INTEGRATED WATER MANAGEMENT

Water and Plant Growth

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(22.08.2007)

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Keywords
Soil water deficit

Introduction

Water is essential for all living organisms and plants are no exception. In fact, most of the actively growing plants may contain almost 90 per cent of water. Although it is generally stated that less than one per cent of the total water used by the plant (consumptive use) is needed for its metabolic activities, water plays a multifaceted role, which can be enumerated as follows:

1. It serves as a solvent for various chemicals present in the cells
2. It acts as a reactant in various biochemical processes, such as photosynthesis, hydrolysis, hydration, etc., and is a source of proton for synthesis of various biochemical molecules.
3. It functions as a medium of transport of minerals from the soil to the plant leaf
4. It also serves as a medium of transport of biochemicals such as products of photosynthesis, hormones, etc. from source tissue to sink tissue
5. It provides the turgor pressure necessary for cell expansion and maintenance of cell shape.
6. Though transpiration is a process of loss of water vapour from the stomata of plant to the atmosphere, it helps in uptake of CO_2, a primary substrate for photosynthesis, and cooling the plant canopy.
7. It acts as buffering agent to maintenance of plant tissue temperature.

Soil Water Relations

Soil has been defined as a three-dimensional, dynamic, natural body occurring on the surface of the earth that is a medium for plant growth and whose characteristics have resulted from the forces of climate and living organisms acting upon parents material, as modified by relief, over a period of time (Tamhane *et al.*, 1970). To serve as a favorable medium for plant growth, soil must store and supply water and nutrients in addition to the anchorage it provides. Soil is a porous medium; therefore, due to the geometry of the pore spaces between the soil particles and the nature of the surfaces, soil has the capacity to hold water. This property of soil enables it to retain precipitation or irrigation water in the root zone to be used by plants over time. The amount of water held depends upon the porosity and pore size distribution and the capillary pressure of water in the soil. The force by which the water is held by soil (soil water suction/tension) is the force that the plant roots have to overcome for extracting water retained by soil. It is expressed in the units of pressure. Earlier, it was generally expressed in bars (or atmospheres) but is now expressed in Pascal's (Pa). The relationship between the various units is given below:

1 bar = 1020 cm of water column*

1 atm = 1030 cm of water column

1 bar = 10^5 Pa = 100 kPa = 0.1 MPa

*Pressure exerted by a column of water 1020 cm high.

Conventionally, the soil water potential is expressed in terms of hydraulic head i.e. soil water potential expressed in terms of height of water column. For example, if the soil water tension is 1 bar (soil water potential of -1 bar), in terms of water column height, it will be 1020 cm. For the sake of convenience, 1 bar is considered equivalent to 1 atm and approximately 1000 cm of water column height. Since these are fairly large numbers and handling such numbers is cumbersome, Schofield (1935) suggested the use of 'pF', which was defined as the logarithm of the negative pressure (tension or suction) head expressed in centimeters of water column. A tension head of 10 cm of water would be pF of 1, a tension head of 1000 cm would be pF of 3.

Soil Moisture Constants

There are many terms that are associated with the water that is contained or retained by the soil. The common ones are saturation, field capacity, permanent wilting point and hygroscopic coefficient. The water held by the soil at these points is shown schematically in Fig. 1.

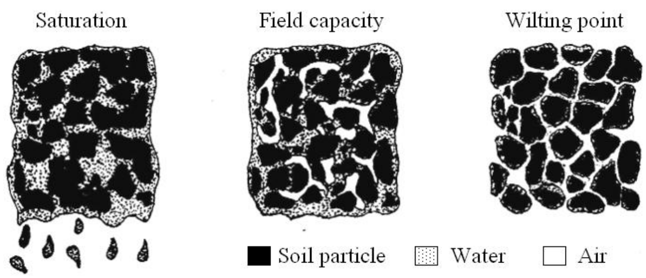

Fig. 1: Volumes water and air associated with soil solids at different moisture levels (Source: Modified from "Irrigation on Western Farms, U.S. Departments of Agriculture and Interior).

Saturation: Soil is a porous medium and when all the pores of the soil are filled with water, it is referred to as saturated soil. Saturation percentage or the water held by soil can be determined by: Bringing the soil core/soil sample in contact with water column at a height corresponding to the mid point of the sample and determining the moisture held by soil, or by using the formula for porosity:

$$P = \{1 - BD/PD\} \times 100 \qquad \text{- - - - - - - - (1)}$$

where P is the porosity in percent, BD is bulk density (g cm^{-3}) and PD is particle density (g cm^{-3}) of soil. PD can be generally assumed to be 2.65 (g cm^{-3}) for mineral soils. It can also be estimated by determining the moisture content of the core of which saturated hydraulic conductivity has been determined without allowing any water to drain out of the sample.

