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Plant and Soil as Hydraulic Systems

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1. Introduction

Soil is usually defined as a natural body consisting of mineral constituent layers that are different in structure and variable in thicknesses. It is composed of particles of broken rock that have been affected by chemical and environmental processes as weathering and erosion. Soil particles are packed loosely, forming a soil structure such containing pore spaces. These pores are filled with soil solution (liquid) and air (gas). This chapter shows that soil and plant are similar hydraulically. The pathway for water moving is from soil through plant to the atmosphere and can be described with the Soil-Plant-Atmosphere Continuum (SPAC) model. Hydraulic conductivity is the property of both soils and higher plants and the resulting analogue model for water transport is supported by the similar structure and the same source for water movement. This continuum hypothesis characterizes the state of water in different components of the SPAC as expressions of the energy level or water potential of each. Also the review of methodology of hydraulic conductivity measurement has been presented in detail.

2. Major physical properties of water

The surface of the Earth is covered in ca. 70% by water - a chemical substance including one atom of oxygen and two of hydrogen connected by covalent bonds (Fig. 1).

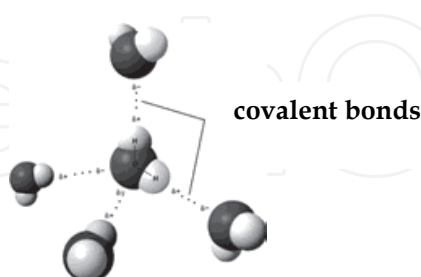


Fig. 1. Model of dipole water structure (http://ffden-2.phys.uaf.edu/212_fall2009.web/Yngve_margaretJ/ice/pg1.htm, modified).

Because water is a polar molecule it has a high surface tension and capillary forces. The capillarity basically makes water move up in narrow tubes against the force of gravity (what occurs in soil and all vascular plants in mechanism of water transport). Polar structure of water causes also the cohesion and the adhesion of water molecules, which contributes to the capillary water threads not to collapse.

The water circulates above and below the surface of the Earth and can change states among liquid, vapour, and ice at various places in its cycle (Fig. 2). Although the balance of water on Earth remains constant over time, individual water molecules can come and go, in and out of the atmosphere. During the physical processes as evaporation, condensation, precipitation, infiltration, runoff, and subsurface flow, water moves from one reservoir to another.

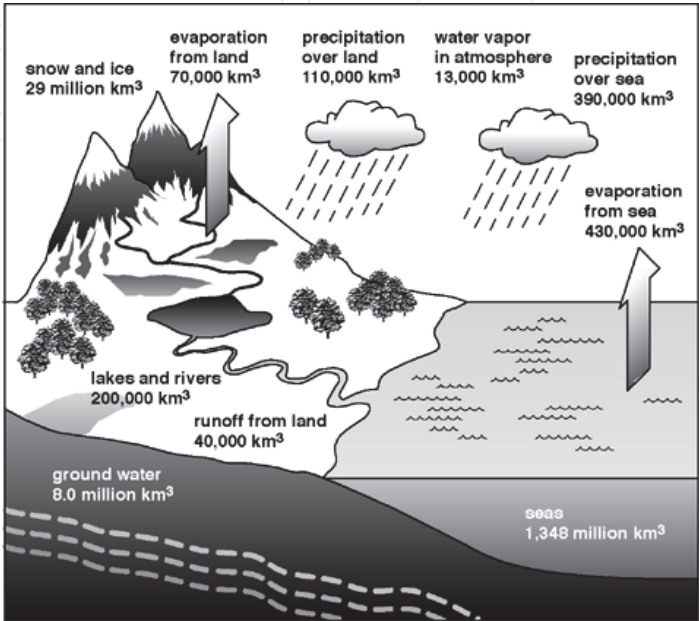


Fig. 2. Water cycle (Clarke, 1991, modified).

According to vertical distribution of water content two main zones in soil profile are distinguished: vadose and saturated (Fig. 3).

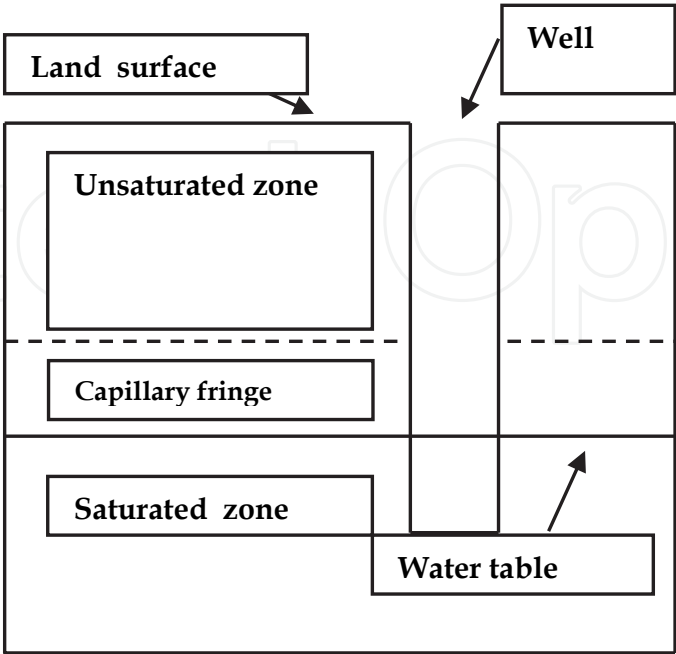


Fig. 3. Vertical distribution of water content in soil profile.

The vadose zone called also unsaturated, is located between the land of Earth surface and zone of saturation and extends from the top of the ground surface to the water table. In this zone water is under less than atmospheric pressure, which is a result of the process of adhesion and capillarity. Water moves predominantly in a vertical direction (Heath, 1983). Within the zone of vadose soil pore spaces usually contain air or other gases. The area below the water table where all open spaces are filled with water under pressure that is equal to or greater than that of the atmosphere makes up the zone of saturation.

