LESSONS IN
SOIL - PLANT WATER RELATIONSHIPS

by

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ABBREVIATIONS

c - concentration of water in vapor air; absolute humidity
cm - centimeter
e - vapor pressure
ha - hectare
hr - hour
KPa - kilopascal
l - liter
m - meter
MPa - megapascal
P - pressure, turgor pressure
r - resistance
s - second
Ψ - water potential
π - osmotic potential, osmotic solute concentration

INTRODUCTION

Water is the most significant environmental factor in Pakistan. Its abundance determines the unusually diverse types of vegetation that occur. The diversity of forest types is exemplified by the mangrove forests of the coasts of Karachi, the riverain forests of the Indus basin, the scrub forests of the foothills, and the coniferous forests that extend from the subtropics through the temperate, and then to the subalpine regions of the Himalaya. These forest types result from variations in the season and amount of precipitation, the evapotranspiration demands of the climate, and the adaptations of plants that maximize the use of available water, yet minimize the stress of water deficit or over abundance.

Pakistan's wood shortage is becoming increasingly critical, and this is compounded by the need to improve the management of watersheds. This demands greater emphasis in the reforestation of cut over lands, and the afforestation of new areas. The success of these new plantings will be improved by foresters who understand the relationships of plants to the water factor.

These lessons were written for M.Sc. students enrolled at the Pakistan Forest Institute, and the topics follow the approved syllabus for the course in plant water relationships. However, the lessons may be studied independently, or individual lessons may be incorporated into courses in botany, ecology, and watershed management. Since the principles apply to both woody and non-woody plants, the lessons may also be studied by students of agriculture.

The illustrations were copied from the references listed as Additional Reading at the end of each lesson. These references have been deposited in the Pakistan Forest Institute library.

Mark Behan, Ph.D.
Peshawar, August, 1992

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LESSON ONE

THE ROLE OF WATER IN PLANTS

By the end of Lesson One you should be able to:

....Recognize the seven roles of water in plants
....Describe how water is responsible for the growth of cells
....Describe how water provides thermal stability of plants

THE ROLE OF WATER IN PLANTS

Water is the single most important constituent of living organisms. In plants water has seven crucial roles.

I. Constituent

Water comprises 80%-90% of the fresh weight of herbaceous plants, and over 50% of the fresh weight of woody plants.

II. Solvent

Water is the universal solvent; more substances dissolve in water than any other substance. Because of this water is the medium in which biochemical reactants are dissolved in the cell, and chemical reactions take place. Cell membranes and cell walls are both very permeable to water, so water can move from place to place in the plant. Water forms a continuous liquid throughout the plant. It fills the central portion (vacuole) of mature cells, the spaces between the cellulose microfibrills of cell walls, and most intercellular spaces. The intercellular spaces of leaves are an exception by being gas filled because of the need for carbon dioxide exchange with the air.

III. Reactant

Water is a reactant in the biochemical reactions of the cell. Among these is photosynthesis, where water contributes electrons ultimately used in the reduction of carbon to a carbohydrate, and hydrogen protons which play a role in ATP (adenosine triphosphate) production. The oxygen evolved in photosynthesis originates in water. Water is also a reactant in the hydrolysis of plant food reserves such as starch. In starch hydrolysis the elements of water are inserted between the glucose units of the starch polymer, converting starch to sugar.

IV. Transport

Minerals absorbed from the soil are transported across the root, up the stem, and throughout the plant by water movement. Carbohydrates formed in photosynthesis are also distributed throughout the plant by water.

V. Growth

At the time of cell division the vacuoles of newly formed cells are scattered and small. Minerals are absorbed and deposited into these small vacuoles. This causes water to diffuse into the small vacuoles, and they enlarge, creating pressure inside the cell. This pressure expands the plastic walls of the young cell, and this expansion is cell growth. Eventually the vacuoles coalesce into a central vacuole, and the walls become so thick they loose plasticity, so that at maturity the cell no longer expands, but does maintain water pressure inside the cell.

VI. Turgidity

Mature cells retain their shape by the force of water pressing against the inside of the cell walls. This pressure keeps the cells turgid, and if the pressure is lost (e.g. from excess evaporation, death, or being placed in salt solutions) they may loose turgidity and become flaccid. It is the turgidity of cells that gives the shape to many tissues such as leaves and annual plants that do not have woody or other strengthening tissues.

VII. Thermal Stability

More calories of heat are required to raise the temperature of water than any other common substance. For this reason plants, which are mostly water, can absorb a considerable amount of heat (e.g. from sunlight), and only slowly gain temperature. Similarly, the same number of calories must be lost in order for the temperature of water (or a plant) to be lowered; thus plant temperatures can remain above air temperature during brief cold periods. The high water content of plants permits them to maintain a more constant temperature than that of the air.

LESSON TWO

PROPERTIES OF WATER AND SOLUTIONS

By the end of Lesson Two you should be able to:

....Describe the atomic basis for hydrogen bonding
....Describe the unique properties of water with respect to liquidity, specific heat, latent heats, viscosity, adhesive and cohesive forces, surface tension, and boiling and freezing points, and how these are affected by H bonding
....Describe why water is referred to as the universal solvent
....Differentiate between bulk flow and diffusion
....Describe the physical cause for diffusion
....List the factors that affect diffusion
....Define vapor pressure and describe the effects of solutes temperature, and pressure on vapor pressure
....Describe the effects of solutes on diffusion
....List the colligative properties of water, and describe how they are related to each other

THE PROPERTIES OF WATER AND SOLUTIONS

I. Hydrogen Bonding

Many of the unique properties of water can be explained by the way its two hydrogen atoms are attached to its oxygen atom. The hydrogens are apart at an angle of only 105 degrees (Fig. 3.3), making the water molecule very polar, i.e., it has a positive end (where the two hydrogens are located) and a negative end (where a pair of oxygen's electrons are exposed).

The positive field of the two hydrogen atoms are attracted to the negative field of oxygen's exposed electrons. This attraction is called hydrogen bonding. The force of hydrogen bonds is generally stronger than covalent bonds, but not as strong as ionic bonds. The result of hydrogen bonding is that water molecules have a great deal of attraction for each other, and it is this molecular attraction that gives water many of its properties (Fig. 3-4).

II. Liquidity

Most substances with molecular weights about that of water (e.g. ammonia, methane) are gases at room temperature, but water is a liquid because hydrogen bonding gives water an apparent molecular weight much greater than 18.

III. Specific Heat

Water requires 1 calorie per gram to raise its temperature 1 degree, the highest heat requirement of nearly any substance. This high requirement is due to strong hydrogen bonding, which requires substantial energy to separate one molecule from another by heat as occurs in vaporization and boiling. This high specific heat also means that substances with high water content require large energy inputs or withdrawals in order to change temperature, thus adding to their thermal stability.

IV. Latent heats of vaporization and fusion

Some 586 calories are required to convert 1 g of water to vapor at 20 degrees, more than five times the heat required to raise the temperature of water from 0 to 100 degrees. This high heat requirement may create "evaporative cooling" effects in transpiration by removing large amounts of heat. An equivalent amount of heat is liberated upon condensation, as in dew formation. These two factors also add temperature stability.

In order to melt 1 g of ice 80 cal must be supplied. This high heat of fusion is again caused by hydrogen bonding. Also during melting the volume of water decreases (and its density increases) because the packing of water molecules in the liquid state is closer than in the solid. This is the feature that causes ice to float, which is fortunate for life on earth. If the density of ice was greater than liquid water, ice would sink, and because of the high specific heat of water it is likely that ice would form at the bottom of lakes and oceans, and not melt.

V. Viscosity

Because the oxygen of a water molecule shares hydrogen bonding with two other water molecules, the viscosity of water is less than that predicted on the basis of the strength of its hydrogen bonds. The sharing weakens the effective bonds, and water flows more readily (is less viscous).

VI. Adhesive and Cohesive Forces; Surface Tension

Adhesion is the attraction of one substance for another, for example, water molecules for cellulose, which both have hydrogen bonding, and thus have strong attraction for each other.

Cohesion is the attraction of one molecule for another of the same species, and as mentioned before, the attraction of water molecules for each other is very high. In other words, it is difficult to separate water molecules, i.e. to form vapor. It is the cohesive and adhesive properties of water that allow it to be transported to the tops of the tallest trees.

Surface tension is associated with water's cohesive force, and it is quite high, permitting some things that have greater density than water to remain on the surface, e.g. a carefully placed needle, or a water beetle.

VII. Water the Universal Solvent

Because of its polar nature and hydrogen bonding, water is able to "cage" many solutes, preventing them from crystallizing and thence precipitating. Because of this caging effect, water can dissolve a very large number of substances.

VIII. Bulk Flow and Diffusion

Many molecules move at a time in bulk flow of liquids, but only one molecule at a time by diffusion. Both methods of transport occur in plants. Bulk flow requires a pressure gradient. Diffusion requires a concentration gradient, i.e., a gradient of chemical activity or potential (Fig.2-4)

IX. Physical Causes of Diffusion

All molecules greater than 0 degree Kelvin (absolute zero or -273 C.) are in motion. In the case of solids this motion is restrained, less so in liquids, and little in gases. During their motion molecules in liquids and gases especially are in nearly constant collision with other molecules, colliding off in random vectors. If a substance is in greater concentration, or has greater potential or activity (e.g. by having a higher temperature) in one area than another, the statistical probability is that these random vectors will travel farther toward the area of less concentration or activity. This tends to equalize the activity or concentration throughout space over time, and this process is called diffusion (Fig. 1-4).

X. Factors Affecting Diffusion

Diffusion occurs in response to differences in concentration. For example, when CO_2 is consummed by photosynthesis a CO_2 concentration gradient develops from air to the chloroplast. CO_2 diffuses in response to this gradient. The chemical potential, or more commonly and accurately in this case, water potential, can also be affected by pressure, temperature, adsorptive surfaces, and by solutes (Fig.1-4).

Pressure increases water potential, and thus the tendency for water to diffuse, and so does an increase in temperature. Adsorptive surfaces, (e.g. clay, cellulose) decrease water potential by restricting the movement of water molecules, and thus the tendency to diffuse is lowered. Water molecules cage solutes, and the motion of these water molecules becomes restricted, thus they are less free to diffuse. The concentration of water molecules <u>with sufficient energy to diffuse</u> is less in the presence of solutes (even though the total concentration of water molecules per unit volume may remain about the same).

Although the above factors determine the *potential* for diffusion, the *rate* of diffusion is determined by the steepness of the diffusion gradient, i.e., the distance over which the changes in concentration or activity occur. The less the distance the more rapid the rate of diffusion.

XI. Vapor Pressure

Water vapor creates a partial pressure that is added to the air in proportion to the amount of water vapor present. Water at 20 degrees and 100% relative humidity contains 17.31 g m^{-3} H_2O (absolute humidity), and this vapor exerts a partial pressure of 2.34 MPa (MegaPascals). Both the density and vapor pressure increase with pressure and temperature (at 100 degrees the vapor pressure of water equals atmospheric pressure at its boiling point.

As noted above, vapor pressures increase with temperature and pressure, and decrease with added solutes (Fig. 1-5)

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XII. The Colligative Properties of Water

The addition of solutes to water causes an increase in boiling point because more energy is required to separate water molecules involved in caging solutes. Solutes cause a decrease in freezing point for a similar reason in that more energy must be removed from caging water molecules so that they can come to rest with other water molecules in the ice crystal. Solutes decrease the vapor pressure of the solution compared to pure water. And since solutes decrease the ability of water to diffuse, water will tend to diffuse into areas where solute diffusion is restricted, even creating a pressure. This special case of diffusion is called *osmosis*.

If any of the colligative values are known, the others can be computed. For example, 1 mol of sugar in 1 kg of water will lower the freezing point to -1.86 degrees, raise the boiling point to 100.56 degrees, lower vapor pressure at 20 degrees by 0.041KPa, and create an osmotic potential of about 2.24 MPa.

Additional Readings:

Salisbury, F. and C. Ross. 1978. Plant Physiology. pp. 18-32
Taiz, L. and E. Zeiger. 1991. Plant Physiology. pp. 61-67

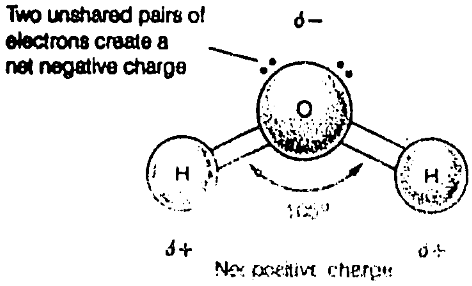

FIGURE 3.3. Diagram of the water molecule. The two intramolecular hydrogen-oxygen bonds form an angle of 105°. The opposite partial charges on the water molecule result in the formation of intermolecular hydrogen bonds with other water molecules. The average distances involved in intermolecular hydrogen bonds and intramolecular hydrogen-oxygen bonds are expressed in nanometers (1 nm = 10^{-9} m).

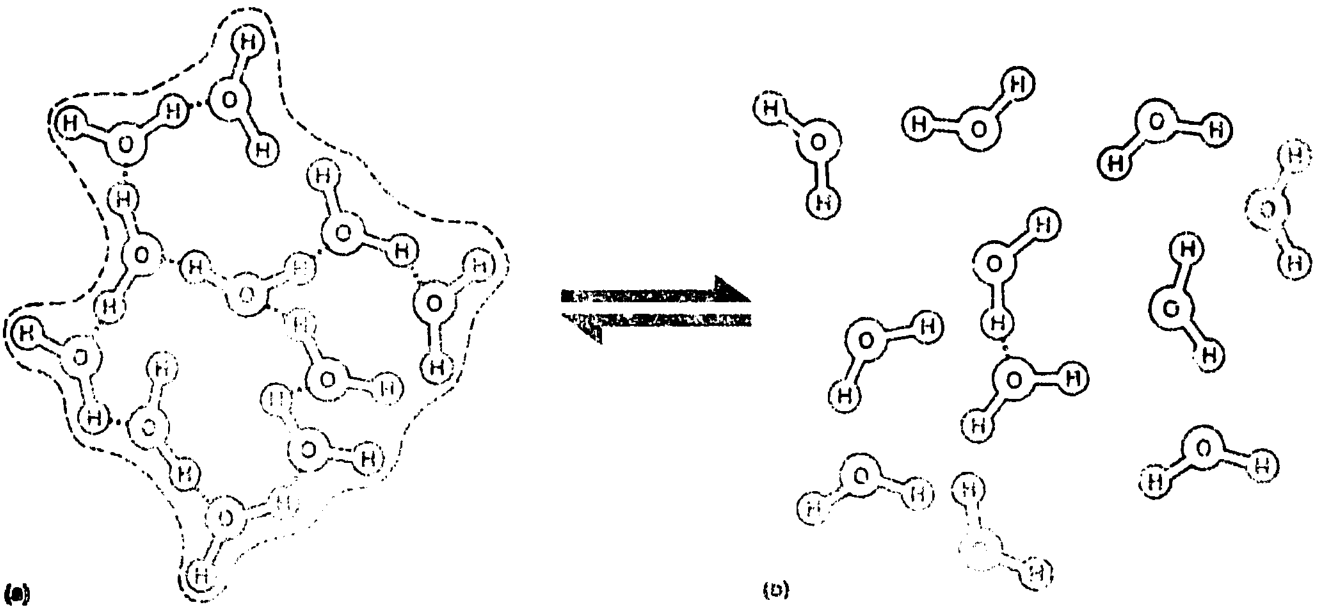

FIGURE 3.4. Hydrogen bonding between water molecules results in local aggregations of ordered, quasi-crystalline water (a). Because of the continuous thermal agitation of the water molecules, these aggregations are very short-lived; they break up rapidly to form much more random configurations (b).