Field Capacity (FC): It is the term used to describe the maximum amount of water that a soil will retain after allowing free drainage. It does not generally correspond to a fixed soil water suction (or potential) varying from 1/10 bar for coarse textured soils to 1/3 bar for fine textured soils. It is, therefore, best estimated in the field by saturating the root zone and determining soil moisture after free internal drainage ceases. It takes about 24 to 36 hrs in coarse and 2-3 days in medium textured soils.

Permanent Wilting Point (PWP): It is the soil water content at which the sunflower or some other indicator plants will wilt and will not recover even when placed in a humid environment. It is important to mention that plants can some time exhibit wilting symptoms but will recover when placed in a humid environment, i.e., the reduction in atmospheric demand. This is referred to as temporary wilting. It is considered equivalent to the water held by the soil against an applied pressure of 15 bars. It is generally estimated in the laboratory using either a pressure plate or a pressure membrane apparatus. It consists of a chamber in which saturated soil samples either disturbed or intact in cores, are placed over a ceramic-plate or cellulose membrane, the bottom of which is connected to the atmosphere. Compressed air is then forced into the chamber (called the extractor). Pressure is maintained at the desired level *e.g.* 15 bars till the outflow of water ceases *i.e.* the soil is in equilibrium with the applied pressure.

Hygroscopic coefficient: It is the water held by the soil at 31 bars (3.1 MPa) soil moisture tension and can be determined using a pressure membrane assembly meant for higher pressures. It can also be approximated by allowing an oven dry soil to absorb moisture from the air till constant weight is attained.

The water between saturation and field capacity is called gravitational water. It flows out under the influence of gravity and is considered unavailable to plants. The water between field capacity and hygroscopic coefficient is referred to as capillary water as it is bound to the soil by capillary forces. The water held by the soil between field capacity and permanent wilting point is termed as available water for plants while the water held between permanent wilting point and hygroscopic coefficient is considered unavailable to plants. Some plants are able to survive even at moisture contents below PWP for short periods. Field capacity can also be determined in the laboratory with this equipment using an applied pressure of 1/3 bar for clayey soils and 0.1 to 0.2 bar for sandy to sandy loam soils. Field capacity is considered as the upper limit of available water to plants and the permanent wilting point as the lower limit.

The relationship between the amounts of water held in a soil and the force by which it is held (capillary pressure or suction or tension) is depicted in the form of a curve commonly referred to as the soil water characteristic or release curve or simply the pF curve (Fig.2). Two points of this curve are of particular interest to agriculturists i.e. the field capacity and the permanent wilting point.

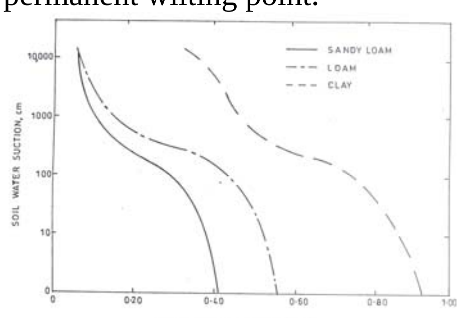

Fig. 2: Soil water retention characteristic curve of three texturally different soils

Soil Water Storage and Availability to Plants

The soil water storage capacity is generally expressed in terms of Available Water Capacity (AWC). The total available water in soil is regarded as the difference between soil moisture content of "field capacity" and "wilting point".

It is customary to express available water capacity in terms of depth dimensions so that it can be considered with irrigation, evaporation rate, rainfall and irrigation water quantity, which are generally expressed in terms of depth. The available water capacity of specific layers, generally available as percent by weight, can be expressed as ‘cm’ if bulk density values and depth of soil layer of the root zone are also determined as illustrated below:

$$D_w = \{(FC - PWP) \times BD \times D_s\}/100 \qquad \text{- - - - - - - - (2)}$$

In which

D_w	=	Depth of water contained in a specific soil layer (cm)
D_s	=	Thickness of the soil layer (cm)
BD	=	Bulk density of the particular soil layer (g cm^{-3})
FC	=	Soil water content at Field Capacity (% by wt)
PWP	=	Soil water content at Permanent Wilting Point (% by wt)

The value of ‘D_w’ is computed for each soil layer and then added up for the entire profile. However, the values of BD, FC and PWP vary from layer to layer within a soil profile, soil to soil and location to location even under the same major soil group for the simple reason that there will be a variation in soil depth and available water capacity limits also. Therefore, as already emphasized earlier the actual determination has to be made for the specific soil under consideration.