3. Hydraulic conductivity of soils and plants

Hydraulic conductivity, which is a property of soils, vascular plants, or rocks describes the ability of water to move through pore spaces or fractures using hydraulic gradient. Saturated hydraulic conductivity expresses water movement *via* saturated media. Symbolically hydraulic conductivity is written as K while saturated conductivity as K_{sat} . The hydraulic conductivity of soil depends on the soil grain size, the soil matrix structure, the type of soil fluid and is defined by Darcy's law that could be written as follows:

$$U = -K/\eta \times dP/dl \quad (1)$$

where U is the velocity of the soil fluid *via* a geometric cross-sectional area within the soil, K is a hydraulic conductivity, η is a coefficient of the viscosity of water, dP/dl is the pressure gradient (Neuman, 1977). On the basis of the above mentioned equation, the hydraulic conductivity is defined as a ratio of soil fluid velocity (U) to the applied hydraulic gradient (dP/dl), because η is a constant.

Soil and vascular plants are similar hydraulically; the same physical laws might be applied to describe soil and plants hydraulic conductivity (Sperry et al., 2003). Both in the soil and the vascular plants structure the pores filled with water occur and although the pores in plants are highly organized in comparison to soil there is a close analogy between the soil and the vascular plants hydraulics. Additionally soil water potential is the driving force behind water movement. The main advantage of the "potential" concept is that it provides a unified measure by which the water state can be evaluated at any time and everywhere within the soil-plant-atmosphere continuum (Hillel, 1980).

For the theoretical calculation of the volume of water flow in the plant conducting elements the law of Hagen-Poiseuille, a special case of Darcy's law, describing the laminar flow through long cylindrical pipe is applied:

$$dV/dt = -K \times dP/dl = -\pi r^4 \times dP/8\eta \times dl \text{ because } K = \pi r^4/8\eta \quad (2)$$

where K is hydraulic conductivity, η is the viscosity of water, r the radius of the capillary and $-dP/dl$ is the pressure gradient along the capillary (Tyree et al., 1994; Tyree & Zimmermann, 2002). K can also be considered as the coefficient of the Hagen-Poiseuille law. It is important to note that flow rate dV/dt , is proportional to the fourth power of the capillary diameter. Thus a slight increase in vessel or tracheid diameter causes a considerable increase in conductivity. In a transverse section of the stem, branch or root many capillaries of different diameters d_i are present in parallel thus the aforementioned formula is written as follows:

$$dv/dt = -dp/dl \times K_i = -dp/dl \times \Sigma \pi r_i^4/8\eta \quad (3)$$

The pressure gradient is the driving force for water flow *via* tracheary elements and is caused by transpiration. Both in the case of soils and plants hydraulics the volume flow of water occurs by reason of decreasing pressure gradient.

4. Methods of hydraulic conductivity determination

To determine the saturated hydraulic conductivity of water in soil both empirical and experimental (field and laboratory) methods could be applied (Jennsen, 1990) (Fig. 4). The empirical approach correlates the hydraulic conductivity with soil properties as: pore and grain size, their distribution and soil texture. The methodology of measurement for laboratory and field experiments is based on Darcy’s law and has been described by Klute and Dirkesen (1986) as well as Amoozegar and Warrick (1986).

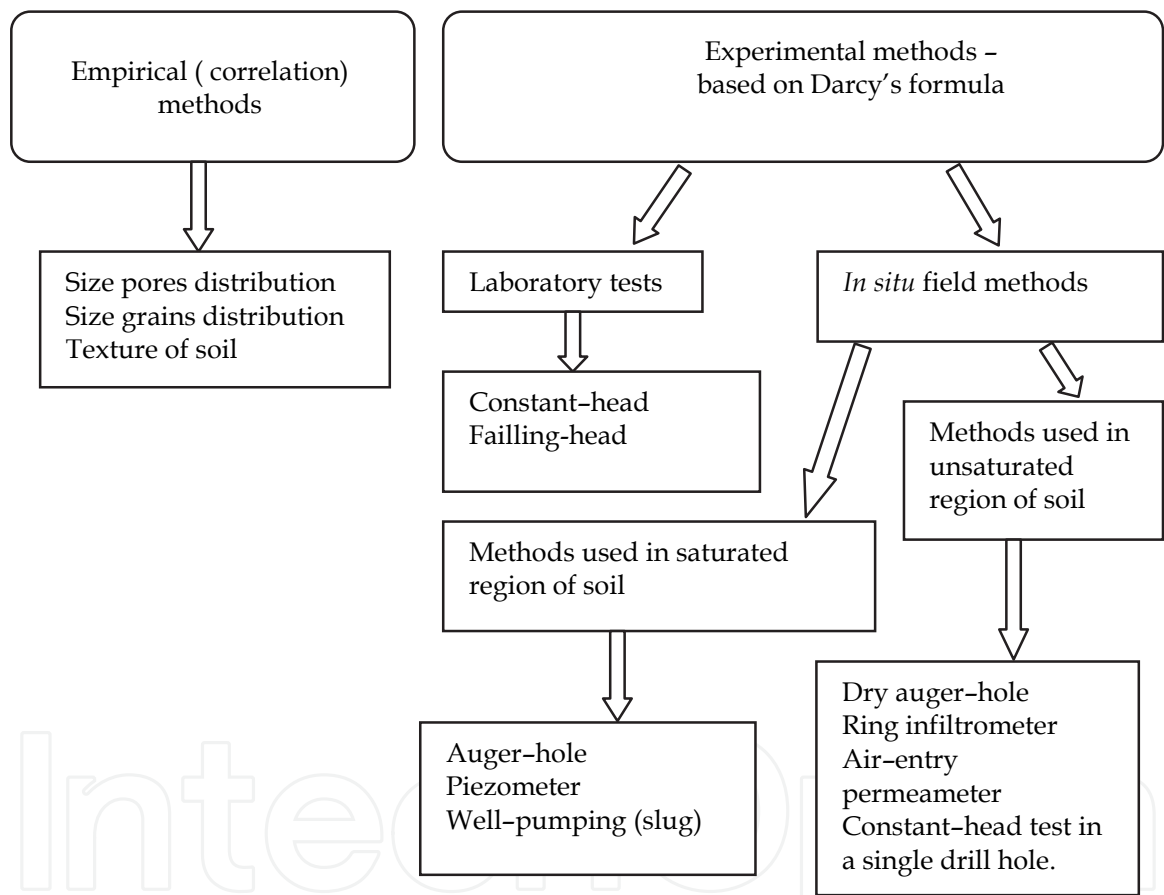


Fig. 4. Scheme of methods for measurement of hydraulic conductivity.

