charge or molecules (e.g. sugars, aminoacids) with protons are frequently transported together in the same direction at the same time by single carrier.

3. **antiport system** – cotransport, where the two ions of the same charge or molecules (e.g. sugars, aminoacids) with protons are frequently transported in opposite directions at the same time by single carrier.

The specific form of uniport system is the ATPase-proton pump.

1.2.3.1. ATPase proton pump

A schematic model relating ATPase proton pumps to solute exchange across membranes is shown in Figure 1.7. Proton-pumping ATPase is localised at the plasma membrane and tonoplast, also. Energy to drive the pumps is provided in the form of ATP, produced by oxidative phosphorylation in the mitochondria or by photophosphorylation in the chloroplast.
The proton pump uses the energy of ATP to establish a proton gradient and potential difference (negative inside) across the membrane. The energy of the proton gradient may active an ion channel or carriers for transport of ions across membrane.

There are several particularly interesting consequences of the ATPase-proton pump. First, a single ion species is translocated in one direction. This form of transport is consequently known as the uniport system. Second, because the ion transported carries a charge, an electrochemical gradient is established across the membrane. In other words, the ATPase-proton pump is electrogenic. It contributes directly to the negative potential difference across the plasma membrane. In fact, the electrogenic proton pump is a major factor in the membrane potential of most plant cell. Since the proton gradient across the plasma membrane is normally on the order of 1:5 to 2.0 pH units, it can account for approximately 90 to 120 mV of the total membrane potential. Third, since the species translocated is protons, the ATPase-proton pump establishes a proton gradient as well as an electrical gradient across the membrane. Energy stored in the resulting electrochemical proton gradient is also known as the proton motive force.