Amitav Bhattacharya

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It is not the quantity of water applied to a crop, it is the quantity of intelligence applied which determines the result - there is more due to intelligence than water in every case.

Alfred Deakin, 1890.

Preface

The semi-arid regions of the Western United States, India, China, and other parts of the world produce a major portion of the world's food and fiber needs—from staple food grains of wheat, rice, and corn to vegetables, fruits, nuts, cotton, and forage crops for cattle and poultry. Most of this production in the semi-arid lands is achieved with irrigation. Due to increase in population, urbanization, and environmental consciousness, the water demands for drinking, sanitation, urban irrigation, industry, and environmental uses for outbidding and reducing the water available for agriculture. Shrinkage of groundwater resources, such as the depletion of aquifers in India, China, and the USA, and prolonged drought in the last few years have aggravated the situation. The greater frequency of more severe drought predicted by some global climate change models is cause of greater concern. In addition, global warming appears to be increasing the water requirements (evaporation demands) of plants and this further decreases the growth and developmental processes in plants and thus reducing the harvestable yields.

Among abiotic stresses, soil water deficit is a serious threat to agriculture and the environment which have been exacerbated in the current century by global warming and industrialization. In the current millennium, an international initiative focusing on increasing our productivity per unit of water has been launched to achieve "more crop per drop." Soil water deficit is the main feature of semi-arid areas. Semi-arid regions represent 30% of the global terrestrial area and are located in the Americas, Oceania, Asia, and Africa. The semi-arid region is characterized by high temperatures and unstable rainfall, both in the temporal and space dimension. The main feature of the semi-arid region is frequent drought caused by the prolonged absence of rain. Efforts to improve the efficiency of agricultural water use while simultaneously reducing adverse environmental impacts will need to draw on results of extensive and diverse research in several areas. Soil water deficit is due to low water potential in the plant as a result of low soil water potential, high evaporative demand, and/or substantial resistance to water flow through the plant. The water deficit affects many processes in the crop, although most of the effects are related to the reduction in growth, the most sensitive process, and to stomatal closure. Mild to moderate deficits do not affect harvest index, and in some species, they may increase it. Instead, severe water deficits reduce the harvest index. The effect of water stress on crop yield can be quantified by Stewart's equation which establishes that the relative reduction in yield is directly proportional to the relative reduction in evaporation, with an empirical coefficient (Ky) which ranges between 0.8 and 1.5. More mechanistic type models may be used to characterize the yield responses to variable water supply, but they need to be locally calibrated for accuracy and this can be achieved with better understanding of different physiological processes as affected by soil water deficit that too at different crop growth stages. Over the last few decades, there has been tremendous progress in understanding the molecular, biochemical, and physiological basis of stress tolerance in plants. Soil water deficit leads to a series of morphological, physiological, biochemical, and molecular changes in plants that adversely affect growth and productivity. Crop yield is the accumulation of energy transformation of solar energy into chemical energy on crops. Soil moisture conditions affect plant root water absorption and leaf transpiration, which further affect dry matter accumulation and ultimately affect crop yield. A frequent result is protein dysfunction. Understanding the mechanisms of protein folding stability and how this knowledge can be utilized is one of the most challenging strategies for aiding organisms undergoing stress conditions. Water deficit also affects the biosynthesis, concentration, transport, and storage of primary and secondary metabolites. As a more comprehensive view of these processes evolve, applications to reducing plant stress are emerging.

Water availability in semi-arid regions is endangered, which is not only due to changing climate conditions, but also to anthropogenic land use changes. While much has been achieved in recent years in developing plants genetically engineered for resistance to herbicides, pests, and diseases, production of plants engineered for soil water deficit has not progressed as rapidly and applications in canola, rice, and maize, for example, have only recently begun to be commercialized. This is due largely to the more complex genetic mechanisms involved in tolerance to water deficit. Many of the gene products differentially expressed under soil water deficit, such as dehydrins, enzymes for the synthesis of osmolytes, and enzymes for the removal of reactive oxygen species, protect plant cells from damage. The production of these functional proteins is widely regulated by specific transcription factors. The use of transcription factors is now under development as an additional biotechnological approach to improving plant response to water deficit. The single greatest abiotic stress factor that limits crop growth worldwide is water availability. Soil water deficit constrains the growth and productivity of major crop species such as cereals, legumes, cotton, sugarcane, etc. While genetic increases in yield potential are best expressed in optimum environments, they are also associated with enhanced yields under drought and nitrogen deficiency.