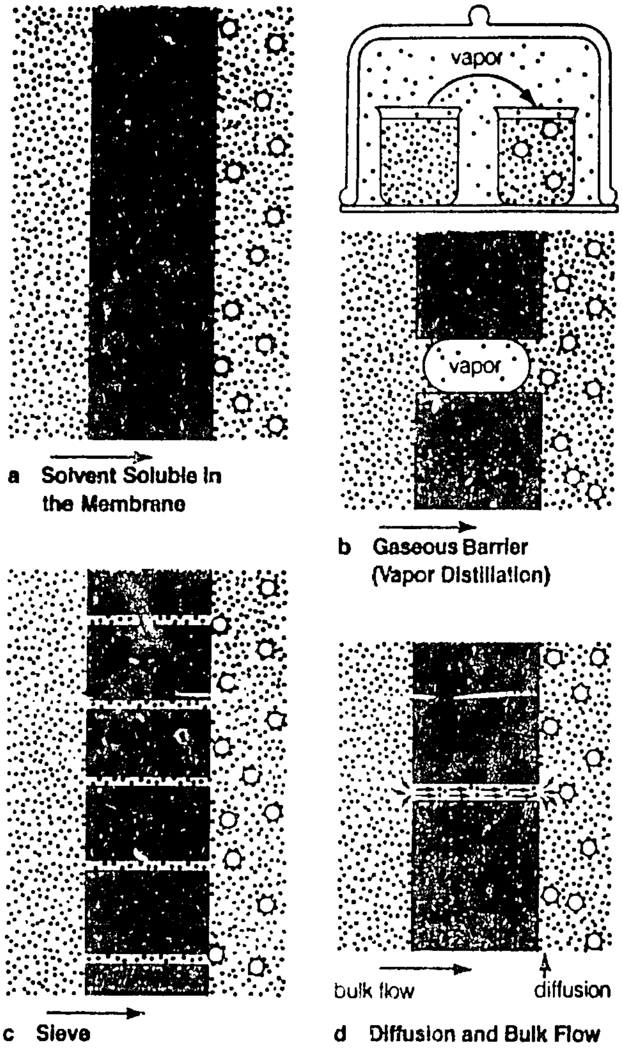

Figure 2-4 Schematic diagram of four conceivable membrane mechanisms. The black dots represent water molecules about 0.3 nm in diameter, open circles represent sucrose molecules about 1.0 nm in diameter, and the membranes are drawn to the scale of most cellular membranes at a thickness of 7.5 nm. Note that water concentration is about the same on both sides of the membranes. Water molecules move rapidly through membranes in cells, possibly by mechanisms similar to those represented by models (**a**) and (**c**). This is discussed in Chapter 6. Model (**d**) is a refinement of model (**c**), as discussed in the text. The vapor model (**b**) may apply in plants and soils in various situations, but no membrane is known to have gas-filled pores.

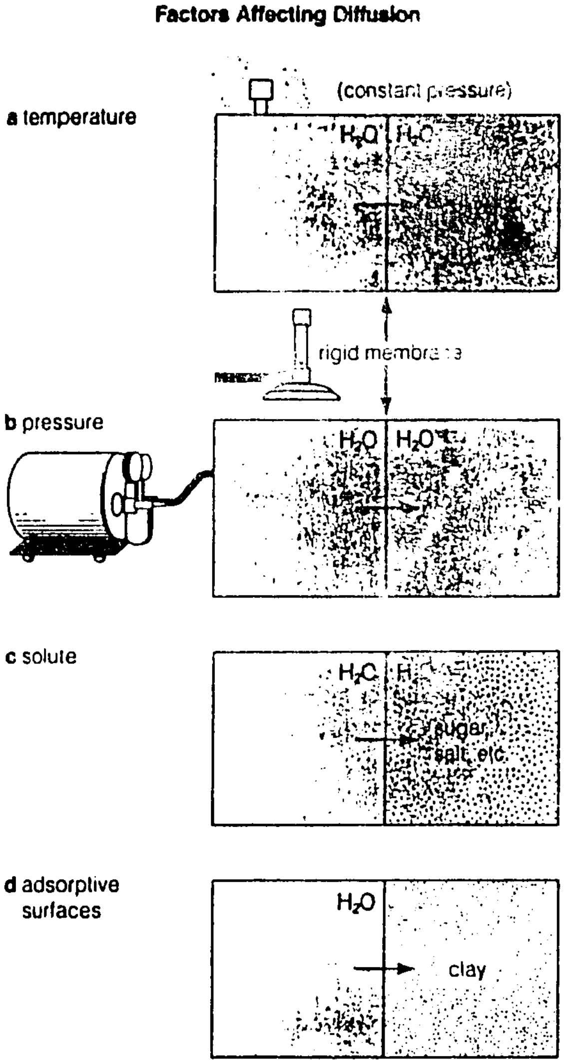

Figure 1-4 Models of diffusional systems.

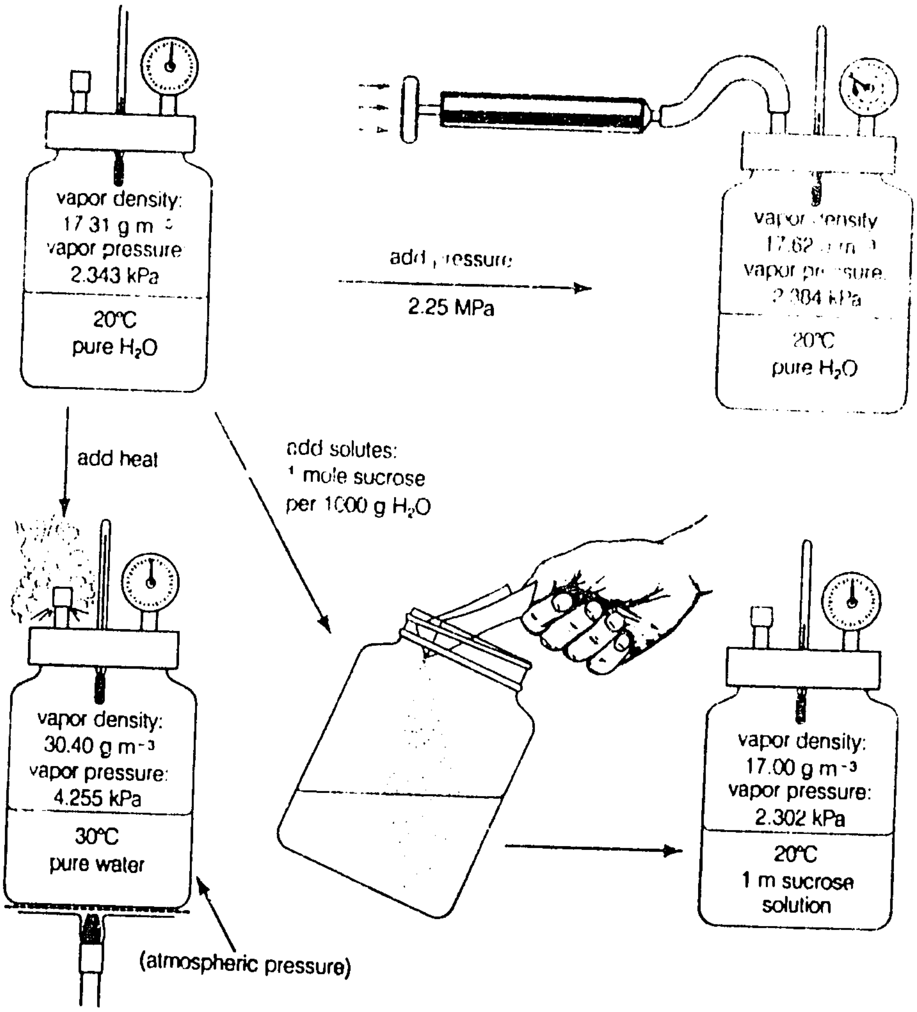

Figure 1-5 Illustrating effects of pressure, temperature, and solutes on vapor density and vapor pressure (and thus indirectly on water potential). Units of vapor density are grams per cubic meter (g m^{-3}); vapor pressure units are kilopascals (kPa). These two ways of expressing the amount of vapor are interconvertible with a suitable equation. The equation for calculating water potentials from vapor pressures is given in Chapter 2 (equations 2.4 and 2.5). Figures for vapor density and pressure of pure water in a closed volume at different temperatures are given in standard tables. Note the relatively large effect of temperature on vapor density or pressure compared with the much smaller effects of pressure and added solutes.

LESSON THREE

CELL WATER RELATIONS AND TERMINOLOGY

By the end of Lesson Three you should be able to:

....List the factors that affect the chemical potential of water, and the relationship between chemical potential and water potential
....Define water potential, osmotic potential, turgor pressure
....Describe plasmolysis and its cause
....Describe osmosis and how it occurs in cells
....Define matrix potential

CELL WATER RELATIONS AND TERMINOLOGY

I. The Chemical Potential of Water

Chemical potential is a term used in thermodynamics. It quantitatively expresses the free energy of a substance. By comparing the free energy at one condition with another, the capacity for work by a change in conditions can be determined. In soil-plant water relations the work is water movement from soil to root, cell to cell, tissue to tissue, etc., and that movement is a form of work, requiring a free energy difference from the origin to destination. The chemical potential of water in this situation is referred to as **water potential.**

There are four factors that affect water potential: solutes, pressure, adsorptive surfaces, and gravity. These same factors that affect the ability of water to diffuse.

II. Water Potential Ψ

Water potential, ψ, expresses the free energy of water in pressure units, usually megapascals (MPa). The reference or standard state of water is taken to be pure water at ambient pressure and at the same temperature as the sample. The ψ at the standard state, is assigned the value of 0, making it easy to calculate the ψ of a sample by difference (Fig. 2-2).

III. Osmotic Potential π

π defines the amount by which the free energy of a solution has been reduced from that of the pure water standard by the presence of dissolved solutes. It is also defined in units of pressure, MPa, expressing the pressure that would have to be exerted on the solution to raise its ψ to that of the water standard (Fig. 2-2).

One mol of a non-ionizing substance,i.e. sugar, dissolved in 1 kg water, will exert π of about 2.25 MPa under ideal conditions. There are deviations from this relationship in all but ideal circumstances in dilute concentrations, but the relationship does provide an estimate. Since π, like the other colligative properties, is determined by the portion of water molecules involved in caging dissolved substances, materials that ionize, i.e. NaCl, exert an π in portion to the ions present. It might be expected that 1 mol of NaCl dissolved in 1 kg water would exert π of 4.5MPa, since NaCl would be expected to ionize to Na^+ and Cl^-, but the actual π is slightly less because the NaCl does not exhibit complete, independent ionization.

IV. Turgor Pressure P

If solutes accumulate inside a cell, water with a greater ψ will diffuse into the cell. If the cell is an animal cell, e.g. a red blood cell (erythrocyte) the cell will burst as the pressure inside the cell exceeds the slight strength of its outer membrane (hemolysis). But plant cells are surrounded by a strong cell wall, so as water diffuses into the plant cell, and since water is virtually incompressible, pressure inside the cell increases. This pressure is termed **turgor pressure P.**

If the cell wall is plastic as occurs in young, newly divided cells, P may cause the cell to expand by stretching the plastic cell wall, causing the cell to grow. As the cell matures additional cellulose is deposited, forming a thicker, less plastic cell wall. In this case P increases until it compensates for the decrease in ψ caused by the added solutes, or π. Because of the small surface area, plant cells can withstand turgor pressures of 3.0 MPa or more, with slight expansion, but without any sign of bursting.

The shape of non-woody plant tissues such as leaves, floral petals, etc., is maintained by turgor pressure, the force of water pressing against the inside of cell walls, making them rigid. If the membranes of such cells is disrupted (e.g.by heating) solutes leak from the cell, and it looses turgor and becomes flaccid. Such tissues also become flaccid if placed in salt solutions.

V. Plasmolysis

If an erythrocyte is placed into a salt solution it shrivels, like a grape shrivels to a raison during drying. This is termed plasmolysis. But if a plant cell is placed in a salt solution the cell wall prevents it from shrivelling. At first the cell looses turgor, just becomes flaccid, and if P = 0, it is termed **incipient plasmolysis.** Plant cells may also undergo negative turgor. In living cells negative turgor may cause membrane disruption as the cytoplasm is pulled away from the cell wall by its attraction to the shrinking vacuole. This kills the cell, and the contents of its vacuole is liberated on death.

Negative turgor can also occur in dead cells. Among these the xylem cells of wood are the most significant, and as will be discussed in a later lesson, it is the negative turgor in xylem cells that permits water transport to the tops of rapidly transpiring trees.

VI. Osmosis

Osmosis occurs when a solvent is allowed to diffuse, but not the solute. A differentially permeable membrane is required to establish this situation, i.e. a membrane permeable to the solvent, in our case water, but not to the solute.

Osmosis can be established physically by placing a cellophane membrane over the mouth of a funnel and securing it so tightly that no leaks occur around its edges. The funnel is then inverted, and sugar solution poured down the stem to the flared end of the funnel. Cellophane is permeable to water, but not to sugar. If the inverted funnel with sugar solution is then placed in a beaker of water, water will diffuse through the cellophane into the funnel, causing the solution to rise up the stem of the funnel. In theory, water should continue to rise up the stem until the hydrostatic pressure of water in the stem equals the osmotic potential of the solution. This phenomena is called osmosis.

