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Water Plant and Soil Relation under Stress Situations

Adrijana Filipović

Abstract

Water is an important component in every plant's life helping them to perform basic metabolic processes. The biggest challenge of today's agriculture is how to ensure sufficient water needs at the key phase of plant development and how they can use the available moisture in the soil through the rhizosphere system.

Keywords: water cycle, water properties, water resources, agriculture, water stress

1. Introduction

Water and sun radiations are the most important environmental factors that make life possible on earth [1]. The lack of fresh water is one of the greatest concerns of humankind [2]. The rivers, lakes, reservoirs, creeks, or streams are natural water resources important for every living organism [3]. Without water, the earth would be a dead desert [4]. Water is a prerequisite for life, is involved in almost all processes of life on our planet, and has many functions in the climate system as well [2]. All organisms contain 50–90% water, some aquatic organisms even 99% [3]. If water becomes scarce or has poor quality, plants and animals die. Humans must drink about 2 L of water per day [5]. Any other substance cannot substitute the function of water. Around 97% of water on the earth is salty and unsuitable for drinking and irrigation, whereas 1.8% was frozen in glaciers and snow [6]. About 20% of the world's population already is suffering from water scarcity [3]. Water will be the most important substance during this century, and therefore, we need a global water policy guided by the United Nations [7]. These surface water resources are extremely important on daily basis for human population too. The earth's surface is 71% covered by the oceans regarding the total water sources of 97% [3]. The freshwater resources make up only 2.5% of total water [6]. In addition, 75% of freshwater is made up of glaciers and polar ice that leaves less than 1% of available fresh water in liquid form [8]. Soil water has many roles but some of the most important are water as a solvent, temperature buffer, and metabolite activator [9]. All of these roles are incorporated through the water-plant-soil relations. During the cultivation of certain plants, many of the farmers found that a number of agronomic measures do not give a good result if the irrigation of crops was omitted or neglected. Water deficit was more often associated with nutrient deficiencies through their reduced solubility and limited distribution to the root system rather than reduction of insufficient nutrient amount. Water needs are increasing on a daily basis that is to be expected compared to population growth; however, water resources are declining and could soon become scarce. Of the total water sources, the most demanding is agriculture and the water used for irrigation for a 68%,

while about 21% used for public supply and about 11% accounted for by industry process. Water use around the world has increased six-fold in the past 100 years, twice as fast as the human population, and is expected to double again before 2030, driven mainly by agriculture and irrigation [1]. Water is an important component in every plant's life helping them to obtain their nutrients (through the process of photosynthesis), growth (cell division, mitosis), respiration (cellular respiration), and turgidity (up standing form). Water helps plants to maintain their formation by transporting water and dissolved nutrients, amino acids, and other osmotic active substances from soil to aboveground plant part. Water help plants to perform the most important process, for them, the photosynthesis. In this chapter, we focused in water cycle and its importance for soil to plant life. The soil consists of different horizons, different thicknesses formed under the influence of pedogenetic factors, and processes that have been going on for millions of years and that are constantly going on. Soil system is consisting of solid (soil particles), liquid (water), and gaseous phases (air). A porous space was built between the soil particles of different shape and dimensions in which there is water, air, or some other gas. Vegetable production largely depends on the quality, type, and types of soil, and the necessary factor for plants is water. It is therefore not surprising that all civilizations in the development of human society have settled in the river valleys. Water is constantly present in the soil or on its surface. Its content in the soil is constant changing and depends on weather conditions and the needs of the plant world. The water is in constant circling, and this movement was called the hydrological cycle. Due to the movement of water in the soil and variable content, there are two major problems. One of those problems is excess water in the soil, so due to such water-air regime, unfavorable living conditions for plants occur. Another problem was the lack of water in the soil for normal growth and development of plants that was negatively reflected on yield. The fact is that producers were increasingly faced with prolonged droughts during the growing season. The only measures to combat the consequences of such troubles are the introduction of programs of the irrigation through reclamation measures as a necessary item for the future of agricultural production and reduction of far-reaching consequences if not prepare for the changes that have taken place. The biggest challenge of today's agriculture is how to ensure sufficient water needs for growing crop. This entails to identify critical plant growth phase in order to meet their water needs. Defining the period, form, role, and amount of available moisture for plants could be useful for obtaining the optimal yields.

2. Chemical and physical water properties

The two hydrogen atoms bonded by covalent bonds to an oxygen atom makes water molecule [10]. A water molecule is a polar molecule meaning that it is electro negatively charged (around oxygen atoms) at one end and electro positively charged (about two hydrogen atoms) at the other end [11]. When water molecules are interconnected, the positively charged end of one molecule (hydrogen atom) connected by a hydrogen bond to the negatively charged end (oxygen atom) to another water molecule [11]. The phenomenon of attracting water molecules is called cohesion [10]. Due to its properties (polarity and the formation of hydrogen bonds), water participates in many interactions and plays a major role in the plant organism (because it makes up between 80 and 95% of the mass of plant tissue) [10]. Polarity makes water the most widespread and most important solvent in nature. The polarity property allows the dissolution of ionic substances and organic molecules containing polar groups (OH^- , NH_4^+ , and COO^-) [10]. Hydrogen bonds formed between water molecules and ions/polar substances reduce electrostatic interactions

between charge-carrying substances and thus allow them to dissolve. The polar parts of the water molecule can form an aqueous mantle (hydration mantle) around the charged particles of the macromolecules, thereby reducing the interactions and binding of the macromolecules, thereby increasing their solubility in water. Due to the large number of hydrogen bonds that connect water molecules, it can absorb heat without large changes in temperature, making it an ideal medium for thermoregulation. As the temperature rises, water molecules movement accelerates. Compared to others liquids, to increase the water, temperature required a relatively large amount of energy (to break hydrogen bonds). From this fact arises one of the basic functions of water in the plant and that is the regulation of plant temperature (thermoregulation) [10]. Since cells contain large amounts of water, they can receive or lose heat with minimal temperature changes. This property can serve to protect organisms from sudden changes in temperature, because organisms that contain larger amounts of water in their tissues were better protected from temperature changes caused by oscillations in heat. Water exists in three different states: ice, liquid, and as steam or water vapor [12]. Water conversion into water vapor requires break down of hydrogen bonds. Therefore, a large amount of energy is used to evaporate the water, which allows the plants to cool efficiently [12]. On the contrary, low temperatures make water molecules approaching. They are closest at 4° C, although they are still moving. At temperatures below 4° C, the molecules just vibrate and the hydrogen bridges become open and rigid [10]. Water in solid state (ice) has a lower density than in liquid, so it floats on the water surface. This property allows many organisms to survive under the frozen water sheet [10]. Water molecules also have a pronounced surface tension. In order to increase the contact area between water and air, it is necessary to break down hydrogen bridges between water molecules [12]. This process requires energy investment, and this energy represents the surface tension. Surface tension has a major role in the transport (movement) of water in the soil-plant system. In addition to surface tension, cohesion and adhesion forces were important in water transport. The attraction between two water molecules is a force called cohesion, while adhesion causes water molecules to adhere to another solid (e.g., a cell wall) [10]. Cohesion, adhesion, and tension allow the appearance of capillarity, that is, the rise of water column through a narrow pipe—capillary, where the water level in the capillary is higher compared to the water level in the source that supplies the capillary [11]. Capillary occurs in various media (soil, root/stem tissue) due to: (1) the attraction of water molecules to the cell wall (adhesion), (2) mutual attraction of water molecules (cohesion), and (3) surface tension of water [13].

The plant tissue consists mostly of water and to a lesser extent of inorganic substances that plants receive from the soil, organic substances formed by photosynthesis and the products of their conversion. Water makes up 80–95% of the mass of metabolically active plant tissue. Majority of the contained water in plant tissue serves for transpiration and less than 1% was used for metabolic activity [14, 15]. High water content is an essential feature of all metabolically active cells. Relative water content reduction up to 70–80% in most plant cells results in the inhibition of central metabolic functions, such as respiratory processes and photosynthesis. In the process of photosynthesis, water is the carrier of electrons and protons. The role of water in plant tissue is multiple. In addition to being the best and most common solvent, water is also a medium for the movement of molecules inside and between cells. It greatly affects the molecular structure and properties of proteins; nucleic acids and other macromolecules indirectly affect the property of cells plasma membranes. Water is the basic constituent of protoplasm.

Water is essential for most of biochemical reactions in plant cells. Water is directly involved in number of chemical reactions, for example, hidrolisis and dehydration reaction (e.g., ADP phosphorylation is actually dehydration of the

ADP molecule, is a donor of hydrogen in photosynthesis). In addition, as water has a high heat capacity, its presence in the plant ensures that temperature changes occur slowly. The polarity and ability to form hydrogen bonds allows water to participate in a number of interactions. Water molecules were arranged around ions or charged groups of macromolecules and cover their charge. This reduces the interactions between the charged substances and increases their solubility. Therefore, water is the best solvent for ionic substances. Water is in liquid phase and medium in which all enzymatic reactions take place. Various substances can enter into a chemical reaction with each other only if they dissolve in water. The uptake of solutes is possible only from an aqueous solution. As the water content in the plant organism decreases, so does the vital activity. Water regulates turgor pressure and upright visual appearance and cell size. A large number of metabolic functions of water were realized by the processes of uptake and release (transpiration).

3. Water uptake and movement through the plant

3.1 Basic process of water uptake

Plants constantly receive water by root system and excrete water by vegetative plant's parts. The root system consists of primary and secondary roots overgrown with root hairs. Root hairs develop on the root surface. Due to their large number, they significantly increase the root area and thus make it easier for the root to absorb water and minerals from the soil. A close contact of the root surface and soil is necessary for the absorption of water by the root. The root hairs penetrate between the soil particles and immerse themselves in the capillary spaces of the soil where the water is located. Under favorable conditions of growth and development, plants scatter the root network and increase its volume. In restrictive plant growth conditions, plant root growth is often primarily restricted. Root hairs were the most susceptible to insufficient water and nutrient demands resulting in decay, especially within the herbaceous plants [16]. The pathway plant-soil-atmosphere water movement occurs through different media (cell walls, double phospholipids layer, cytoplasm, etc.), and the transmission mechanism changes depending on the type of medium through which it passes (**Figure 1**).