This book is intended to cover the major effects of soil water deficit on the various aspects of physiological processes in plants through review articles. The book has seven chapters altogether. Under soil water deficit condition, the first issue faced by plant is lowering of plant water content and thus the first chapter deals with *plant–water relationship* under soil water deficit. Following lowering of plant water content the most affected physiological process in carbon metabolism, e.g., photosynthesis, photorespiration, and respiration. The second chapter deals with the effects of soil water deficit on *photosynthesis, photorespiration, and respiration*. Apart from water relationship and carbon metabolism, under, nitrogen uptake and its metabolism is also affected by soil water deficit. In the third chapter, the effects of soil water deficit on *nitrogen metabolism* have been reviewed. *Mineral nutrition* under soil water deficit condition and roles of different nutrient to overcome water deficit have been discussed in the fourth chapter. Changes in carbon and nitrogen metabolism bring about changes in the growth and development pattern of plant under soil water deficit condition and the fifth chapter deals with *growth and development* under soil water conditions. The sixth chapter deals with the effect of *plant growth regulator* under soil water deficit condition and efforts were made to review the means to overcome the effects of water deficit through growth hormone application. The seventh chapter reviews the effects of soil water deficit on *dry matter accumulation, dry matter partitioning, and seed yield*. These review chapters address how knowledge of the physiological mechanisms of crops can contribute to reaching these goals.

These seven review chapters address knowledge of the physiological mechanisms of crops which can contribute to overcoming the adverse effects of soil water deficit in plants. Suggestions and advice are most welcome for improvement in the chapters of this. The author is hopeful that this text will be of use to readers, and suggestions for any future edition from researchers, teachers, and students, who use the book, are welcomed. It is hoped that this book will serve the needs of students, faculty members, and researchers. The author sincerely hopes the review chapters in this book will meet the requirements of postgraduate students as well as faculty members of plant physiology and will be glad to receive constructive criticism and suggestions from faculties.

Kanpur, India
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About the Author

Amitav Bhattacharya, Principal Scientist (Retired), Indian Institute of Pulses Research, Kanpur, India. The author earned his M.Sc. degree in Botany (with specialization in Plant Physiology) from Allahabad University, Allahabad, India and his PhD Degree in Plant Physiology from Indian Agricultural Research Institute, New Delhi, India. He is now retired from his role as Principal Scientist at the Indian Institute of Pulses Research, Kanpur, India, where he served over 40 years actively engaging in laboratory studies and conducting field experiments of pulses (Grain Legumes). During his service tenure the author also performed the duties of Principal Investigators (Plant Physiology) for All India Pulse Improvement Programme and looking after the field experiments of different pulses (e.g., green gram, black gram, lentil, field pea, french bean, and pigeonpea.

Effect of Soil Water Deficits on Plant–Water Relationship: A Review

1

Abstract

Plants are often subjected to periods of soil and atmospheric water deficit during their life cycle. The frequency of such phenomena is likely to increase in the future even outside today's arid/semi-arid regions. Under the climatic changing context, soil water deficit has been, and is becoming an acute problem most constraining plant growth, terrestrial ecosystem productivity, in many regions all over the world, particularly in arid and semi-arid area. With global warming, it is expected that soil water deficit would be escalated by increasing evapotranspiration, increasing the frequency and intensity of soil water deficit with an increase from 1% to 30% in extreme water deficit land area by 2100, which would offset the beneficial effect from the elevated CO_2 concentration, further limiting the structure and function of the terrestrial ecosystem. Thus, an understanding of stress due to soil water deficit and water use in relation to plant growth is of importance for sustainable agriculture. Soil water deficit affects the growth, dry mater, and harvestable yield in a number of plant species, but the tolerance of any species to this menace varies remarkably. Plant responses to water scarcity are complex, involving deleterious and/or adaptive changes, and under field conditions these responses can be synergistically or antagonistically modified by the superimposition of other stresses. A ramified root system has been implicated in the tolerance to water deficit and high biomass production primarily due to its ability to extract more water from soil and its transport to above-ground parts for photosynthesis. In addition to other factors, changes in photosynthetic pigments are of paramount importance for tolerance to soil water deficit. Of the two photosynthetic pigments classes, carotenoids show multifarious roles in tolerance to water deficit including light harvesting and protection from oxidative damage caused by soil water deficit. Thus, increased contents specifically of carotenoids are important for stress tolerance. Differences among species that can be traced to different capacities for water acquisition, rather than to

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differences in metabolism at a given water status, are described. Changes in the root: shoot ratio or the temporary accumulation of reserves in the stem are accompanied by alterations in nitrogen and carbon metabolism, the fine regulation of which is still largely unknown. At the leaf level, the dissipation of excitation energy through processes other than photosynthetic carbon metabolism is an important defense mechanism under conditions of water stress and is accompanied by down-regulation of photochemistry and, in the longer term, of carbon metabolism.

