Plant Stress Physiology and Climate Change

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How Plants Struggle in Our New World

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To my biological and spiritual parents

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PREFACE

This is a book that started very humbly: Some notes useful for teaching classes and a couple of proposals that were considered to be too long and convoluted. After a while, they all needed to be treated a little better by their writer.

My primary intention was to gather the most interesting research on Plant Physiology and present a big picture for students and researchers. Obviously, the book cannot cover every topic and every interesting research I came across. My intention was also to show how I see these topics connecting to each other.

I hope this book can become a useful and effective tool in mastering the major topics of Plant Stress Physiology. I also hope you will keep on learning more about these fantastic green creatures that surround us in their humble silence when they have so much to teach us.

PREAMBLE

The first part of this book consists of basic, undergraduate-level knowledge of Plant Physiology. The purpose of Part A is to help students understand the most important chapters of Plant Physiology, not to explore the full extent of it. For more information, a number of scientific books and publications are mentioned in the text and included in the bibliography sections of Part A and Part B separately. The figures included in Part A were designed to be as simple as possible for easier and faster understanding of the complex processes in Plant Physiology. The intention of the writer was not to teach organic chemistry. This means certain details of the biochemical compounds and pathways are included only when they fulfil the primary purpose of Part A: to explain the basics of Plant Physiology as a preparation step for Part B, Plant Stress Physiology.

IMPORTANT MORPHOLOGY TERMS

The Plant Cell

The cell is an autonomous, independent unit of life with its own genetic material that is capable of reproducing itself (Figure 1).

The cell membrane or plasma membrane or cytoplasmic membrane or plasmalemma is a biological membrane that separates and protects cells from their environment, i.e. the extracellular space. It surrounds the symplastic space.

The cell wall is the outer layer of the plant cell, a rigid envelope of polysaccharides outside the plasma membrane of the cells of plants, fungi and bacteria. The cell wall of algae and higher plant cells consists mainly of cellulose, but also of hemicellulose and pectin. There are two types of cell walls, the primary and the secondary. The secondary cell wall is formed in mature, non-dividing cells inside the primary cell wall. Compared to the primary cell wall, it is stiffer and thicker and contains a higher proportion of cellulose as well as lignin, suberin and cutin.

The apoplast or apoplastic space consists of the intercellular space, the cell walls, and the xylem.

Plasmodesmata are pores in the cell wall that enable communication and transport between cells.

The cytosol or intracellular fluid or cytoplasmic matrix is the aqueous part of the cell cytoplasm in which the organelles are suspended. The cytosol is divided into compartments by membranes.

The cytoplasm is the cell substance between the cell membrane and the cell nucleus and contains the cytosol, the organelles, the cytoskeleton and other particles. It is a gel-like matrix and controls cell metabolism and cell signalling.

In eukaryotic cells, the cell **nucleus** is an organelle that contains the majority of the cell's genetic (hereditary) material. The cell nucleus is a kind of control centre. The genetic material is organised in DNA molecules and a large number of proteins to form chromosomes.

Protoplasm is the cytoplasm including the nucleus (it also includes the nucleoplasm) and other organelles.

Ribosomes are the smallest and most abundant organelles. They consist of RNA and protein and are themselves macromolecular machines of protein synthesis. Ribosomes link amino acids together to form polypeptide chains.

The endoplasmic reticulum is a network of membranous tubes/tunnels that connect to the nuclear membrane, lie next to each other like flattened sacs and to which ribosomes are attached. The endoplasmic reticulum has two subunits: the rough endoplasmic reticulum (for protein synthesis) and the smooth endoplasmic reticulum (for lipid synthesis).

The Golgi bodies (or apparatus or complex) are a complex of vesicles and folded membranes (cisternae) near the cell nucleus. They are involved in the secretion and intracellular transport of proteins and carbohydrates, which they package in membrane-bound vesicles and export from the cell.

Plastids are organelles with double membranes (an outer and an inner membrane) that are responsible for the production and storage of “food” or the synthesis of cell building blocks. They often contain pigments.