Living cells may accumulate solutes inside the vacuole to concentrations of 100 fold or more that of the environment. The accumulation of solutes and maintenance of them inside the cell requires metabolic energy. Cells may also synthesize an increase in solutes, e.g. by converting starch to sugar. Such solute accumulation decreases ψ in cell, cellular membranes are differentially permeable, and water diffuses into the cell by osmosis in response to the ψ gradient (Fig. 2.1).

VII. Matrix Potential

In addition to caging solutes, the free energy of water may be lowered by attraction to the surfaces of substances too large to dissolve. Colloids (e.g.clay particles) attract a surface film of water, with a force termed **matrix potential.**

Consider water held by a piece of blotter paper. Water is first attracted to the surfaces of the cellulose fibers that comprise the paper, then water molecules bridge the spaces between fibers by their attraction to each other, i.e. the matrix or composition of the paper. Water is held in the paper by matrix potential, and it is less free to diffuse the pure water. Water in soils is also held by matrix forces. The matrix potential of soil water plus its π determines Ψ_{soil}.

VIII. Measurement of Cellular Water Attributes

A. Water Potential

The water potential of tissues (e.g. leaves, potato disks) can be measured by the Chardakov method in which the tissue is immersed in a graded series sugar solutions of increasing concentration. If the ψ_{tissue} is less than $\psi_{solution}$, water will leave the tissue and dilute the solution. The treated solution is then compared with a paired untreated solution by transferring a drop. In this case the drop should rise in the control solution, because the treated solution has become less dense. When a drop from the treated solution is placed into its paired control and it neither rises nor sinks, the Ψ_{tissue} equals $\Psi_{solution}$ which equals $\pi_{solution}$ (Fig. 2-5).

Water potential can also be determined by placing a soil or plant tissue sample in a small chamber with strict temperature control, and determining the vapor pressure in the chamber by measuring the dew point by isopiestic psychrometry (Fig. 2-5).

The water potential of soils may be also be determined by placing the soil in a pressure membrane apparatus, applying pressure to extract soil water, and measuring the amount of water that remains after extraction at various pressures.

B. Osmotic Potential π

π can be determined by expressing cell sap and determining freezing point depression (Fig. 2-10). It can also be determined by placing tissues in a graded series of sugar solutions and determining which solution causes the tissue to just loose turgor, a condition defined as incipient plasmolysis. At zero turgor the π of the bathing solution equals π of the tissue. This method is illustrated in Fig. 2-11.

Table 2.1 gives the osmotic potential for several plants.

C. Turgor Pressure

P is generally determined by differences after measuring ψ and π. It can be measured directly on a few, specialized cells. The negative turgor that occurs in rapidly transpiring plants may be determined by a pressure bomb, which will be described in a later lesson.

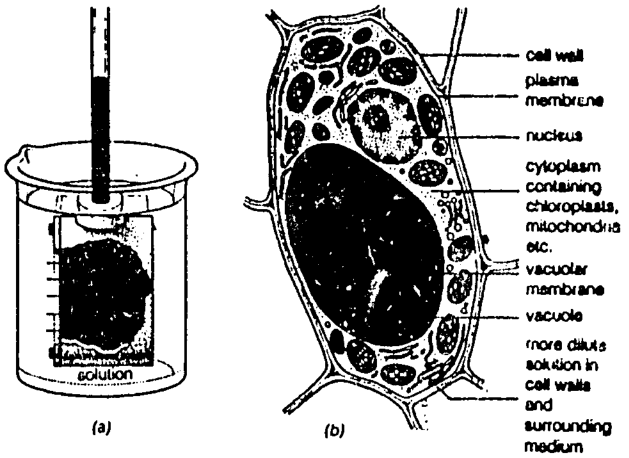

Figure 2-1 **(a)** A mechanical osmometer in a beaker. **(b)** A cell as an osmotic system.

Additional Reading:

Salisbury, F., and C. Ross. 1978. Plant Physiology. pp. 33-39
Taiz, L. and E. Zeiger. 1991. Plant Physiology. pp. 67-76

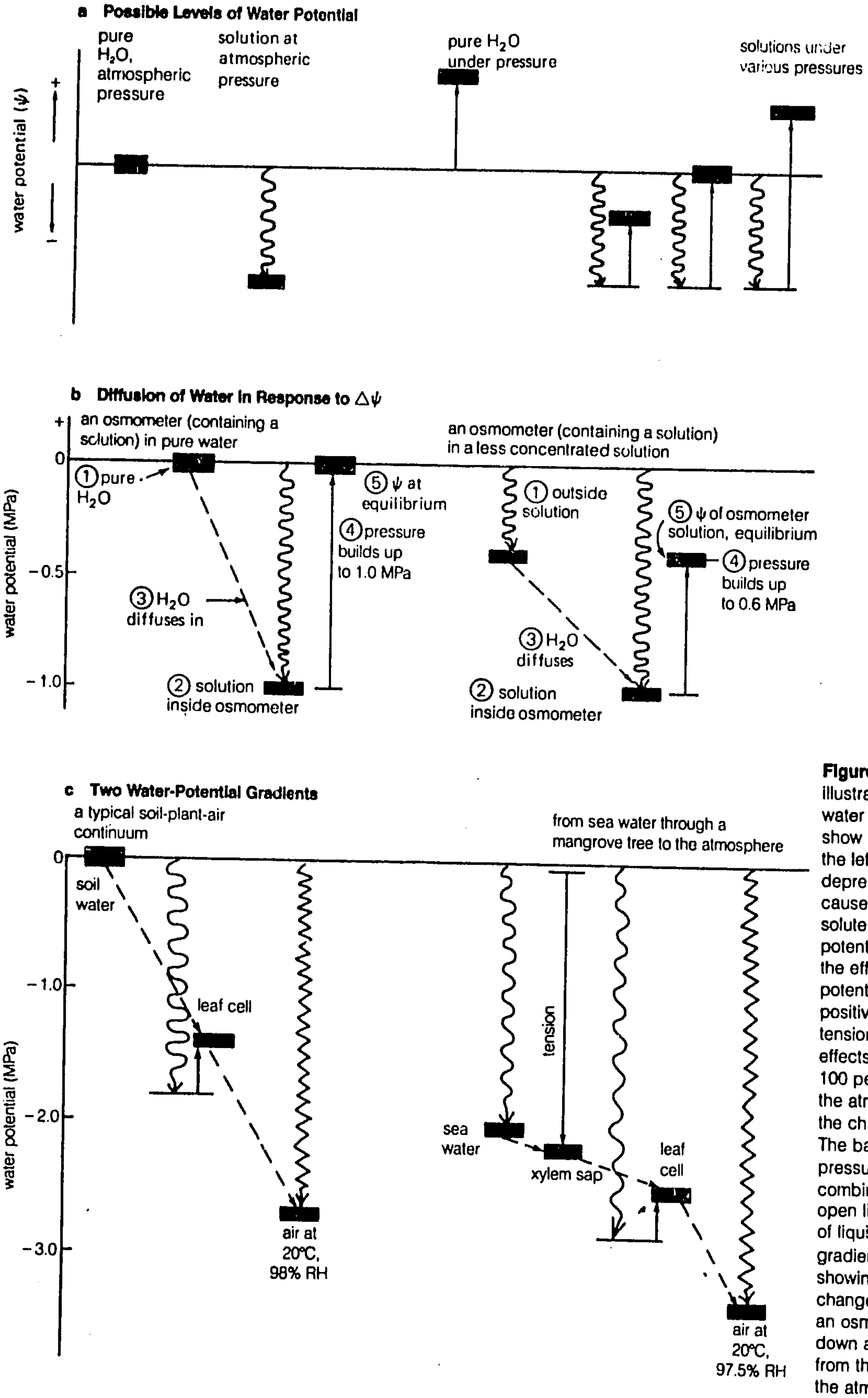

Figure 2-2 A schematic illustration of various effects on water potential. Black rectangles show the water potential (scale on the left). Wavy lines indicate depression in water potential caused by solutes (the osmotic or solute component of water potential). Unbroken lines suggest the effect of pressure on water potential. (Arrows point up for positive pressure, down for tension.) Zig-zag lines indicate effects of relative humidities below 100 percent on water potential of the atmosphere (discussed later in the chapter and in Chapter 4). (**a**) The basic effects of solutes and pressures, alone and in combination, on water potential of open liquid water. (**b**) Diffusion of liquid water in response to gradients in water potential, showing how water potential changes as diffusion occurs into an osmometer. (**c**) Water diffusion down a water potential gradient from the soil through a plant into the atmosphere and from sea water through a plant into the atmosphere. The sea-water example (note *tension* in the xylem sap) is discussed in Chapter 4 (see Figure 4-13).

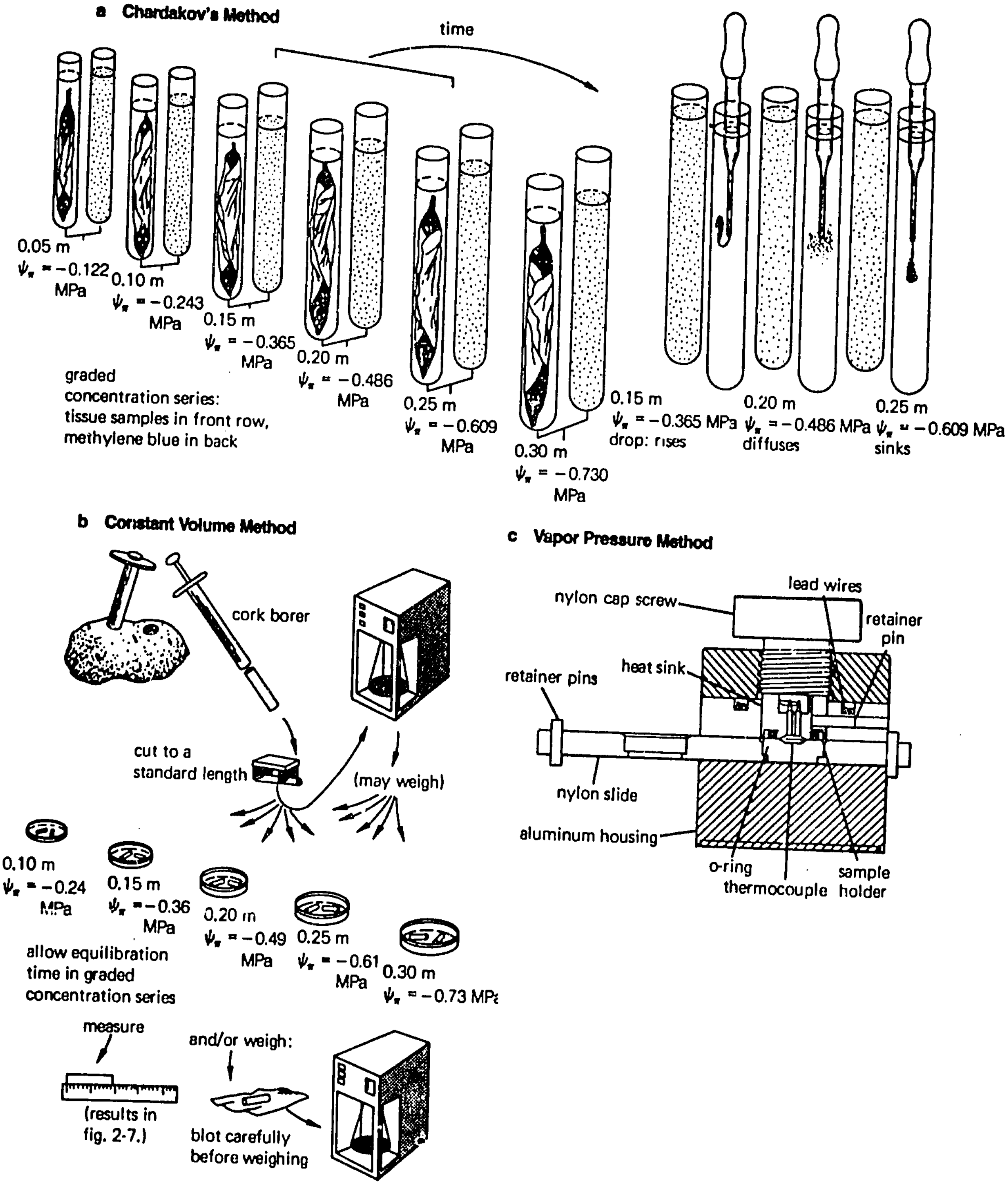

Figure 2-5 Three different ways to measure water potential. Osmotic potentials are calculated at 20°C by equation 2.2. The vapor-pressure device is made by Wescor, Inc., Logan, Utah. (Drawing and photograph used by permission.)

