

WATER UPTAKE BY PLANTS

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Summary

This chapter deals with the processes involved in water uptake by plants. Following a natural order, we first focus on describing water availability and water movement in the soil. Then we pay attention to water absorption through roots, describing how water moves from the soil into the root xylem, and then up to the leaves. Structures for water uptake, hydraulic characteristics of the conductive tissues and main physical aspects

related to the water flow within the plant are considered. Once this picture has been completed, we move on to how water uptake can be determined, describing the latest advances in methodology for quantifying changes in soil water content around roots and water flows within the plant. Finally, we try to give a comprehensive picture on root morphology and function, describing main features of the hydraulic performance of roots, root growth, distribution and activity, and the influence of main environmental factors on the behavior of the root system.

1. Introduction

The use of water, since population pressures and human activities are constantly increasing, is a matter of crucial interest. If we were bound to summarize the overall problem of water use in just a few sentences, those will probably include: the distribution of water resources for agricultural, industrial and urban use is causing frequent social conflicts in arid and semiarid areas; environmental anxiety is increasing as a consequence of the degradation in the quality of ground and surface water due to non-sustainable practices in the use of water and agrochemicals; planners are demanding more information on the fate of water in natural and cropped systems, and on how the use of this natural resource can be optimized. Over recent decades, some positive developments have occurred: first, the problem has been identified, which is always the first step to solve it. Biologists, growers, environmentalists, planners, and society, in general, are now well aware of the need for optimizing the use of water. Second, technological improvements are giving us an invaluable hand in understanding water transport and consumption processes.

There are different components to the hydrological cycle, and this article deals with the rootzone, the soil region explored by roots. The aim of this article is to give a comprehensive picture of the processes involved in water uptake by plants: how water moves in the soil and into the roots, and how it is transported within the plant up to the aerial parts and to the atmosphere. Many of those processes are not yet well understood. This is due, on the one hand, to the fact that they occur mostly below the ground surface. Being out of sight has curtailed the amount of research on the subject. On the other hand, the processes involved are certainly complex. There is a strong relation between root structure and function, but the existing knowledge is far from capable of giving a clear picture. It is well known that root behavior not only depends on the plant species, but it changes with time and growth conditions.

The reader, therefore, may be disappointed when, after reading this article, many of his or her detailed questions still remain unanswered. The good news is that the development of new instruments and novel techniques for determining the fate of water in the soil-plant-atmosphere system is improving. The speed of these developments would have been unthinkable just a few years ago. The use of these techniques are changing our view of the root structure and functioning, and new insight is being added to our understanding of water uptake, and certain aspects of theories that had been accepted for decades are now being clarified. This article shows the main advances in the understanding of water movement in the soil-plant system, and the newest theories describing the nature of water uptake.

2. Water in the Root Environment

One of the factors influencing more the root behavior is water availability in the rootzone (see Section 5.4). Rather than being related to the soil's volumetric water content, water uptake by roots depends on the energy with which the soil particles retain water, i.e. the thermodynamic potential of the state of the water in the soil. In fact, water uptake only takes place when the energy created by the roots in the absorption process is greater than the water potential in the soil in which they reside. The water potential is markedly affected by the textural characteristics of the soil, and its value, in turn, depends on the soil moisture content. Since this latter variable is easier to measure than the water potential, it is also widely used when considering water status in the root environment.

2.1. Water Content

After wetting by rainfall or irrigation, water infiltrates the soil under the action of capillarity, and it is also drawn in by gravity. If the amount supplied is large enough, the soil can become saturated. When the water supply ceases, a fraction of the water drains out of the larger pores, because gravity is stronger than the capillary forces with which water is retained in those pores. After equilibrium between both forces is attained, downward drainage can soon become negligible. The soil then can be regarded as being at 'field capacity'.

Sandy soils usually attain equilibrium sooner than clay soils. In these latter soils, the size of the soil particles is smaller than in sandy soils, which causes greater forces for water retention by capillarity. Therefore, the moisture content at field capacity is usually greater in clay soils than in sandy soils. A soil can reach field capacity from a few hours, to several days, after the water supply, depending on the soil characteristics. The soil water content at field capacity can be measured *in situ*, or in the laboratory, where the soil samples are subjected to a pressure of about -0.03 MPa. The soil of the rootzone often remains around field capacity only briefly, since water is continuously lost by evaporation from the soil surface, or by water uptake by roots, or by lateral movement away from the wetting surface.