Keywords

Soil water deficit · Absorption and water flow · Soil plant water dynamics · Water deficit and morphological traits · Physiological and biochemical traits · Plant growth · Photosynthesis · Membrane stability · Water use efficiency · Stomata metabolism · Aquaporins · Mechanism of resistance to soil water deficit · Mechanism of regulation · Enhancing productivity

1.1 Soil Water Deficit

Although water is abundant on Earth—covering 71% of the total surface—its distribution is not uniform and can easily cause restrictions in availability to vegetal production. At global scale, these restrictions are easily observed in dry climates and can appear in other regions which do not currently experience soil water deficit, as provided by the future backdrop of climate change (IPCC 2007). The influences of water restriction on losses in the production and distribution of vegetation on the terrestrial surface are significantly larger than all other losses combined which are caused by biotic and abiotic factors (Boyer 1985). This striking effect of water on plants emerges from its physiological importance, being an essential factor for successful plant growth, involving photosynthesis and several other biochemical processes such as the synthesis of energetic composites and new tissue. Therefore, in order to characterize the growth and productive behavior of plant species it is essential to have an understanding of plant water relations, as well as the consequences of an inadequate water supply. Broadly, the water state of a plant is controlled by relative rates of loss and absorption, moreover it depends on the ability to adjust and keep an adequate water status (Chavarria and dos Santos 2012).

Water being considered as universal solvent occupies 75% of our planet in the form of oceans. Added to this water is also found in the atmosphere in the form of hydrospheric mantle. The evaporation of water from the surface of ocean, the formation clouds and raining, is a natural cycle evolved during course of evolution of this planet. Nearly 3.8 billion years ago, life took its origin as a speck of protoplasm in the churning oceanic water which was not salty as it is today. In the course of Chemical Evolution, the birth of life has chosen H_2O as the medium of biochemical activities. Thus water has become mother of life or “Solvent of Life.” Cells of all organisms are made up 90% or more of water. And all other components are either dissolved or suspended in water to form protoplasm, which is often referred to as physical basis of life. In this context one is tempted to know why water is so important and how water is useful to life forms.

Water is the major component of living cells and constitutes more than 90% of protoplasm by volume and weight. In acts as medium for all biochemical reaction that takes place in the cell, and also acts a medium of transportation from one region to another region. Water is a remarkable compound made up of hydrogen and oxygen (2, 1) and it has high specific heat, high heat of vaporization, high heat of fusion and expansion (colligative properties). Water because of its bipolar nature acts as universal solvent because it dissolves more substances than any other solvent. Electrolytes and non-electrolytes like sugars and proteins dissolve very well. Even some hydrophobic lipid molecules show some solubility in water, it acts as a good buffer against changes in the hydrogen ion concentration (pH). This is because of its ionization property. Certain xerophytes use water as buffer system against high temperature. Water also exhibits viscosity and adhesive properties. Because of hydrogen bonds, water molecules are attracted towards each other, they are held to each other with considerable force. This force of attraction is called cohesive force. Thus water possesses a high tensile strength. If this water is confined in very narrow columns of dimensions of xylem vessels, its tensile and cohesive forces reach very high values (1000–1200 Gms). And this force is very helpful in ascent of sap. Water is of great importance in osmoregulation, particularly in the maintenance of turgidity of cells, opening and closing of stomata, and growth of the plant body. Water is an important substrate in photosynthesis, for it provides reducing power in CO_2 fixation; water is also used in breaking or making chemical bonds of polypeptides, polynucleotides, carbohydrates, etc.

Green Revolution technologies and significant expansion in the use of land, water, and other natural resources for agricultural purposes have led to a tripling in agricultural production between 1960 and 2015 (FAO 2017). Despite this success, the high costs to the natural environment that accompany elevated productivity and changes in the food supply chain threaten the sustainability of food production (FAO 2017). Global food security is further challenged by climate change, with a predicted increase in frequency of water deficit (Spinoni et al. 2014; Trenberth et al. 2014). While 2 L of water are often sufficient for daily drinking purposes, it takes about 3000 L to produce the daily food needs of a person. Globally, agriculture accounts for at least 70% of withdrawals from freshwater resources, with large effects on ecosystems (Morison et al. 2008; Jobbágy and Jackson 2004). Despite this high water deployment, major yield losses due to water deficits are experienced in crops (Fahad et al. 2017). At the same time, global population growth increases the demand for food, feed, and fuel, which intensifies the pressure to improve water use efficiency of crops (Spiertz and Ewert 2009; Rockström et al. 2007). While better crop and water management practices provide an immediate opportunity to increase crop water productivity, breeding for superior varieties can achieve a medium and long-term increase (Sadras et al. 2012; Parry et al. 2005). The consequences of recent global temperature rise for soil water deficit severity are not well understood. An increase in the water pressure deficit driven by higher temperatures is expected to increase atmospheric evaporative demand (Wang et al. 2012a), resulting in more frequent and severe water deficit (Dai 2011). The hypothesis that there will be an increase in the severity of climate-driven soil water deficit as a consequence of temperature-enhanced atmospheric evaporative demand appears reasonable (Breshears et al. 2005; Teuling et al. 2013). The expected consequences include enhanced biological stress (Williams et al. 2013; Peng et al. 2011; Carnicer et al. 2011) and reduced soil water content, runoff generation, stream flow, and groundwater recharge (Cai and Cowan 2008; Cho et al. 2011). Nevertheless, the relationship between climate warming and increased evapotranspiration is the subject of large scientific debate (Sanchez-Lorenzo et al. 2014). Several studies have shown no effect of temperature increase on the soil water deficit through increased evaporation, as other meteorological variables that affect the evaporative demand of the atmosphere may compensate for the temperature increase (McVicar et al. 2012; Roderick et al. 2008), and potential evaporation may in fact have decreased in recent decades (Roderick et al. 2008).