The selection of methods could depend on the objectives to be achieved (Tab. 1). The laboratory methods are used to delimit the vertical and horizontal hydraulic conductivity in small soil samples collected in accordance with core drilling programs. The results of these methods are considered as point representation of the soil features because of the small sizes of the soil samples. If the structure of soil samples is not disturbed (naturally) the measurement of hydraulic conductivity represents the *in situ* saturated hydraulic conductivity at the particular sampling point. In the case of the field methods, the evaluation of the hydraulic conductivity is based on a large region of soil, therefore the results of these tests should present the effects of both

vertical and horizontal directions and the main value of K . It is important if soil is highly stratified and the values of K measured by means of field methods could reflect the most permeable and dominate layer in soil profile.

4.1 Empirical methods

Empirical approach contains the Shepherd formula (1989) that correlates grain size and hydraulic conductivity. The formula expresses the approximate hydraulic conductivity from grain size analyses:

$$K = a(D_{10})^b \quad (4)$$

where a and b are empirically derived terms based on the soil type, and D_{10} is the diameter of the 10 percentile grain size of the material.

Another specialized empirical estimation of hydraulic conductivity is the pedotransfer function method (PTF). It is described primarily in the soil science literature, but has been increasingly applied in hydrogeology. There are many different PTF methods, however, they all attempt to evaluate soil properties, such as hydraulic conductivity, several given measured soil properties, such as soil particle size, and bulk density.

The hydraulic conductivity is affected not only by grain size but also by the viscosity and quality of the water, the shape of the soil particles, density of the soil, cementation of the soil and the degree of soil saturation. All these factors strongly influence hydraulic conductivity and relationship between these factors and hydraulic conductivity can be expressed by following formula based on Darcy law:

$$K = 2gD^2e^3/vC_s1 + e \quad (5)$$

where:

K – hydraulic conductivity,

g – the acceleration due to gravity,

v – the kinematic viscosity of water,

C_s – particle shape factor,

D – the weighted or characteristic particle diameter,

e – void ratio.

The characteristic particle diameter D is calculated from a grain size distribution analysis using the following equation:

$$D = \Sigma M_i / \Sigma [M_i / D_i] \quad (6)$$

where:

M_i – the mass retained between two adjacent sieves,

D_i – the mean diameter of two adjacent sieves.

Gülser and Candemir (2008) using pedotransfer method to determine the saturated hydraulic conductivity on the base of the soil physical properties concluded that direct effect of some physical properties on K in soils could be expressed in following order: permanent wilting point > bulk density > clay > silt > field capacity. The hydraulic conductivity generally decreases according to soil textural class (Fig. 5) and it may be described as follows: sandy soil > loamy soil > clay soil. If sand and silt contents in soil texture increase the soil bulk density increases generally (Hillel, 1982) while total porosity decreases and ratio of macro porosity in total porosity increases.

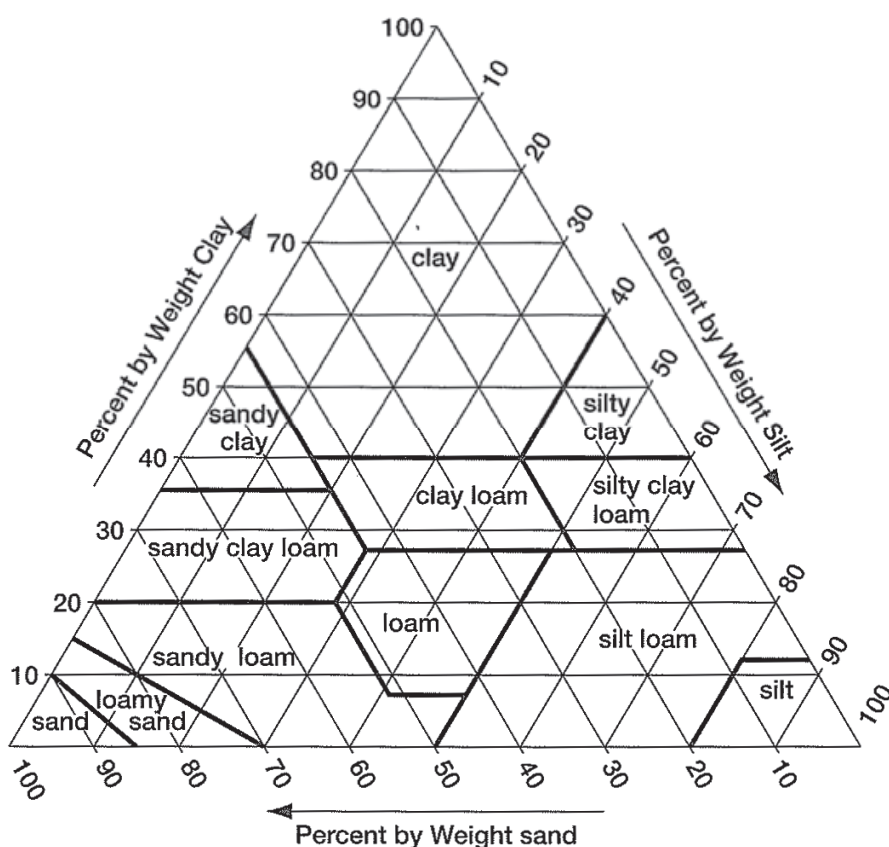


Fig. 5. Diagram of soil textural classes.