The **chloroplast** is a plastid in green plant cells that contains the pigment chlorophyll and is responsible for Photosynthesis. Inside the chloroplast, in the **stroma**, disc-like **thylakoids** are piled up in a **granum** (Figure 2). Many grana together are connected to each other with a bridge-like structure, **lamella**. The inside of a thylakoid is known as **lumen**.

Chromoplasts produce and store yellow and orange pigments, which give colour to petals and fruits.

Leucoplasts do not contain pigments and are found in non-photosynthetic tissues and root cells, where they store starch, lipid, or protein.

Amyloplast is a type of organelle that is responsible for producing and storing starch within plant cells.

Elaioplasts are a type of leucoplasts that play a crucial role in storing fats or lipids within fat droplets, which are also known as plastoglobuli.

Proteinoplast, also known as proteoplast, aleuroplast, or aleuronoplast is a type of leucoplast that stores proteins.

Mitochondria are semi-autonomous organelles responsible for cell respiration generating energy from glucose to produce energy as adenosine triphosphate (ATP) molecules. Mitochondria are surrounded by an outer membrane and an inner membrane. The space between them is known as the intermembrane space. The folds of the inner membrane, the **cristae**, extend into the matrix, the space within the inner membrane (Figure 2).

Peroxisomes are small organelles involved in lipid metabolism and photorespiration. They have a simple membrane surrounding them and often contain a crystalline structure at their centre. They contain catalase, a reducing enzyme that converts Reactive Oxygen Species (ROS) into water and oxygen.

Glyoxysome is a type of peroxisome found in fat-storage tissues such as those present in germinating seeds.

Spherosomes, also known as oleosomes, are small, single-membrane organelles that participate in lipid storage and synthesis.

The cytoskeleton is comprised of protein polymers that make up microtubules.

A vacuole is an organelle in the cytoplasm that is separated by a membrane called a tonoplast. It looks like a cyst and is primarily used for storage purposes, ranging from water, ions, and sugars to even toxic compounds. Besides storage, it also maintains the turgor pressure of the cell and facilitates cell growth. Vacuoles can be quite large, occupying 30-90% of the cell's volume.

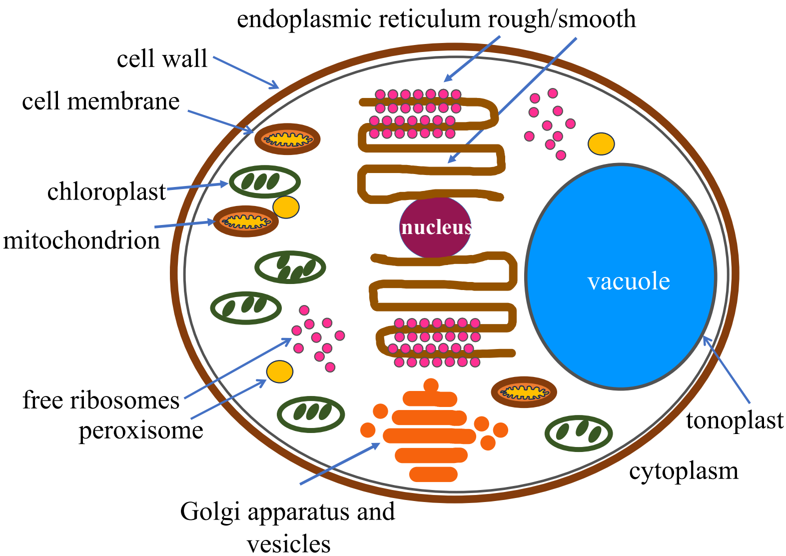

Figure 1: A simplified graphic of a plant cell structure. A cell is surrounded by the plasma membrane, which is surrounded by the cell wall. Inside a cell, there are various organelles depending on the cell type. There is also a nucleus, where the majority of the cell’s genetic material is stored, and at least one vacuole, where various molecules are stored in significant quantities.