A school of thought led by Veihmeyer and Hendrickson (1948) maintains that soil moisture is available for plant growth equally over the range between field capacity and permanent wilting point. According to this view, transpiration/plant growth is unaffected by the magnitude of soil moisture content unless PWP is reached when the water suddenly becomes non-available. Another view point states that the water held by the soil becomes progressively less available with a linear decreasing trend as the water content decreases from FC to PWP (Thornthwaite and Mather, 1955). Yet another school of thought maintains that transpiration/plant growth is unaffected by the magnitude of soil moisture content from field capacity up to certain threshold value below which almost linear decrease in rate of transpiration occurs (Ritchie *et al.*, 1972). The magnitude of the threshold value would, however, depend upon a variety of factors related to soil, plant and atmospheric conditions. The approach of Ritchie *et al*. (1992) is the one generally subscribed to by most workers for its practicality. All the three approaches have been depicted in Fig. 3.

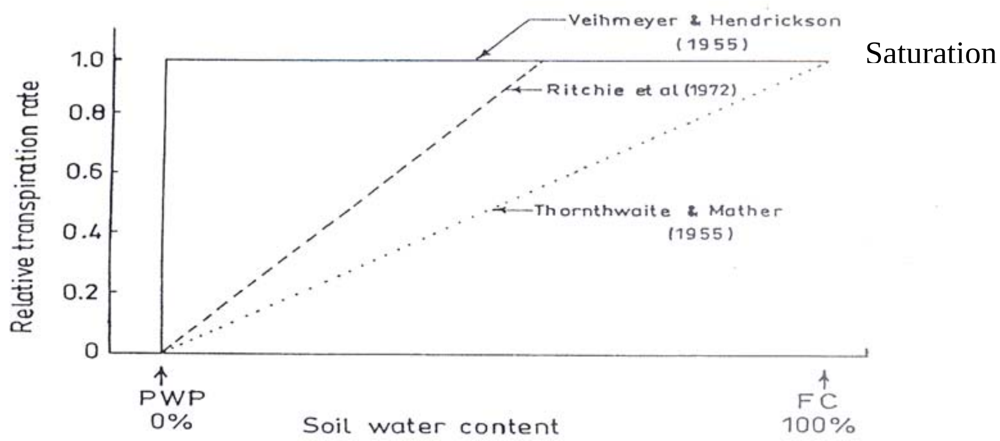

Fig 3. Concepts of soil water availability to plants

Different views regarding availability of water to plants appear apparently contrasting, however, they can be reconciled if consideration is given to the water transmission characteristics of soils, crop rooting depth and density, and evaporative potential of atmosphere. In general, a greater soil water depletion can be tolerated by plants under the conditions of low evaporativity, deep and dense rooting of plants and medium to fine textured soils. In contrast, under the conditions of high evaporativity, sparse rooting and coarse textured soils, only a small depletion of soil water can be tolerated by plants and frequent light irrigations will be needed to maximize crop growth. Irrigation schedule needs to be optimized in terms of time and amount of irrigation on the basis of permissible water depletion for a given combination of crop, soil and climate. Under limited water supply situations, crop water deficit may be planned by identifying optimal and sub optimal water deficit sequences.

Water Transmission Characteristics

Hydro-physical properties of soil, *viz.*, moisture retention characteristics and hydraulic conductivity, greatly influence the availability of water to plant roots. As suction increases i.e. moisture content decreases, hydraulic conductivity decreases more steeply in coarse textured soils than in fine textured soils. Thus, not only is the amount of moisture retained in a coarse textured soil less (Table 1), but also the movement of moisture from the bulk soil to the site of moisture absorption *i.e.* the root surface is much slower as compared with the fine textured soil.

Table 1: Available water capacity of soils of different textural classes

Textured class	**Available water (cm/cm of soil)**
Loamy sand	0.074
Sandy Loam	0.146
Loam	0.191
Silt Loam	0.234
Sandy clay loam	0.209
Silty clay loam	0.204

Water retention curves for soil plotted in terms of per cent depletion of available water (Table 2) suggest that a coarse textured soil would get depleted of available water to a large extent even at a relatively lower water tension while a fine textured soil would retain a considerable portion of available water even at a relatively higher tension. Thus, the availability of water in a coarse textured soil would decrease further.

Table 2: Depletion of available water in light and heavy soils

Suction (bar)	Per cent depletion	
	Light soil	Heavy soil
0.1	0	0
0.3	48	0
0.5	75	15
1.0	83	26
5.0	98	75

Crop Rooting behaviour

Crop rooting behaviour influences the soil water availability to a very large extent. In general, the greater the proliferation and density of roots, the less is the sensitivity of the crop to soil water depletion. Moreover, compared with the roots in the upper layers, the lower lying roots, although less abundant, are more effective in water uptake because of being younger, less crowded and often growing in a better soil moisture regime. The root completely fills the soil pore under adequate soil moisture conditions, while, under severe stress, shrinkage of cortical cells of root results in root shrinkage and thus, significantly reduces soil-root contact (Fig. 4).