(<http://keys.lucidcentral.org/keys/sweetpotato/key/sweetpotato%20diagnoses/media/html/TheCrop/CropManagement/SoilFertilityManagement/Soil%20structure.htm>)

Generally, large particles (sand and stones) pack loosely with large spaces between. Very fine particles (clay) pack very densely with little space. A well structured soil has small particles clumped together in aggregates, so that there are both small spaces (between the particles within the aggregates) and larger spaces (between the aggregates).

Larger spaces allow water to infiltrate easily, and to drain freely enabling air to re-enter after wetting. Smaller spaces are primarily important to hold water, and to ensure contact between soil particles and soil water so that nutrients can dissolve and become available to plant roots.

4.2 Experimental methods

4.2.1 Laboratory tests

While estimating of the hydraulic conductivity of soil by means of laboratory methods, different instruments are used. They contain permeameters, pressure chambers and consolidometers. The samples of soil are placed in a small cylindrical receptacle representing one-dimensional soil configuration which, the circulating liquid is forced to flow through. On the basis of the flow pattern *via* the soil samples some kinds of the laboratory methods for measuring of K are distinguished. The first one is constant-head test with a steady-state flow regimen and the second with unsteady flow regimen called falling-head test. The constant-head method is mainly used on granular soil with an estimated K

above 1.0×10^2 m/yr, while the falling-head method is used on soil samples with K below 1.0×10^2 m/yr (Freeze & Cherry, 1979). The important considerations concerning the estimation of value of the hydraulic conductivity by means of laboratory methods are the procedure of the soil collection and preparation of the test specimen and circulating liquid. The collection of the soil samples should be performed so as to avoid changes in matrix structure of the soil. It is possible to apply walled tube sampling methods. In this technique undisturbed soil sample is received by pressing a thin walled metal tube into the soil, removing the metal tube filled with soil and then sealing its ends to avoid physical disturbance in the structure of the soil matrix.

4.2.1.1 Constant-head method

The procedure of constant-head method allows water to move through the soil under a steady state head condition while the quantity (volume) of water flowing through the soil specimen is measured over a period of time (Fig. 6). By knowing the quantity Q of water measured, length of specimen L , cross-sectional area of the specimen A , time required for the quantity of water t , and head h , the hydraulic conductivity can be calculated thus:

$$Q = Avt \quad (7)$$

where v is the flow velocity. Using Darcy's Law:

$$v = Ki \quad (8)$$

and expressing the hydraulic gradient i as:

$$i = h/L \quad (9)$$

where h is the difference of hydraulic head over distance L :

$$Q = AKht/L \quad (10)$$

solving for K gives:

$$K = QL/Ath \quad (11)$$

4.2.1.2 Failing-head method

The basis of this test is very similar to the foregoing constant-head method, but it is used for both fine-grained and coarse-grained soils. The soil sample is first saturated under a specific head condition. The water is then allowed to flow through the soil, a constant pressure head not to be maintained. To determine the hydraulic conductivity by use of the failing-head method, a cylindrical soil sample of cross-sectional area A , and length L is placed between two high conductivity plates. The soil sample column is connected to a standpipe of cross-sectional area a , in which the percolating fluid is introduced into the system. Therefore, by measuring the changes in head in the standpipe from h_1 to h_2 during the time t , the hydraulic conductivity can be expressed as follows:

$$K = (aL/At) \ln (h_1/h_2) \quad (12)$$

A common problem of the foregoing, two laboratory methods using permeameter is related to the degree of saturation achieved within the samples of soil during the test. Air bubbles are usually trapped within the pore space, and although they could disappear slowly by

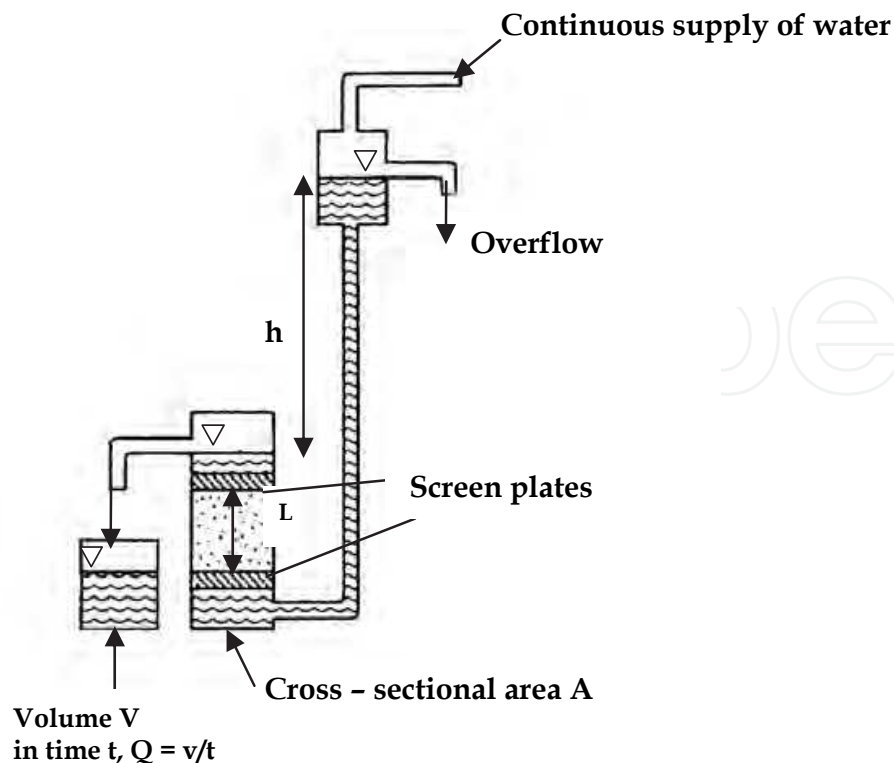


Fig. 6. Constant head permeameter (Beers, 1983, modified).

dissolving into the deaerated water, their presence in the system may influence the results of measurement. For more accurate results of K measurement in soil samples in which the air bubbles could appear and be critical, the conductivity test with back pressure is recommended.