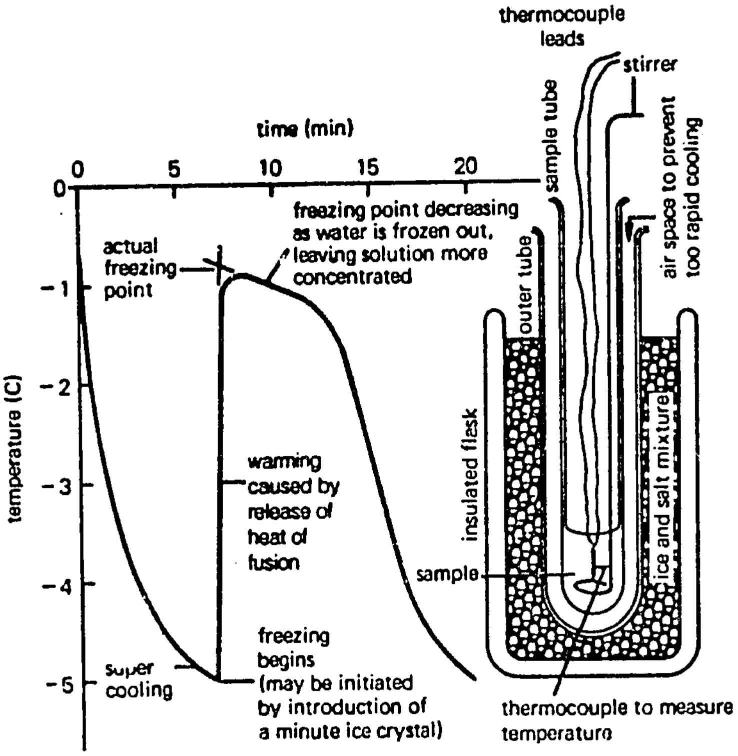

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Figure 2-10 Determination of the freezing point of a solution

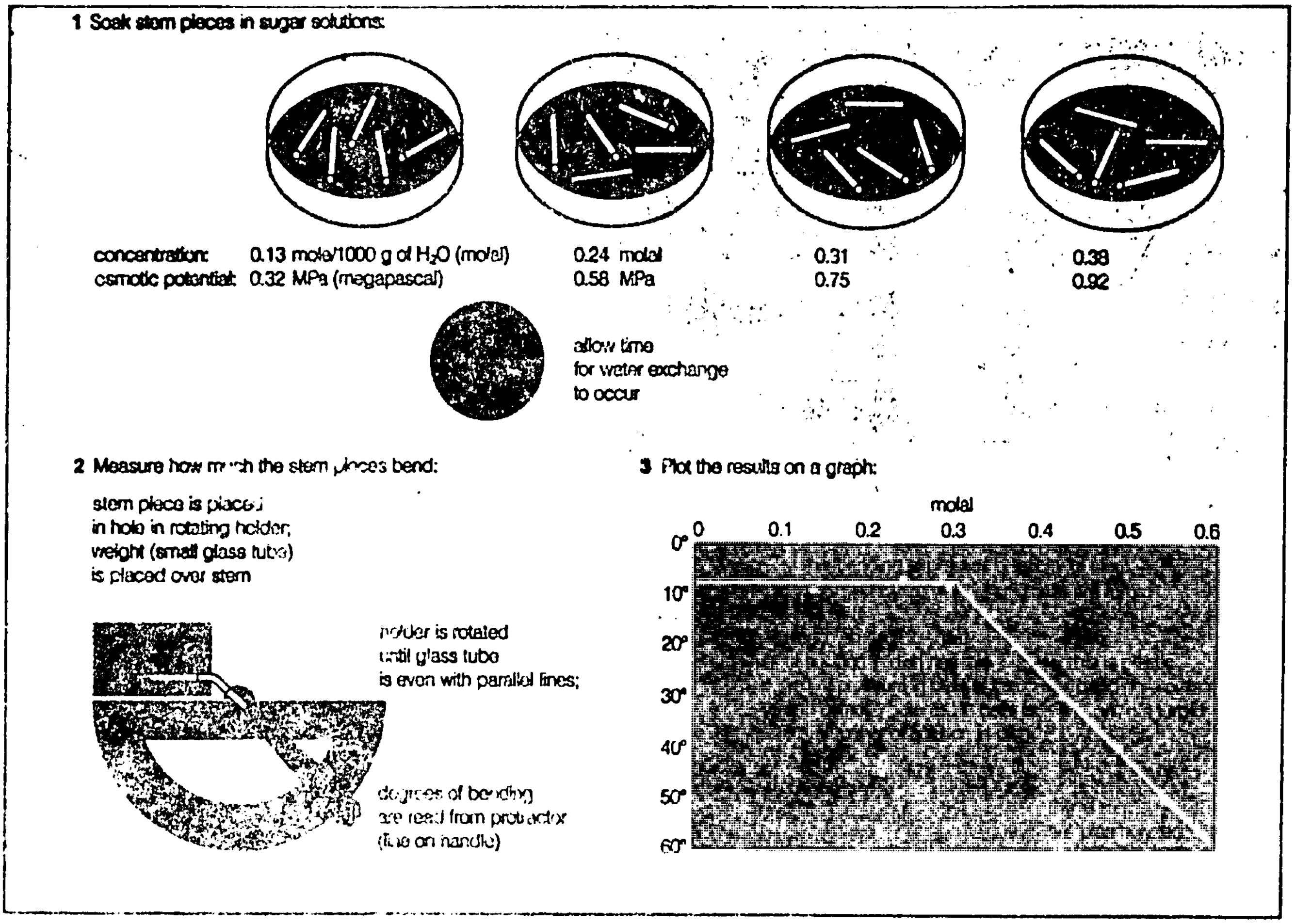

Figure 2-11 How to detect when cells are just beginning to plasmolyze without actually looking at them. At the moment when the turgor pressure in the cells reaches zero, the tissues (stem, in this case) become much more flexible and much less elastic. (Jensen and Salisbury, *Botany*, 1984, [illegible]; see Lockhart, 1959.)

Table 2-1 Some Examples of Empirically Determined Osmotic Potentials of Leaves.

Species	Osmotic Potential ψ_π (MPa)
Shadscale (*Atriplex confertifolia*)[a] (The most negative values are highly questionable.)	−2.4 to −20.5
Pickleweed (*Allenrolfea occidentalis*)[b]	−8.9
Sagebrush (*Artemisia tridentata*)[a]	−1.4 to −7.4
Salicornia (*Salicornia rubra*)[a]	−3.2 to −7.3
Blue spruce (*Picea pungens*)[b]	−5.2
Mandarin orange (*Citrus reticulata*)[b]	−4.8
Willow (*Salix babylonica*)[b]	−3.6
Cottonwood (*Populus deltoides*)[c]	−2.1
White oak (*Quercus alba*)[c]	−2.0
Sunflower (*Helianthus annuus*)[c]	−1.9
Red maple (*Acer rubrum*)[c]	−1.7
Waterlily (*Nymphaea odorata*)[c]	−1.5
Bluegrass (*Poa pratensis*)[c]	−1.4
Dandelion (*Taraxacum officinale*)[c]	−1.4
Cocklebur (*Xanthium spp.*)[c]	−1.2
Chickweed (*Stellaria media*)[c]	−0.74
Wandering Jew (*Zebrina pendula*)[c]	−0.49
White pine (*Pinus monticola*)[d], dry site, August, exposed to sun	−2.5
White pine (*Pinus monticola*)[d], moist site, April, more shaded	−2.0
Big sage (*Artemisia tridentata*)[d], March to June, 1973	−1.4 to −2.3
Big sage (*Artemisia tridentata*)[d], July to August, 1973	−3.8 to −5.9
Herbs of moist forests[e]	−0.6 to −1.4
Herbs of dry forests[e]	−1.1 to −3.0
Deciduous trees and shrubs[e]	−1.4 to −2.5
Evergreen conifers and Ericaceous plants[e]	−1.6 to −3.1
Herbs of the alpine zone[e]	−0.7 to −1.7

LESSON FOUR

MOVEMENT OF WATER IN AND OUT OF CELLS

By the end of Lesson Four you should be able to:

....Use the Water Potential Equation to solve problems in:
    movement of water between cells and solutions
    movement of water between cells
    movement of water between tissues
....Define imbibition potential
....Use the Water Potential Equation to solve problems involving
    imbibition

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MOVEMENT OF WATER IN AND OUT CELLS

I. Water Potential Equation

$$\psi^* = P - \pi - \psi_{matrix} - \psi_{temp} - \psi_{gravity}$$

Water potential*$^{(total)}$ = Pressure - osmotic potential - matrix potential - WP due to temp. difference - WP due to gravity

The above equation includes all of the common factors that affect ψ. In previous lessons you noted that an increase in P increased ψ^*, and that an increase in solute concentration, which caused π to become more negative, decreased ψ^*. Water can also be attracted to surfaces, and to itself across spaces such as capillaries. This attraction is expressed as ψ_{matrix} and also decreases ψ^*. Differences in temperature can also affect ψ^*; cold water has less free energy than hot water. This is the reason water vapor in the air condenses on a glass of iced tea, and vapor is released from a cup of hot tea. Finally, $\psi_{gravity}$ is a special form of P taking into account the hydrostatic head created by a standing water column such as in the xylem at the base of a tall tree. Not all of these factors are used in most water potential calculations.

II. Movement of water between solutions and cells

Example Problem 1. Suppose a cell with $\pi = 1.0$MPa is immersed in pure water ($\psi = 0$). What will be the ψ^*, P, and π of the cell at equilibrium?

Answer: $\psi = P - \pi$; ψ pure water = 0 (see Fig. 3.10 (a))

at equilibrium $\psi_{cell} = 0 = \Psi_{pure\ water}$

in order for the $\Psi_{cell} = 0$ the water potential equation is used:

$\Psi_{cell} = P_{cell} - \pi_{cell}$ or $0 = 1.0$ MPa P - 1.0 MPa π

By definition the cell $\pi = 1$MPa, therefore the only way the cell could achieve $\psi = 0$ would be to increase turgor pressure to 1MPa.

Example Problem 2. Cell A and Cell B are adjacent and can freely exchange water. Cell A has $\pi = 0.7$MPa and $P = 0.8$MPa. Cell B has $\pi = 1.5$MPa and $P = 1.0$MPa. Will water diffuse from Cell A to B, or B to A?

Answer: $\psi^*_A = 0.8$MPa P - 0.9MPa π = -0.1MPa ψ^*

$\psi^*_B = 1.0$MPa P - 1.5MPa π = -0.5MPa ψ^*

Since the ψ_B is more negative, water will move from Cell A to Cell B.

III. Practice Problems (Figure 3.10)

1. A cell with π = 0.8MPa is allowed to come into equilibrium with pure water. What will the ψ, π, and P of the cell be when it reaches equilibrium?

2. A chain of three cells are connected by their ends, and water is allowed to diffuse through them. The end of Cell A has been dipped into a sucrose solution with π = 0.2MPa.
Cell A π = 0.4; Cell B π = 0.3MPa; Cell C π = 0.6MPa.
What will the ψ ,π, and P of Cells A,B,and C be at equilibrium?

3. A root is in a soil with ψ_{matrix} = -0.2 and π = -0.05. What is the ψ^*_{soil} ?
Water in the xylem of this root is under a negative pressure (tension) P = -0.5, because of rapid transpiration.
The cells of the root cortex has P = 0.4MPa and π = -0.8MPa
Determine whether the ψ gradient from soil water to xylem sap is sufficient for soil water to enter the xylem.

4. A leaf has π = -1.5MPa. What is the maximum ψ_{soil} that this plant can extract without loosing turgor?

5. What is π of a solution consisting of 0.5 mols $CaCl_2$ in per kg water, assuming the $CaCl_2$ becomes 80% ionized?

IV. Imbibition

Imbibition is a special case of matrix potential. The term is used to express the attraction that substances such as seeds and wood have for water. The absorption of water by such substances is termed imbibition. Water that has been imbibed is held with considerable force. Water first absorbed is held with greater force than that absorbed later, as the distance between the absorbing surface (or diameter of capillary space) increases. The process of imbibition causes the imbibant to swell, and there is a liberation of detectable heat (why?).

Stone cutters have used imbibitional forces to split rock by driving dry wooden wedges into cracks and then filling the crack with water. The swelling wood can crack rocks. Similarly, seeds absorb water and hold it with considerable force, swelling enough to rupture hard ground.

Practice Problem 6. Bean seeds were immersed in a graded series of sucrose solutions, and it was found that water was imbibed in lesser amounts from solutions as the concentration increased until the seeds were placed in a sugar solution containing 4 mols sugar kg^{-1} water. What is the imbibitional potential of the bean seeds? (Hint: use the relationship of 1 mol kg^{-1} exerts π = 2.25MPa even though this relationship is unlikely at such high concentrations.)

Additional Reading:

Kramer, P.J. 1983. Water Relations of Plants. pp 46-53
Salisbury, F., and C. Ross. 1985. Plant Physiology. pp 33-49
Taiz, L., and E. Zeiger. 1991. Plant Physiology. pp 68-79

Answers to Problems

1. The cell will come into equilibrium at $\psi = 0$.
Since it has $\pi = 0.8\text{MPa}$, P must also = 0.8 MPa.

2. All three cells will come into equilibrium with the solution into which Cell A was placed, namely with $\psi_{\text{solultion}} = -0.2\text{MPa}$. For the different cells:

General Equation
$P = \psi - \pi$

Cell A $0.2\text{MPa}P = -0.2\psi - (-0.4\pi)$
Cell B $0.1\text{MPa}P = -0.2\psi - (-0.3\pi)$
Cell C $0.4\text{MPa}P = -0.2\psi - (-0.6\pi)$

3. a. $\psi_{\text{soil}} = -0.2\psi_{\text{matrix}} + (-.05\pi) = -0.25$
b. $\psi_{\text{xylem}} = -0.5\ P = -0.5$
c. $\psi_{\text{cortex}} = 0.4P + (-0.8\pi) = -0.4$
A ψ gradient exists from soil, across cortex, to xylem, and water should flow in response to that gradient.