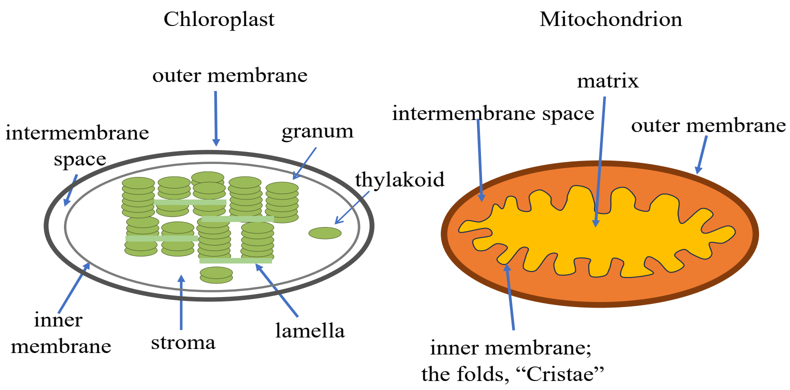

Figure 2: A simplified graphic of the structure of a Chloroplast and a Mitochondrion. In the chloroplasts, thylakoids are organised in grana inside the stroma. In the mitochondria, folds of the inner membrane, the cristae, extend into the matrix, the space within the inner membrane. The chloroplast is where photosynthesis takes place. The mitochondrion is where cell respiration takes place.

The Plant

Plants are generally divided into **angiosperms** and **gymnosperms**. Angiosperms have flowers and fruits and their seeds are enclosed within an ovary. Gymnosperms are non-flowering plants with unenclosed seeds and they rely on the wind (not on pollinators) for their reproduction. They include conifers, cycads and Ginkgo. The flowering plants are divided into monocotyledon and dicotyledon species. Monocotyledon seeds contain one embryonic leaf (one cotyledon), while the latter have two cotyledons. In contrast to dicotyledons, monocotyledons have parallel leaf veins and fibrous roots and their vascular tissue is scattered throughout the stem. Characteristic monocotyledon species include grains. The present book will focus more on dicotyledon species. Plants consist of four main types of tissues, which include meristematic, dermal, ground, and vascular tissues.

Meristems are specialised tissues responsible for the growth and development of plants. They are constantly dividing and producing young, undifferentiated cells that have the ability to proliferate. There are three types of meristems: apical, lateral, and intercalary. Apical meristems are located at the tips of shoots and roots and are responsible for primary growth, which is vertical. The cambium is a meristematic tissue but not all meristems are cambium. Meristems are responsible for primary and secondary growth.

Lateral meristems, which consist of vascular cambium and cork cambium, are responsible for secondary growth, which is horizontal. The vascular cambium is responsible for increasing the diameter of stems and roots, which leads to the formation of woody tissue. On the other hand, cork cambium produces bark. Intercalary meristems are found in plants that do not have a vascular cambium or a cork cambium because they do not increase in girth. They are responsible for the length increase of plants and the regrowth of cut grass.

The **epidermal** tissues in plants consist of several types of cells, including epidermal cells, guard cells, subsidiary cells, and trichomes (epidermal hairs). Among these, the basic epidermal cells are the most common and least specialised. They have an irregular shape and do not contain any chloroplasts. Elongated epidermal cells are typically found in elongated organs. The epidermis on the upper and lower surfaces of leaves may differ. In some species, the wall of the epidermal cells on the leaf's surface is thicker, especially in the epidermis of conifer needles and leaves of xerophytes.

The epidermal cells of plants are bound tightly to each other, providing mechanical strength and protection to the inner plant cells. These cells are further shielded by a cuticle, protecting them against water loss, intense sunlight, and wind. In dry climates, leaves have extra thick cuticles. Bark, on the other hand, is the secondary external tissue that surrounds the stems or roots of dicotyledonous plants.

Trichomes, or plant hairs, are elongated extensions of the epidermal cells and usually have secretory functions.

Stomata are tiny openings on the surface of leaves. They are formed of two symmetrical, kidney-shaped **guard cells** that can change their size to create an opening between them. This opening allows for the exchange of gases needed for photosynthesis, respiration, and transpiration. Surrounding the guard cells are subsidiary cells that support their function.

The **ground** tissue of a plant consists of three types of cells: **parenchyma, collenchyma**, and **sclerenchyma**. This tissue comprises the majority of the plant's primary body.

Parenchyma cells are a highly abundant type of cell that can be found in all parts of higher plants. They have thin walls and large vacuoles, which make them capable of storing materials. These cells also have the ability to repair damage in plant tissues by dividing when they are mature.