4.2.2 Field methods

The field methods contain several tests for *in situ* determination of hydraulic conductivity that could be divided into two groups: (1) those which refer to sites near or below a shallow water table and (2) those that are applicable to sites above a deep water table or in absence of water table. Similarly to the laboratory procedures, in these groups, to determine the hydraulic conductivity (K), the Darcy's formula is used after the measuring the gradient of hydraulic head at the site and the resulting soil water flux.

4.2.2.1 Field methods used in saturated regions of the soil

These methods will be applied to determine the hydraulic conductivity for saturated zones of soil within a groundwater formation under unconfined and confined conditions. This method contains (1) the auger-hole and piezometer methods, which are used in unconfined shallow water table conditions and (2) well pumping tests, which are used for determination of aquifer properties in confined and unconfined groundwater systems.

4.2.2.1.1 Auger-hole method

If the water table is shallow, the auger-hole method could be used for evaluating the hydraulic conductivity below the water table. This method concerns four steps as follows:

- a. drilling of the augerholes

- b. removal of water from the augerhole
- c. measurement of the rate of rise
- d. computation of the value of K from the measurement data.

This method is fast, simple and usually used to design drainage systems in waterlogged land and in canal seepage studies.

4.2.2.1.2 Piezometer method

The piezometer method is designed for applications in layered soil aquifers and for determining either horizontal or vertical components of the saturated hydraulic conductivity. In this method piezometer tube or long pipe are used to penetrate the unconfined system.

4.2.2.1.3 Well-pumping (slug) method

A slug test is a particular type of aquifer test where water is quickly added or removed from a groundwater well, and the change in hydraulic head is monitored over time, to determine the near-well aquifer characteristics. It is a method used by hydrogeologists and civil engineers to determine the transmissivity/hydraulic conductivity.

4.2.2.2 Field methods used in the unsaturated region of the soil

The measurement of the value of hydraulic conductivity of unsaturated soils located above the water table (or if there is no water table) by *in situ* methods is more difficult in comparison to estimation of K for saturated soils because primarily unsaturated soil must be first saturated to perform the measurements. Therefore, the results of these *in situ* measurements are commonly called the field-saturated hydraulic conductivity. The available methods for measuring field saturated K comprise: (1) the shallow-well pump-in or dry auger-hole, (2) the double-tube, (3) the ring infiltrometer, (4) the air-entry permeameter, (5) the constant-head test in a single drill hole.

The shallow-well pump-in, is otherwise known as dry auger-hole method or well permeameter method. It is used to measure the rate of water flow from a cased or uncased auger-hole when a constant height of water is maintained in hole. To maintain a water level with a large water tank providing the water supply a float valve is usually used. The hydraulic conductivity values are calculated by use the steady state outflow rate and a shape factor determined from nomographs or equation. The position of water table or impermeable layer below the bottom of the well must be known. This procedure is easy but is limited by the time requirements needed to reach steady state and to replicate measurements.

Double tube method uses two concentric tubes that are placed in the soil to a given depth. The water flow is manipulated to move from the inner to outer tube at a high and changing rate of hydraulic head. Hydraulic conductivity values are then determined from tables and graphs and express the combination of vertical and horizontal hydraulic conductivities.

Ring infiltrometer method is similar to cylinder permeameter procedure. A large hole is prepared to appropriate depth. A metal sleeve is installed in the center of the hole. The same water level is maintained outside and inside the sleeve. The saturated hydraulic conductivity is taken to be the rate of infiltration when soil suction at the bottom of the ring equals zero (saturated conditions). This method allows measuring the vertical conductivity of layered soils.

Air-entry permeameter method. In this method a small covered cylinder is driven into ground. To this cylinder water is applied until all air is driven out. At the top of cylinder a

Type of methods	Name of method	Application of method	Description of method	Literature
LABORATORY	A. Constant-head conductivity with permeameter cylinder	For disturbed soil samples of cohesionless coarse-grained soils with $K > 1.0 \times 10^{-2} \text{m/yr}$	It is used to estimate the original, in undisturbed state conductivity in a horizontal direction	Klute & Drikson, 1986
	B. Falling-head conductivity with permeameter cylinder	For disturbed samples of cohesionless coarse-grained soils with $K < 1.0 \times 10^{-2} \text{m/yr}$	As in A method	Klute & Drikson, 1986
	C. Conductivity test with sampling tubes	For unchanged cohesionless soil samples that can not be removed from the tube without disturbance	In depends on the estimated conductivity of samples, it is carried out under constant or falling head flow regimen, the conductivity is evaluated in accordance with direction in which samples has been collected (mainly in vertical direction)	Reddi, 2003
	D. Conductivity test with pressure chamber	For cohesive fine-grained soil, with changed, unchanged structure or in compacted state in a fully saturated condition	It is used only for originally fully saturated soil samples under falling-head flow conditions	Reddi, 2003
	E. Conductivity test with back pressure	As in D case, but soil samples are not fully saturated	The back pressure is used to reduce the size of the gas bubbles in the soil sample pores resulting in increase of the degree of water saturated, it is conductive under constant-head flow regimen	Reddi, 2003
	F. Conductivity test with consolidometer	As in D case	As an alternative method to method D	O'Kelly, 2009
FIELD	A. Auger-hole	For saturated soil samples located near the ground surface in the presence of a shallow water table	Used for saturated soil samples, gives average value of horizontal conductivity for dominate layers in soil profile	Amoozegar & Warrick, 1986
	B. Piezometer	As above	It is used for determination the hydraulic conductivity in both directions and it allows to measure K in each layer of stratified soils. The piezometer tube or pipe are installed into an auger – hole with a cavity at the bottom. Water is transferred from the tube and the rate of its rise in tube is measured.	Amoozegar and Warrick, 1986