Well-watered plants are turgid. Their cells, which are enclosed in a strong but slightly elastic wall, are distended by an internal pressure that may be as high as 1 MPa, 5 times the pressure in a car tire and 10 times the pressure of the atmosphere. Plants perform best when they are turgid. Many of the structures of higher plants serve to maintain their cells sufficiently hydrated to function—to grow, to photosynthesize, and to respire—even though most of these cells are in the shoots of the plants and so are not only remote from the supply of water in the soil, but are also exposed to a dry environment. A well-hydrated leaf may transpire several times its own volume of water during a day. Water evaporates from wet cell walls into the internal gas spaces of the leaf. It then flows away as vapor, largely through stomata, which are variable pores in the surface of the leaf. The loss is an unavoidable consequence of the stomata being open, as they must be to allow carbon dioxide to enter the leaf. The relative humidity inside a leaf is typically >99%, and thus there is usually a large difference of absolute humidity across the stomata that induce rapid diffusion of water vapor out of the leaf. Although a leaf may lose much water by evaporation, its net loss of water is usually small. Evaporation from cell walls creates in them a large suction that replenishes water by drawing it from the soil, principally not only via the plant's vascular system, but also through flow across cells in the roots and leaves.

Generally stress due to soil water deficit occurs when the available water in the soil is reduced and atmospheric conditions cause continuous loss of water by transpiration or evaporation. Tolerance to soil water deficit is seen in almost all plants but its extent varies from species to species and even within species. Soil water deficit and salt stresses are global issues to ensure survival of agricultural crops and sustainable food production (Jaleel et al. 2007a, b, c, d; Nakayama et al. 2007). Conventional plant breeding attempts have changed over to use physiological selection criteria since they are time consuming and rely on present genetic variability (Zhu 2002). High yield potential under soil water deficit is the target of crop breeding. In many cases, high yield potential can contribute to yield in moderate stress environment (Blum 1996a). Stress due to soil water deficit is

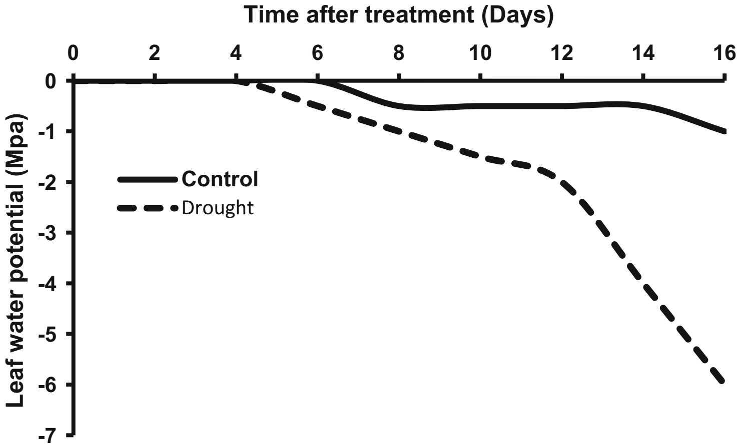

Fig. 1.1 Changes in leaf water potential and relative water content in sorghum leave during drought progression

considered to be a moderate loss of water and is characterized by reduction of water content, diminished leaf water potential (Fig. 1.1), and turgor loss, closure of stomata, and decrease in cell enlargement and growth (Fig. 1.1). Severe soil water deficit may result in the arrest of photosynthesis, disturbance of metabolism, and finally the death of plant (Jaleel et al. 2008c).

Soil water deficit inhibits cell enlargement more than cell division. It reduces plant growth by affecting various physiological and biochemical processes, such as photosynthesis, respiration, translocation, ion uptake, carbohydrates, nutrient metabolism, and growth promoters (Jaleel et al. 2008a, b, c, d, e; Farooq et al. 2008). In plants, a better understanding of the morphoanatomical and physiological basis of changes in water stress resistance could be used to select or create new varieties of crops to obtain a better productivity under water stress conditions (Nam et al. 2001; Martinez et al. 2007). The reactions of plants to water stress differ significantly at various organizational levels depending upon intensity and duration of stress as well as plant species and its stage of growth (Chaves et al. 2002; Jaleel et al. 2008b). Understanding plant responses to soil water deficit is of great importance and also a fundamental part for making the crops stress tolerant (Reddy et al. 2004; Zhao et al. 2008).