Basic processes that enable the water uptake and conduction of water in the plants are swelling and osmosis. Both processes were conducted by the reduction

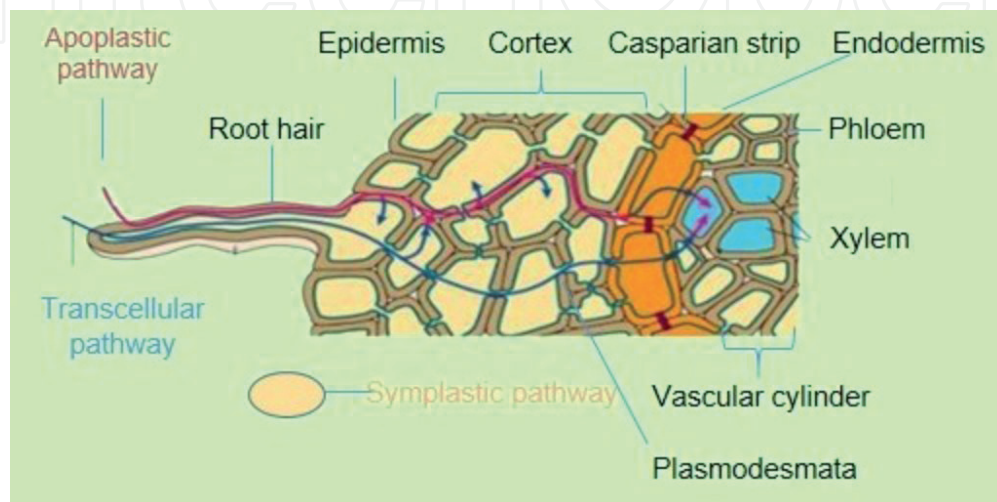


Figure 1.
Water movement and different pathway of water uptaking in roots.

of water chemical potential and by the process of diffusion. Diffusion process presents water movement from the medium of high-water potential to the medium of low water potential. In an aqueous solution of a substance, the gradient of the water chemical potential is opposite to the gradient of the electrochemical potential of the solute, so water diffuses in the opposite direction from the solute. During this process, there is no chemical reaction. The diffusion rate presents amount of substance that diffuses in certain period proportional to the concentration gradient. First Fick's law defines diffusion rate of solvent across the membrane. The process of diffusion is important for small molecules in aqueous solution effective on cell level as for entering of solution in root cell or for a stomata transpiration rate. Diffusion is not effective enough to transmit solutes to the too long pathway. The rate of diffusion is rapid over short distance but extremely slow over long distance. The process of diffusion has great importance in receiving water from the soil, the movement of solutes over short distances, and the loss of gaseous water from the vegetative plant's part, but it is not important in the transfer of water over long distances that occur in the main stream. The cohesion-tension theory explains the mechanism of water transport without consuming metabolic energy. Xylem water transport is closely related to cohesion (water molecules bind to each other) and adhesion forces (where water molecules adhere strongly to the conductive elements of the xylem), forming a transpiration column for which upward movement is responsible for the negative hydrostatic pressure [11]. Unlike diffusion driven by a difference in concentration (concentration gradient), mass bulk or mass flow represents water molecule mass flow often driven by differences in pressure (pressure gradient). This mass flow mechanism by xylem elements frequently is used for water transport over the long-distance pathway.

Mass or free flow of water plays a significant role for absorption of nutrients from soil solution of high concentrations even when transpiration is high. Then significant amounts of water move toward root carrying with it dissolved substances (nutrients) which the plant receives. Certainly, if there is not enough water in the soil, there is no flow of nutrients, while too much water can increase leaching of nutrients or asphyxiation of root.

The root hairs penetrate into spaces between soil particles and allow water to enter the apoplasmic space of the root cells. To receive water from the soil, corresponding reduction of water potential between the soil and roots has to occur. The drier the soil, the more negative the water potential becomes, and the potential swelling pressure increases, as moisture is still retained only between the soil capillaries. The water enters root hairs by imbibitions and osmotic transporting into the central cylinder of the root. Further, the plant uses water potential reduction between the soil and the atmosphere to conduct water from the soil through the plant body to the atmosphere without consuming energy. A process leading to water transport in plant cells is osmosis referring to movement of a solvent such water and other substances across a membrane. The membrane for all living cells presents certain barriers: they separate different parts of the cells from each other and greatly impede movement of substances between compartments. The plant cells membranes are semi-permeable, since they are well permeable to water molecules and other smaller particles with a weakly charged charge and quite limited permeability to larger molecules and particles with a pronounced charge [5]. Osmosis similarly to the diffusion and mass flow occurs and it appears unpredictably as a response to the suction forces.

Water is a key factor in initiating the germination of dry seeds when they reach the soil. The water in the seed stimulates the swelling process by imbibitions; hydrolytic enzymes were activated; and the germination process begins. The entry of water into the seed is wrapped from the hardness of the seed coat, and sometimes

with tightly closed seeds, a negative pressure of -100 MPA [17] can occur when entering the seed coat. Activated hydrolytic enzymes also activate other biochemical processes on which the germination process depends.

Water uptake by seeds is a process called imbibition, after which a certain period causes swelling and rupture of the seed coat. Germinating seeds use reserve nutrients stored in the seed endosperm. This nutrient reserve ensures the growth of the embryo. When the seed absorbs water, hydrolysis enzymes are activated that break down these stored reserve substances into metabolically useful chemicals. After the germ emerges from the seed layer and begins to grow roots and leaves, food supplies are usually depleted; in this case, photosynthesis provides the energy needed for further seedling growth, which now requires a continuous supply of water, nutrients, and light.

The swelling degree depends on the balance between the soil solution water potential and water potential of seeds, described as acting as repulsive and attractive forces between the two charges [18]. Imbibition is a physical process in which water enters the seed coat, where the volume of the seed changes significantly, exceeding its actual seed surface [19].

3.2 Water chemical potential

The term water potential is the most important factor for understanding the way of water moves in plant cells and through the conducted elements of the plant [20]. The chemical potential represents the water potential when it comes to water. The chemical potential of water or any substance is a measure of the available energy per mole by which that substance will react or move. Because the water molecule is neutral, the electrical potential has no effect on the chemical potential of the water. The chemical potential of water is a relative quantity and expressed as the difference between the potencies of a substance under certain conditions and the potential of that same substance under standard conditions. The unit for chemical potential is the energy per mole of a substance (J mol^{-1}) but for better understanding, we use term water potential. The unit of water potential presents the free energy per unit volume of water solution in relation to the standard state of water, as a result of the combined action of solution concentration, pressure, and gravity in ambient temperature regime [19]. Presented equation express water potential as:

$$\Psi = \mu_{w1} - \mu_{w2} / V_m \quad (1)$$

Ψ , water potential; μ_{w1} , chemical potential of water; μ_{w2} , chemical potential of pure water; V_m , molar volume of water.

The molar volume of water presents the molar mass (w) divided by the mass density (ρ) expressed cubic meter per mole ($\text{m}^3 \text{mol}^{-1}$). The soil particles and plant tissue cells absorb water, and the level of absorbed water depends on different factors. Absorbed water depends on soil pore size, water regime, ambient temperature, and pressure, and working adsorption forces depend on concentration of solutes in water. Uncontrolled movement and movement speed of some solutes in water depends on their concentration. Restricted movement of water molecules reduce chemical potential of water expressed as the Brownian's irregular water movement. A plant cell does not have mechanism of "water pumps" for water potential incensement so the water uses gradient water potential reduction. To determine the value of the water potential, equilibrium methods are most often used in which the plant tissue is brought into balance with solutions of known water potential. Water

potential of pure water is always equal to zero but water in natural system, in plant cells, or soil pores has always dissolved some solutes as organic molecules, sugars, enzymes, or other substances making water potential more negative [19].

This formula describes the energy state of water as the sum of the solute potential, the pressure potential, and the gravitation potential in a mixture of water and other particles in relation to standard conditions. The main factors contributing to the water potential can be expressed by the following equation:

$$\Psi = \Psi_p + \Psi_s + \Psi_m + \Psi_g \quad (2)$$

Ψ , water potential; Ψ_p , pressure potential; Ψ_s , solute potential; Ψ_m , matrix potential; Ψ_g , gravitation potential.

The pressure potential expresses the effects of pressure within the water potential of solution and refers to the hydrostatic pressure. Water potential has elevated by positive pressure, whereas negative pressure has an opposite effect. Plant cells have solid cell walls and can produce strong positive hydrostatic pressure called turgor. In xylem elements and apoplastic space, negative hydrostatic pressure can develop which is important for water distance moving through the vascular tissue.

The solute potential expresses the effects of dissolve solutes within the water potential of solution and refers to the osmotic potential. Dissolved substances dilute water and therefore reduce its free energy. On the contrary, diluting a solution with water leads to a decrease in the concentration potential of dissolved particles and to an increase in the concentration potential of water. The effect of the osmotic potential on the water potential of the solution is negative, which means that the solutes reduce the water concentration and it is potential. The values of the osmotic potential and the osmotic pressure differ only in sign. In other words, the values of the osmotic potential are negative, and the values of the osmotic pressure are positive.

The gravity potential (Ψ_g) represents the gravity effects on water potential of some solution. Gravity causes the water to move downward, and the potential affects the movement of the water depending on the height or transport distance. The effect of gravity on the potential can be neglected in the case of the transfer of solutes between cells or when the substances transported at a shorter height than 5 m.

One of the important components of water potential is potential of matrix (Ψ_m). This parameter is important for reducing the water potential because of the action of water on a solid surface such as a cell wall or soil particles. Such interactions of water and solid reduce the tendency of water molecules to chemically react or evaporate. In addition to dissolved particles and colloidal dissolved macromolecules, the cell has membrane surfaces and hydrated structural elements that can affect the water potential. For example, the water potential of a cell wall is not equal to zero even when the solution in the cell is pure water. The contribution of the cell wall structure to the water potential consists of a negative pressure component caused by water bound in the capillaries and an osmotic component that can theoretically be included in both the osmotic and turgor potential. For a practical reason, these potentials were often combined into one called the matrix potential. In an adult vacuolated cell, the matrix potential of the protoplasm and cell wall is small compared to the osmotic potential that was often neglected. The more negative the water potential of a cell, the higher its suction force. In water-saturated cells, the water potential is equal to zero, and the turgor potential corresponds to the sum of the osmotic and matrix potentials. The water potential increases with increasing turgor pressure and decreases with increasing osmotic pressure. The values of turgor and osmotic pressure depend on temperature and increase with increasing temperature. Water moves exclusively from the area of higher water potential to the

area of lower water potential, that is, down the chemical gradient. On the contrary, water from the area of lower water potential can be transferred to higher area only with energy consumption (endogenous process). Water will enter the cell until the water potential inside the cell equals that outside the cell. The flow of water into the cell resulting from the water potential gradient causes a hydrostatic pressure (turgor) in the vacuole. This pressure gives the cell tension and strength. Since the cell wall is quite solid but also elastic, small changes in cell volume can cause large changes in turgor pressure.