The parenchyma tissue is responsible for most of the edible portion of fruits. Parenchyma cells have several functions such as storage, photosynthesis, and making up the bulk of the ground and vascular tissues.

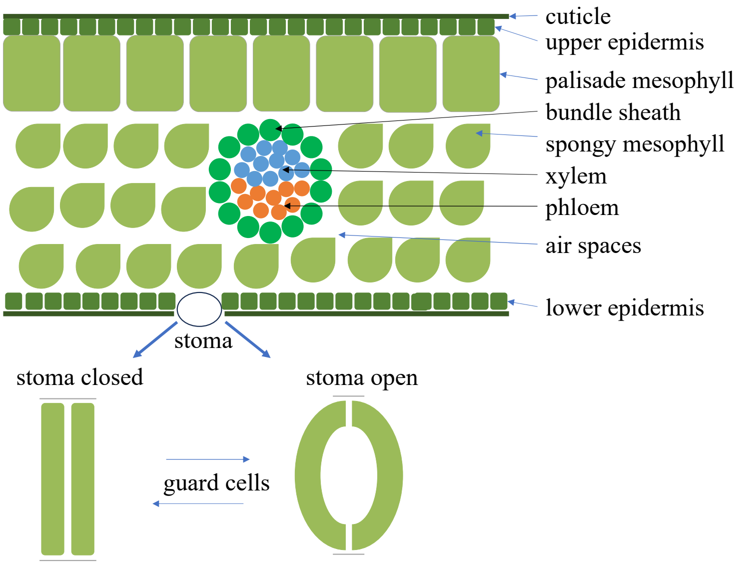

Figure 3: A simplified graphic of the leaf structure of a dicotyledon. The palisade structure takes full advantage of the light falling on the leaf. The spongy mesophyll leaves space for the gas exchange to take place through the stomata. Stomata (*mouths* in Greek) open when the guard cells swell via a complex mechanism that increases their cell turgor. Stomata close again when their turgor decreases. Water comes via the xylem and is diffused in the tissue. The cells in the circle surrounding the xylem and phloem cells are very characteristic in "C4 plants".

Chlorenchyma cells are a type of parenchyma cells containing chloroplasts, which are found in green tissues and leaves where they play a key role in photosynthesis. **Palisade** parenchyma cells are found in leaves in the mesophyll below the epidermis. **Spongy** mesophyll cells are located beneath the first layers of palisade cells (Figure 3). Ray parenchyma cells are found in wood rays that carry nutrients laterally in a woody stem.

Finally, **Aerenchyma** cells are loosely packed parenchyma cells that contain large interconnected air spaces. They are typically found in aquatic plants like water lilies where they facilitate oxygen transport.

Strengthening tissue consists of collenchyma and sclerenchyma. **Collenchyma** cells are elongated cells with extra thick cell walls of cellulose and pectin. They have a living protoplasm, like the parenchyma cells, but the difference is the increased thickness of their walls. Collenchyma is found beneath the epidermis (the first layer under the cuticle) and provides mechanical tissue for the flexible support of the plant organs. **Sclerenchyma** are cells with thick, tough secondary walls with lignin. Reaching maturity these cells die and serve as support of the structure. There are two subtypes: Sclereids (they are as long as they are wide) and fibres (they are much longer than they are wide).

The Vasculature

Vascular tissue forms the transport system in plants, consisting of **the xylem, phloem, parenchyma, and cambium cells.**

The xylem is the tissue responsible for transporting water and minerals from the roots to the shoots (Figure 4). It is composed of several types of cells, including **tracheids, vessels, xylem fibres, and xylem parenchyma**. Tracheids are long, thick cells with lignified walls that die once they mature. Vessels are tubes formed by a chain of elongated cells. Xylem fibres are sclerenchyma fibres that are associated with the xylem. Xylem parenchyma cells are living cells that accompany the xylem tissue.