If no additional water is supplied, the roots dry the soil down until reaching the 'permanent wilting point'. At this point the energy developed by the roots during the absorption process cannot overcome the energy with which the water is retained by the soil. Consequently, the plants become wilted. It is widely accepted that the wilting point is reached when the water potential in the soil decreases to -1.5 MPa. It has to be taken into account, however, that this value depends on the plant species. Some species can remain wilted overnight at low values of water potential, while others, typically those well adapted to arid conditions, can recover turgidity during the night when growing in soils at -2.5 MPa or lower. Both these concepts of field capacity and permanent wilting point, are widely used by agronomists, environmentalists and researchers. Despite obvious utility, some soil scientists have recommended to abandon these concepts, arguing that they are not really soil constants, but depend on the conditions under which measurements have been made and on the plant species.

The ‘total available water’ for the plants growing in a particular soil is often calculated from the difference between the soil water content at field capacity and at wilting point, and taken into account the depth of the soil layer explored by the roots. It is normally expressed in millimeters (mm), i.e. liters per square meter of soil surface. Generally the total available water is greater in finer-textured soils, than in coarse textured soils. Another concept used by agronomists is that of “readily-available soil water”. This is the water that can be extracted from the soil before the water stress suffered by the plants causes a significant decrease on crop water use and productivity. For crops growing in arid and semiarid areas, the readily-available water can be about 60-70% of the total available water. Replenishment of the readily available water is important for the sustainable management of irrigation.

The soil water content, normally expressed as volumetric water content (θ , $\text{m}^3 \text{m}^{-3}$), can be measured by different techniques. The gravimetric method simply requires weighing before and after drying, needing only inexpensive equipment and little training, but it is destructive. The water content determined is on a per unit weight basis, which can be converted into volumetric units just multiplying by the soil bulk density. The neutron scattering method has been, and still is, widely used to determine θ . It is less time consuming and not as laborious as the gravimetric method, and repeated measurements can be made at the same locations, using access tubes installed in the soil until the desired depth. The neutron probe, itself, has the main disadvantage of emitting neutron and gamma radiation. Therefore, the equipment must be used by licensed people and it must be regularly checked. The technique is becoming used less and less. Another nuclear method for measuring θ is gamma densitometry. The instrument is used similarly to a neutron probe, but the technique has never really become popular. Time domain reflectometry (TDR) and the frequency domain method (FD) are two so called dielectric methods, whose popularity has increased in the last years. The value of θ is derived from the measurement of the electrical capacitance of the soil, the value of which depends to a large extent on the water content. TDR is the most widely used of the two methods. It can be used with confidence in nearly all types of soil, without site-specific calibration. Saline or cracking soils may pose some limitations for use of the technique. The system can be automated for continuous monitoring. Several works published in the last decade confirm that TDR is a powerful technique for studying root water uptake (see Section 4.1).

2.2. Water Potential

The chemical potential of the water of an aqueous solution is a measure of the ability of that water to do work. The water potential is the chemical potential of the water component of a solution compared to some reference state, usually taken as being pure water at the same temperature and elevation. Basically, the water potential is referenced to different parts of the soil-plant-atmosphere system to determine the continuous and causal link for transport from the soil, to the plant and to the atmosphere. The water potential in the soil (Ψ_{soil} , MPa) results from the effect of four components:

$$\Psi_{\text{soil}} = \Psi_{\text{m}} + \Psi_{\text{s}} + \Psi_{\text{g}} + \Psi_{\text{p}} \quad (1)$$

In this equation, Ψ_m is the matric potential that results from the capillary and absorptive forces that attract the water to the soil matrix; Ψ_s (which can also be represented as Ψ_π) is the osmotic potential produced by solutes in the soil water; Ψ_g is the gravitational potential of the soil water, determined by the elevation of any given point at which the water potential is measured, relative to a reference level, usually taken to the soil surface, or the water table depending on the purpose; Ψ_p represents the effect of hydrostatic pressures exerted on the system. This last component is usually disregarded because the pressure is near atmospheric in the rootzone. From these potential components, Ψ_m is the one which generally most influences Ψ_{soil} . The value of Ψ_s is usually negligible, except in saline soils when the amount of solutes in the soil solution is high. The sign of Ψ_g depends on whether the given point in which Ψ_{soil} is measured is either above (+) or below (-) the reference level. For each meter of distance from the datum $\Psi_g = 0.01$ MPa.