The turgor pressure is very important for the upright appearance of the plant and the strength of the cells. In conditions when the plant loses water, due to the limited availability of moisture, the turgor pressure decreases, the cell walls relax, and the plants take on a withered appearance. The turgor pressure acts against further osmotic flow of water in the vacuole, as the actual operating pressure for osmotic flow and at disposal, it has only a part of the potential osmotic pressure that was not compensated by turgor and was called the tension or suction force. The positive value of the suction force corresponds to the negative value of the water potential. The difference in water potential between the outer and inner membrane space is the force that allows water to be transported osmotically. The potential osmotic pressure of a cell decreases due to water intake and increases with water excretion. The cell sap contains a relatively high concentration of solutes and entering of water molecule through the cell wall has controlled by pressure. The turgid cells have a suction force equal to zero, whereas turgor and osmotic pressures were equalized. Plant cells between the saturated state and the wilting state have a suction force corresponding to the negative value of the water potential. When the plant cells are partially dehydrated, the turgor pressure corresponds to zero and the suction force corresponds to the value of the potential osmotic pressure. When the plant cell is saturated, the turgor pressure takes a negative sign, and the suction force corresponds to the sum of the turgor and osmotic pressure. Small changes in Ψ s usually accompanied such changes of turgor pressure. The water uptake to the cells leads to positive sign of pressure potential Ψ_p . Water absorption through the roots is possible only when there is a corresponding drop in water potential. The water potential was significantly affected by humidity, because in conditions of high humidity, the water potential is quite high, while in conditions when the air is quite dry, there are large differences between aboveground plant parts and the atmosphere. The amount of water available to the plant is in balance with the physiological capacity of the plant to absorb water and the environmental conditions that affect the intensity of plant transpiration. The movement of water in the plant-environment system always takes the place of water and solutes movement from the area of higher potential to the area of lower potential until the concentrations equalize. The water potential in the leaves of plants rating from -10 to -100 bar, while in the atmosphere, in the conditions of relative humidity, up to 50% of the potential reaches up to -1000 bar. A large difference in the water potential gradient of plant leaves and the atmosphere causes transpiration. Negative water potential usually occurs in leaves than the root cells. Similar happens when water enters the root of plants, through the apoplast where the driving force is the difference between the water potential of the xylem and the soil solution. When the water potential of a xylem solution is more negative than the water potential of soil solution, water enters the root and moves all the way to the endoderm. Van den Honert [21] explains the differences in potential that occurs when water enters into the root or exits by transpiration. An increase in the water potential due to an increase in relative humidity of air and a decrease in the water potential of the soil due to desiccation leads to a slower transfer of water from the roots to the aboveground organs of the plant. The lack of water is most reflected in the decline in turgidity of plant

cells and thus in the overall appearance of the plant, with the leaves falling down, twisting, decreasing the intensity of photosynthesis, and reducing all other metabolic activities [22]. Any deviation of the available amount of moisture from the optimal in plants results in stress and the plant wilting and earlier the deterioration of plant tissue occurs [23]. In conditions when the plants are short of moisture for a long time, it passes into the phase of permanent or reversible wilting and then dies.

3.3 Plant water balance water status

Plant water balance water status in plants is very important for plant growth and development, and metabolic activities, and especially, the lack of water drastically affects the length of the growing season and crop yields [23]. The total ratio between the water absorbed by the root system and the water released by transpiration from aboveground plant part is referred to as water balance. In cases when the transpiration of water exceeds its absorption from the substrate, water deficit occurs. The physiological processes in a plant depend on the amount of available moisture. The lack of water leads to inhibition of growth and photosynthesis. In addition, it acts on cell division and inhibits the synthesis of cell wall components and proteins, causing a stomata closure. Environmental conditions significantly affect the water potential, which is negative in conditions of well-available humidity, and in arid environments, the negative pressure was even more pronounced. Water potential was not only response to the environmental condition but also to the plant genetic characteristics [19]. The water transfer presents passive process so water movement to the plants occurs due to the low water potential of the plant in regard to the water potential of the soil. Since turgor pressure cannot be directly affected, the plant cell can regulate the water balance only by active regulation of the osmotic potential. Osmoregulation is the adaptation of osmotically active substances in the cell to the newly occurring environmental changes that largely control the water potential of the cell. This adjustment can be achieved by receiving/releasing or synthesis/decomposition of osmotically active substances. Under drought stress, plants are able to maintain water adsorption by increasing the cellular solute concentration, a process called osmotic adjustment. Osmotic adjustment occurs when the osmotic potential of a cell changes due to an increase or decrease in the content of osmotically active substances. Many cells respond to water stress by increasing the water potential of the cell. In this way, the decline in turgor can be prevented or minimized. Osmotic adaptation is an important feature of delaying dehydration in water-constrained environments because it maintains cell turgor and physiological processes with the development of water deficit [24]. Osmoregulation and osmotic adjustment are two different mechanisms. Glycophytes and halophytes have the ability to adapt to stress in two ways. One is that under conditions of water deficiency, plants can synthesize organic substances such as organic soluble substances, such as glycine betaine or proline, or high concentrations of inorganic ions [25]. The water balance of a plant depends on the rate of water uptake and excretion.

3.4 Absorption, transport, and transpiration of water

Water movement in the plant occurs predominantly regarding the passive or active transport of osmotic active substances along with water across the membrane. Main trigger for such solutes moving through the plant cells is difference in water potential followed by a difference in pressure (**Figure 2**).

The entry of water into the root cells occurs passively, that is, diffusely, and the solution moves freely through the apoplasmic space. Since the water molecule uncharged, it can very easily cross the membrane without hindrance and continue to

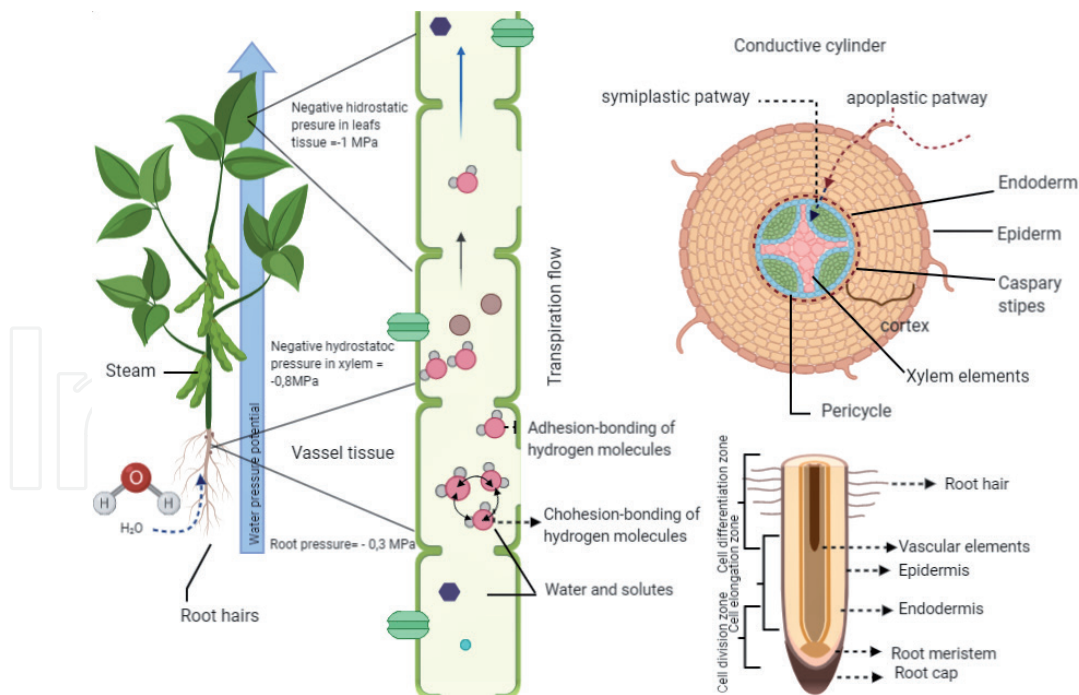


Figure 2.
Water movement through the plant root and root elements.

move upward through the conductive elements of the xylem by mass flow. Mass flow is also a passive mode of water transport, which is used for long-distance transport. While diffusion is a way of moving water and solutes over shorter distances which mainly occurs at the entry of water into the root cells and the exit of water through the stoma into the atmosphere, which occurs mainly in nonvascular tissues [26]. In the rhizosphere layer, water generally moves by mass flow to the site of adsorption. However, after contact of water and solutes with the root hairs, the mode of uptake changes significantly as other forces occur that affect the uptake mechanism. Water movement through the rhizosphere layer depends on the texture and structure of the soil. Since more permeable, sandy soils have weaker buffering capacity, so they tend to dry out quickly, while compacted, clayey soils have very limited capacity to receive and conduct water and nutrients, and transitional soil types are in terms of permeability and moisture retention and nutrients mobility of moderate capacity.

3.4.1 Absorption of water

Absorption of water requires a close contact of the roots of an intact plant and soil particles in the aqueous soil phase. The larger the volume of the roots and the root zone in the rhizosphere layer of the soil the greater the possibility of absorption. Root hair presents a tissue of the rhizoderm (root epidermis) that pronounces the root surface area affecting the root capacity to absorb water and minerals. Water enters the root in the root hair growth zone and in the root tip zone. Older parts of the root are often impermeable to water. Cracks in the root bark, as well as the growth of the secondary (lateral) root, allow water to be received by older parts of the root as well. Plants have relatively low water use efficiency and therefore need to receive large amounts of water. The water potential reduction among soil particles and the root hair occurs in order to root absorb the moisture from the soil. Water potentials in the soil (expressed as the suction tension in the soil) determine the potential imbibitions pressure caused by hydration and capillary forces. Water potential becomes more negative as soil dries out, and the imbibitions pressure increases potential, because water retained only in narrow capillaries, which is also

case with potential osmotic pressure. Root growth usually follows soil moisture sources and growth intensively while those parts that are no longer actively involved in absorption die off, resulting in asymmetric root growth.

3.4.2 Water transport

Water can move from the epidermis to the root endoderm in such a way that in apoplastic cells, water passes exclusively through cell walls and intercellular spaces, without passing through the membrane, while in the cell pathway, water passes through protoplasts. The cell pathway has two components: the transmembrane pathway in which water passes from cell to cell through plasma membranes and the symplasmic pathway through which water from cell to cell passes through plasmodesmata [11]. When passing water to the root endoderm, all three types of pathways were usually combined. The root endoderm is single layered and separates the conductive cylinder from the root cortex.

The movement of water through the apoplast of the endoderm of the cortex blocks the Casparian stripes located in the radial cells of the endoderm. Casparian cells are narrower or wider suberized cells, located around vascular elements of plant tissue. In younger cells, these stripes are similar in thickness to other cell sections, while older cells show these sites as more pronounced. Casparian stripes are barriers, so the water flow and solutes at that point cannot pass through the intercellular space of the root parenchyma, but must take place through the plasma membrane all the way to the endodermal cells—*apoplastic pathway of water movement*.

The *symplastic pathway* of water movement takes place from cell to cell through plasmodesmata where water does not cross cell membranes. Unlike the apoplast, the symplast is the living part plants composed of interconnected cytoplasmic cells with the help of plasmodesmata that grow on the cell wall interconnecting cells into a symplast. When water moves through the apoplast and symplast, water does not cross the cell membrane, because this water movement caused by difference in hydrostatic potential.

Water channels as the integrated part of membranes mostly responsible for transcellular transport of water, of which aquaporin's standout, which originate from larger protein families of major intrinsic proteins (MIP) forming pore channels in cell membranes and mediate in many other physiological processes [27]. The transcellular pathway is the movement of water from cell to cell where water crosses cell membranes, entering and getting out of the cells. The transcellular pathway also includes the entry of water into the vacuole, that is, the transport of water through the tonoplast. Because of that, the transcellular water movement was driven by the difference in gradient of water potential.