4. -1.5MPa

5. (0.5)(3)(2.25)(0.8) = 2.7MPa

6. (4)(2.25) = 9MPa

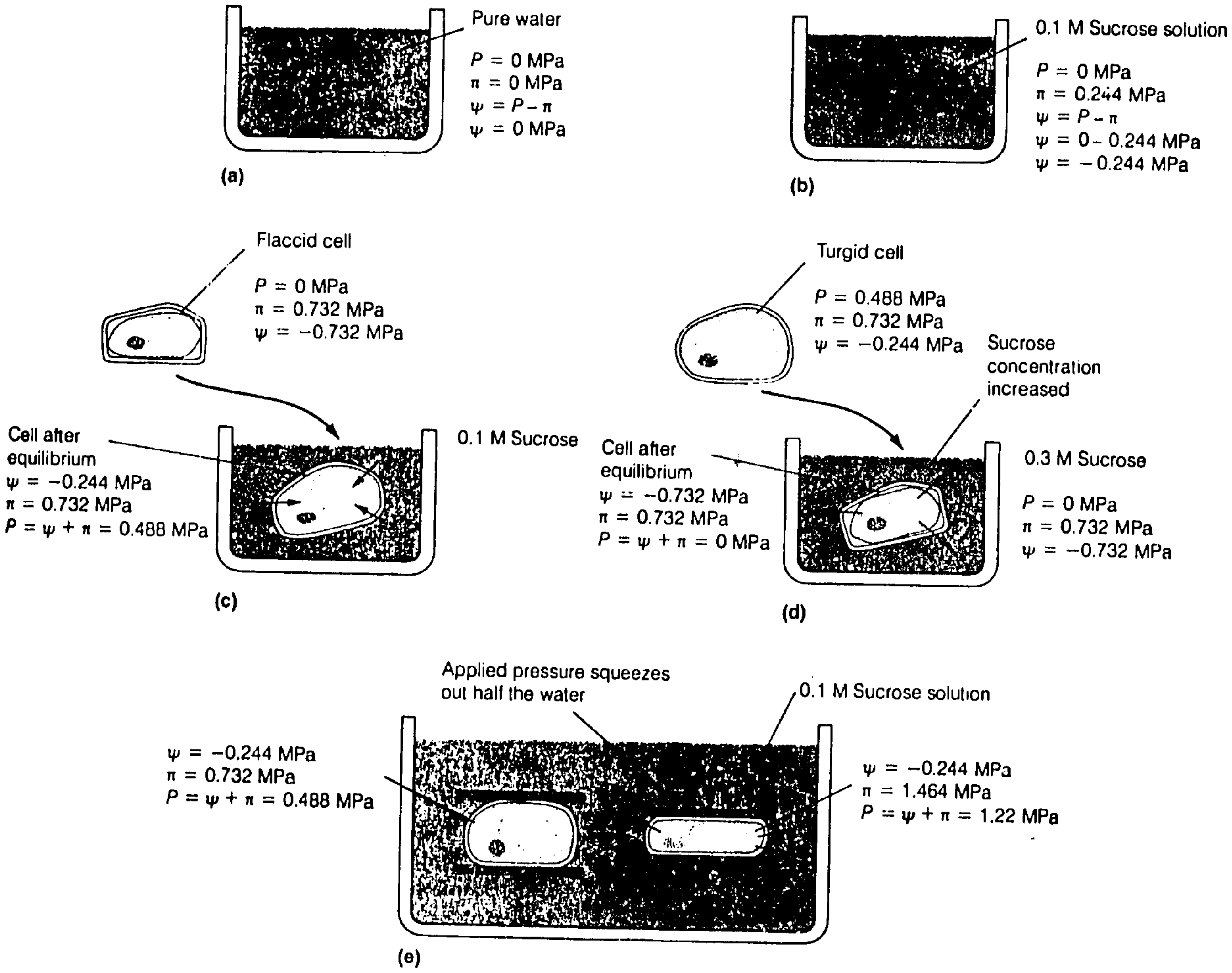


FIGURE 3.10. Five examples to illustrate the concept of water potential and its components. In (a), the water potential and its components are illustrated for pure water. (b) shows a solution containing 0.1 M sucrose. In (c), a flaccid cell is dropped in the 0.1 M sucrose solution. Because the cell's starting water potential is less than the solution water potential, the cell takes up water. After equilibration, the cell's water potential rises to equal the water potential of the solution, and the result is a cell with a positive turgor pressure. (d) illustrates how the cell is made to lose water by increasing the concentration of sucrose in the solution. The increased sucrose concentration lowers the solution water potential, draws out water from the cell, and thereby reduces the cell's turgor pressure. Another way to make the cell lose water is by slowly pressing it between two plates (e). In this case, half of the cell water is removed, so cell osmotic pressure doubles and turgor pressure increases correspondingly.

LESSON FIVE

PRECIPITATION AND WATER CYCLE

By the end of Lesson Five you should be able to:

....Describe the cause of precipitation and the three major ways in which the causative factor occurs
....Describe the effect of season of precipitation on vegetation
....Explain how type, duration, and intensity of precipitation influence precipitation effectiveness and vegetation
....Describe the fate of precipitation with respect to interception and redistribution
....Give examples of the effect of vegetation on precipitation
....Summarize the role of precipitation in the water cycle by identifying precipitation sources, fates of water striking plants, routes of water flow overland and underground, and the eventual return of water to water bodies or ground water recharge.

PRECIPITATION AND THE WATER CYCLE

I. The Cause of Precipitation

The major source of the water vapor in the atmosphere is evaporation from large water bodies, principally the oceans. In the equatorial regions especially, intense solar radiation warms the atmosphere and evaporates enormous amounts of water from the oceans. This warm, humid air rises, and in doing so cools, condensing into clouds, and if cooled enough, precipitation occurs. Rainfall is heavy over the tropics for this reason.

These warm, humid, tropical air masses arise as cells which flow as a mass north and south of the equator. Some of these masses are spun off their polar routes by the earth's rotation, causing them to travel westward over land masses. If these humid masses encounter heavy, high pressure, cold air masses, the low pressure warm air tends to over ride them, gaining additional altitude, cooling further, and precipitation occurs. These types of storms are termed frontal or cyclonic systems.

The westward movement is confounded by the monsoons, but essentially the same process occurs in which warm, humid air masses from the seas are thrust into high elevation, either by over riding heavy cool air masses, or by convection from air rising from hot land surfaces.

At about 20 - 30 degrees north and south latitude (the horse latitudes) cells of surface air flow back toward the equator to replenish air that arose because of equatorial heating. This causes atmospheric air cells to descend over the horse latitudes, completing the circulation of the cell which rose because of heating over the equator, spread north or southward, and descended at the horse latitudes, then returned to the equator.

Air warms as it descends. The air's capacity to hold water increases as it warms, discouraging precipitation, and thus the great deserts and arid regions occur in the horse latitudes around the world.

Warm, humid air masses may be forced to higher, cooling elevations by two other means. If such air masses are forced against mountains the air mass rises, cools, and precipitation generally occurs on the windward side of the mountain system. As this same air descends on the lee side it is drier, having lost water on the windward side, and is warmed by descending into higher pressure, thus its capacity to hold water increases. Lee sides of mountains are in the "rain shadow" for this reason. Mountain system cooling causes **orographic** precipitation. The cooling process is termed adiabatic cooling, and amounts to about 1 degree $100m^{-1}$. (See Figure 19-3)

In the summer air is heated near the ground, becomes lighter, and rises. If water vapor is added such as by transpiring plants, the water vapor rises with the air mass, cools, and if it rises high enough, condenses to form clouds. The heat of condensation can cause the air mass to warm and continue to rise forming the tall, cumulus clouds of summer. This is termed convectional precipitation, and it essentially recycles past cyclonic precipitation in place.

II. Season of Precipitation Occurrence

In a few climates precipitation is distributed evenly throughout the year, but in most climates it is seasonal. The season of occurrence affects vegetation, depending whether it occurs during or outside the growing season.

Both the northeast and northwest sections of North America receive about 100 cm yr^{-1} precipitation. In the northeast it occurs primarily during summer, and the forests are mostly deciduous broadleaves such as maple, hickory and oak. Because broadleaves display such a large leaf surface to gather sunlight they are quite productive, but also would heat if not provided water for transpirational cooling. They occur in the northeast because the summer rains supply this requirement.

In the northwest most precipitation occurs during winter. The forests are the more xeric conifers, because the summers are arid even though annual precipitation is similar to the northeast. (See Figure 19-7)

Seasonal variations may also cause substantial changes in productivity. For example, in Nepal the monsoon usually begins in mid-June. In some years the monsoon is delayed to early or mid-July. When the delay occurs rice production is markedly reduced because the final, enlarging grain development occurs in the cooler, shorter photoperiod of September instead of August.

III. Types, Duration, and Intensity of Precipitation

Precipitation may occur as rain, snow, drizzle, fog, hail, or dew. There may be variations over space of the amount of rain, and especially snow fall. These are generally caused by wind. The crown of an exposed tree will intercept more rain than a tree inside the forest because wind causes the rain to fall at an angle. Snow will be deposited deeper in a clearing than in the forest because of wind turbulence over the clearing.

Snow may also cause mechanical damage to trees if their shape does not allow snow to shed, or if they have retained snow-collecting large leaves. Hail may also cause extensive injury to plants, even causing bark wounds on some thin barked trees.

Fog is an important source of moisture for some forests, especially in coastal regions. The crowns of such trees are generally cooler than oceanic air, either because the land mass is cooler, or the crowns have been cooled by nocturnal re-radiation to space. When warm, foggy air encounters these cool surfaces the fog condenses and drips off the crown to the ground below. (See Table 5-A)

Some species of desert plants appear to absorb dew into their leaves. Dew formation in the desert occurs because strong, nocturnal radiational cooling of surfaces causes condensation, even of air of low daytime humidity.

Slow drizzles are generally more effective forms of precipitation than brief intense storms because less of the precipitation is lost by evaporation, interception, and runoff.

IV. Fate of Precipitation

A. Interception. The crowns, branches, and leaves of plants intercept precipitation to varying amounts depending upon their geometry. A broad, spreading crown intercepts more than the conical, tapered crown. (See Figure 5 B)

Forests and individual trees have an interception storage capacity, and this capacity must be filled before precipitation can fall through the canopy to the ground. Examples of interception storage include snow on branches, water films on leaves, stems, and bark, and water droplets on leaves and in needle angles. (See Table 5 -1, 5 - 2)

An important aspect of interception is that foliage and stems absorb the impact of falling rain. Even though the force of each raindrop is hardly significant, the accumulation of millions of drops, if allowed to fall on bare ground, is sufficient to compact the soil so that water infiltration is reduced and the water either evaporates from the surface or runs off without penetrating into the soil.

B. Redistribution. Although precipitation may fall evenly over the forest canopy, as soon as it strikes the crowns it is redistributed. Some of the precipitation is intercepted, some is throughfall, and another amount may be directed toward the stem by the geometry of leaves and branches. Precipitation is focused to stemflow by trees with spreading, upturned canopies such as palms. Palms and other trees with upturned canopies generally have taproot systems and stemflow is directed to them.

Other trees have a geometry that directs precipitation to flow across the crown and fall at the canopy edge. The most active root systems of these trees are located just below the projection of the canopy rim, and they tend to be more spreading.

C. Infiltration into the soil

D. Transpiration (see Figure 19-14 and Table 11.5)

V. Contribution of Forests to Atmospheric Water Vapor and Desertification

About 20% of the global water vapor in the atmosphere is the result of evapotranspiration from forests. It has been estimated that 70% of the precipitation in North America originates from water vapor transpired from forests. Deforestation removes the plant water system that pumps water from the soil into the atmosphere, and therefore it reduces rainfall because there is less water vapor in the atmosphere.

Deforestation is an important component of desertification. Once the process of desertification commences it is difficult to reverse. The climate becomes too arid for tree growth, soils become compacted because of the absence of foliage to intercept the impact of raindrops, runoff increases as a result of soil compaction, thus less water infiltrates into the soil, and this compounds the reduced precipitation. This process is believed to be the cause for the expansion of the Sahara desert by steppe woodland removal by grazing and fuel wood extraction.

The deforestation of the Amazon rain forest is of global concern not just because of the loss of species by extinction from this special habitat, but because the humid, tropical forests contribute about 50% of the water vapor from evapotranspiration that falls as precipitation. This means that about one-half Amazonian precipitation originates from water vapor transpired into the atmosphere, and not from oceanic sources. Loss of the enormous component of transpired water vapor in this huge ecosystem could affect continental if not global climates if the Amazon were deforested.

Deforestation can also cause forests to convert to marshlands in the high latitudes where precipitation equals or exceeds evapotranspiration potential. After World War II Russia imposed a heavy war damages debt upon Finland that required Finland to log extensive areas of forest to obtain funds for debt payment. After tree removal transpiration ceased, and the water table rose to the surface. Most tree seedlings cannot tolerate flooded soils, so attempts at regeneration failed. Some of these lands were eventually reclaimed at great cost by installing drainage canals to lower the water table enough to allow the seedlings to establish.

VI. The Water Cycle.

Examine Figure 5-C in order to familiarize yourself with the inputs of water to the atmosphere from water bodies, evaporation from interception and surfaces, and transpiration; precipitation as rain, snow, fog, and rime (water deposits as ice on very cold surfaces); runoff and evaporation from soil surfaces; infiltration into the soil, to perched water tables and to deep seepage, and into the ground water table which may recharge streams and lakes by seeps and springs. Each aspect of the water cycle will be discussed in future lessons.

<u>Additional Reading:</u>

Kimmins, J. P. 1987. Forest Ecology. pp. 263-270

Spurr, S. H. and B. V. Barnes. Forest Ecology. pp. 155-162;

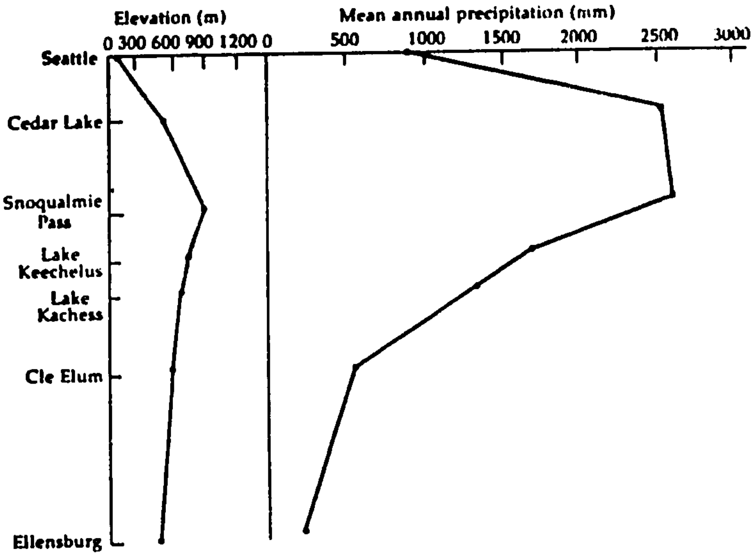


Figure 19-3 Precipitation along a cross section of the Cascade Range in the vicinity of Snoqualmie Pass, Washington (47° 25′ N. lat.); the distance from Seattle to Ellensburg is approximately 152 km. (From Franklin and Dyrness 1969, *Natural vegetation of Oregon and Washington*, U.S. Dept. of Agriculture Forest Service Research Paper PNW-80.)

Note the heavy windward precipitation and the lee side rain shadow

Figure 5-A Fog Drip Under Vegetation at 1783 m Elevation on Mt. Wilson, California (Data from Kittredge, 1948)

Vegetation Type	Precipitation Beneath the Vegetation, cm	Fog Drip, cm
Open (no vegetation)	58	0
Shrubs:		
Ceanothus sp., 2.4 m tall	58	0
Trees		
Canyon live oaks, 13.7 m tall	121	63
Pseudotsuga macrocarpa, 12.2 m tall	122	64
Pinus ponderosa, 24.4 m tall	154	96

Table 5-1 Annual Percent Interception Loss in Various Different Mature Forest Types in the U.S. (Data from Kittredge, 1948)

Forest Type	Location	Interception, %
Mature hardwoods	S. Appalachian Mts.	12
Oak-pine	New Jersey	13
Quaking aspen	Colorado	16
Ponderosa pine	Idaho	22
Lodgepole pine	Colorado	32
Douglas-fir	Washington	34
Ponderosa pine	Arizona	40
Maple-beech	New York	43
Eastern hemlock	Connecticut	48

Table 5-2 Effects of Stand Age and Tree Spacing on Interception Loss

	Age, yr	Interception Loss, cm	Interception, %
Eastern white pine, S. Appalachian Mts.[a]	10	30.5	15
	35	38.1	19
	60	53.3	26
	Spacing Stems/ha		
Douglas-fir, 18 yr old, Coastal British Columbia[b]	10,000	12.7	15
	3,000	19.5	23
	1,370	20.4	24
	730	22.0	26

[a] The data for white pine are for annual interception losses (Kittredge, 1948).
[b] The data for Douglas-fir apply to an 8-month period, May–December (Kimmins, unpublished data).