FIELD	C. Single-well (slug) in moderately permeable formations under unconfined conditions	Saturated soil samples of moderate K	Pump out test, K in horizontal direction is measured. It comprises the removing of a slug of water from a well and then measuring the recovery of the water in the well.	Bouwer & Rice, 1976
	D. Single-well (slug) in moderately permeable formations under confined conditions	As above but in confined conditions, entirely open to the well screen or open borehole	As above, for saturated zone of the soil under confined condition	Kessler & Oosterbaan, 1974
	E. Constant-head conductivity test by the well permeameter method, referred to shallow-well	For measurement field-saturated hydraulic conductivity of soil samples in unsaturated zone near the ground surface	Pump in test, consisting of measuring the rate at which water flows out of an uncased well into the soil under constant-head flow conditions, could be also used for saturated zones	Amoozegar and Warrick, 1986
	F. Pump in or dry-auger-hole	For soil types ranging among sand, silt and clay mixture with K larger than $1,0 \times 10^0$ m/yr and relatively clean sand or sandy gravel with $K < 1,0 \times 10^4$ m/yr	Pump out test, K is measurement in horizontal direction for uniform soil, it is used to determine the conductivity of the most permeable layer of the soil profile	Engqvist et al., 1978
	G. Double-tube	To measure field-saturated K of soil samples in the unsaturated zone near the ground surface	Two concentric cylinders are installed in auger-hole, water is pumped into these cylinders and K is estimated by measuring the flow in the cylinders, K represents conductivity in both directions	Amoozegar & Warrick, 1986
	H. Infiltrrometer	As above for soil samples with ranging between $1,0 \times 10^{-3}$ m/yr and $1,0 \times 10^3$ m/yr	For measurement K in the vertical direction near the ground surface. It consists of pending water within a cylindrical ring placed over the soil surface and measuring the volumetric rate of water needed to maintain a constant head	Amoozegar & Warrick, 1986
	I. Constant-head conductivity test in single drill hole	To measure field-saturated K of soil samples at any depth within unsaturated zone, Soil or rock materials within K ranging between $1,0 \times 10^0$ and $1,0 \times 10^4$ m/yr	Pump in test consisting of injecting water into an isolated interval of a drill hole in soil or rock under constant-head flow conditions	Amoozegar & Warrick, 1986

Table 1. The review of standard experimental methods applied in measurements of soil saturated hydraulic conductivity (K).

large constant head is kept in a reservoir until saturation is reached at the bottom of the cylinder. The water level is then allowed to fall and the conductivity is calculated by the use of falling head equations. Due to air-entry permeameter method the hydraulic conductivity in vertical direction is obtained.

5. Wood elements as structural basis for hydraulic conductivity of higher plants

Vascular plants also known as tracheophytes or higher plants are those that have developed specialized conductive (vascular) tissues which circulate resources through the plant's body. In these plants, the xylem tissue is a space where long-distance transport of water takes place. The xylem tissue consists primarily of dead, lignified cells named tracheary elements. Either of two types of water conductive cells, tracheids and vessel elements, are found in xylem of vascular plants. Tracheids are found in all vascular plants and are the chief water-conducting elements in most of living gymnosperms and seedless vascular plants (Bailey & Tupper, 1918; Gifford & Foster, 1989), whereas vessel elements are unique to angiosperms and are the chief water-conducting elements for these plants. Both kinds of cells are elongated, die at maturity, but their lignified cell walls remain as the conduits through which water is carried in the xylem. Tracheids are closed at both ends but have pits where the cell wall is modified into a thin membrane, through which water flows from tracheid to tracheid. Vessel elements are stacked one on top of another in long columns, called vessels. In contrast to the tracheids the final walls of the single vessel element are perforated (composed plate) or, completely resolved (simple plate). Water flows almost unimpeded from cell to cell along these columns through perforations in the cell walls.

The size of tracheids is limited as they comprise a single cell. By the end of the Devonian, tracheid diameter had already increased to its maximum of ca. 80 μm (Niklas, 1985). Greater tracheid diameter would be advantageous only if accompanied by increased conduit length. Actually the wider tracheids are longer – up to 10 mm (Schweingruber, 1990). However, further increase in length and diameter of tracheid may be impossible because of limits to the maximum cell volume. Vessels, consisting of a number of cells overcame this limit and allowed larger conduits to form, reaching diameters of up to 500 μm , and lengths of up to 10 m (Zimmerman, 1983).

Important feature of the xylem structure is its connectivity i.e. the interconnected conduits form a network (Cruciat et al., 2002; Tyree & Zimmerman, 2002). The spatial arrangement of conduits was investigated by Burgraff (1972), Zimmerman (1971) and more recently by other authors (Steppe et al., 2004; Kittin et al., 2004) giving the support to define vascular system as a network integrating all main parts of the plant's body, i.e. roots, branches and leaves. Any root in the system is more or less directly connected with any branch and not with a single one. Moreover, the xylem network is redundant in two meanings: at a given level of the stem several xylem element are present in parallel and they develop lateral contacts with other tracks of vessels or tracheids.

Scholander et al. (1957) proposed and experimentally tested the hypothesis that the water-conducting xylem in the stem is essentially a flooded, continuous, micropore system, scattered with elongate macrocavities (vessels). The stem may accordingly be compared to a pipe filled with a sinter of fine sand, throughout which large longitudinal cavities are dispersed. If water fills such a system and flows through it, the cavities will offer the paths of least resistance, and through them most of the water will flow. If the hydrostatic pressure

is below atmospheric and outside air enters a cavity, this will press the water out of the cavity, but no farther, as the air-water menisci will hang up in the micropores of the cavity walls.

The above way of describing the stem xylem emphasises that there is a great degree of structural similarities between the stem xylem of plants and the soil pore system. Tracheary elements have dimensions of capillaries and thus the same mechanism as for soil hydraulic conductivity might have been applied. Water moves spontaneously through tracheary elements only from places of higher water potential (ψ) to places of lower water potential, i.e. along a decreasing ψ gradient (Fig. 7).