Xylem water transport presents the longest path taken by water in a plant (long distance transport). Almost total amount of water moved through the vascular cells was transported by xylem. Compared to transporting water through living cells, the xylem built of dead cell that provides little resistance to water movement. Xylem presents specialized tissue cells for the water and solutes transport. The xylem elements anatomy allows very efficient transport of large amounts of water for long distance. The two types of dead cells that make up the xylem elements: tracheid and trachea. These are cells with lignified, thickened secondary cell walls. Tracheids are spindle cells that communicate with neighboring cells through numerous pores in the walls. Pores are microscopic areas in which there is no secondary wall, and the primary wall is thin and porous. The tracheae were shorter and wider than the tracheid and have perforated walls that form perforated plates at the end. The conduction of water by xylem elements is the result of the action of cohesion and adhesion forces on the conductive wall elements. Within the conductive elements of

the xylem, continuous water columns are formed, which can, due to high tension, cause the interruption and appearance of air bubbles or the so-called embolism. The xylem transport presents of water movement for a long distance pathway from soil to aboveground vegetative plants part under the differences in pressure gradient [28]. The pressure gradient is responsible for the main transpiration flow of water, however, sometimes although less efficient transpiration of water can take over the root pressure in certain condition. In that condition, root pressure mostly show values less than 0.1 MPa [29] that correspond very high humidity as result of the high difference between daily and night temperatures. In such terms, guttation could occur as a result of water transport on leaf edges through specialized pores called hydathode [30]. In addition to guttation, root pressure is also responsible for the appearance of exudates of plant tissue in the case of mechanical injuries or cuts [31]. The amount of exudate that the plant secretes primarily depends on the condition of the plant and environment. Root pressure consumes metabolic energy and can therefore be inhibited by respiratory toxins or low temperatures in the root area. Water movement through the xylem requires the differences in gradient pressure; it can also occur due to the negative pressure (vacuum) that develops by transpiration (loss of water through the coup). The root pressure (0.05–0.5 MPa) cannot develop in conditions of low soil water potential or intensive transpiration and given that the pressure required for long-distance water transport is up to 3 MPa. Due to the loss of water by transpiration, tension (negative hydrostatic pressure) occurs which moves the water upward in xylem. For the transport of water and solutes from the roots to the aboveground parts, the most significant suction force is the aboveground organs of the plant, which create a negative pressure as a result of transpiration and root pressure. The mechanism by which tension drives water by xylem called transpiration suction.

3.4.3 Transpiration of water

Negative hydrostatic pressure develops on the surface of the cell walls below the stomata due to the loss of water by transpiration. The water movement in vascular elements of plant tissue was explained by transpiration cohesion tension model due to the forces that act based on the existence of soil-plant atmosphere continuum. Transpiration makes releases of water through the stomata on leaf surfaces. The capillary and cohesive forces cause water to enter the root cells from the soil, then go through the xylem elements all the way to the leaves of the plant to make up for the lost water. Xylem is a passive conductive element through which water columns move under pressure. Therefore, on the upper side of the water column, the water is sucked due to transpiration, which allows the entire column to move upward. In order to increase the contact area between water and air, it is necessary to break the hydrogen bonds between water molecules, for which energy must be invested, and this energy represents the surface tension. Surface tension plays an important role in the transport (movement) of water in the soil-plant-atmosphere system. In addition to surface tension, cohesion and adhesion forces are important in water transport. Cohesion is the force by which water molecules are attracted to each other, while adhesion causes water molecules to adhere to another solid (e.g., a cell wall). Cohesion, adhesion, and tension allow the appearance of capillarity, that is, the rise of a column of water through a narrow tube—capillary, where the water level in the capillary is higher compared to the water level in the source that supplies the capillary. Adhesion and surface tension together pull the water column in the capillary allowing it to move upward. The height of the water column depends on its mass, and the water column will rise through the capillary until the mass of the

water column equals the action of surface tension and adhesion forces. The narrower the capillary, the higher the water column in it will be because it will have less mass and the adhesion and surface tension will be higher.

The leaf cell wall system acts as a network of microscopic pores filled with water that adheres to cellulose microfibrils of the walls. Leaf mesophilic cells are located below the stomata, and in conditions when the stomas are open, they are in direct contact with the surrounding atmosphere. As water evaporates into the surrounding atmosphere, the surface of the water retreats into the interspaces between the cells where curves of the contact surface between air and water are created. Because of the surface water tension, menisci cause tension, that is, negative hydrostatic pressure. As water evaporates more and more, the menisci become deeper (more curved) and the tension increases (more and more negative hydrostatic pressure).

By moving water from the root to the stem through the xylem, water enters the leaves via the petiole. The petiole xylem redistributes water to the edge of the main leaf vessel, which then branches into progressively smaller veins and is incorporated into the leaf mesophyll. Since different plant species have different anatomical leaf structure and thus the arrangement of veins on the leaf for dicotyledonous plants, it is considered that most of the water used for transpiration of this plant is stored in smaller veins [32, 33]. After the water leaves the xylem, it moves through the bundle cells that surround the veins. It is not yet clear which exact path of water follows after exiting the xylem through bundle cells and enters into mesophilic cells, but the apoplastic pathway during transpiration probably dominates [32].

Xylem elements are structurally adapted to large changes in pressure. Pressure changes are dependent on temperature oscillations and, as mentioned earlier, can cause bubbles to appear in the conductive elements—embolism or cavitation. Such bubbles only briefly interfere with transpiration flow, and this problem easily overcomes, thanks to the numerous pores in the walls of the trachea and tracheid. Such occurrences of bubbles in the conductive elements interfere with the normal transpiration flow and the established pressure, so they can often affect the photosynthetic activity and other physiological processes of the intact plant [34]. Embolic or cavitation is often occurred in very high tree that can develop high tension needed for transpiration flow. The cell wall balances the volume changes without major change in water potential that occurs because of water loss by transpiration. Changes in water potential are related to changes in volume in cells that are mainly the result of transpiration. Differences in hydrostatic potential (Ψ_p) result in changes in cellular water potential (Ψ_w) with respect to the cell wall strength. On the way out of the leaf to the atmosphere, water passes from the xylem to the cellular walls of mesophilic cells and from there evaporates into intercellular spaces of leaves. From the leaves, water released by diffusion in the form of water vapor through the small openings of the dental apparatus (stomata), which are located in the epidermis of the leaf, a process that is called transpiration.

The actual flow rate of the xylem content is difficult to determine because the substances traveling through the xylem were constantly alternating with the environment of the conductive elements. The rate of transpiration flow increases with increasing transpiration rate until rupture control begins to operate, and there are no difficulties in water supply. In this case, short-term fluctuations in transpiration can be manifested as changes in the speed of transpiration flow. The speed of the transpiration flow shows the daily rhythm: in the morning, the transpiration begins and the water movement starts, and in the evening when the stoma close, the transpiration flow is interrupted. This process does not require energy and it is a passive way of water flow. The plants transpire most of the water over the stoma and release the water in the form of water vapor. Some of the moisture can be

evaporated by plants through lenticels or cuticles, although it is a very small amount of moisture. The intensity of transpiration is related to the size of the leaf area, the number and size of stoma, the appearance of the leaf surface, and of course, the environmental conditions in which the plant is located. If the plant suffers more damage during intensive transpiration, it must compensate for the water by receiving it from the soil. The numerous open stomata allow the exchange of O_2 and CO_2 gases and the evaporation of water. If the air immediately around the leaf is dry, water vapor molecules move from saturated air to the unsaturated external atmosphere according to the law of diffusion. The function of the stoma is to facilitate the excretion of water vapor by opening it, and on the other hand, to make it difficult for stomata transpiration by closing it with the insufficient water supply [35]. The mechanism of opening and closing of the stomata works based on the water and osmotic potential of the gate cells. In order to act by opening of stomata, the gate cells after the water entering should have water potential lower than the water potential of the surrounding cells. The water potential of the gate cells largely depends on the osmotic potential. Since gate cells contain chloroplasts, they also show photosynthetic activity. The leaves under daily conditions where maximum transpiration occurs release 50–70% water vapor. In the light period, intensity of photosynthesis may decrease for 50% or more due to the limited water supply [36, 37]. Since the gate cells are photosynthetically active, this enable them the accumulation of sugars, which reflected the osmotic potential, and the regulation of turgor pressure, responding on the mechanism of closing and opening the stomata [38]. Water has important role in the mechanism of opening and closing of stomata. When the plants are well supplied with water, the guard cells are turgescient and the stomates are open, while in conditions of water deficit, the guard cells lose turgor and the stomata are closed. Model of opening and closing of stomata would be used in genetic engineering for producing of species with reduced water requirements and better production rate [35]. The physiological activity of plants is significantly disrupted by interfering with the process of photosynthesis either through a process of reduced transpiration or altered gas uptake and release [39]. This is one of the reasons of balance maintaining between process of photosynthesis and transpiration. Concept soil-plant-atmosphere continuum is based on the decrement of tension of sap flow through the vessels, and transpiration flux is proportional to the pressure gradient in leaves [40]. Transpiration into cormophytes mostly shows

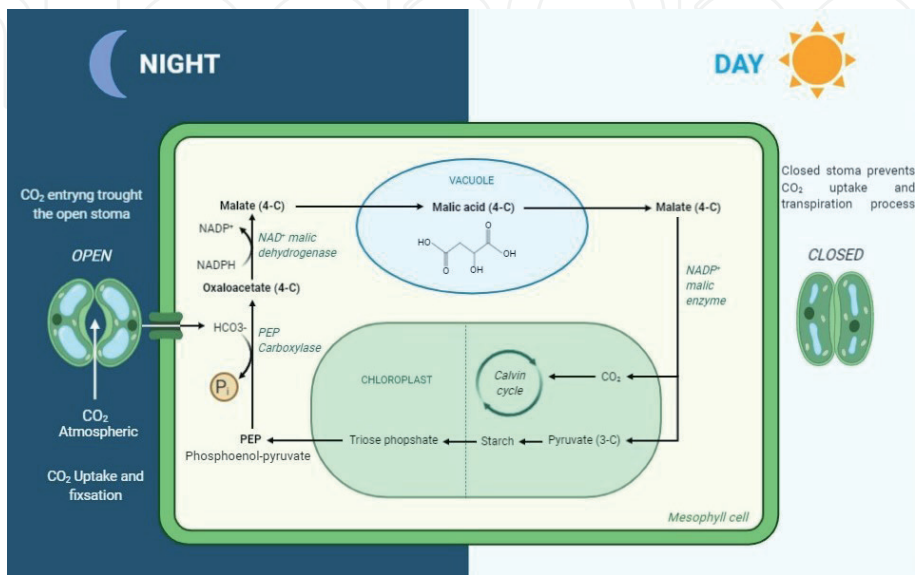


Figure 3.
CAM—Crassulacean acid metabolism in plant cells of arid area.

a characteristic diurnal rhythm. Time control of the opening and closing of the stomata serves to maximize photosynthesis and minimize transpiration. At night when there is no photosynthesis, there is no need for CO₂ absorption either, the stomates are closed and unnecessary water loss is prevented. While in the morning, when the water supply is abundant and the sun's radiation is conducive to strong photosynthetic activity, CO₂ requirements are pronounced and stomates are open. Some succulent's plant have crassulacean acid metabolism (CAM) that enables plant to keep stoma open during the night and uptaking the CO₂ and water making the acidification process through the malic acid building up in vacuole (**Figure 3**). During the day, stomas are close and transpiration as well as CO₂ fixation stopped, and in Calvin process, starch compounds were created.