In short, to absorb water, roots must generate internal water potentials low enough to overcome Ψ_{soil} . As well, the value of Ψ_{soil} is also important in the study of how water moves in the soil, for the soil's hydraulic conductivity is a highly non-linear function of Ψ_{soil} . Generally water moves through the soil to locations of lower water potential. Note that the sign of Ψ_{soil} is negative, so that low potential means drier soil, whereas higher potential means wetter soil, such that the soil is saturated when $\Psi_{\text{soil}} = 0$, namely there is free water at the given point. This need not always be true (see Section 2.3). The different components of Ψ_{soil} (Eq. (1)) have a varying influence in the movement of the water in the soil-plant system, depending on which part of the system we are considering. For example, Ψ_s has little effect on the water movement within the soil, but it has a marked effect on the movement of water from the soil into roots because the soil solution is separated from the plant solution by differentially permeable membranes. A membrane may allow free passage of water, while at the same time it restricts the passage of solutes, which then results in a built-up in the osmotic potential. Water movement from the soil to the roots, and within the plant, is discussed later (see Section 3).

The matric potential, Ψ_m , which is the main component of Ψ_{soil} , can be measured in the field with either resistance blocks, or more directly with tensiometers. The tensiometer works well in moist soils, until a minimum Ψ_m of about -0.08 MPa. The resistance blocks can give reasonably accurate measurements at matric potentials down to -3.0 MPa. Both instruments are widely used to schedule irrigation. The measurement of Ψ_m in the field with batteries of tensiometers each placed at different depths can be used, together with Darcy's Law (see Section 2.3), to monitor fluxes of water in the soil. Microtensiometers can be used for *in situ* measurements of Ψ_m close to the roots. Total soil water potential can be measured with soil psychrometers. These are thermocouple psychrometers housed in a ceramic cup. They can measure below the tensiometer range, but they are not accurate above -0.2 MPa. The value of Ψ_{soil} is rarely lower than -2

MPa. The water potential in the leaves of plants, growing under relatively high atmospheric demand for water, can easily drop to -4 MPa, or even lower in some plants. In the ambient air surrounding the plants the water potential is commonly lower than -50 MPa. This strong gradient in water potential in the soil-plant-atmosphere system is responsible, to a great extent, for water uptake (see Section 3.2). In addition, the value of Ψ_{soil} in the rootzone can, by feedback, alter stomatal behavior, thereby influencing water uptake and transpiration (see Section 4.4).

2.3. Water Movement in the Rootzone

The major portion of water movement within the soil takes place in the liquid phase. In this case, the forces that determine water potential (Eq. 1) lead to water movement in the particular direction of the potential field. *In situ* determination of water movement in the vadose zone is not easy. The natural heterogeneity, both in space and time, of soil hydraulic properties, can create a significant variability in both θ and Ψ_m across the rootzone. As a consequence, the hydraulic conductivity of the soil (K , m s^{-1}) is also highly variable, because K is a strongly non-linear function of both θ and Ψ_m . In addition, root decay, worm burrows and ant holes, plus structural cracks can create a network of macropores through the soil's matrix which can have a great impact on the soil's ability to conduct water, especially when the soil is saturated, or at near saturation. As a result, K , especially the saturated $K_s = K(\Psi_m = 0)$, can often be raised several orders of magnitude by the presence of just a few connected macropores. The influence on water entry and storage in the rootzone caused by macropores must therefore be taken into account in irrigation practice. The key is to avoid saturated or near-saturated conditions. Water flow through the macropores is often called preferential flow. One approach that can be used to model water transport through the soil profile is to consider that the soil has two complementary domains; a mobile and an immobile pathway for water transport. The mobile domain represents the soil's macropores, and the immobile domain represents the soil matrix. After the water supply at the surface ceases and the water content drops somewhat below saturation, equilibrium between the mobile and immobile phases is progressively achieved, and this exchange is driven by a difference in water content between the two domains.