The phloem tissue is responsible for transporting sugars from the leaves to other parts of the plant. It runs alongside the xylem and it consists of sieve elements, companion cells, phloem fibres and phloem parenchyma. The sieve elements comprise sieve cells and sieve tubes. Sieve cells are thin, long, and alive. Sieve tubes have sieve plates that help circulate the sugars throughout the plant. Companion cells are also alive and have a dense, granular cytoplasm with a prominent nucleus. They perform important functions that sieve tubes lose as they mature. Phloem fibres, on the other hand, consist of lignified sclerenchyma cells and have small, rounded, simple pits. Finally, phloem parenchyma cells are present in the phloem of dicots, which are plants whose seeds have two embryonic leaves or cotyledons.

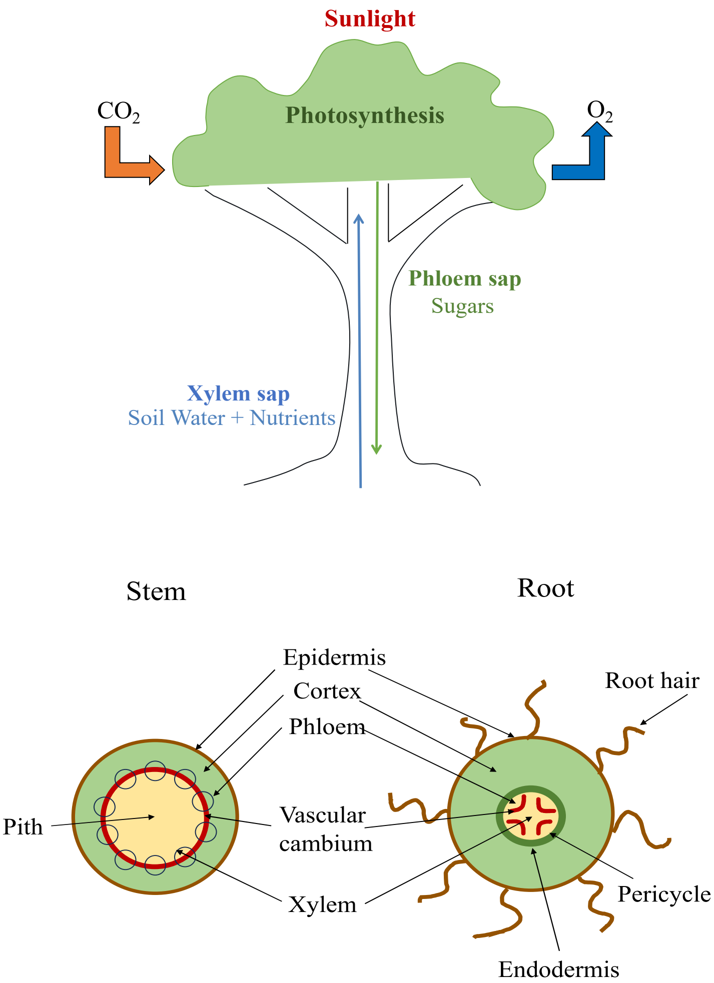

Figure 4: A simplified graphic representing the plant's fundamental processes. Plants absorb atmospheric CO_2, soil water, and sunlight to produce sugars in the leaves during photosynthesis and release O_2 into the atmosphere. The xylem brings soil water and nutrients to the leaves, while the phloem distributes the sugars produced throughout the plant body. However, the cross-section of the stem (left) and the root (right) are different. In the stem, the vascular cambium (red circle) produces phloem cells towards the epidermis, while xylem cells toward the pith. In the root, the vascular cambium (the open red cross) is surrounded by the pericycle which is surrounded by the endodermis. The scheme represents a dicotyledon structure.

Roots

There are three main types of roots: primary, secondary, and adventitious. The primary root consists of the **stele**, which is a central cylinder of vascular tissue surrounded by the **cortex**, large storage parenchyma, and on the outside the epidermis. The innermost layer of the cortex is called the endodermis, which is characterised by the presence of suberin in the "Casparian" strip. The endodermis controls the movement of water and nutrients through plasma membranes and plasmodesmata. The pericycle inside it generates meristematic cells to support secondary growth and the cambium that produces xylem and phloem. The root can be divided into four main zones, including the root cap, the zone of cell division, the zone of cell elongation, and the zone of cell differentiation (Figure 5). As the primary root grows, secondary roots emerge from its body.