4. Plant adaptation to the soil moisture regime

Soil moisture is primarily important for water circulation in continuum soil-plant-atmosphere system. The importance of moisture is especially emphasized for the life of terrestrial plants, which are tied to the soil by their roots. Plant roots from the soil absorb water and solutes, so that they can grow and develop. The water that the plants absorb passes through the conductive elements of the plant, reaches the vegetative parts, and then comes out as water vapor through the stomata. We say for this process that the plant transpires. The needs of plants for water vary, but the fact remains that water in agricultural production is one of the main limiting resources in gaining the optimal yields, with the implementation of regular agro-technical measures. Soil is supplied with moisture through precipitation; however, soil moisture and moisture retention in soil pores and the pathways by which it reaches plants are different depending on the buffering capabilities of the soil. It is clear that some plants remain viable even after a long drought, because their roots manage to find moisture in the deeper layers of the soil. There are also those plants that, due to their anatomical structure, have adapted to life in arid environments. This mode of survival allows them to have large water storage capacities in mesophilic leaf cells as they have succulent leaves. Their leaves transpire in very limited quantities of water, because otherwise they would die very quickly. There are thousands of different species of plants that are adapted to living in desert conditions. Among them are common plants that are classified as succulents. The term succulent can be explained from different perspectives but is most commonly used in terms of a plant that has specialized tissues for water storage, resulting in their special morphological characteristics: thick, fleshy stems, leaves, and/or roots. Sometimes the leaves are transformed into thorns, with the photosynthetic function taken over by a thickened green stem, in other cases by geophytes that have most of their thickened water storage tissue underground, and the third is large trees that store water in huge swollen trunks. Of course, there is a continuum among plants from those that have almost no water storage tissues to those that possess highly developed tissues intended for that purpose so it is difficult, or even impossible and inaccurate, to speak of plants that are and are not succulents. It might be more accurate to use the term "plants with pronounced succulent characteristics," but for simplicity, the term "succulent" is used. Terrestrial plants usually adapt to moisture conditions and soil type by developing roots that provide them with water and nutrients. There are plants that grow on soil with very little water supply and where the plant faces drought for most of the year. In such plants, the roots are often adapted in such a way that they exceed the volume of the aboveground part of the plant. In desire, they stretched and branched to the extent that there was favorable moisture content in the soil, from which it draws strength for its growth. Often such plants show both

weak growth and progression but manage to survive dry periods. Because water in deserts does not stay in one place for long and often drains very quickly, without roots penetrating deep into the soil succulents depend on the root network close to the surface (the first 5–40 cm below the surface) to collect most of the water after rain. Therefore, many species of cactus, agaves, and other succulents’ groups have many shallow and extremely widespread roots, which is an adaptation to rains that are sudden and short-lived. Within a few hours after the rain comes, many additional fast-growing lateral roots appear that have thin walls and increase water absorption. When water disappears, they degrade [41, 42]. Often, as an example of a drought-adapted plant, one specific plant, the Jericho rose or *Anastatica hierochuntica*, is found in the list. In addition, succulents were defined by their morphological characteristics, it is important to define them from an eco-physiological point of view: succulents plants have ability to survive in a water-restricted habitat using special strategies for water use. Succulents can be in different life forms (annuals or perennials, shrubs, and trees) and from completely different genera and families.

Some economically important plants do not have the ability to adapt to drought (Figure 4), such as the aforementioned wild plants of arid areas. In complete lack of water or prolonged drought, they dry out completely and die. In addition, during periods of water deficits, these plants show a completely different course of development, in a way that they often discard their leaves and fruits and slow down growth.

Therefore, it is extremely important that plants receive adequate amounts of moisture during growth and development in order to be able to optimize the level of expected yield. Moisture from the soil is a much more favorable factor that affects the uptake and utilization of water in the plant compared to the moisture that the plant receives through precipitation [42, 43]. The biological importance of precipitation for the plant itself is questioned, because short-term rainfall does not have high efficiency, unlike longer weather conditions or sudden precipitation,



Figure 4. Economically important crop *Vitis vinifera* L. on plantation under drip irrigation (left: Cover crop system with irrigation) and individual farm with open filed crop growing system (right: Consequences of drought).



Figure 5. Soil desiccation and cracking (left), aromatic plant root adaptation to arid land (middle), and very fertile sinkholes supplied by runoff water (right).

and in terms of their effectiveness, same authors have discussed, the distribution of precipitation during the growing season when the plant has the greatest moisture needs is questioned [43]. Meaning that distribution of rainfall over the vegetation season is a key factor in plant productivity because of variability in plant phenology requires a suitable frequency of precipitation periods rather than suitable total amount during the total year (**Figure 5**).

5. Soil moisture sources

Soil supplied with moisture from the atmosphere and/or from deeper soil layers. The precipitation from atmosphere could be in the form of rainfall, snow, ice rain of some other forms in which enriches the soil. From the deeper layers of the soil, the earth was supplied from groundwater. Groundwater was created by the underground discharge of water from precipitation from the hills to the lowlands. Sometimes these waters can appear on the surface, which we call natural springs. Groundwater varies in its depth. The one located 1–2 m below the soil surface is very useful for plants because it protects them from drought. The agroclimatology as a science pays more and more attention to temporal and spatial variations of moisture as an essential element in the surface distribution of moisture and energy source that are reflected in the complete ecosystem influencing the soil-plant-atmosphere continuum [44].

All soils are water permeable, because water can move through the space of interconnected pores between solid particles. Soil moisture behavior due to gravity and other factors such as moisture quantity, distribution, and moisture pressure significantly affect soil properties. In conditions when the soil was saturated with moisture, all soil pores are filled with water, and gases are expelled, which often results in anoxia in plants, especially if the water overloading conditions are prolonged. If not, all pores were filled with water; the soil is partially saturated or unsaturated. The highest plant yields are achieved when the most favorable ratio of air and water in the soil was achieved and especially in the critical periods of each crop [45]. Since different plant species may have different water needs, which also depend on the developmental stages of each plant, it is necessary to provide the required amount of water in critical periods of plant [44]. Climatic characteristics and soil water regime and their interrelationship is hard to have in balance due to the high production needs, as the most of the agriculture land is placed in arid area [46]. Regarding the arable agriculture land, the total of 1.5 billion hectares were estimated, which about 250 million are under irrigation or about 17% total used land and for agricultural food production is estimated about 40% [47]. It was estimated that between 2000 and 2500 km³ of water is consumed annually for irrigation. It is a well-known fact that on a global scale, about 70% of the affected quantities of water were consumed for agriculture [3], and irrigation is the main consumer of that water.

Water uptake relies on the osmotic potential of the soil solution, and the decrease in uptake can occur in the summer months on saline soils. At low temperatures, water uptake was reduced and then the plants experience physiological drought. This phenomenon can often occur in the spring; when due to the relatively high air temperature and low soil temperature, there is an imbalance in the water regime of plants, despite the fact that the soil contains sufficient amounts of water.

5.1 Soil water type

Water that results from precipitation or flooding was called surface water and it causes erosion and landslides. Free and bound water were most occurred

states of soil water. The bounded water can occur as: chemically bound water, hygroscopic water, membrane water, water in the form of water vapor and capillary water, while the free water includes gravitational, groundwater, and water in the form of ice [48]. Water in the soil is bound by various forces that the root system must overcome when adopted, so the water in the soil is divided into two classes: accessible and inaccessible.

Bound water in the soil is in the following forms:

1. Chemically bound water has no significance for the plant because it was bound within a solid lattice of minerals and as such belongs to the solid phase of the soil. Chemically bound water does not participate in physical processes and does not evaporate at a temperature of 100° C. It is present as constitutive and crystallized water. If water in the form of H^+ and OH^- ions enters the composition of different minerals, it was called crystal water. If it is bound to minerals as a molecule, then it is constitutional water. Chemically bound water is not available to the plant.
2. Hygroscopic water is water that is adsorbed on absolutely dry soil by surface forces at a relative humidity of less than 100%. The ability of soil particles to absorb relative moisture from the air was called hygroscopic water. Hygroscopic water in the soil is held at a high pressure of 50 bar; since the suction force of the root system is between 6 and 16 bar, it is inaccessible to plants. Maximum hygroscopic water is water constant but has no practical application other than being used to calculate other water constants. It is also adsorbed on dry soil by surface forces at a relative humidity of 95–100%.
3. Membrane or film water is located around soil particles and is used by plants only when the soil dries to membrane moisture. Membrane water binds to the surface of the particle after completion, that is, saturation of water binding to the maximum hygroscopy, if the particles can attract and to what extent there is available water. It was water bound by dipole forces that were weakening toward the periphery. Limestone water moves very slowly in the soil. According to Škorić [49], it is possible to divide film water into: stationary film water that corresponds to twice the value of hygroscopy and is inaccessible to plants, and mobile film water, where the water membrane is thick enough for water to move through plants is affordable. There are different zones: hygroscopic, which do forces greater than 50 bar, lentocapillary (6.25–50 bar) and membrane water of 0.50–6.25 bar hold, which is accessible to the plant.
4. Water in a gaseous state (water vapor) is physiologically useful if it turns into a liquid state by condensation, and it is a constant component of the soil air. The air in the soil saturated with water vapor with 98%. Water vapor in the soil moves from a warmer to a colder area or from an area of higher tension to lower tension.
5. Capillary water is very mobile and is of great importance in providing plants with water, as well as for physical and chemical processes in the soil. In dry climates, it is the only reserve for the plant, and the measures that allow the retention of capillary water were deep tillage, application of mulch, and cultivation. Capillary water is water that fills the narrowest pores of the soil due to the action of surface tension and occurs by increasing soil moisture. Capillary water is the most ecologically important form of water and is a basic factor in soil dynamics and fertility.

Free water in the soil is in the following forms: gravitational, groundwater, and ice-shaped water. For all forms of free water, one thing is common and that is when they are in liquid form, they move laterally and vertically under the influence of inclination or under the influence of gravity. The forces that hold water against soil particles are on the one hand the tension of moisture (surface, hydrostatic, and gravitational forces), and on the other hand, the osmotic pressure of the aqueous phase of the soil. Cohesion forces connect water molecules (hydrogen bridges and Van der Waals-London forces), whereas adhesion is responsible for their binding to soil particles and the formation of a double layer. Adhesion water is water that is located in the surface soil layer and retained by the forces of mutual molecular action between the soil particles and the absorbed water.