Some 150 years ago, the French engineer Henry Darcy discovered that the water flow through a saturated soil is proportional to the hydraulic gradient in potential head, which is, in fact, the driving force. At the beginning of the last century, Buckingham demonstrated that Darcy's Law also applies to unsaturated soil. For flow in porous media, and in capillaries, the appropriate driving force is the hydrostatic pressure gradient ($\partial P/\partial x$). Therefore

$$J_v = -L\partial P/\partial x \quad (2)$$

where J_v is the volumetric flux density ($\text{m}^3 \text{m}^{-2} \text{s}^{-1}$) which is equal to an average velocity of water flow (m s^{-1}) times the soil's water content θ , and L is a hydraulic conductivity coefficient ($\text{m}^2 \text{s}^{-1} \text{Pa}^{-1}$) which is analogous to the diffusion coefficient in Fick's First Law. The choice of hydrostatic pressure, rather than total water potential as

the driving force, is because a gradient of osmotic potential can only affect volume flow when there is a semi-permeable membrane present to sustain a pressure differential. As with Fick's First Law, it is often more convenient to apply the equation in an integrated form, and to include the path length in the coefficient to give

$$J_v = L\Delta P/l = L_p \Delta P, \quad (3)$$

where L_p is now a hydraulic conductance ($\text{m s}^{-1} \text{Pa}^{-1}$) which, for a uniform path is given by L/l (where l is the path length) so is analogous to diffusive conductance (g). So, L_p , the conductance, therefore depends on path length, while L , the conductivity, is a property of the material through which the flow occurs and also depends on the fluid's viscosity.

Characterizing water movement in the soil becomes even more complicated when plants are present. In this case, the root capacity for water uptake must be taken into account. Water movement in the root environment is best described by the Richards' equation, which is a combination of the Darcy-Buckingham Law for flow due to capillary and gravity, and an expression for mass conservation:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left(D(\theta) \frac{\partial \theta}{\partial z} - K(\theta) \right) - S(z, t). \quad (4)$$

In this equation z is depth (m); D is the soil water diffusivity function ($\text{m}^2 \text{s}^{-1}$), which is the ratio of the soil's hydraulic conductivity to the specific water capacity; t is time (s). The component $S(z, t)$ is a sink function included to represent the uptake of water by a root system which is distributed, in some way, with both depth and time. Reasonably good results have been obtained when applying Eq. (4) to experiments under controlled conditions. But there are often difficulties when trying to describe water movement at the mesoscale in the field. This is due to the spatio-temporal variability on the hydraulic characteristics of the soil, and also to the fact that the $S(z, t)$ sink term has not been appropriately described from first principles based on root system topology. The processes involved in the distribution and activity of the root system in the soil are so complex, that the various forms of the sink term used until now are just coarse empirical descriptions of what has been observed to happen (see Section 4.3).

3. Water Absorption through Roots

Of all the functions of the root system, water uptake is most likely the one that generates the most interest. This is because water is the key substrate for plant activity. So not only do biologists want to know the processes involved, agronomists and environmentalists also demand information on root behavior and functioning. This knowledge is important for both optimizing water management in agriculture, and for minimizing the contamination of groundwater by agrichemicals. Water flow from the soil into the root xylem, and then up to the leaves is the result of a complex of interrelated processes. In part, the flows are driven by hydrostatic gradients. Purely

hydraulic characteristics of soil and roots need therefore to be considered. Also, there are flows driven by gradients in osmotic pressure. To complicate things further, water channels in the cell membranes also have a role in generating the radial water flow within roots. The key processes of this complex water-uptake phenomenon are discussed in the following section, and points of current controversy are also mentioned.