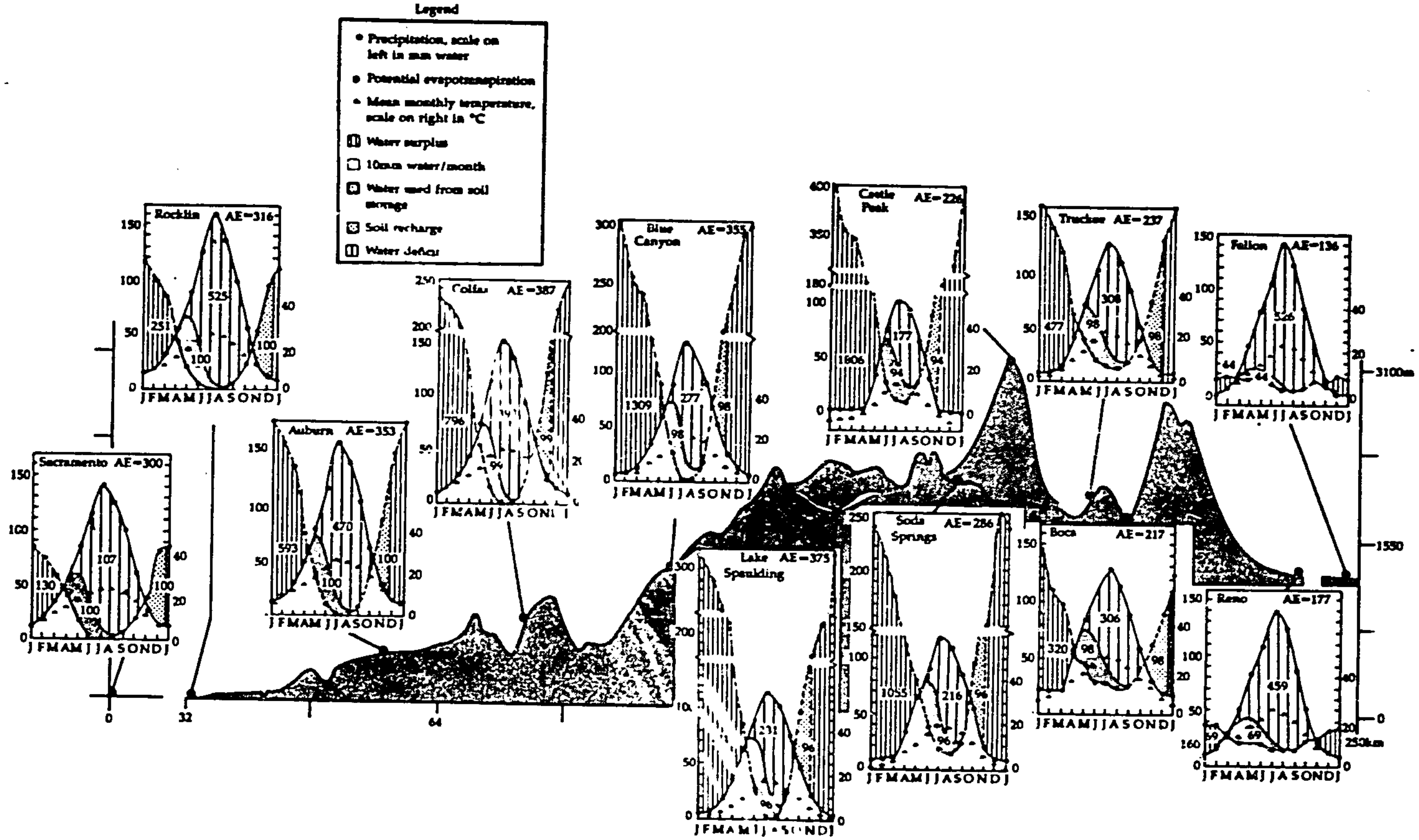


Figure 19-7 A transect over the Sierra Nevada from Sacramento (38.5°N), over Donner Summit (39.3°N), to Reno and Fallon, Nevada (39.5°N), showing water balances. Vertical exaggeration 14.5×. (From Major 1977. In *Terrestrial Vegetation of California*.

Note the heavy winter precipitation (snow) in the mountain stations (e.g. Lake Spaulding, Castle Peak), but still these stations have a water deficit in mid-summer. Also note periods of soil water use and re-charge. Reno is in the desert.

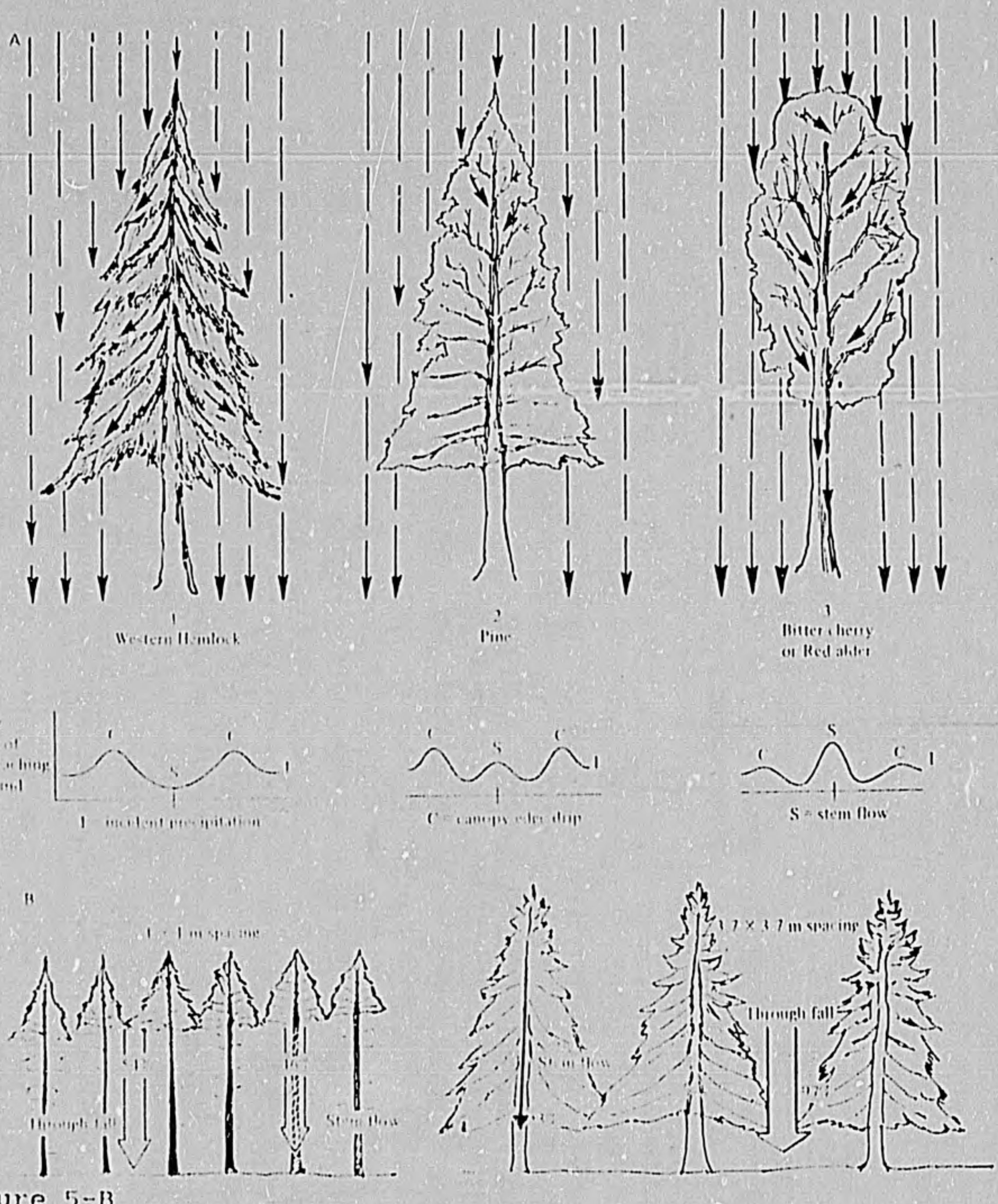


Figure 5-B

Effect of variation in crown morphology and stand density on the relative importance of stemflow and throughfall. (A) Tree species with pendulous branches tend to have little stem flow and redistribute much of the precipitation into canopy edge drip. Species with erect or acute angled branches have much more stemflow and less canopy drip. (B) The closer the spacing in a stand, the higher the proportion of acute angled branches and the greater the importance of stemflow: data from an 18 year old Douglas fir plantation.

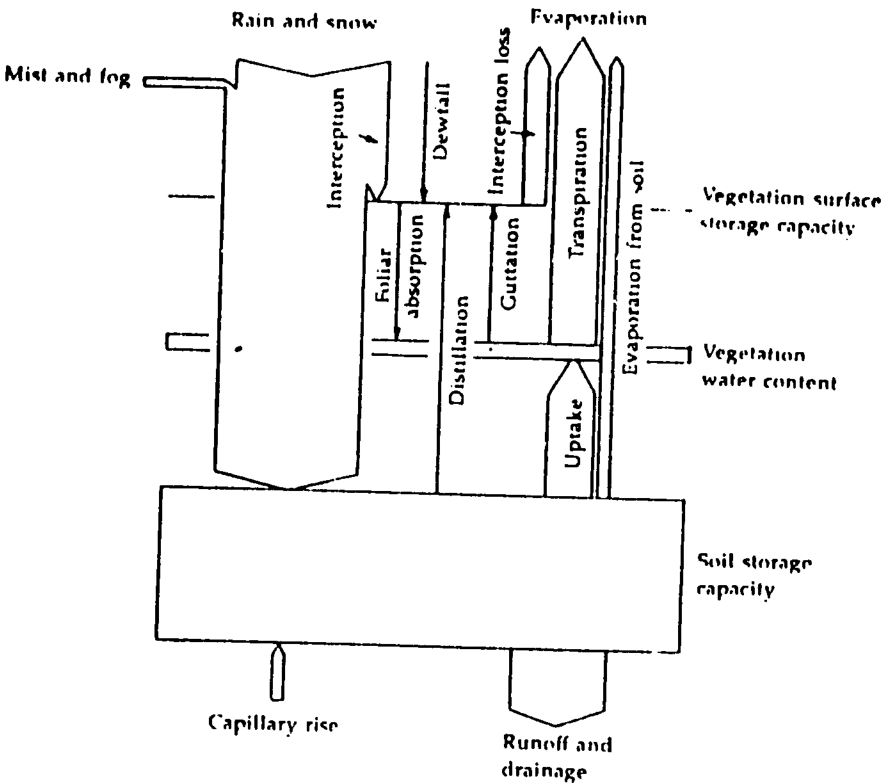


Figure 19-14 Diagram summarizing the hydrological cycle in a vegetation-soil system; the components are approximately to scale for an annual rainfall of 1000 mm and evaporation of 500 mm. (Guttation is the exudation of liquid water from leaves.) (From Rutter 1975. "The hydrological cycle in vegetation" in *Vegetation and the Atmosphere*, vol. 1, ed. J. L. Monteith. By permission of Academic Press, London.)

Table 11.5 Utilization of Water by Forests in Various Parts of the World (After Rutter, 1968)

Forest Type	Annual Precipitation, cm	Annual Evapotranspiration Loss		Growing Season Soil Water Deficit
		cm	%	
Northern taiga conifer forest, USSR	52.5	28.6	54	Negligible
Southern taiga conifer forest, USSR	60.0	32.9	55	Negligible
Spruce stand, Great Britain	135.0	80.0	59	Negligible
Mixed conifer and deciduous stand, Switzerland	165.0	86.1	52	Negligible
Mixed conifer and deciduous stand, N. Japan	261.7	54.2	21	Negligible
Evergreen rain forest, Kenya	195.0	157.0	81	Small
Deciduous forest, European USSR	45.7	42.4	93	Moderate
Coulter pine, California	123.0	63.7	52	Severe
Ponderosa pine,	126.0	58.0	46	Severe

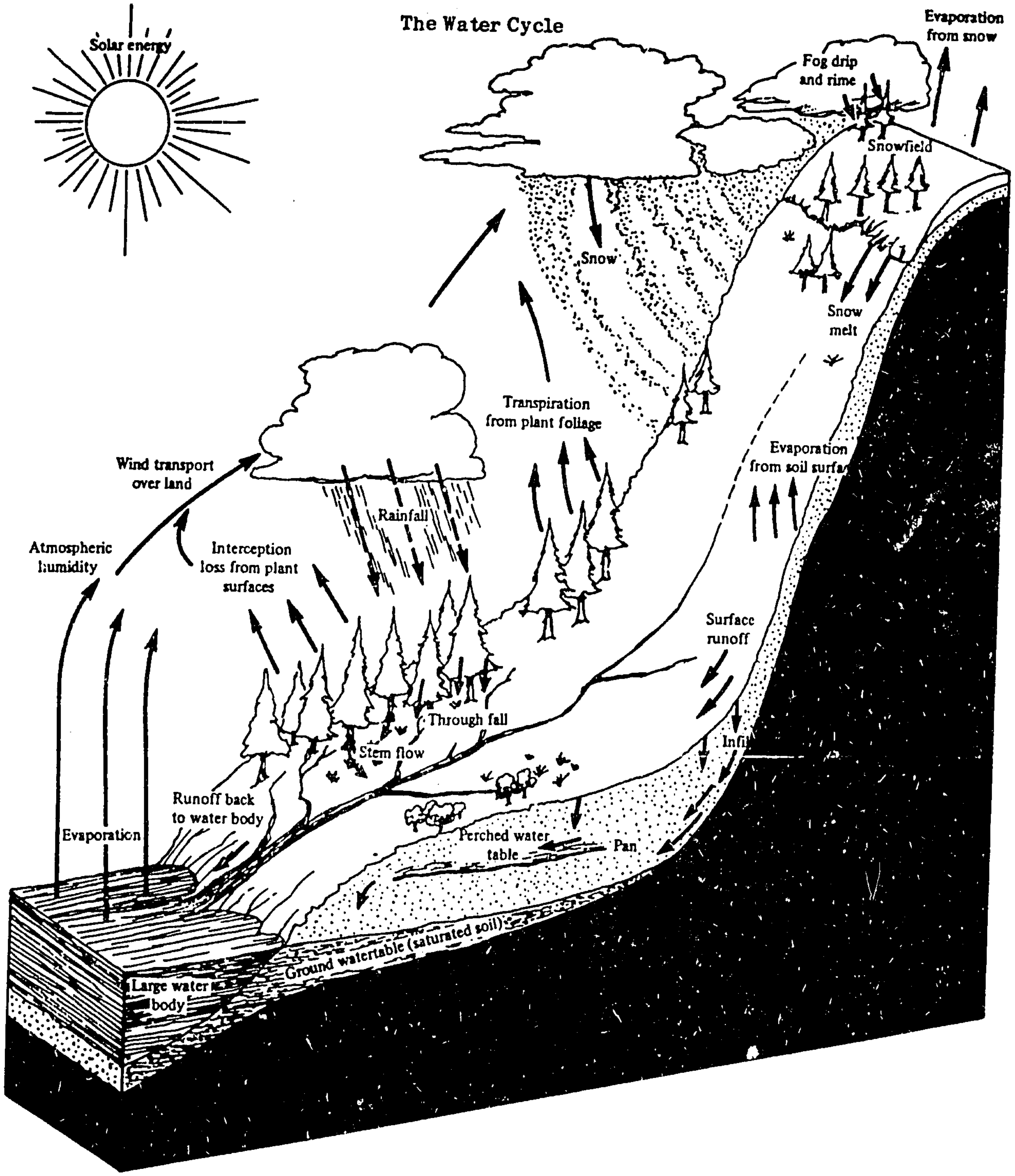


Figure 5-C
Diagrammatic summary of the major components of the water cycle. This cycle is driven by inputs of solar energy that generate evaporation and atmospheric stirring.