1. Gravitational or leach water is formed in occasion of fully saturated soil pores with water. In such a state of saturation, water seeps through macropores by gravity and is not bound to the soil. Gravitational water is the basic form of free water in the soil. After the precipitation layer, soil pores were fulfilled and, under the gravity, flows into the depth or sideways, down the slope. The size of the pores in the soil or soil texture was highly dependent on water flow movement in soil profile. If the soil has a lighter mechanical composition and contains a higher content of noncapillary pores, gravitational water will pass through the soil faster and less water will remain in the soil. There are two forms of gravitational water: fast gravitational water (for larger pores) and water that gradually drains away (for smaller pores). Gravitational water can be retained in the smallest noncapillary pores for several days during the wet period. She then swells with the help of her own weight.
2. Groundwater that is under a certain pressure in a water-permeable layer between water-impermeable layers. Groundwater is another form of free water and it formed if gravitational water encounters an impermeable layer of soil. Groundwater can also be associated with river water and then this water is close to the surface (1.0–2.5 m). The impact of groundwater on the soil depends on its depth and composition. Groundwater has no significance for plants if it is at great depth, but if it is located high and too close to the soil surfaces, it has a negative effect on plants. Groundwater is useful to plants when it is accessible to the roots due to capillary uplift or when the plants can absorb water from the deeper layer with long root system. Groundwater has a great impact on plants and soil if it contains soluble salts.
3. Ice form water or water in solid form is a special form of free water. This form of water is not of great importance for our climatic areas. Freezing and melting have a negative effect on the soil.

5.2 Movement of water in the soil

The three basic forms of water movement in liquid form are capillary movement, infiltration, and filtration. The movement of water is possible through unsaturated and saturated soil. Movement is possible descending, ascending, and lateral. The water direction of movement and speed were highly related to the occurrence state of the water, amount, texture, structure, porosity, the amount of organic matter, and the forces that cause the movement. The primary causes of soil water movement are capillary forces, gravity, and hydrostatic pressure.

The capillary movement of water occurs from the area of higher humidity to the area of lower humidity, that is, in unsaturated soil in micropores.

Infiltration is the uneven absorption by vertical and lateral motion into unsaturated soil, by the action of capillary, gravitational, and osmotic forces.

Filtration is the leaching of excess water from saturated soil into deeper layers through soil macropores, which causes gravity (and hydrostatic pressure).

Water in the soil moves in three basic directions: descending, ascending, and lateral. The descending flow of water is downward, with water draining freely through the macropores of the soil, primarily under the influence of gravitational force. This steady flow of water in cultural engineering corresponds to the concept of filtration. The ascending movement of water is ascending toward the soil surface and interpreted by capillary theory, membrane water theory, or potential difference (suction force—tension). According to capillary theory, water rises in profile due to the adhesion force that occurs between soil and water particles. Due to the adhesion, the capillaries fill and the water rises with the strength of the meniscus (adhesion) and due to the surface tension. According to the theory of membrane water, the ions in the outer diffuse shell have a suction power (osmosis) that fills the capillaries. Soil particles that have a thinner mantle accept water than those with a larger mantle. The last is the potential theory where water moves due to tension from a wetter to drier area. Lateral (lateral and radial) movement of water is interpreted by capillary theory, the theory of membrane water, and osmotic pressure, and the theory of potential.

The supply of soil with water from deeper soil layers depends on the type and composition but also on the method of soil cultivation depending on its purpose. Precipitation, which falls to the ground, is not equally abundant everywhere. Long-term hydrometeorological and agrometeorological measurements determine the daily, monthly, and annual average amount of precipitation for a particular area, which is logical to vary from place to place. Almost half of the water that enters the soil evaporates out into the atmosphere, about $\frac{2}{6}$ is lost by leaching and runoff into depressions, streams, streams, and various standing waters, while only $\frac{1}{6}$ is absorbed into the soil, which means that about $\frac{1}{6}$ of the total precipitation and moisture that enters the soil remains available to the plants. Water retention is a very important factor in soil composition. This means that, for example, sandy soils differ significantly from clay soils in terms of moisture retention, absorption, and loss. Every soil has a certain degree of porosity because the soil made up of tiny fractions of sand and even tiny dust particles. Depending on the sand fraction, the pore size will also vary, or the permeability rate of such soil. Clay soil, on the other hand, consists largely of the finest particles of powder and clay, between which a very small number and diameter of pores were formed or have the ability to form, which limits the porosity of this type of soil.

5.3 Soil water constants

Water or hydrological constants defined as the equilibrium states between the suction force of soil particles and water. Most authors include the following in water constants:

- Hygroscopic water form
- Soil water capacities
- Maximum water capacity for soil
- Water retention and absolute water capacity for soil

- Field water capacity for soil
- Minimum water capacity for soil
- Humidity equivalent
- Lento-capillary point (humidity) or wilting point.

Water retention and water movement in soil were characterized by above mentioned water constants. Water constants were defined as the concept of water content, shape, and form in the soil related to the texture and structure of the soil, organic matter content, and applied agrotechnical measures. There were a number of water constants and various names were used in the literature and practice. Water constants that are of practical importance for the needs of soil hydro melioration and primarily for irrigation and drainage were listed here.

Hygroscopic water is, as mentioned earlier, the ability of soil particles to absorb relative moisture from the air. Humidity in contact with dry soil, allows the absorption of moisture that increases the volume of soil particles, until an equilibrium ratio is achieved. The established ratio represents the maximum absorption capacity with the achieved maximum hygroscopic effect, which for soils with sandy texture is 1%, for loamy soil texture up to 7%, and for clay soil texture up to 17% measured on dry matter. There is a difference between the maximum hygroscopy (Hm) according to Lebedev [50] and the hygroscopy according to Mitscherlich [51] (Hy). If the soil is placed in the conditions of complete saturation of the air with water vapor, then it will attract the maximum layer of hygroscopic water, this called maximum hygroscopy. Mitscherlich hygroscopy [51] corresponds to the moisture content, which is obtained by placing a soil sample in an evacuated desiccator above 10% sulfuric acid. The acid creates conditions of 96% relative humidity of the air that the soil absorbs. After establishing the equilibrium state by gravimetric method by weighing the moistened sample to hygroscopic moisture and completely dry soil, and by calculation in mass percentages, the moisture content corresponding to the hygroscopy is obtained. Hygroscopic moisture held in the soil, as mentioned earlier, by a suction force of 50 bar and is inaccessible to plants because the root of the plant has a suction force between 6 and 16 bar. The double value of Mitscherlich hygroscopy corresponds to the equilibrium state between the suction force of the plant root and the soil particles called the wilting point.

Soil water capacity presents a soil capacity for water retention in micropores after squeezing water from macropores under the influence of gravity. Depending on the method of determination, there were retention and absolute, field soil water capacity, minimum water capacity, and moisture equivalent according to Briggs and McLane [52].

Maximum soil water capacity (MWC) is a constant that represents the water content in the soil when water saturation is in maximum fulfilling the micropores and they are theoretically equal to the total porosity (**Figure 3**). When the maximum water capacity is then all other water constants were maximally realized. The state of maximum water capacity is short, especially in normal soils. Maximum water capacity is undesirable because anaerobic conditions occur, which puts the plants in a state of stress and puts maximum pressure on the metabolic activities of the plant. MWC occurs due to heavy rains and sudden melting of snow. In addition, the soil maximally saturated with water both when groundwater reaches the surface and during major floods. In rare situations and for a short period, the soil saturated to the MWC value. When the soil oversaturated with water, oxygen is lost in the soil and anaerobic conditions occur. This phenomenon is very harmful to soil and plants.

Excess water in the soil causes problems in the plant's oxygen supply (occurrence of anoxia = complete lack of oxygen and occurrence of hypoxia = reduced amounts of oxygen). Anoxia occurs more often if the temperature 12°C of the air is above 20°C, when the consumption of oxygen by breathing the roots of plants, soil fauna, and microorganisms is higher than at lower temperatures. Under such anaerobic conditions or at insufficient oxygen concentration, changes in the metabolism of plant tissue cells occur. Cell intoxication with alcoholic fermentation products and increase in cytoplasm acidity occurs. These phenomena can result in cell death. Plants suffering from the lack of oxygen show signs of wilting, due to the inability to active transfer water, and the leaves show epinastic growth (downward) due to increased ethylene synthesis. In such leaves, the concentration of abscisic acid increased, which initiates the closure of the shoot. This interrupts the transpiration flow and distribution of osmolytes and water to up ground plant parts which resulting in growth retardation.

The absolute soil water capacity according to Kopecky [53] corresponds to the water content in the micropores after complete saturation of the sample in a cylinder with a volume of 100 cm³ and squeezing of excess water from the soil macropores after 24 hours. Horvat et al. [54] introduced the retention capacity of soil for water due to certain soil losses in determining the absolute capacity. According to this method, the soil sample in the cylinder, according to Kopecky [53] placed on a stand with filter papers whose edges immersed in water. The soil absorbs water and holds it in the micropores by adhesion, hydration, capillary, and surface tension forces. After squeezing, the excess water from the gravitational pores (the soil sample stands on the filter paper for half an hour) and the water content in volume % which corresponds to the retention capacity of the soil for water are is determined gravimetrically. The values of absolute and retention capacity of soil for water correspond to the soil layer above the groundwater level and are higher than those determined in field condition.

Field water capacity (FWC) is a condition where micropores are filled with water and macropores with air, after maximum saturation and seepage of free water under the influence of gravity. Soil moisture at FWC is retaining longer provided there is no evaporation or the influence of groundwater (capillary). For field water capacity, there are many names such as retention capacity, maximum water capacity, capillary capacity, and water retention at 0.33 bar. However, this constant (FWC) is determined in field conditions, and therefore, the name filed water capacity is the most appropriate (**Figure 6**). Field water capacity is extremely important because

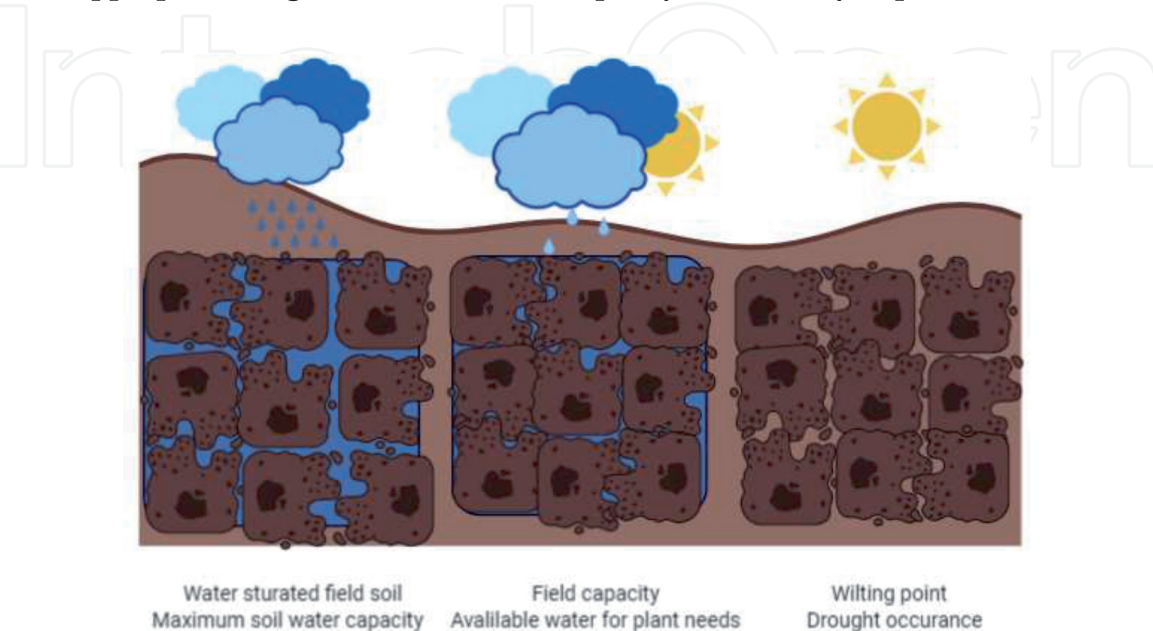


Figure 6.
Diffèrent water soil capacity.