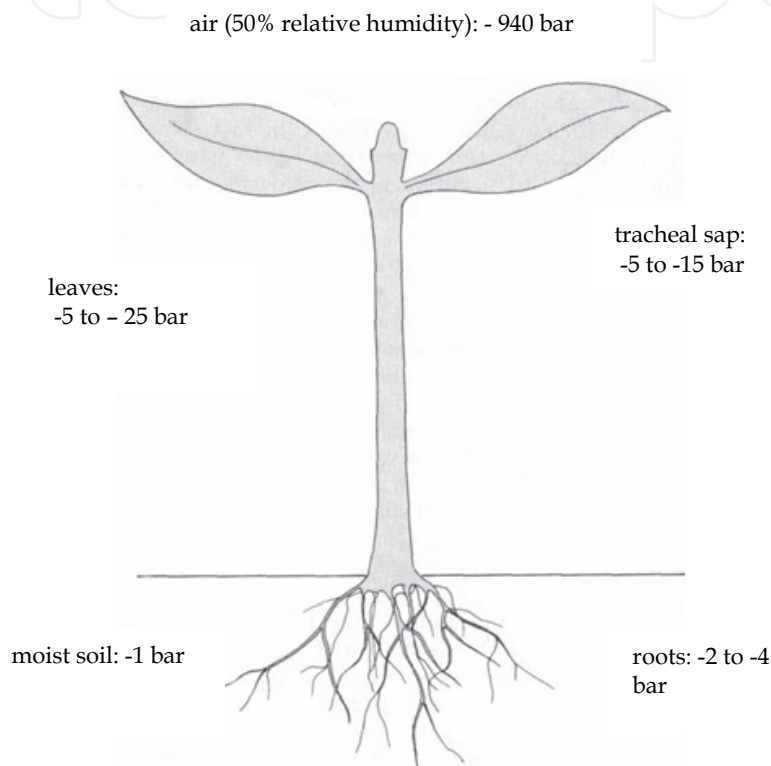


Fig. 7. The scheme of the pathway of water in the soil-plant-atmosphere continuum with the representative values for the water potential ψ (Mohr & Schopfer, 1995, modified).

6. Mechanism of water transport in vascular plants

The water transport in xylem of vascular plants is explained by the cohesion - tension theory formulated by Dixon and Joly (1894) as well as Askenasy (1895). The attractive force between water molecules is one of the principal factors responsible for the occurrence of surface tension in liquid water allowing plant to draw water from the root through the xylem to the leaf. Two phenomena cause xylem sap to flow: transpirational pull and root pressure.

Water is constantly lost by transpiration in the leaf. This creates tension (negative pressure) in the mesophyll cells. Because of this tension water is being pulled up from the roots into leaves, helped by cohesion (the pull between individual water molecules, due to hydrogen bonds) and adhesion (the stickiness between water molecules and the hydrophilic components of cell walls of plants). This mechanism of water flow works because of water

potential (waters flows from high to low potential) and rules of diffusion. Transpirational pull requires that conduits transporting the water are small in diameter, otherwise cavitation would break the water column. As water evaporates from leaves, more is drawn up through plant to replace it. When the water pressure within the xylem reaches extreme levels due to low water input from roots, then the gases come out solution and form a bubble – an embolism forms, which will spread to adjacent cells, unless bordered pits are present.

Water potential of the root cells is more negative than that of the soil, usually due to high concentrations of solute, water can move by osmosis into the root from the soil. This causes a positive pressure that forces sap up the xylem towards the leaves. In some circumstances the sap will be forced from the leave through a hydathode in a phenomenon known as guttation. Root pressure is highest in the morning, before stomata open allowing transpiration to begin.

Comparing plant to a hydraulic system evokes the search for basic elements of such a system i.e. a driving force, pipes, reservoirs and regulating systems. In case of plants the driving force is most of the time, the transpiration, which pulls water from the soil to the leaves and creates and maintains a variable gradient of water potential throughout the plant. Pipes in the hydraulic systems correspond to very complex network of fine capillaries (vessels and tracheids) forming plant conducting system.

7. Environmental factors affecting hydraulic conductivity of SPAC

The root hairs play role in water uptake from the soil into plants: having close contact with soil solution they prevent the formation of air-filled cavities between root and soil particles during the process of water uptake. Such spaces could be a barrier zone to the transfer of water from soil to the roots. (Fig. 8.).

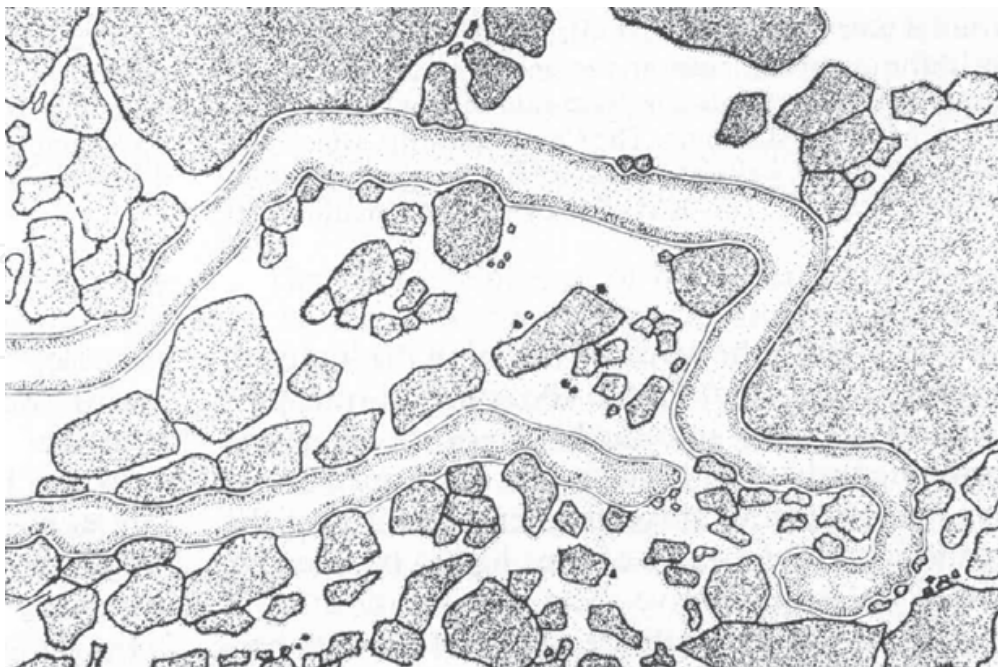


Fig. 8. Longitudinal section of soil profile with root hairs that increase the root surface and have extensive contact with the soil solution (Stocker, 1952 modified).