1.2 Properties of Water

A substance with the molecular weight of water should exist as a gas at room temperature and have a melting point of below 100 °C. Instead, water is liquid at room temperature and its melting point is O °C. It has the highest specific heat of any known substance except liquid ammonia, which is about 13% higher. The high specific heat of water tends to stabilize temperatures and is reflected in the relatively uniform temperature of islands and land near large bodies of water. This is important with respect to agriculture and natural vegetation. The standard unit for measuring heat, the calorie, is 4.18 joules and is based on the specific heat of water or the amount of energy required to warm 1 gram of water 1°, from 14.5° to 15.5 °C. The heat of vaporization is the highest known, 540 cal. g^{-1} at 100 °C, and the heat of fusion, 80 cal. g^{-1}, is also unusually high. Because of the high heat of vaporization, evaporation of water has a pronounced cooling effect and condensation has a warming effect. Water is also an extremely good conductor of heat compared with other liquids and nonmetallic solids although it is poor compared with metals. Water is transparent to visible radiation (390–760 nm). It allows light to penetrate bodies of water and makes it possible for algae to carry on photosynthesis and grow to considerable depths. It is nearly opaque to longer wavelengths in the infrared range so that water filters are fairly good heat absorbers.

Water has a much higher surface tension than most other liquids because of the high internal cohesive forces between molecules. This provides the tensile strength required by the cohesion theory of the ascent of sap. Water also has a high density and is remarkable in having its maximum density at 4 °C instead of at the freezing point. Even more remarkable is the fact that water expands on freezing, so that ice has a volume about 9% greater than the liquid water from which it was formed. This explains why ice floats and pipes and radiators burst when the water in them freezes. Incidentally, if ice sank, bodies of water in the cooler parts of the world would all be filled permanently with ice, with disastrous effects on the climate and on aquatic organisms.

Water is very slightly ionized; only one molecule in 55.5×10^7 is dissociated. It also has a high dielectric constant (ability to neutralize attraction between electrical charges) which contributes to its behavior as an almost universal solvent. It is a good solvent for electrolytes because the attraction of ions to the partially positive and negative charges on water molecules results in each ion being surrounded by a shell of water molecules which keeps ions of opposite charge separated. It is a good solvent for many non-electrolytes because it can form hydrogen bonds with nitrogen in amino groups and oxygen in carbonyl groups. It tends to be adsorbed, or bound strongly, to the surfaces of clay micelles, cellulose, protein molecules, and many other substances. This characteristic is of great importance in soil and plant water relations.

One of the most important features of water is that it forms strong hydrogen bonds. These greatly influence several biologically important bulk properties. Water has unusually large latent heats of evaporation and freezing, which help plants cope with frosts or heat loads. It has great cohesive strength, which enables it to withstand the very large tensions that develop in the xylem and thus to maintain continuity of liquid water throughout the plant. It has a large surface tension at an air–water interface, which creates a strong skin that ensures that suitably small pores in soil or plant remain filled with water even if the water is under great tension, as is often the case. The physico-chemical properties of water have shaped many of the processes in plants and, indeed, in all organisms. Several of these properties, together with selected values, are listed in Table 1.1.

Table 1.1 Some of the physico-chemical properties of water and aqueous solutions

Properties	Value and units
Cohesive strength	>25 MPs
Surface tension	0.073 mN m^{-2} at 20 °C
Viscosity	0.0018 Pa s at 0 °C
	0.0010 Pa s at 20 °C
Diffusion coefficient of small solutes in water	~1×10^{-9} m^2 s^{-1}
Molar volume (pure water at 10 °C)	1.51×10^{-5} m^3 mol^{-1}
Latent heat of evaporation at 20 °C	2.5 MJ kg^{-1}
Latent of melting	0.34 MJ kg^{-1}
Saturated vapor pressure of pure water	0.61 kPa at 0 °C
	1.25 kPa at 10 °C
	2.34 kPa at 20 °C
	4.24 kPa at 30 °C

After Passioura J.B. (2001)

On the molecular scale, hydrogen bonds ensure that macromolecules such as proteins and DNA (deoxyribonucleic acid) are surrounded by a shell of water molecules that acts as a spatial buffer between the macromolecules, preventing them from adhering to each other and thereby precipitating. This shell also penetrates interstices in such molecules, thus helping to maintain the three-dimensional structures on which their reactions depend.