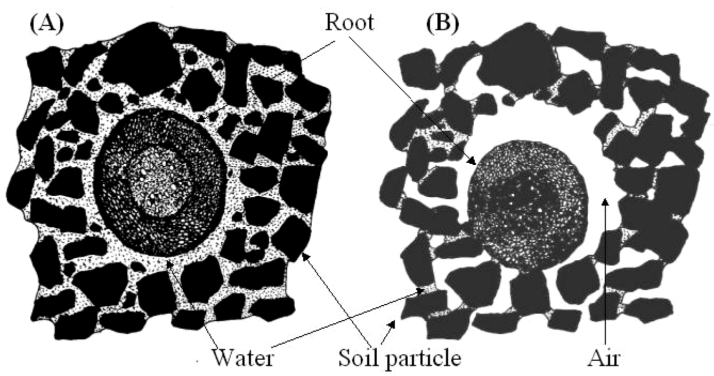

Fig. 4: Cross-section of root surrounded by soil.
A) Adequate soil moisture; B) Severe water deficit stress

Evaporation potential of the atmosphere

The extent of soil water depletion that leads to the reduction in the rate of transpiration, depends upon evaporative conditions of the atmosphere. Greater soil water depletion can be tolerated by plants without any adverse effect on growth when they grow under conditions of low evaporative potential of the atmosphere. But permissible depletion would be less when plants are exposed to high evaporative potential. According to a report, the actual ET of maize began to fall below the potential rate at a suction value of

0.3 bar under an evaporative potential of 1.4 mm/day (Denmead and Shaw, 1962). Information has been compiled showing critical value of available water fraction in the root zone at a given environmental setting below which water availability to crops is constrained (Table 3).

Table3: Available water fraction for maximum, evapotranspiration in various crops

Crop group	**Max. Evapotranspiration (mm day^{-1})**				
	2	**4**	**6**	**8**	**10**
Onion, potato	0.50	0.65	0.75	0.80	0.825
Cabbage, pea, tomato	0.375	0.525	0.65	0.725	0.775
Beans, groundnut, sunflower, wheat	0.20	0.40	0.55	0.625	0.70
Cotton, maize, sorghum, safflower, soybean, sugarbeet, sugarcane	0.125	0.30	0.45	0.55	0.60

When one has control over the amount and time of irrigation within the constraints of water supply at hand, crop water deficit may be planned by identifying optimal and suboptimal water deficit sequences. An optimal water deficit sequence results in minimum yield reduction while a sub-optimal one gives lower yields depending upon ET deficit sequences. Thus maximization of water use efficiency under limited water supply condition can be achieved by planning water deficit to correspond with optimal water sequence based on experimentally determined water deficit-crop yield reduction relationships and applying fertilizers at a rate which will not promote crop growth more than the available water can sustain till maturity.

When crops are raised with stored soil water, fertilizer application increases crop yields not only by correcting nutrient deficiency but also by enhancing water use (Singh et al. 1975). The data presented in Table 4 indicate an increase of 4.6 cm in water use by wheat with application of 80 kg N ha^{-1} resulting mainly from greater sub-soil water extraction compared with unfertilized control. However, fertilizer application must be proportional to soil water availability as excess application might cause luxuriant vegetative growth in earlier phase and development of stress in later growth resulting into lower yield.

Table4: Profile water use by unirrigated wheat as influenced by fertilizer N application

Profile depth (cm)	**Water use (cm)**	
	Control	**80 kg N ha^{-1}**
0-90	10.8	11.2
90-180	4.5	8.7
0-180	15.3	19.9

Plant Water Relations

Concept of water potential

The energy status of water is expressed in terms of water potential, which is a measure of chemical potential of water. Water potential can be defined as the free energy of water available (without temperature change) to do work. Simply water potential is the potential energy of water in a system relative to pure water in the same temperature and pressure. It measures the tendency of water to move through soil plant atmosphere continuum.

The chemical potential of the water depends on the mean free energy per molecule and the concentration of water molecules, i.e., on the mole fraction of the water. The degree to which the presence of solute reduces the chemical potential of the water in the solution below that of pure free water can be expressed as

$$\mu_w - \mu°_w = RT \ln N_w \text{ - - - - - - - - - - (3)}$$

μ_w is the chemical potential of water in the solution

$\mu°_w$ is the chemical potential of pure water at the same temperature and pressure (ergs per mole)

R = the gas constant

T = the absolute temperature in °K.