3.1. Structures for Water Uptake

The hydraulic architecture of roots remains less known than that of the more accessible aerial parts of plants. However, new techniques have appeared recently for measuring water uptake by the main structural roots of woody plants under field conditions (see Section 4). Nonetheless, to quantify fully the uptake of water from different parts of root system is still a difficult task. There are, therefore, uncertainties about root functioning. Usually, most of the water is absorbed via young, unsubsized roots. In most species, and under non-stressed soil-water conditions, these young absorbing roots may represent most of the total active root surface. Consequently, most of the water and solutes that are absorbed by these roots enter the plant in a region just a few centimeters from the root tips. Here root hairs are at their most abundant. Root hairs develop from cells of the root epidermis close to the apex. They extend the effective root surface area for absorption. Also they improve root-soil contact and thereby enhance water uptake. There is some controversy, however, about the amount of water entering through the meristematic regions very close to the root tip. Here the xylem, namely the tissue responsible for carrying the water up to the aerial parts, is not yet functional. In experiments with maize, for instance, the diameter of protoxylem vessels near the root tip was found to be of 5-10 μm . At about 25 mm from the root tips, metaxylem vessels had a mean diameter of 23 μm . At about 250 mm or more from the root tip, the older metaxylem elements had a diameter of about 100 μm . From Poiseuille's law we can predict that the conductance of one vessel of 100 μm is equivalent to that of 357 vessels of 23 μm diameter! So on the one hand, these data suggest that the younger part of the root, a few millimeters from the tip, would seem to be unable to contribute much to water absorption. On the other hand, the axial hydraulic conductance provided by the young metaxylem is probably more than sufficient to transport water to the shoot. Furthermore, in the intact root, it is the radial resistance, rather than the axial resistance, which limits water uptake. It can be concluded, therefore, that those parts of the root in which there are no mature metaxylem vessels are by no means hydraulically isolated from the rest of the plant.

At a certain distance from the root tip, suberization and lignification of the hypodermis, and the endodermis reduces the permeability in older parts of the roots. Suberization of roots increases with age. This can also occur as a result of stress caused by drought, high salinity, nutrient deprivation, anoxia, and other inhospitable conditions. Young roots suberize as they pass through the different stages of development of the endodermis and exodermis. During state I, Casparian bands are formed in the radial walls of the endodermis. During state II, suberin lamellae are laid down in both the radial and tangential walls. Eventually, cell walls are thickened during state III, and this results in the characteristic u-shaped cross section of the endodermal cells. It has been shown that the exodermis also develops Casparian bands, and that this structure then passes through similar states as the endodermis. This also includes the formation of

passage cells. The formation of an exodermis with Casparian bands plays an important role in reducing the axial hydraulic conductance of roots. The appearance of this structure is related to stress conditions. In drying, or saline soils the decrease on Ψ_{soil} may result in water flowing from the roots into to the surrounding soil. This can lead to the process of hydraulic lift, whereby water drawn from deeper down, is ‘leaked’ via the roots into surface dry soil. The appearance of the exodermis can help to prevent excessive water loss from the roots to the soil. Little is known, however, about the contribution of older thickened roots to overall water uptake. Absorption through suberized roots must be important, at least in certain cases, such as for perennial plants growing in cold, or dry soil, where unsuberized roots are often scarce, or even absent. Cracks and other pathways for water uptake that have been observed in the suberized layers of old roots are also supposed to increase water absorption in the older regions of the root system.

Often roots are invaded by fungi, thereby forming symbiotic associations called mycorrhizae. This association normally has mutual benefits; the plant receives mineral nutrients, and the fungus receives carbon compounds derived from the plant’s photosynthesis. In some cases, with so-called endotrophic mycorrhizae or endomycorrhizae, the fungus actually penetrates the root cells;