Water is polar: despite being electrically neutral, it has a slight excess of electrons on one side of each molecule and a slight deficit on the other. Its polar nature, coupled with its ability to form hydrogen bonds, makes it a very good solvent for ions and small organic molecules such as sugars. Molar concentrations of these are possible, and often occur, thereby enabling cells to generate osmotic pressures of several MPa, a requirement for plants to remain turgid in a saline or water deficit environment. The polar nature is especially important in enabling fatty acids to organize themselves into the membranes that bind cells and organelles. Fatty acids have a nonpolar hydrocarbon tail attached to a polar carboxylic acid group. These nonpolar tails, eschewing an aqueous environment, line up to form two sheets that are appressed together to form a lipid bilayer, with the polar heads presenting a hydrophilic surface on each side. Other biologically important properties of water include: its viscosity, which influences how fast water flows in response to a pressure gradient; and its ability to dissociate into hydrogen- and hydroxyl ions, which is central to the pH scale. As with all materials above absolute zero temperature, water and solute molecules are in thermal motion. This motion ensures that gradients in solute concentration or temperature are eventually dissipated by diffusion.

1.2.1 Water Potential

In most fully differentiated plant cells the cytoplasm takes up only 5–10% of the cell volume, while the rest is filled by a huge vacuole. The cytoplasm and vacuole contain large quantities of dissolved ions and organic compounds, which impart to them an osmotic potential or solute potential (ψs). The osmotic potential can be calculated from van't Hoff equation $\psi s = -RTc_s$, where R is the gas constant (8.32 J mol^{-1} K^{-1}), T is the absolute temperature (in degrees Kelvin), and c_s the osmolality of the solute concentration (moles of total dissolved solutes per liter of water, mol L^{-1}). Hence, the osmotic potential of pure water is zero. The more solutes there are in the solution, the more negative the osmotic potential will be.

There are other things that affect the state of water inside the cells: these are the pressure, the gravity, and the presence of large organic molecules (or matrix), which may collect a sheet of water molecules around them. Now, these have been given the terms ψ_p (p for pressure), ψ_g (g for gravity), and ψ_m (m for matrix). All these potentials added together form the water potential (ψw) of the cell, and hence we can write the equation:

$$\psi_w = \psi_s + \psi_p + \psi_g + \psi_m$$

While the osmotic potential is either 0 or a negative figure, the pressure potential can vary between positive (turgid cell) and negative (transpirational "pull" in vessels) values. Gravity would impart a positive value, but under normal conditions, when vertical distances are small, it is negligible. The matrix potential can be a positive or negative value depending on the matrix. Normally, all the polymer surfaces of the plant cells are covered by a layer of water molecules, and hence matrix potential is negligible, except in germinating seeds, which contain large amounts of starch and other dry compounds that draw a lot of water molecules to their hydrophilic surfaces, and hence impart a negative ψm to the system. Now, we see that the ψ_w can have either 0, a negative or a positive value although in normal living cells ψ_w is practically always a negative value. The water potential of a particular cell gives us an idea how water molecules travel in the tissues. If two adjacent cells have different water potentials, this means that water is going to pass from one cell to the other until the pressures are equalized. Water moves from higher water potential to lower (more negative) water potential. The passage of water is allowed through particular pores in the plasma membrane called aquaporins. Until a few years ago their existence was not known, but nowadays there is ample information on their presence in membranes. Earlier it was thought that water molecules could work their way between the membrane lipid molecules, and hence pass the membrane. This was, however, against the basic theory of membrane properties, which states that all ions or molecules that are charged or polar cannot pass the membrane, and only small, uncharged (and hence hydrophobic) atoms or molecules can go through the plasma membrane. It is now known that the aquaporins allow the passage of water through the otherwise impermeable membrane. Water flow is regulated by the expression of aquaporins (i.e., their number per area) and by their regulation through protein phosphorylation.

The water content in the soil, plants, and atmosphere is usually described as water potential (Ψw). This is based on the relation between the water content in the part of a system and pure water at the same temperature and atmospheric pressure, measured in pressure units (megapascal-MPa or bars-Bar). By definition, the potential of free pure water at atmospheric pressure and at a temperature of 25 °C corresponds to 0 (zero) MPa. The contrast in the water potential between two points invariably determines the direction of water transport in a system. More precisely, the water potential represents all the water pressure in a given system and it is the sum of osmotic potential (Ψπ), matrix potential (Ψm), hydrostatic pressure or the turgor potential (Ψρ), and the gravitational potential (Ψg). The osmotic potential (Ψπ) is the chemical potential of water in a solution due to the presence of dissolved substances (solutes). This is always negative because the water moves from one point with a lower concentration of solutes (for example, pure water) to a point with a higher concentration. So, the higher concentration of the solutes at a point which makes the system more negative will be the osmotic potential in this place. The water potential can also be influenced by a charged surface—mainly by soil components and cell walls—which compose the influence of the matrix potential (Ψm). In the soil, this influence of the matrix is so great that water potential is assumed negligible and therefore equivalent to the matrix potential. Concerning the potential of hydrostatic pressure (Ψρ), it is noted that this component of the water potential can be positive or negative and it refers to the physical pressure that water exerts on a given system. For example, a turgid cell of a root cortex or a leaf mesophyll, the hydrostatic pressure is positive. However, in a xylem vessel subjected to a stressful condition—in a transpiring plant—this component of hydrostatic pressure is negative. Finally the gravitational potential (Ψg)—ignored in most cases—is very important in studies of the water potential of tree species, where plant height exerts a great influence on water flow. Considering that this gravitational component fluctuates at a rate of 0.1 MPa for every 10 m of vertical displacement, it is suggested to consider if when plant height is 10 m or more.