Nw = the mole fraction of water

For use with ionic solutions, the mole fraction is replaced by the activity of water, a_w and for general use, by the relative vapor pressure, $e/e°$.

$$\mu_w - \mu°_w = RT \ln (e/e°) \text{ - - - - - - - - - - (4)}$$

- *When the vapor pressure of the water in the system under consideration is the same as that of pure free water, ln e/e° is zero, and the potential difference is also zero. Thus,* ***pure free water is defined as having a potential of zero****.*

- *When the vapor pressure of the system is less than that of pure water, ln e/e° is a negative number; hence, the potential of the system is less than that of pure free water and is expressed as a negative number.*

Since the expression of chemical potential in units of ergs per mole is inconvenient in discussions of cell water relations, units of energy per unit of volume was chosen. The measurements are compatible with pressure units, which can be obtained by dividing both sides of above equation by the partial molal volume of water, V_w (cm^3/mol). The resultant term is called the water potential, Ψw. The symbol for water potential is the Greek letter Psi (Ψ).

$$\Psi_w = (\mu_w - \mu°_w)/Vw = (RT/V_w) \ln (e/e°) \text{ - - - - - - - - - - (5)}$$

Water potential = the chemical potential of water / the partial molar volume

$= J\ mol^{-1} / L\ mol^{-1}$

$= N \times m\ mol^{-1} / m^3\ mol^{-1}$

$= N\ m^{-2} = MPa$

1 MPa = 10 bars = 10 atm. (1 atm = 760 mm Hg = 14. 7 lbs sq in^{-1})

Plant water potential expresses the chemical potential of water in the plant system relative to the chemical potential of pure water at the same temperature and pressure.

Note:

- Water always moves from high water potential to low water potential.
- The addition of solute decreases water potential.
- Pressure increases water potential.
- In cells, water moves by osmosis to areas where water potential is lower.

Components of water potential

The total water potential (Ψ) of a system can be partitioned in to different component potentials.

$$\Psi = \Psi_s + \Psi_p + \Psi_m + \Psi_g \quad \text{- - - - - - - - - -} \ (6)$$

where, Ψ_p, Ψ_s, Ψ_m and Ψ_g are referred to as pressure, solute/osmotic, matric, and gravitational potential, respectively.

Solute/osmotic potential (Ψ_s): It arises due to the presence of dissolved solutes in water. Since presence of solutes reduces the potential of water to below that of pure water, the osmotic potential is below zero or a negative value. Thus, Ψ_s of a system is determined by the osmolality, i.e., the total concentration of dissolved particles in a solution without regard for the particle size, density, configuration or electrical charge. The vapor pressure of water in a solution is lowered in proportion to the extent to which the mole fraction of water in the solution is decreased by adding solute. Hence, when water is separated from a solution by a membrane permeable to water but impermeable to the solute, water will move across the membrane along a gradient of decreasing vapor pressure or chemical potential into the solution until the vapor pressures of solution and pure water become equal. The pressure that must be applied to the solution to prevent movement of water in to solution when separated by semi-permeable membrane is termed the osmotic pressure. The negative value of osmotic pressure is equal to osmotic potential.

Van't Hoff equation can be used to calculate osmotic pressure of solutions:

$$\pi = (n_s / V)RT \quad \text{- - - - - - - - - -} \ (7)$$

π = the osmotic pressure in pascals

V = the volume of solvent in liters

n_s = the moles of solute

R = the gas constant (0.00832 literMPa/degree mol at 273°K)

T = the temperature in °K.

For 1 mol of solute in 1 liter of solvent at 273°K (0°C), $\pi = 22.7 \times 10^5$ Pa or 2.27 MPa (22.4 atm or 22.7 bars). In case of soil, osmotic potential plays a significant role where high concentration of salts occur, for example, in saline soils or waters with high salinity are being used, as that influences the uptake of water by plant. In soil, osmotic potential is given by

$$\Psi_s = -0.36 \times EC \quad \text{- - - - - - - - - -} \ (8)$$

where, EC is electrical conductivity (dS m^{-1}). Osmotic potential is generally ignored as far as movement of water within the soil is considered.

Pressure potential (Ψ_P): It is equivalent to the hydrostatic pressure exerted on the cell wall by plasma membrane due to water uptake induced inflation of protoplast. When a plant cell is having sufficient water, it inflates the cell membrane and hence develops a pressure against the cell wall. At incipient plasmolysis when the cell faces water deficit, turgor potential will be zero. Immediately after cell division, plant cells take up water and expand. Cell expansion ceases once cell wall is fully developed. Hence final size of the cell, and thus size and shape of plant organs depends upon the water availability. Water deficit at any period of plant growth thus may result in smaller organs such as small leaves, fruits and short plant. Loss of cell turgor leads to drooping of shoots, leaves, etc.