As mentioned above the continuous movement of water molecule from the soil *via* plant into atmosphere is driven by the differences in water potential between the perirhizal soil and the atmosphere and is maintained by solar energy. Resulting continuity of water columns from soil pores throughout the plant to leaf cells, linked to evaporative flux, is known as the soil-plant-atmosphere continuum (SPAC). Maintenance of this “hydraulic rope” is needed to ensure a continuous water supply to leaves.

The traditional view of plant hydraulics considered stomatal conductance and root conductivity as the main controlling factors of water flow in plants (Jones, 1983). This view is now expanding to include dynamic responses of xylem flow resistance to environment. Xylem conductivity is determined by the structure and size of the vessels (Schultz & Matthews, 1993; Tyree & Ewers, 1991) and by their efficiency, which may be affected by presence of embolism (Tyree & Sperry, 1989). One of the consequence of the cohesion-tension theory of water ascent in plants is the state of tension in the xylem sap and the occurrence of cavitation, which is the abrupt change from liquid water under tension to water vapour. As water is withdrawn from the cavitating conduit, vapour expands filling the entire lumen. Then air diffuses in causing the pressure rising to atmospheric. The conduit becomes embolized i.e. air-blocked. The same occurs in soil, where the larger pores in soil became filled in air, leaving only the smaller pores to hold and transmit water under the drought conditions.

Several reports have shown that water stress induces embolism and loss of function of the vessels (Sperry & Tyree, 1990; Hargrave et al., 1994) contributing to the reduction of water flow across the shoot (Schultz & Matthews, 1988). The resistance to cavitation and embolism is thus an important parameter determining the drought resistance of a plant and its hydraulic conductivity. The relation between the tension of the sap in the xylem and the corresponding degree of embolism is called a vulnerability curve. These curves are measures of the plants drought resistance (Cruziat et al., 2002; Sperry et al., 2003) and to much extend correspond to the unsaturated conductivity of soil while drying and wetting cycles (Sperry et al., 2002).

A negative effect of water stress on vessels size, hypothesized by Zimmermann and Milburn (1982) and implied in the observation that in periods of drought, wood xylem rings are narrower was directly evidenced in experiments with grapevine plants subjected to water stress of different intensity (Lovisolo & Schubert, 1998). It is also suggested that in large - vessel species reduction of vessel size may be an adaptation to a persistent situation of moderate waters stress, while embolism may be induced by a short or more severe water stress. Drought stress is frequently mentioned as an environmental factor implicated in the induction of trees decline recently observed in case of several species in Europe (Lygis et al., 2005; Kowalski & Łukomska, 2005) and North America (Ward et al., 2007; Bricker & Stutz, 2004).

Recently the relevance of xylem network structure for plant hydraulics (Loepfe et al., 2007) has been introduced into the theoretical discussion emphasizing that maximum hydraulic conductivity and vulnerability depend on multiple factors, including the connectivity of the network. The aforementioned authors have stated that connectivity increases both maximum hydraulic conductivity and vulnerability to drought-induced embolism and is therefore an element to be taken into account in any discussion on the efficiency vs. safety trade-off in the xylem. Our own preliminary data on connectivity in *Fraxinus excelsior* L. xylem in relation to the decline process were shown at the 55th Congress of Polish Botanical Society in 2010 and further investigations are currently carried out on that issue.

8. Conclusions

Soil and xylem are similar hydraulically and can be described as systems consisting of the same basic elements: a driving force, pipes, reservoirs, regulating systems. For plants the driving force is mainly the transpiration pulling water from the soil to the leaves and creating and maintaining a variable gradient of water potential throughout the plant. Pipes in plants correspond to a complex and highly organized network of very fine capillaries (vessels and tracheids), which form the xylem conducting system.

The water transport models for soils have been much mechanically based and complete than the corresponding description of plant hydraulics. The physical nature of flow throughout the soil makes it to some extent more amenable to quantitative treatment. An unsaturated conductivity curve for soil corresponds to the vulnerability curve for xylem and the underlying physical basis is the same. Thus any transport model that treats unsaturated soil conductivity provides an opportunity for the SPAC model to incorporate more mechanistic and predictive treatment of plant hydraulics and a better understanding of how the SPAC model is influenced by repeated droughts.

9. Acknowledgments

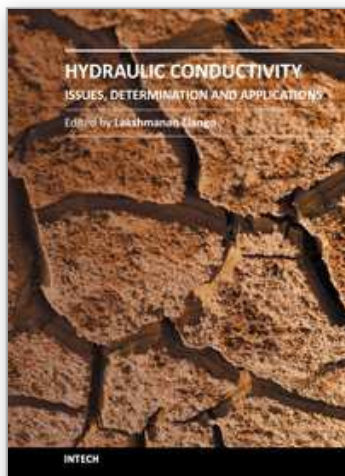
The publication was, in part, supported by Grant, No N N309 077438 from The Ministry of Science and Higher Education.

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Hydraulic Conductivity - Issues, Determination and Applications

Edited by Prof. Lakshmanan Elango

ISBN 978-953-307-288-3

Hard cover, 434 pages

Publisher InTech

Published online 23, November, 2011

Published in print edition November, 2011

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