1.3 Absorption and Water Flow Through Plants

Independent of the species, plants require from the soil a water volume that overcomes its metabolic necessities. Through the transpiration process plants transmit to the atmosphere the majority of the water absorbed from soil (generally around 90%). From this perspective, it is noted that the plant water requirements are defined primarily by the atmosphere evapotranspirative demand, which is a predominately passive process. Figuratively, and with some caveats, we can compare a plant water flow with the principles of oil flow in the wick of an old fashion lampion.

1.3.1 Water Dynamics in Soil–Plant–Atmosphere System

From these components of water potential we return to our lampion scheme and show how the potential can vary over the continuum soil–plant–atmosphere, exposing the control points of each step of water flow from the soil to the atmosphere.

The water potential in soil affects water reservoir and its availability for plants, hence it has a large impact on plant growth and production. Furthermore, the soil water content exerts a great influence on some physical and chemical properties of soil, such as the oxygen content, which interferes with root breathing, microbial activity, and soil chemical status. Water potential is directly dependent on soil physical characteristics, and varies with time and space, depending on soil water balance. That balance is determined by input (rain, irrigation) and output of the soil (drainage, evaporation, and root absorption). It is noteworthy that the amount of rain affecting soil water reservoir is only the effective precipitation. This is the amount of precipitation that is actually added and stored in the soil. For example, during drier periods <5 mm of daily rainfall would not be considered effective, as this amount of precipitation would likely evaporate from the surface before soaking into the ground. It is important to emphasize that behavior of water into soil differs from that in a pot, like the oil in the lampion reservoir. That is, soil water interacts with the matrix and solutes, and it is under pressure or tension, resulting in various energy states, relative to free water (Kirkham 2005). With regard to the physiological aspect, it is important to point out that the water content in soil is associated with three terms: field capacity, the permanent wilting point, and the available water content.

The term "field capacity" corresponds to the maximum water content that a given soil can retain by capillarity, after saturation and gravity drainage, and it is conventionally estimated as the water content when the matrix potential is −0.03 MPa (−0.3 bar). In spite of the great applicability of this term to irrigation management, field capacity has been recognized as an imprecise term due to theoretical advances and precise irrigation techniques. It is because the capillary soil water constantly (even slowly) decreases (due to evaporation from soil surface or drainage losses) and never stabilizes, it turn the soil water potential decreases while the matrix potential increases. This is most evident with medium and fine texture soils (for example, those rich in clay and organic matter), which maintain a significant drainage rate over a long time. Therefore, there is no real and unique value for accurately characterizing the field capacity of a given soil. Furthermore, the continuous drainage can induce an overestimation of the water consumption of the plant. Despite these uncertainties, the term field capacity is still useful for a qualitative understanding—rather than a quantitative understanding—of the water behavior of a particular soil, providing an estimate of the maximum limit of water accumulation. It is noteworthy that the inaccuracy of the field capacity determination occurs mainly when analysis takes place on samples in the laboratory, which can be contoured with evaluations directly in the soil, with specific sensors and considering together all characteristics of each site. In general, clay soils or those with higher content of organic matter (upper to 5% of organic matter) present a higher soil water holding capacity (average field capacity ranging from 35 to 40%vol). In contrast, sandy soils have a lower water holding capacity and field capacity typically ranges from 10 to 15% vol. It is important to observe that field capacity cannot be regarded as a maximum limit of the water available to plants, due to the fact that plants also use free water that is in contact with the roots at the moment of soil drainage.