its knowledge used in various calculations in the design and use of hydromelioration systems. FWC is especially important for irrigation because it is water constant without is impossible to accurate calculate the irrigation rate to moisten the active rhizosphere. FWC is also the largest amount of water that can be giving during irrigation because water above the FWC value is considered harmful to the plant. Irrigation practice depends on soil conditions, moisture and plant's requirements. Field capacity corresponds to the state of moisture that occurs in the soil immediately after rain, before evaporation and transpiration begin. It is expressed as the percentage of water in the soil that is found in such a state of humidity. Therefore, it corresponds to the water content in the well-drained, permeable soil from which all the gravitational water had drained. However, soil moisture that would correspond to the absence of gravitational water alone must be determined relatively soon after rain. This is possible only with light and well-drained soils, because in others, the process of rain infiltration through the ecological profile takes a long time, often several days. Meanwhile, after rain, the surface layers lose water by evaporation and transpiration, so the field capacity values that obtained after several days do not correspond to the actual water content of the soil.

Kramer [55] states that FWC will depend on soil temperature, that is, soil moisture in FWC will decrease as the soil temperature rises. Kirkham et al. [56] cite the influence of groundwater level, soil moisture depth, and impermeable layers in the soil on the FWC value. The author explains that the depth of soil moisture during infiltration will be greater the wetter the soil. Furthermore, the author states that the presence of an impermeable or less permeable soil layer increases the value of FWC.

The equivalent of moisture according to Briggs and McLane [52] is the water constant obtained by centrifuging a soil sample with a force of thousand times greater than the gravitational force. The value roughly corresponds to the field capacity of the soil for water. The lentocapillary point (Lkt) was defined as the lower limit of optimal soil moisture and corresponds to a soil water pressure of 6.25 bar ($pF = 3.8$). It is obtained by subjecting a saturated fine to the specified pressure in the pressure membrane. The wilting point (T_v) is the equilibrium state between the suction force of the root system and the soil particles and plants starts to lose turgor. A pressure that occurs in soil depends on available water and for this hydropedological constant is 15 bar ($pF = 4.2$). The point of wilting can be determined by vegetation experiments, using a pressure membrane and calculate from hygroscoy. Plant-accessible water is in the range between the value of soil water capacity and the wilting point (**Figure 7**)



Figure 7.
Philodendron in well turgid (left) and in less turgid condition (right).

and called physiologically active water. Within this interval, not all water is equally accessible, so the soil should maintain a moisture state between the water capacity and the lentocapillary point, which corresponds to the optimal moisture interval.

6. Drought stress

Drought is a common occurrence for many areas that recurs without noticeable regularity. Drought is one of the abiotic factors that have the greatest impact on agricultural production. It occurs when soil moisture decreases to an amount that negatively affects the yield and profitability of agricultural production [57]. Drought as an abiotic stress can directly affect agricultural production and even in some extreme situations lead to the complete destruction of yields. It is very important to distinguish the meaning of drought in agronomy and the definitions of drought in meteorology, hydrology, and the socio-economic concept of drought. The amount of physiologically active water in the soil, which is the only available water for plants, and the ratio of capillary and noncapillary pores in the soil are also important. The water content in the soil also depends on the texture of a particular soil type (i.e., on the water balance in the soil; fine sand has a lower possibility of water retention than clay loam). The ratio of humus in the soil is significant, because it has a great ability to absorb water (it acts like a sponge). The term drought should not be confused with the term “aridity,” which refers to the permanent property of a naturally dry (waterless, arid) climate. A dry or dry area (“aryland”) is an environment that was constantly, seasonally, or occasionally exposed to a significant lack of moisture. It was estimated that about 36% of the planet’s continental surface, which is approximately 45 million km², can be classified as dry area. It is estimated that between 15 and 21% of the earth’s population live in this area [4].

Regarding the extreme climatic conditions and rising temperatures, the need for irrigation of agricultural land is increasing; according to some statistic report, as much as 69% of drinking water is used in agriculture (irrigation of plants, watering livestock, etc.). FAO estimates that water consumption for plantation irrigation will increase by 5.5% from 2008 to 2050. These data show that the world’s demand for water is increasing, and the increase in agricultural production results in higher consumption of drinking water. In order to reduce the need for irrigation, scientists studied the drought resistance of plants and sought to investigate the associated adaptation mechanisms. Geneticists are already creating varieties that contain drought-resistant genes; however, drought tolerance is only possible up to a certain percentage of moisture reduction. For example, chickpea (*Cicero arietinum* L.) is extremely drought resistant, its root is spindle-shaped and branched, and it reaches a depth of 1 m where there is a higher amount of moisture in the soil, and also many Mediterranean plant species are resistant to both high temperatures and lack of moisture in the soil.

Different time of drought periods also cause different changes in plants. Some plants increase synthesis of secondary metabolite as a response to drought occurrence resulting in leaf or fruit abscission and leading a plant cell, tissue, or organs to death (**Figure 8**). Transient wilting occurs during the hottest part of the day, when there is increased transpiration in plants. Permanent wilting occurs due to the low water content in the soil, root hairs die off, which blocks the plant’s connection with nutrients from the soil (lost water can no longer be compensated). It is necessary to distinguish: desiccation (delay of drying ability to maintain hydrated tissue), tolerance to drying (retention of functions during drying), and avoidance of drought completion of the plant life cycle before drought occurs [13]. The point of wilting is the phase in which the plant begins to die, resulting in permanent death, and the plant when it reaches this stage (critical lack of moisture depends on the plant



Figure 8.
Citrus fruit abscission under the drought occurrence in critical phase (left) and leaf scrolling in tomato plant to avoid excess transpiration rate under stress condition (right).

species and type of cultivar) will not recover after irrigation. When a critical water deficit occurs, necrotic changes first appear on the plants, and finally, the lethal phase occurs. Plants have the greatest need for water during the growth phase, and during fruit formation, when plants are most sensitive to drought. According to the requirements of plants against water, they are divided into three main groups: hygrophytes (wetland plants), mesophytes (plants of temperate areas, which include most agricultural plants), and xerophytes (plants of arid areas).

One of the first defense mechanisms of the plant on drought is the reduction of the leaf surface, because with the reduction of water in the soil, the turgor pressure in the cells decreases, which ultimately results in a decrease in the concentration of cell content and cell volume. Turgor affects cell growth, and by reducing it, cell growth also decreases affecting the growth of the leaf surface and thus transpiration. Plants can reduce the surface area of transpiration by leaf scrolling and abscission (leaf rejection) or increased secretion of ethylene, which affects cell death. One of the most effective adaptations to drought is the closure of the stomata, to prevent further dehydration, this mechanism occurs when the plants have already fully developed their leaf surface. However, many plants lose water through the stomata because they remain open, and much of the water is lost through the epidermis by the cuticle, especially if the cuticle is thin.

Although it can be found in almost all parts of the world, the characteristics of drought vary from region to region. Defining drought is therefore difficult and depends on regional differences and needs, but also on the perspective from which this phenomenon is viewed. Regardless of the needs for which drought is defined, it is necessary that this definition includes the deviation of the current relationship between precipitation and evapo-transpiration in an area from the normal value of this relationship determined for a multi-year data set. It is also important to take into account the time distribution (precipitation regime, delay of the beginning of the rainy season, the relationship between precipitation, and phenological phases of the most important field crops in the observed area), as well as precipitation efficiency (precipitation intensity and number of rain episodes). Other climatic factors, such as high temperatures, high wind speeds and strengths, and low relative humidity, are often associated with drought in many parts of the world and can significantly worsen its consequences (**Figure 9**). Drought is an insidious natural disaster that, unlike other natural disasters, occurs slowly, lasts a long time, and affects large areas. It can be considered from four aspects (meteorological, hydrological, agricultural, and socio-economic).

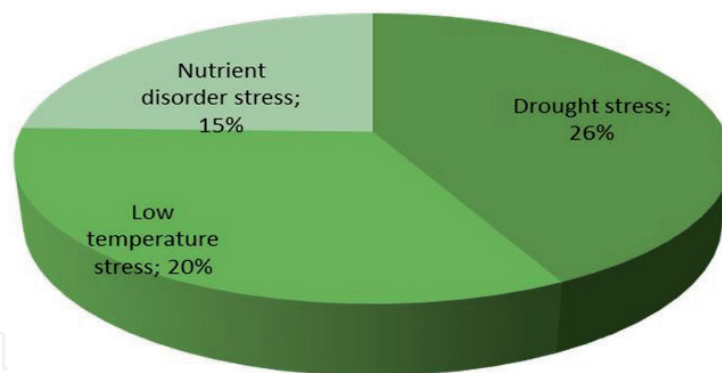


Figure 9. Current trends of most abundant abiotic stress occurrence in agriculture sector estimated for around 50% of world's arable land.

Short-term water shortage over a period of several weeks in the surface layer of the soil, which occurs at a critical time for plant development, can cause agronomic drought. The agronomic droughts may lag behind meteorological droughts, depending on the condition of the surface layer soil. High temperatures, low relative humidity, and wind amplify the negative consequences agronomic droughts. The agronomic droughts, precipitation deficits are taken into account along with the physical and biological aspects of plants, interactions within the soil-plant-atmosphere system and the balance between plants' water needs and available water reserves, which may result in declining yields. Beside agronomical drought, we can also distinct the meteorological and hydrological drought.

Meteorological drought occurs as a consequence of lack or complete absence of precipitation over a long period of time in a certain area. This deficiency is defined as the deviation of precipitation from normal, that is, from the multi-year average. Meteorological drought can develop abruptly and stop abruptly.

Deficit of precipitation over a long period of time affects surface and ground-water supplies: to the flow of water in rivers and streams, level of water in lakes, and level of groundwater. When flows and levels decrease, we talk about hydrological drought. The onset of hydrological drought may lag a few months behind the beginning of the meteorological drought, but also continue after the end of the meteorological droughts. Finally, socio-economic drought could be defined as an event when the need for water is greater than the possibility to provide it with agrotechnical measures. The mentioned concept of drought reflects a strong connection between drought and human activities. The droughts in recent years have had a significant impact on the economies and environment of agricultural production, increasing the vulnerability of society as well as a whole ecosystem.