Matric potential (Ψ_m): Interaction of water with matrix (capillary or electrostatic) reduces the potential of water to below that of pure water and hence it is a negative value. Normally matric potential is a negligible component of plant water potential, but it is the most important component of soil water potential. Soil water movement essentially occurs in reference to the hydraulic gradient expressed as change in soil matric potential per unit length.

Gravitational potential (Ψ_g): It arises due to gravitational forces acting on water. It may be positive or negative depending up on whether the system is above or below the reference point. The contribution of Ψ_g to Ψ is negligible except for tall trees as the contribution of Ψ_g to the Ψ is about 0.01MPa per meter height. Gravitational component in case of soils will play a significant role depends upon the magnitude of soil matric potential when movement in the vertical direction is being considered.

Among these components, the major components of water potential in plants are the turgor potential and osmotic potential, while in soil, the major component of water potential is the matric and gravitational potential.

Water Uptake by Roots

In terrestrial plants, the roots mediate water and nutrient uptake from soil. The maximum water uptake is mediated by 20-200 mm root region from the growing meristem. This region contains large amount of root hairs, which increases the surface area of root and thus, the extraction of soil moisture from a larger soil volume. Root water uptake decreases with the age of the roots, as older roots become suberized. Hence, the root system continuously grows and extracts water and nutrients from the soil. Soil water enters the root apoplast and moves mainly through apoplastic pathway till it reaches the Casparian strip, which seals the radial and transverse walls of endodermis cells, i.e., apoplastic pathway is blocked. At this point water enters the symplatic pathway. A cross-section of a cereal plant root showing types of cells in root and pathway of water and nutrient transport is depicted in Figure 5. Thus at this point of water transport in roots, maximum resistance occurs. Water channel proteins called aquaporins, which are located on the plasma membrane, mediate entry of water through plasma membrane into the symplast. Once water crosses the Casparian strip, water can move both in symplast and apoplast till it reaches apoplastic xylem in the stele. Through xylem water reaches the leaves, where it can take either symplastic or apoplastic pathway until it reaches the stomatal cavity.

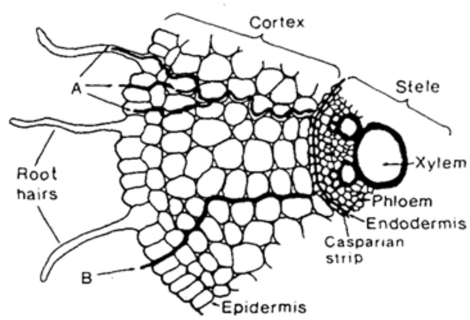

Fig. 5: A cross-section of a cereal plant root showing types of cells in root and pathway of water and nutrient transport. A) symplasmic and B) apoplasmic pathway
(Source: Marschner H. 1986. *Mineral nutrition of higher plants,* Academic Press, New York)

Ascent of sap or movement of water from root to leaf is explained by the cohesion-tension theory. It relies on the physical properties of water, on mechanisms of liquid transport, and on the anatomical features of the xylem, the sap conducting system. Water within the whole plant forms a continuous network of liquid columns (due to hydrogen bonding of water molecules with each other) from the absorbing surfaces of roots to the evaporating surfaces. About 99% of these water columns consist of xylem vessels and tracheids and remaining 1% is constituted by the wall and cytoplasm of living cells. Surface tension of water at the evaporating surface provides the driving force for movement of water. Due to surface tension and the small radius of the curvature of the capillary menisci at the evaporative surfaces, water potential of adjacent cells is lowered by evaporation. Since water column is continuous in vascular pathway, it transfers the variations of water potential throughout the plant instantaneously. From the stomatal cavity, water vapor evaporates to the atmosphere through stomatal pores present in the epidermis. This loss of water through evaporation from the stomata contained in the leaves of plants is called transpiration. The rate of transpiration is controlled by the energy gradient of water or the water potential gradient.