LESSON SIX

SOIL AS A MEDIUM FOR PLANT GROWTH, AND HOW WATER OCCURS IN SOIL

By the end of Lesson Six you should be able to:

....List the functions of soil with respect to plants
....Describe the factors that affect the ability of the soil to anchor plants
....List the factors that affect soil fertility
....Describe soil pore space
....Define the forms of water in the soil
....Describe the factors that affect the ability of the soil to store water

SOIL AS A MEDIUM FOR PLANT GROWTH, AND HOW WATER OCCURS IN THE SOIL

I. Functions of the Soil for Plant Growth

The soil serves three main functions in plant growth: to anchor the plant; to serve as a reservoir and supply of mineral nutrients; and to provide a water supply and reservoir.

II. Factors affecting the ability of the soil to anchor plants

A. Soil texture

Sandy and gravelly soils with little internal cohesion may not provide a good anchoring medium. Soils on steep slopes that are subject to plastic flow may disrupt rooting and also provide poor anchorage.

B. Soil depth

Shallow soils underlain by a hard pan or rock, or effectively shallow because of poor root growth may provide poor anchorage. Root growth may be restricted to surface layers by poor aeration caused by water saturation.

C. Plant characteristics

1. Genetic. Species differ in their rooting patterns, and this affects how well anchored they are. Some species develop shallow, spreading roots, others taproots, others deep spreading roots, and still others have little root development.

2. Environment. The environment in which a plant develops affects rooting. Trees that develop in the shade generally have less root development than tress that develop in open sunlight. Trees that develop as members of an even age stand have less root development than those that develop individually. These environmental factors become apparent after a forest is clear cut when windthrow of trees at the boundary of the cutting block may occur because such trees are often shallow rooted having developed as members of an even aged stand or in the shade.

III. The Soil as a Mineral Nutrient Reservoir and Supply

A. Parent Material

The ability of the soil to supply minerals depends in part upon their parent material. Residual soils that developed in place from granitic rocks tend to be less fertile because of low base ion (e.g. Ca, Mg) content of granitic rocks. Soils that develop from calcareous rocks and basalt tend to be more fertile because of the high base ion content of these rocks.

Most soils have not developed in place, but on parent materials that have been transported by wind (loess, dunes), gravity (colluvial), water (alluvial), ice (moraine, till), lake bottom (lacustrine), or ocean bottom (marine). The mineral supplying power of these soils is a composite of the mixture of transported parent materials.

B. Soil depth

The actual or effective (e.g. limited by water table,etc.) soil depth and root penetration throughout the soil determines the volume of soil available to the plant. The greater the soil volume occupied by roots the greater the minerals available.

C. Exchange Capacity

Cations such as K^+, Ca^{++}, and Mg^{++}, are prevented from being leached from the soil by being attracted to clay particles and organic matter. Clay, and to a lessor extent organic matter, possess a cation exchange capacity (Table 3.1). That is, they can bind one ion, but this ion can be exchanged for another, e.g., a H^+ can replace a K^+ bound on the exchange complex. Although the chemistry of cation exchange is beyond the content of these lessons, it should be recognized that the greater the clay content the greater the ability of the soil to store mineral nutrients by preventing them from being leached, and the more fertile the soil. Thus, loam soils are more fertile than sandy soils.

D. Organic Matter

The organic matter in the soil functions as a reservoir of minerals that is made available for absorption after organic matter decomposition.

E. Decomposition Rate

The rate of organic matter decomposition varies greatly with climate and vegetation type. In grasslands decomposition of organic matter to humus is rapid, but the decomposition of humus less so. The dark color of grassland soils is due to their high humus content.

Organic matter decomposition in humid tropical forest soils is so rapid, and leaching so intense, that the nutrient cycle requires minerals be transferred back into twigs efficiently before the leaf fall. Mycorrhizae fungi at the soil surface absorb the minerals released by decomposition within a few centimeters of the surface before the minerals can be leached.

The litter of conifers tends to be acidic and contain tannin, terpene, resins, and other substances that resist bacterial decomposition. The cool climate and short growing season where some of these species are found in also discourages bacterial activity, so much of the decomposition is by less efficient fungi. As a result minerals remain in the undecomposed litter. This is a transfer of the mineral capital of the forest soil to soil litter, where it no longer is available for nutrient cycling, and the forest soil fertility is reduced as a consequence.

A common way in which these minerals are leased is by fire. Burning removes the acidity and antibiotic chemicals, encouraging bacterial activity on the remaining organic matter, and releasing "pot ash" by fire. Ash contains inorganic minerals that are available for absorption by roots.

IV. Characteristics of Soil

Soil includes four major components: the mineral or rock material plus the non-living organic matter that forms the solid matrix of the soil; the soil solution and the air that occupies the pore space; and the living organisms - bacteria, fungi, algae, protozoa, insects, small animals, and living roots that give soils their special characteristics.

The pore space is an important characteristic of soils. This space is continuous, but geometrically complex. In saturated soils it may be water filled, and in dry soils air filled. Pore space occupies 30% - 60% of soils. At field capacity, i.e. filled with the amount of water the soil can hold against gravity, 40% - 60% of the pore space is water filled.

More important than total pore volume is the portion of pores that are of capillary dimensions in the soil compared with larger pores. The portion of pore space of capillary dimension (30-6-um or less) determines the amount of water available to plants. Capillary pores hold water at a potential of -1.5MPa or less, and this is available for plant absorption (Fig. 3.4).

The soil atmosphere must contain a substantial amount of oxygen and low CO_2 for root growth, mineral, and water absorption. These conditions are maintained by exchanges between the soil atmosphere and the air. Good soil aeration is promoted by large pore spaces, absence of surface compaction, and periodic flushing from downward moving water fronts.

Soil texture is defined by the portions of sand, silt and clays in the soil (Fig.3.3). Sand, silt, and clay are defined by their size (Table 3.1). The least complex soil is a sand, which contains less than 15% silt and clay. Sandy soils have good drainage and aeration because of the large portion of large pore spaces, but sandy soils have a much lower capacity for wate storage because of few capillary spaces. In contrast, clay soi have a large portion of capillary pore spaces, a large capacity for water storage, but may have poor drainage and aeration because of the absence of large pore spaces. A good soil for root growth and water retention has pore space about equally divided between small capillary and large non-capillary spaces.

V. Forms of Water in the Soil

The water content of a soil is measured as the amount of water lost when the soil is dried at 105º. Water may occur in soils in three forms:

A. Gravitational water

Gravitational water moves down through the soil in response to gravity. If a soil is flooded with 3 cm of water, a wetting front will move through the soil in large pores to a depth of about 20 cm, filling capillary spaces as the front moves. There are enough capillary spaces in a common soil to absorb 3 cm of water in 20 cm of soil, so when the wetting front reaches the

20 cm level, no further downward movement occurs because all of the gravitational water has been used to fill capillary spaces.

B. Capillary water

Capillary water is held in the soil at tensions greater than -0.03MPa, the approximate force of gravity.

C. Unavailable water

Unavailable water occurs as a film on colloidal and larger particle surfaces (hygroscopic water), or in capillary pores so small that it is held at forces greater than -1.5MPa. Some plants, especially some that occur in arid regions, can extract water unavailable to crop species, but as each component is removed at one force, e.g. -2.0MPa, the water remaining is held at nearly exponentially increasing force (Fig. 10.2)

D. Available water

Available water is that portion of soil water held against gravity at a force greater than -0.03MPa, but less than -1.5MPa, the generally accepted permanent wilting percentage for crop species.

Soils differ in Water Holding Capacity (WHC). Most of the difference can be accounted for by soil texture and the organic matter content of the soil. Soil texture determines the distribution of pore sizes. Sandy soils contain large pore spaces, and most of the water that falls on sandy soils percolates through it as gravitational water. Clay soils, at the opposite extreme, contain a large portion of capillary spaces, and thus have a high water holding capacity. Clay soils also have a large portion of capillary spaces so small that the water is unavailable (i.e. held at tensions greater than -1.5MPa), and a large amount of water still remains in such soils after plant roots have extracted all that they can. Soil organic matter also contains a large amount of capillary space which can act as a sponge in soaking up and maintaining water for future plant absorption.

VI. The Development of Soils

Soils development is determined by climate and the type of vegetation that occurs on them, and it is recognized by the appearance and type of soil horizons that develop. Figure 10.15 illustrates the soil development processes that typically occur in coniferous forests such as blue pine forests in Pakistan. The Ac horizon in this figure is typical of a coniferous forest podzol soil. It develops because coniferous litter is slow to decompose and acid, and leaches iron and aluminum from the Ac horizon to the B horizon, where it is deposited. The other major soil groups that occur in Pakistan are laterites of hot regions, and the pedocal and desert soils of arid regions.

Additional Reading:

Kramer, P. J. 1983. Water Relations of Plants. pp. 57-69.

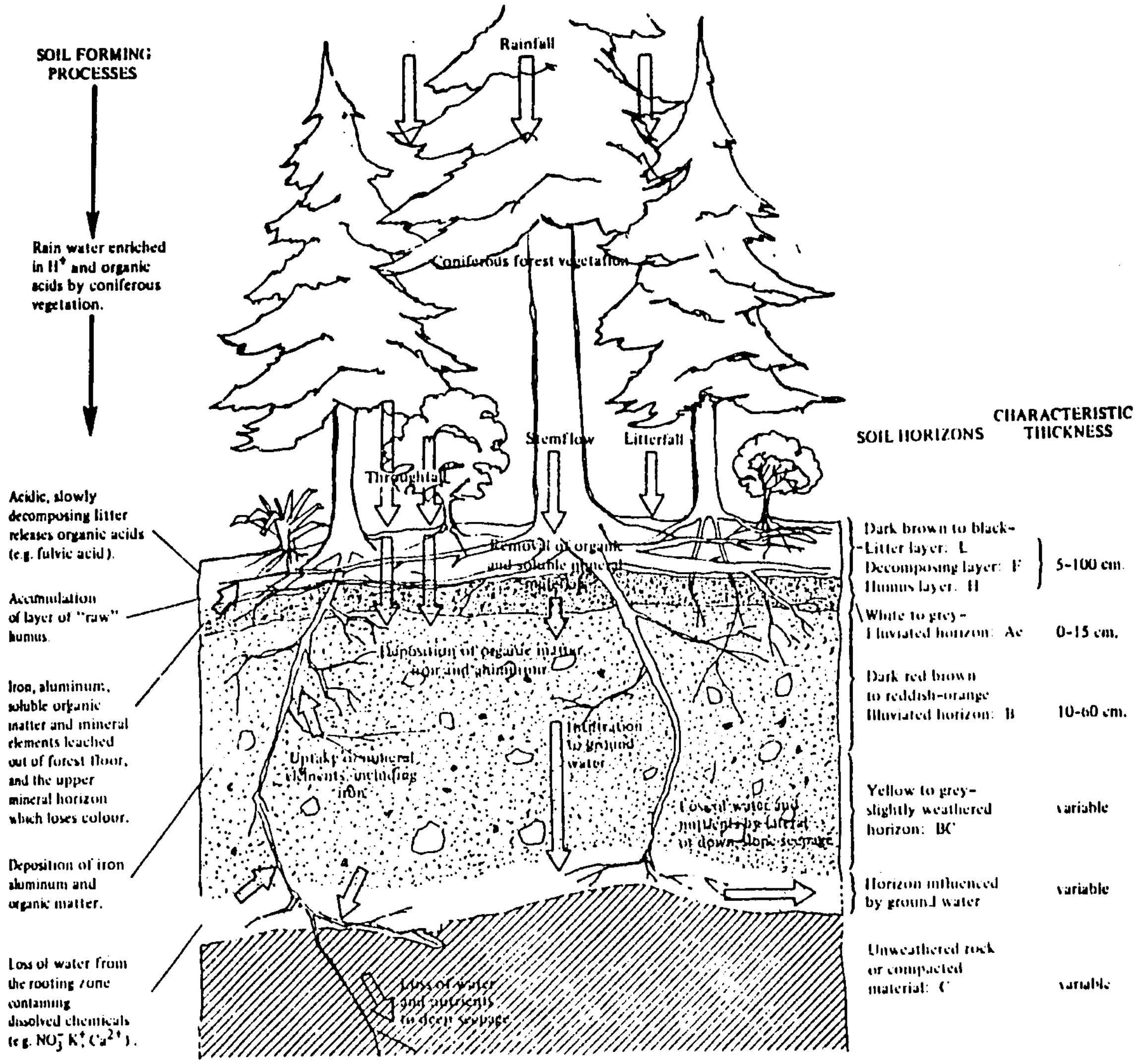


Figure 10.15
Characteristic major horizons and soil-forming processes of a typical coniferous forest podzol, a pedalfer type of soil. (After Clarke, 1967. Copyright 1967 by John Wiley & Sons, Inc., New York. Used by permission.)

TABLE 3.1 Cation Exchange Capacity of Humus and Clay Minerals in Milliequivalents per 100 g Dry Soil[a]

Vermiculite	160
Humus	100–300
Montmorillonite	100
Illite	30
Kaolinite	10

[a] From data of Thompson (1952).