Root hairs are elongations of the epidermal cells of roots. These cells provide a large surface area for the absorption of water and nutrients from the soil. Root hairs are essential in expanding the surface foraging capabilities of the root. Rhizomes, on the other hand, are underground stems that undergo structural modifications. They have branches and are used for storage purposes.

Roots exhibit a variety of shapes. Fibrous roots are small, thin and of uniform length. Examples include onion, rice, and maize. Taproots are thick, straight and deep roots such as those found in cotton, coffee, carrots and gymnosperms. Creeping roots are shallow and extend far from the plant, covering a wide area instead of penetrating deeply into the soil (e.g. trees). Tuberous roots are very thick and can store large amounts of reserves (e.g. Cassava). Adventitious roots start from the stem above the collar and then grow down into the soil (e.g. maize and rice).

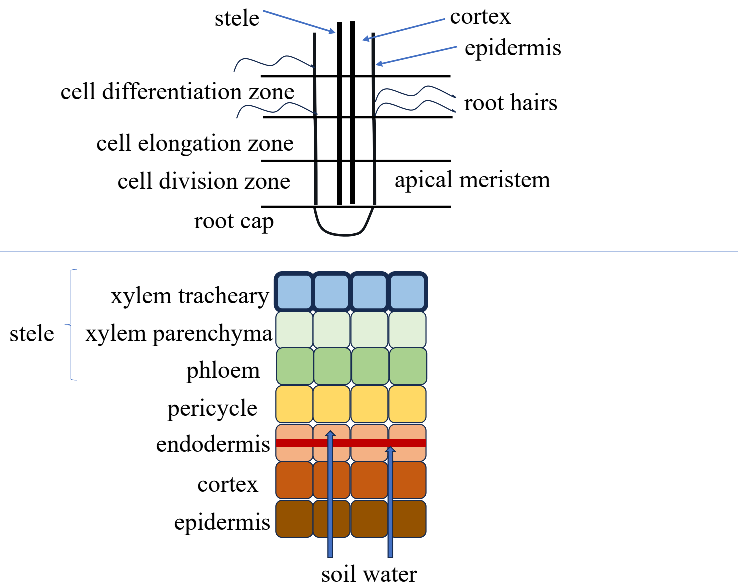

Figure 5: A simple graphic representation of the fine root. Above the root cap, there is a cell division zone, a cell elongation zone, and a zone where cells can differentiate in root hairs where absorption of nutrients takes place. The soil water approaches first the epidermis cells and several layers of cells before arriving at the xylem. The red zone in the endodermis cells represents the "Casparian strip". It forces the soil water that enters around the cell walls (the apoplast) to move through the cell plasma membranes (symplast).

PART A

PLANT PHYSIOLOGY

1

FUNDAMENTAL ENVIRONMENTAL FACTORS FOR PLANT LIFE

Temperature

Temperature sets limits for plant development, having as a minimum limit the freezing point of water and as a maximum the temperature where denaturation of proteins occurs. Survival in extreme environments depends on a species' specific characteristics, its specific temperature limitations and the optimum temperature for its growth and photosynthesis. Plants can be classified depending on their temperature limitations:

Psychrophiles grow optimally at temperatures of 0°C to 10°C. **Mesophiles** at temperatures of 10°C to 30°C. **Thermophiles** at temperatures of 30°C to 65°C. Most higher plants are mesophiles, although most plants survive temperatures from 0°C to 45°C. Survival also depends on the duration of exposure to extreme temperatures (Hopkins and Hüner 2009).

Temperature signals the change of season and sets developmental changes. In autumn decreasing temperature in combination with changes in sunlight induces **dormancy** in buds with low respiratory rate and inability to grow, even if other parameters are supportive. Dormant buds usually have a chilling requirement, before dormancy can be broken. Dormancy is also a property of seeds. Seeds may fail to germinate because they require fluctuating temperatures or at least a period of low temperature (pre-chilling or stratification) to break the dormancy (Hopkins and Hüner 2009).

On the other hand, with increasing temperature elongation increases and flowering accelerates (thermomorphogenesis) (Jung et al. 2016). Enhanced temperature stimulates the growth of meristems and organs, however, this makes the duration of the growing phases shorter, resulting in fewer and smaller organs with less biomass accumulation (Sallas et al. 2003). Temperature is a principal factor in **biogeography**, the distribution of plants.