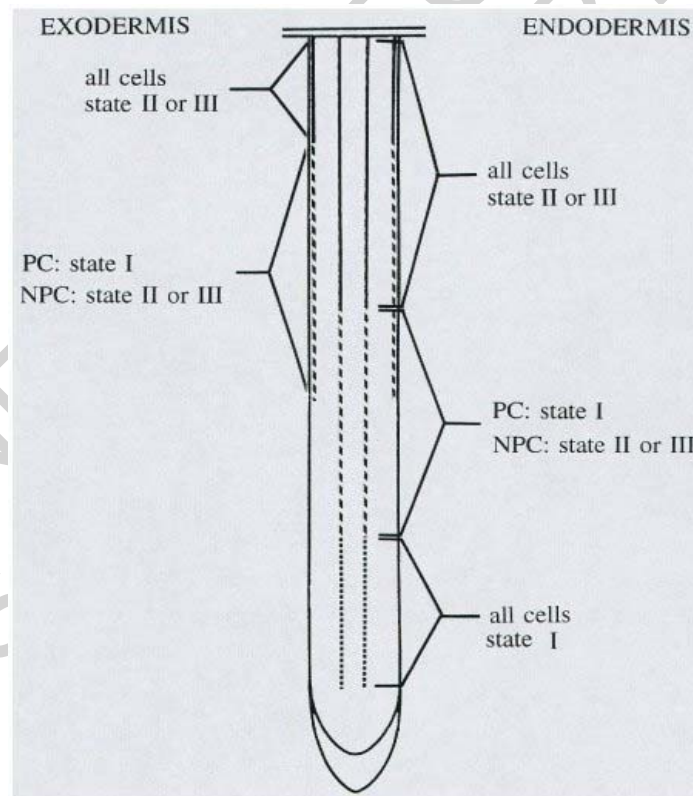


Figure 1. Diagram of median longitudinal section of a root, indicating sequential development of the endodermis and exodermis. PC, passage cells; NPC, nonpassage cells. (Source: C.A. Peterson and D.E. Enstone, 1996. Functions of passage cells in the endodermis and exodermis of roots. *Physiologia Plantarum*, 97: 592-598. With kind permission from the Journal)

In other cases, termed ectotrophic mycorrhizae or ectomycorrhizae, the fungus covers the external surface and causes marked hypertrophy, and extensive branching of roots. In addition, arbuscular mycorrhizae have internal fungal structures and mycelium external to the root. These are the most widespread, and are involved with many agriculturally and ecologically important plant species. Ectotrophic mycorrhizae involve most forest tree species, and it seems that they increase the competitive capacity of trees. This advantage can be due to the fungal hyphae extending out into the soil, and thereby increasing the absorption surface.

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Biographical Sketches

José Enrique Fernández was born in Castilleja del Campo, close to Seville, Spain. He was trained as an agriculture engineer (1986) and has a Ph.D. (1989) from the University of Córdoba. He carried out his Thesis' work in the *Instituto de Recursos Naturales y Agrobiología* of Seville, which belongs to the Spanish Research Council (CSIC). He got a permanent position in the CSIC in December 1993, after working for two years at the Silsoe Research Institute (UK). Currently he is *investigador científico* of the CSIC. His areas of expertise are related to water management in crops of Mediterranean areas. His current research activities are focused to high-frequency irrigation control and to the modeling of transpiration and photosynthesis at the crop level. He is mainly dedicated to research, although occasionally teaches undergraduate and graduate students in the Universities of Cordoba and Seville. He has directed several doctoral theses. Dr. Fernández is author of more than 30 scientific publications in refereed journals and more than 50 presentations in international congresses. He has written more than 10 chapters for different books, as well as several technical articles. He has participated in about 20 research projects, being the main researcher in some of them. In addition, he has carried out technical works for some commercial European companies. Dr. Fernández is a member of the Consulting Editorial Board of the journal *Plant &*

Soil, and works occasionally as a reviewer for other journals. He also evaluates national and international research projects.

Brent E. Clothier is New Zealander who, in 1974, obtained his B.Sc. degree with first class honors from the University of Canterbury, Christchurch, New Zealand. He then graduated with a Ph.D. in soil physics from Massey University, Palmerston North, New Zealand in 1977. In 2002, Dr Clothier was awarded a D.Sc. degree from Massey University for his thesis entitled “Water and solutes in soil: Hydraulic characterization, sustainable production and environmental protection”. Dr Clothier’s research has focused on measuring and modeling the transport and fate of water and chemicals in the rootzone. Presently, he is Leader for the Environment Sector of HortResearch, a Crown Research Institute, and he is based at HortResearch’s Palmerston North Science Centre. Dr Clothier has published over 142 scientific papers, and he has been elected Fellow of the Royal Society of New Zealand, the New Zealand Soil Science Society, the Soil Science Society of America, and the American Society of Agronomy. In 2000, he was awarded the Don & Betty Kirkham Soil Physics Award of the Soil Science Society of America, and in 2001 he was awarded the J.A. Prescott Medal of the Australian Soil Science Society Inc. Dr Clothier has worked collaboratively with scientists in government laboratories and universities in Australia, Canada, USA, France, Spain, China, and Japan.