The pathway of movement of water from soil to atmosphere through plant is called Soil-Plant-Atmosphere Continuum (SPAC), an anology to Ohm's law of flow of electrical current through a system. Water uptake and transport in the plant driven by the energy status of water present in the soil-plant-atmosphere continuum (SPAC). Water moves from high-energy status i.e. high water potential (in soil) to low energy status i.e. low water potential (in atm). Water flow in the SPAC depends on water potential gradients and resistances according to the following equations, valid for steady state conditions:

$$Jv = \text{Potential gradient/resistance} = \Delta\Psi/R \quad \text{- - - - - - - - - - (9)}$$

where, Jv = rate of water flow or transpiration; ΔΨ= water potential gradient; R = resistance to water flow. The rate of water flow from soil to root depends upon water potential gradient between root and soil and the resistance in the soil. This can be expressed as:

$$Jv = (\Psi_{soil} - \Psi_{root}) / R_{soil} \quad \text{- - - - - - - - - - (10)}$$

Similarly, the rates of water flow from root to xylem and xylem to leaf and leaf to air are expressed as:

$$Jv = (\Psi_{root} - \Psi_{xylem})/R_{root} \quad \text{- - - - - - - - - - (11)}$$

$$Jv = (\Psi_{xylem} - \Psi_{leaf})/(R_{xylem\ to\ leaf}) \quad \text{- - - - - - - - - - (12)}$$

$$Jv = (\Psi_{leaf} - \Psi_{air})/(R_{leaf\ to\ air}) \quad \text{- - - - - - - - - - (13)}$$

Hence, the rate of transpiration or the rate of flow of water from soil to air through plant system depends upon the water potential gradient between soil and air, and the resistances to water movement in the various paths of soil and plant. Thus, the rate of transpiration (Jv) can be expressed as:

$$Jv = (\Psi_{soil} - \Psi_{air}) / R_{(soil+root+xylem+leaf)} \quad \text{- - - - - - - - - - (14)}$$

In reality, steady state conditions seldom exist, and water potential in plants quickly decreases after sunrise, and recovers during the night if soil has adequate moisture.

Transpiration

About 99% of the water taken up by the plant is lost to the atmosphere through transpiration. Evaporation of water from leaf surface occurs through two pathways: 1) direct evaporation from the outer epidermal cell walls through cuticle to the atmosphere, 2) from cell wall to stomatal cavity and then to atmosphere through stomata. Depending upon the thickness and wax load, the water loss through cuticle varies. Majority of the water lost in transpiration through stomatal pathway.

Water deficit stress develops when water removed by plant from soil is not replenished through irrigation/rainfall. When water uptake is less than the rate of transpiration cellular water deficit occurs. Figure 6 shows development of water deficit stress in plants after withholding irrigation (Slatyer, 1967). It is assumed the same evaporative demand was constant for the period.

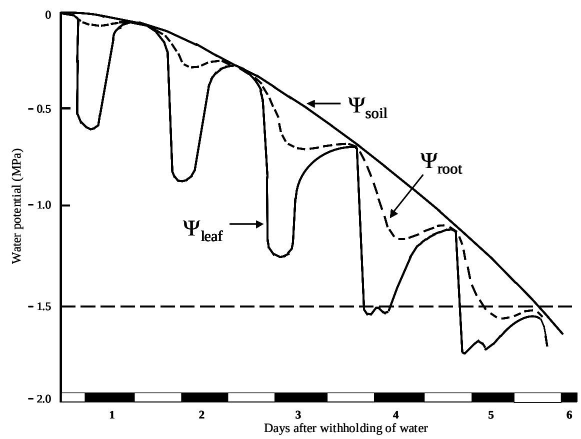

Fig. 6 Changes in soil-, root- and leaf-water potential as transpiration proceeds from a plant grown in limited soil volume irrigated to field capacity initially
(The horizontal broken line indicates the value of leaf water potential at which wilting occurs. Periods of light and dark are indicated by the unfilled and filled bars, respectively, on the X-axis).

The leaf water potential has to be maintained at a critical value in order to maintain cell turgidity and open stomata to support photosynthesis. The sensitivity of the plant processes to water potential changes vary greatly. Hsiao (1973) identified cell expansion as most sensitive plant process to cellular water deficits (Fig. 7). However, wide genetic variation in plant processes for water deficit stress tolerance is found within and across species.