Water

Water creates the matrix and medium where most biochemical processes take place. Plant cells absorb and release water. The rate of water transport across a membrane depends on the hydraulic conductivity of the membrane and the water potential difference across the membrane (Smith et al. 2010).

Hydraulic conductivity measures the ease, with which water moves through pores or any spaces and fractures. **Cohesion** is the strong mutual attraction between water molecules. **Adhesion** is the attraction of water molecules to solid surfaces. The cohesion-tension theory explains the water movement hydraulically. Due to cohesion-adhesion, a narrow column of water will not rupture even under considerable negative pressure, because water has high tensile strength (Taiz and Zeiger 2002).

Water potential quantifies the tendency of water to move from one area to another. A water potential measurement combines the effects of **pressure** and **solute concentration** and determines the direction of the movement of water. **Pressure potential** is created by physical pressure on water (positive) or by vacuum/sucking (negative). The solute **potential** is created by a higher concentration of solutes (=lower concentration of water). Water moves from areas of higher (=more positive) potential to lower (=more negative) potential (Hopkins and Hüner 2009).

Diffusion is the movement of molecules of a material from an area of high concentration to a low concentration area. Note that solutes can move independently of water. Different substances move independently depending on their concentration gradients. Water will diffuse from areas of low solute concentration (high potential) to areas of high solute concentration (low potential). Diffusion does not work well over long distances (e.g. from leaves to roots) (Hopkins and Hüner 2009).

Bulk flow, mass flow or mass transfer is the movement of fluids down a **pressure** or **temperature** gradient. Water will move from areas of high pressure to areas of low pressure by bulk flow. Water moves by diffusion, bulk flow, or their combination. Gravity becomes important only when there is a large vertical distance to the ground (Hopkins and Hüner 2009, Smith et al. 2010).

Cellular membranes control local and long-distance transport. **Membrane permeability** is the ability of membranes to permit or restrict the movement of compounds. It depends on the chemical properties of each solute, the lipid composition of a membrane and the membrane proteins, which enable the transport of a substance.

O**smosis** is the movement of water **across membranes** into the cell (or a region of higher solute concentration) and depends on a gradient measured as a **difference in water potential**. Osmosis occurs in the direction that tends to equalise the solute concentrations on the two sides. **Osmotic pressure** is a measure of the tendency for water to move into a solution by osmosis and it is **positive**. Osmotic pressure is the pressure applied by a solution to prevent the inward flow of water across a semi-permeable membrane. In other words, osmotic pressure is the pressure required, so that there is no net movement of solvent (water) across the membrane (Hopkins and Hüner 2009, Smith et al. 2010).

Osmotic potential is a measure of the tendency of a solution to draw water from distilled (pure) water due to its high osmotic content, across a differentially permeable membrane (Taiz and Zeiger 2002). Osmotic potential is also the potential of water to move from a hypotonic solution to a hypertonic solution across a semi-permeable membrane. The osmotic potential of a solution is **negative**. Pure water's osmotic potential is zero when the pressure is one atmosphere. The difference between osmotic pressure and osmotic potential is that the first refers to the solution, while the latter refers to the water. The **pressure flow theory** supports that water together with dissolved sugars in it flows from a higher pressure point to a lower pressure point (Taiz and Zeiger 2002).

When cations and anions move passively across a membrane at different rates, an electric potential is developed. The diffusion potential, voltage difference or **membrane potential**, is caused by the asymmetric ion distributions between the inside and outside of the cells. This has a significant impact on the transport processes.

Passive transport is the transport of solutes down a chemical gradient (such as diffusion**)**. Active transport is the movement of solutes against a chemical potential gradient i.e. **it requires energy input**. Membranes contain specialised proteins - pumps, channels, carriers - to enable solute transport. **Electrogenic pumps** carry out active transport and carry a net charge. They alter the membrane potential that diffusion would have created. **Channels** are transport proteins that form pores through the membrane. Solutes diffuse down their gradient of electrochemical potentials. **Carriers** bind a solute on one side of the membrane and release it on the other side. Transport specificity depends on the properties of channels and carriers (Smith et al. 2010).