6.1 Mechanisms of plant adaptation to drought

The lack of water especially in agricultural sector presents important limitation of world food production. The strategies for promoting the mechanisms of plant tolerance to drought:

- Desiccation delay is the ability to maintain hydration of the tissue
- Desiccation tolerance is the retention of cell functions during drought
- Drought avoidance is the end of the plant vegetation cycle before drought occurs.

It is already clear from this division that the mechanisms and strategies of drought resistance may differ. Water deficiency could be explained as amount of water in a cell tissue that is lacking until optimal hydration. When water deficit gradually occurs, the impact of water scarcity on plant growth and development comes to the fore. The basic acclimatization strategies that occur in conditions of water scarcity are:

- reduction of leaf area,
- leaf rejection (abscissa),
- increased root growth,
- retaining the stomata,
- osmotic adjustment,
- thickening of the cuticle.

Decrement of water plant status affects the turgor pressure, which also decreases. As turgor falls, cell volume decreases, cell contents become more concentrated, and cell membrane becomes less tense and thicker. Cell growth is highly influenced by turgor and consequently declining of turgor will restrict cell growth. In addition to reducing turgor, the lack of water also reduces the elasticity of cell walls, which also affects cell growth. Decreased cell growth results in smaller leaves, that is, reduced leaf area. Reduced leaf area helps conserve water because smaller leaves breathe less (lose water more slowly). Therefore, a plant usually starts to decrease leaves surface and afterwards its number as a result on water stress conditions. The leaves age and fall off faster (there is an increased synthesis of ethylene, which encourages leaves fall).

Beside leaves, plant root is also susceptible to the lack of water. The balance between the uptake of water through the root and the photosynthetic activity of the aboveground part influences the ratio of the root mass and aboveground part. Simply, the aboveground organs will grow as long as the root supplies them with sufficient water and nutrients, and conversely, the root will grow as long as the aboveground organs supply it with sufficient assimilates. As already mentioned, water deficiency causes leaf area and number of leaves decrease in the early phase, while the intensity of photosynthesis tends to remain unchanged. Reducing the leaf area allows less water consumption, but also energy, so more carbohydrates were translocated to the root and allowed it to grow. However, in dry soil, the root tip loses turgor very quickly, so the root grows where the soil is still moist. As water scarcity (drought) progresses, stress most often occurs. Stress caused by the lack of water due to drying out of the upper soil layers so the plants develop deeper roots. The development of deeper roots is also one of the reaction pathways to the drought. Increased root elongation during drought requires translocation of assimilates from aboveground organs to the root. In the generative phase, a significant outflow is represented by fruits (assimilates are spent on fruit growth), so the roots get less assimilates. Therefore, if the stress of water deficiency occurs in the generative phase of plant development, the effect of enhanced root growth will be less pronounced [10].

In conditions of intense stress (rapid) occurrence as a result of water deficit or the phase where plants have already developed the maximum leaf area, other mechanisms activated to prevent the plant from drying out. One of the most important such mechanisms is the closure of the stoma, which reduces transpiration, that is, water loss. Therefore, the “third line” of drought protection can be considering the

mechanism of stomata closing. The change of turgor in the guardian cells regulates the opening and closing mechanism of the leaves stomata. The guardian cells are modified cells of the leaf epidermis and that is why they can lose turgor as they loss of water (transpiration) into the atmosphere. Such a way of holding, stomata (due to direct water loss and falling turgor) called hydro-passive stoma detention. The second mechanism called hydro-active stomata closing occurs in conditions when the whole leaf and/or root is dried. This mechanism is triggered by metabolic processes in the stomata cells. Concentration decrement of osmotic active substances in the stomata results in water release in guardian cells and turgor pressure decrease. Hydro-active detention of the stoma occurs due to a decrease in osmotic potential, which leads to the release of water and a decrease in turgor in the guardian cells. The abscisic acid (ABA) affects the decrement of concentration in osmotic active substance in the stoma. Absciscic acid in very low concentrations is constantly synthesized in mesophilic cells and accumulates in chloroplasts. Under conditions of mild dehydration of mesophylls, two processes activated: (1) part of the abscise acid stored in chloroplasts is released into the apoplast (intercellular spaces) of mesophilic cells and then the transpiration current of water carries ABA to the guardian cells and (2) the synthesis of ABA intensifies and its higher concentrations accumulate in the apoplast of the leaf. This second process (ABA synthesis) prolongs, that is, maintains the process of coupling retention that occurs due to the release of ABA from the chloroplast. In addition, during stress caused by the lack of water, chemical signals (ABA) transmitted from the root to the leaf, leading to the stomata closing. In fact, the conductivity of the shoot indirectly was managed by the soil water status rather than the water status of the leaves, afterward root show high sensitivity respond to lac of soil moisture.

As the amount of water in the soil decreases, the water potential of the soil decreases. In condition when root water potential is more negative then soil water potential plants can receive necessary water. The process of accumulation of solutes (osmotic active substances) in cells presents osmotic adaptation. Thus, the cell reduces the water potential (the water potential becomes more negative) without a significant change in the turgor or volume of the cell. During osmotic adaptation, various solutes accumulate in the cell, mainly sugars, organic acids, amino acids, and inorganic ions (especially K^+). Ions mainly accumulate in the vacuole because their high concentration in the cytosol can inhibit many enzymes. However, due to the increased concentration of ions in the vacuole, and in the cytoplasm, there must be an increase in the concentration of solutes in order to maintain the balance of water potential within the cell. Dissolved substances that accumulate in the cytoplasm called compatible osmotic active substances and are substances that do not inhibit enzymes. Compatible osmotic active substances were proline as amino acids, and sugar alcohols and glycine betaine as amine. The synthesis of compatible osmotic substances also occurs under conditions caused by increased salinity. The osmotic adjustment takes place slowly over several days. Osmotic adjustment of leaves can provide turgor maintenance with lower water potential compared to leaves that have not undergone osmotic adjustment. The maintenance of turgor enables the normal course of cell growth (cell elongation) and greater stomata conductivity at lower water potential, which leads to the conclusion that the osmotic adaptation is actually a process of acclimatization.

The cuticle is a waxy coat located above the epidermal cells, and its function is to reduce water loss (cuticular transpiration). In conditions of lack of water, plants often synthesize a thicker cuticle. The thicker cuticle also reduces the entry of CO_2 , but photosynthesis usually remains unchanged because the epidermal cells located below the cuticle do not conduct photosynthesis (CO_2 for photosynthesis enters the leaf through the stoma). Cuticular transpiration makes up only 5–10% of the total transpiration, so the thickness of the cuticle is important only in conditions of more severe drought or when the cuticle is damaged (e.g., due to wind). The lack of

water reduces the intensity of photosynthesis although this process does not react as pronouncedly to lack of water, as is the case with leaf area. The reason for this is that photosynthesis is not as sensitive to turgor decline as cell growth. However, due to the detention of the stoma under drought stress conditions, the entry of CO₂ into the leaf reduced and the intensity of photosynthesis decreases.

Each plant species has its own root growth characteristics, which can be substantially, modify by the plant's environment. In most arable land used in agriculture, the roots occupy the largest volume of soil, although it is dictated by the physical and chemical properties of the soil. The main roots and root hairs are responsible for transporting water through the conductive elements, while the lateral roots play an important role in the absorption of water and minerals [58–60]. The roots are under the extremely high influence of soil factors, its buffering abilities, surrounding environment as one of the most important parameters that reflected in the development of the roots [58]. The soil water and nutrient content, soil type, vegetation, and agrotechnical measures strongly reflect root growth [61–63, 60, 64]. In the early growth phase, roots behave as sink for assimilates which are distributed in vegetative parts of plant until generative phase occurs this role become weaker [61]. Richards [65] found that wheat root shows significant changes if grown in water deficit conditions and also this state reflects root development. Dry soil may intensify growth of root in depth searching for water [66] but elongation of root cells could be restricted [67].

The balance between the aboveground and underground part of the plant is very important in terms of regulating the status of water in the tissue, and it was found that some plants tolerate drought conditions better if the ratio between aboveground and underground plant parts were lower [68]. Under favorable water conditions in the soil and the wheat phase of vegetation, better rooting and increase in root volume can occur [69]. Taylor and Klepper [70] found that minor changes in water potential did not significantly affect the increase in plant root volume.

A large number of studies regarding the influence of water stress on the plant conclude that not only the root results in certain changes but also certain changes occur in the aboveground part of the plant. Beside arid area also water saturated soil can provide certain changes on root (**Figure 10**) and affect root development as



Figure 10.
Salix sp. root adaptation to water level changing or species tolerant to hypoxic conditions by forming abounded fibrous root.

a result of anaerobic conditions [71] even some species have adapted to this condition developing a special root [72]. The reaction of the plant to stressful conditions in most cases was reflected in the unfavorable status of water in plant tissues and organs. The main mechanism of plant cell resistance to stress is to maintain favorable turgor pressure in cells, tissues, and organs (stress is first reflected in important physiological processes in the plant such as photosynthesis, respiration, transpiration, nutrient, and water uptake) [64, 73, 74].

The roots of plants are most often adapted to stressful conditions in a way that changes the structure of the tissue and changes in root volume occur, which was closely related to the reclamation of the osmotic activity of root cells. Cells most often try to protect cells from protoplast dehydration through metabolic exchange of water molecules and some osmotic active substance that result tissue adaptation to newly state that occurred (wall thickness, cell size, osmolite concentration, etc.) [66, 75, 76].

7. Conclusion

Life on earth originated in water and depends on water which is necessary for the life of all beings. Plants are constantly receiving and excreting water that has a number of biochemical and physiological functions in the plant organism. Plant species as well as individual plant parts differ in terms of water demand. Of all the factors that affect the growth and development of a plant, water have become the most important and common limiting factor. Plant tolerance to abiotic stresses, especially drought stress is a very complex process consisting of a series of physiological, biochemical, and genetic adaptations, that is, evolutionary adaptations of certain plant species. The biggest challenge is to determine exactly which genes activate certain chemical compounds and substances which control the plant's response on drought stresses and how exactly the plant physiologically manages to respond to stimuli. The agricultural production is dependence on weather conditions as of today it is becoming more and more pronounced due to the increasingly frequent weather extremes caused by the climate changes. The lack of precipitation or their uneven distribution, pronounced dry periods almost regularly monitored by above-average temperatures, and extreme weather conditions such as hail, floods, and strong winds negatively affect agricultural production. Yield drop or total loss of yield and financial losses are the main direct consequences of adverse weather conditions. One of the most important factors that affect plant habitat and available source of water is soil capacity and physical properties of soil. Some agrotechnical measures can improve soil water capacity but in fact for all agricultural produces always remain as challenge—how to manage water in a way to provide optimal crop yields during the vegetation season.

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Conflict of interest

The authors declare no conflict of interest.

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