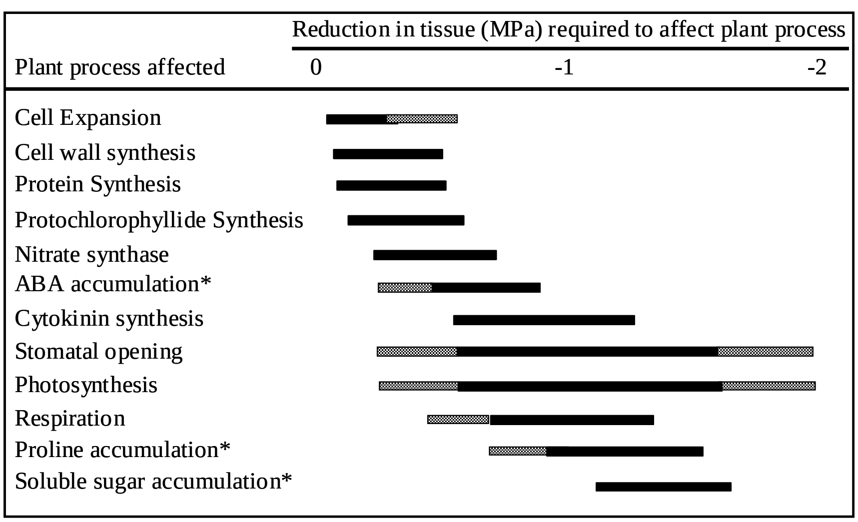

Fig. 7. Generalized sensitivities of plant processes to water deficits

* : *These processes are induced by cellular water deficit. ABA is a plant stress hormone, which promote root growth, reduces shoot growth and closes stomata and thus helps in enhancing water uptake and reducing rate of transpiration. Organic solutes such as*

proline and soluble sugars accumulate under cell water deficit conditions. These solutes act as osmolytes and osmoprotectants.

For a given genotype, the transpiration rate is regulated by the stomatal opening and closing, depending upon the water availability. The rate of transpiration varies widely in different plant species due to the differences in root architecture, leaf area, leaf structure, leaf number, cuticle thickness and wax load and stomatal characters. Since water vapor is lost to the atmosphere and CO_2 is taken inside the leaf for photosynthesis through the stomata, any reduction in transpiration through stomata will also reduce rate of photosynthesis. Hence, crop yield can be expressed as:

$$\text{Yield} = T \times WUE \times HI \qquad \text{- - - - - - - - - - (15)}$$

where T = total seasonal crop transpiration, WUE = crop water-use efficiency and HI = crop harvest index (the ratio of economic yield to total biomass).

Hence, to increase the crop yield, either the transpiration or WUE must be increased, keeping HI at its maximum value for each species. Since water is a scarce resource, it is imperative to enhance WUE of crops plants. Water use efficiency (WUE) is defined as the ratio of photosynthesis (**A**) to water loss in transpiration (**E**). Simply WUE is the yield per unit amount of water used in evapotranspiration. High WUE is crucial for crop production under water-limited environments. WUE is influenced the rate of transpiration and photosynthesis. C3 plants such as rice, wheat, etc., fix CO_2 in photosynthesis through Calvin cycle in to a three carbon compound. The enzyme Rubisco, which fix CO_2 is can also fix O_2 in a process called photorespiration, which leads to about 40 % reduction in photosynthetic carbon fixation. C4 plants such as maize, sugarcane, sorghum, etc., first fix CO_2 in photosynthesis through HATCH- SLACK-cycle in to a four carbon compound, which is then exported to specialized buddle sheath cells, where CO_2 is released and converted in to sugars by Calvin cycle. Because of this CO_2 concentrating mechanism, which increases CO_2 to high level at the site of carbon fixation by Rubisco, photorespiration in these plants is negligible. In general water use efficiency of C4 plants is higher than the C3 plants, mainly due to minimal or negligible amount of photorespiration in C4 plants. Nevertheless, significant variation exists in water use efficiency within each of these categories of plants.

Drought (Soil-water deficit) resistance of plants

From the point of view of plant growth, drought can be defined as plant water deficit, caused by shortage in precipitation and soil water availability (soil water deficit) and excess of evapotranspiration (atmospheric water deficit) that impairs normal growth and development of plants. The nature of drought stress for a crop depends upon 1) quantity - duration-distribution of rainfall for a rainfed crop, 2) soil moisture availability when crop depends upon stored soil moisture, 3) quantity - frequency of irrigation in irrigated crop, 4) soil type, and 5) evapotranspiration in that environment. In addition to the above factors, occurrence of plant water deficit depends upon the biology of plants, i.e., species, genotype and sensitivity to water deficit at various growth and development stages of plants. Plants may employ the following mechanisms of drought resistance:

1) **Drought avoidance:** It refers to the ability of the plant to tolerate prolonged soil water deficit periods by maintaining high plant water status. It depends upon maintaining the plants capacity of water uptake (by increasing the rooting depth, root density and hydraulic conductance, osmotic adjustment) and/or minimizing water loss from plants (by increased stomatal and cuticular resistance, reduced radiation absorption and reduced leaf area).

2) **Drought tolerance:** The ability of plants to tolerate prolonged soil water deficit periods by enhancing cellular tolerance to low tissue water potential. It depends upon remodeling of cell ultrastructure and reprogramming of cell metabolism, activation of plant defense mechanisms such as reactive oxygen species management, and protection of membranes and macromolecules.

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