The wilting point is another important parameter in soil water dynamics as it dramatically affects plant physiology. This term is also known as the permanent wilting point, and can be defined as the amount of water per unit weight (or volume) of soil that is so tightly retained by the soil matrix that roots are unable to absorb causing the wilting of plant. In others words, it corresponds to the water potential of soil under which plants cannot maintain turgor pressure, even if a series of defense mechanisms have been triggered (e.g. increased abscisic acid synthesis, stomatal closure, osmotic adjustment, leaf fall). Similarly with field capacity, the value of water content in a soil at wilting point is not a unique and precise value despite it is conventionally measure at −1.5 MPa (−15 bar). The wilting point is influenced by the physical and chemical characteristics of soil, but also by the plant species considered. This is because various plant species differ in their ability to deal with low soil water content due to differences in roots anatomy and depth, osmotic adjustment capacity, and other defense mechanisms. Conventionally, the wilting point is estimated as the water content when the matrix potential of the soil is −1.5 MPa (−15 bar). Nevertheless, some species of plants can absorb water soil at a potential much smaller than this limit. For example, olive trees can set a water potential gradient between dry soil (−3 MPa) and leaf (−7 MPa) (Dichio et al. 2006). Similarly, *Larrea divaricata* (commonly known as chaparral) may absorb water at −6.0 MPa soil water potential (Kirkham 2005). Another species of the same genus of desert plant (*Larrea tridentata*) can survive with soil water potentials up to −11.5 MPa, maintaining the photosynthetic activity of leaves within the range between −5 and −8 MPa (Fitter and Hay 2002). These examples serve to explain that the permanent wilting point does not exclusively depend on the soil but also on the plant species. At the permanent wilting point, the water potential of soil tends to be less than or equal to the osmotic potential of the plant, which is extremely low in plants adapted to dry environments.

The indiscriminate use of a fixed value to estimate field capacity and the permanent wilting point can generate false interpretations. However, this reference to the water content in the soil is essential for calculating the available water content for the plants. The available water content for plant is calculated considering the soil volume explored by roots and the percent of water content determined as the difference between field capacity and wilting point. Due to this interval of water availability, one may assume that water could be absorbed by the roots with the same facility in the range between field capacity and wilting point. For some plants this may be true, given that the energy to extract water from the soil is small, compared to the energy needed to transport the water from the root system to the atmosphere. However, with the reduction of soil water potential, there is also a reduction in its hydraulic conductivity (i.e. water moves slowly in the soil), limiting the water absorption capacity of the roots. In this scene—and for a majority of crops—the yields are reduced if the water content in the soil approaches the wilting point. Thus, the available water content should be considered as a relative value and, for the same soil water potential, it may have different proportions of accessibility, depending on the ability of each species to exploit or capture available water.

1.3.2 Water Absorption by the Roots

The water flow of a plant is primarily controlled by the transpiration rate. In this flow system it is essential indeed that there are no limitations on water absorption by the root system. As the roots absorb water, there is a reduction in the water potential in the soil that is in contact with the roots (rhizosphere). This process establishes a water potential gradient between the rhizosphere and a neighboring region of the soil which presents a higher water potential and which coordinates the water movement towards the roots of a transpiring plant (Fig. 1.1). This water movement in the soil occurs mainly through mass flow due to the fact that the water filled micropores of the soil are interconnected. Therefore, water flows from soil to root at a rate depending on the water potential gradient between soil and plant which is affected by plant water need, hydraulic conductivity of the soil, soil type, and soil water content. Sandy soils have higher conductivity due to greater porosity, but they also retain less water in relation to clay soils or soils rich in organic matter. At field capacity, water is initially removed from the center of the largest pores (spaces $\geq$50 nm, that are too large to have any significant capillary force) between the soil particles, maintaining the water next to the particles due to adhesive forces. The reduction in water content causes a drastic decrease in soil hydraulic conductivity, because the water is replaced by air in the spaces between the soil particles (Fig. 1.2). Thus, the water movement in the soil is limited to the periphery of soil pores, which can promote restrictions in the hydraulic conductivity to the root surface and reach the permanent wilting point.

The water absorption by the roots is related to its surface directly in contact with soil. Thus, longer and younger (less suberized) roots with more root hairs are essential for increasing the contact surface and improving the water absorption capacity of the soil. Moreover, the distribution and proportion of the roots are very important for meeting the water demand of a plant. In humid regions, as tropical rain forest, plants usually do not require very extensive root systems (i.e. root:shoot ratio $<$0.15, Abdala et al. 1998), because a small volume of soil can meet the demands of transpiration. In addition, the water absorbed from that small soil volume is frequently replenished by rainfall. This condition in turn induces a reduction of the root: shoot ratio. On the other hand, in dry regions, the plants invest more in their roots, increasing the root:shoot ratio such that the roots can represent upper to 90% of a plant biomass in some species of a desert climate, such as observed in some species from open areas of the Bana woodland in southern Venezuela (i.e. root:shoot $>$5, Bongers et al. 1985) and from savanna in Brazil (Abdala et al. 1998). It is important to note that the use of this root:shoot relation in the classification of plants with respect to their habitat must be made with caution. In many species, a higher investment in roots is more related to the accumulation of reserves and not