TABLE 3.2 Classification of Soil Particles According to the System of the International Society of Soil Science, and Mechanical Analysis of Three Soils[a]

Fraction	Diameter (mm)	Sandy loam (%)	Loam (%)	Heavy clay (%)
Coarse sand	2.00–0.20	66.6	27.1	0.9
Fine sand	0.20–0.02	17.8	30.3	7.1
Silt	0.02–0.002	5.6	20.2	21.4
Clay	Below 0.002	8.5	19.3	65.8

[a] Lyon and Buckman (1943, p. 43).

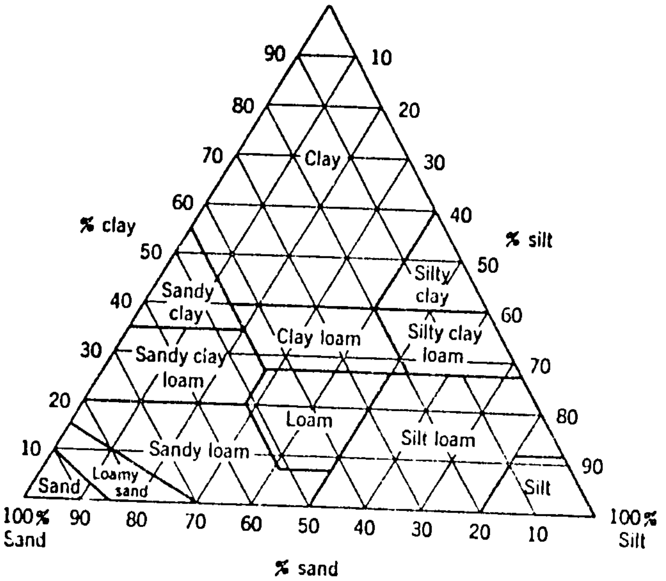


Fig. 3.3. Diagram showing the percentage of sand, silt, and clay in various soil classes. (From *Soil Sci. Soc. Am. Proc.* 29, 347, 1965.)

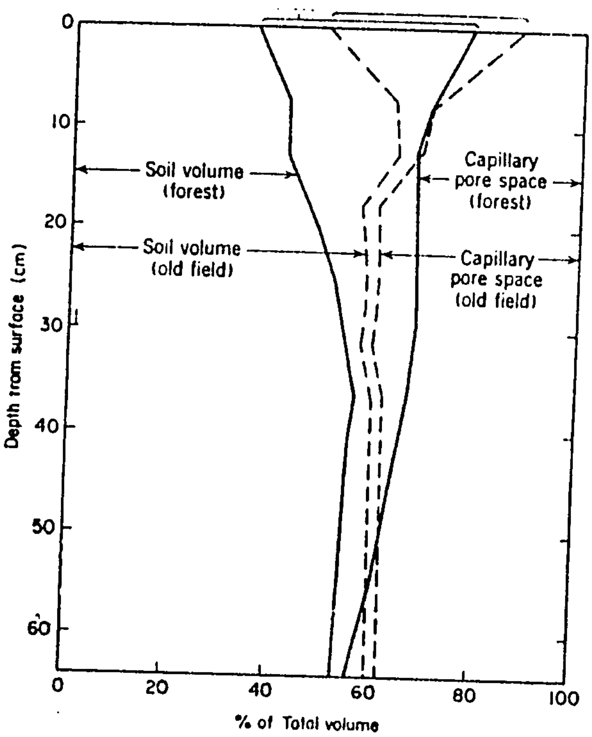


Fig. 3.4. Differences in amount of capillary pore space in an old field and in an adjacent forest on the same type of soil. The large percentage by volume occupied by noncapillary pore space in the forest soil provides better aeration for roots. It also increases the rate of infiltration, as shown in Fig. 3.13, and decreases runoff during heavy rains. (From Hoover, 1949.)

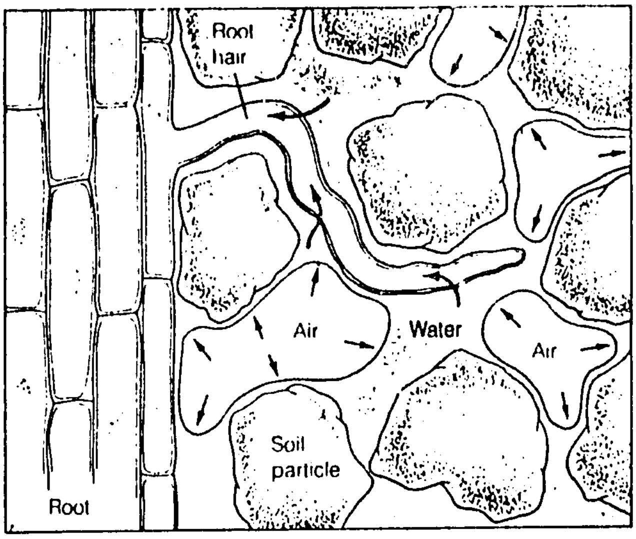


FIGURE 4.1. Root hairs make intimate contact with soil particles and amplify the surface area needed for water absorption by the plant. The soil is a mixture of particles (both mineral and organic), water, dissolved solutes, and air. As water is absorbed by the plant, the soil solution recedes into smaller pockets, channels, and crevices between the soil particles. This recession causes the surface of the soil solution to develop concave menisci (curved interfaces between air and water), which brings the solution into tension, or negative pressure, by surface tension. As more water is removed from the soil, more acute menisci are formed, resulting in greater tensions (more negative pressures).

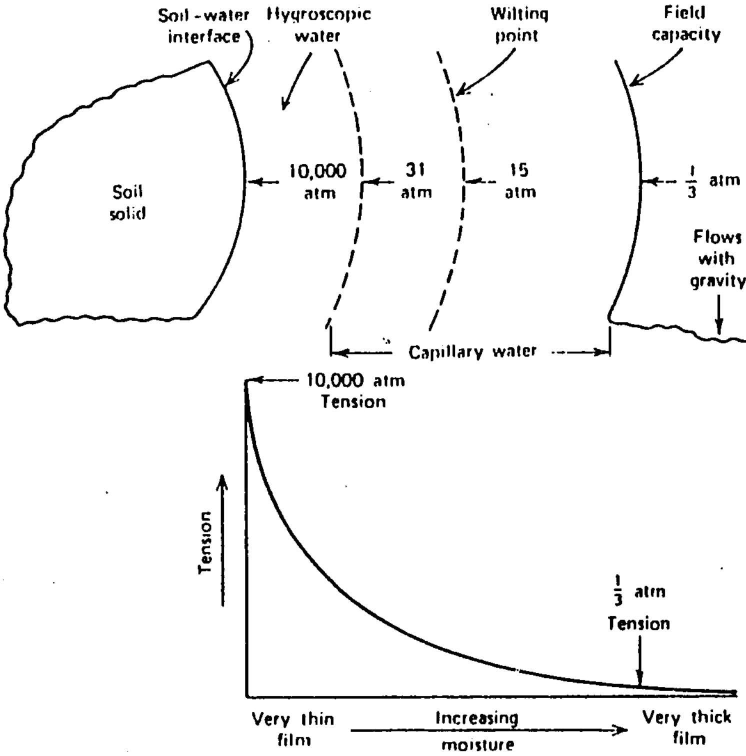


Figure 10.2. Diagrams showing relationship between thickness of water films and the tension with which the water is held at the liquid-air interface. The tension is shown in atmospheres. *(Upper)* Sketch of water film thickness at several moisture levels. *(Lower)* Logarithmic change in tension with increase in thickness of moisture film.

LESSON SEVEN

INFILTRATION, MOVEMENT, AND MEASUREMENT OF SOIL WATER

By the end of this lesson you should be able to:

....List the possible fates of a raindrop after it strikes the forest floor
....Describe the properties of the forest floor and the mineral soil that affect infiltration and water movement
....Describe the effect of compaction on infiltration
....List the results of poor infiltration
....List the factors that affect the movement of water in the soil
....Describe why the forest floor is sometimes disrupted to encourage tree seedling establishment
....Describe the effect of mulching on soil water
....Describe one method each for measuring soil water content, field capacity, permanent wilting percentage, available water, soil moisture tension, and salinity

INFILTRATION, MOVEMENT, AND MEASUREMENT OF SOIL WATER

I. Infiltration into the Forest Floor

Infiltration is the movement of water from the atmosphere into the soil. In forest soils the soil consists of two major components: the organic forest floor, and the underlying mineral soil.

The forest floor is composed of twigs, leaves, needles, rotting logs, etc, that are still recognizable. After decomposition the origin of the litter becomes unrecognizable. It is then termed humus, and becomes incorporated into the mineral soil.

Large pores and water holding capacity allow rapid movement and retention of water into the forest floor. The forest floor can hold one to five times its weight in water, and only after the water holding capacity of the forest floor has been saturated can water continue its downward movement into the mineral soil. It may take many weeks and many centimeters of precipitation for moisture recharge of the mineral soil following a prolonged dry period because of water retention in the forest floor.

Very little surface flow occurs across the forest floor. Such flow can occur on slopes or because needles or leaves have been arranged like roof tiles, but it is then for just a few cm or meters before the water forms pools in micro-depressions, behind logs, etc., allowing additional time for infiltration.

The presence of the forest floor prevents the soil from becoming compacted or forming surface crusts. The impact of raindrops on mineral soil is the most common cause of compaction, but it can also be caused by trampling, harvesting, and grazing.

There is one instance in which the forester may wish to disrupt the forest floor temporarily, and that is when the forest floor interferes with tree seedling establishment. Because of the large water holding capacity of the forest floor, it may become wetted while the underlying mineral soil remains dry. In such a case the roots of tree seedlings may grow entirely in the forest floor, never tapping the large water reservoir that occurs after the mineral soil becomes recharged. Because the forest floor is porous it dries quickly, often killing the tender roots of young seedlings. For this reason seeding is often more successful when placed directly on the mineral soil. However, if the forest floor is disrupted, additional measures should be taken to reduce erosion.

II. Infiltration into Mineral Soil

Infiltration into the mineral soil is affected by soil texture, structure, root channels, capillary pore size, and the permeability of the soil surface. (Fig. 4.1)

Soil texture, the proportions of sand, silt, and clay in the soil, determines the size of pores in the soil. In sandy and gravelly soils infiltration is very rapid as is water movement through the soil because the pore sizes are large. In clay soils initial infiltration is rapid because the small capillary pores have a high attraction for water, but movement is slow for the same reason.

Soil structure is important to good infiltration and water movement. Structure refers to the aggregation of soil particles into clumps or crumbs. When crumbs are formed, water and root penetration occurs with ease, as does good soil aeration. Crumb structure is affected by the ratio of calcium and sodium in the soil; calcium dominated soil aggregates into crumbs, whereas the clays of sodium dominated soils remain dispersed. Compaction and plowing cause the crumb structure to deteriorate.

The large pores created by root channels and animal burrows also encourage rapid infiltration into the mineral soil.

Recall that water will rise in a glass capillary tube of 1 mm diameter or less, and that the smaller the diameter the higher the water will rise in the tube. The alignment of sand, silt, and clay particles in the soil forms many spaces of capillary dimensions of varying sizes. These spaces may become clogged from clays powdered on the surface by compaction, in sodium dominated soils, or by swelling of the clay following hydration. Clogging reduces infiltration.

Poor infiltration results in surface puddling whereby water is evaporated without entering the soil. Puddling may also reduce infiltration by clogging pores. On slopes poor infiltration causes runoff, and runoff in turn causes erosion. The sediment carrying capacity of water is a function of its velocity; i.e. fast moving water can carry more sediment than slow moving water. Therefore, water moving down steep slopes can be very erosive unless the soil is protected by the forest floor.

An extreme example of the continental effects of erosion for denuded forest lands can be observed in Nepal and India. In Nepal runoff from the steep mountainsides of the Himalaya erodes enormous amounts of soil, and during the monsoon the fast moving, swollen rivers carry this sediment load to the plains of India. As river velocity decreases in the plains, the rivers can no longer carry as much sediment, and it is deposited in the river channels, reducing the ability of the rivers to contain water within their channels. During periods of high runoff flooding occurs, and serious flooding is now a near annual occurrence in these regions, such as Bangladesh.

Sheet erosion may be recognized by the accumulation of stones 1 cm and larger on the soil surface. They appear because the soil matrix of finer material has been washed away, leaving the heavier stones behind. More extensive erosion causes gullies. Erosion reduces soil fertility and the water holding capability of the soil.

You should also recall that runoff and surface evaporation represent precipitation lost, and when it occurs the area is more arid than would be indicated by precipitation records. This is one more process leading to desertification.

III. Movement of Water in the Mineral Soil

Water movement in soils is termed percolation. The rate of movement is determined by the hydraulic conductivity of the soil.

A. Factors affecting soil hydraulic conductivity

1. Initial water content. Water moves as a wetting front through the soil in the large pore spaces by saturated flow. Water in these large pores is called *gravitational water*. The capillary spaces in the soil remove water from the large pores, and hold the water in place against gravity. No further liquid water movement occurs after all the water has been removed from the large pores into the capillary spaces. A light rainfall may saturate the first few cm of soil, leaving the lower depths dry. (Fig. 4-11)

A soil which has been saturated and allowed to have all gravitational water drained away is said to be at *field capacity*. It is not possible to irrigate a field to 50% field capacity, only to field capacity to a certain depth. An estimate for common soils is that 3 cm rain will wet a soil to field capacity to a depth of about 15 cm.

2. Surface permeability or crusts affect the hydraulic conductivity of the soil.

3. The amount and size of the pore spaces affect conductivity as mentioned above

4. The swelling of soil colloids and organic matter reduces permeability. Some clays swell more than others.

5. Duration of rainfall. Slow, steady rains allow for greater conductivity.

6. Percolation barriers such as clay pans, hard pans, underlaying rock, restrict hydraulic conductivity.

B. Hydraulic conductivity

The hydraulic conductivity of soils range from 0.002 cm hr^{-1} in poorly drained soils to 25 cm hr^{-1} in soils such as sands that have little water holding capacity. Hydraulic conductivity is determined by the hydraulic gradient (degree of saturation of the soil at different depths), capillary forces, and gravity. The hydraulic gradient is downward in wet periods, but in dry periods the hydraulic gradient may be upwards against gravity because of evaporative loss of water at the surface. Upward movement of liquid water in capillary spaces is much more rapid than the movement of water vapor. Thus, when the surface of the soil dries, capillary channels are broken, and continued evaporative loss occurs at the much slower rate because the slow movement of water vapor in the drying soil. Mulching, the application of organic matter such as straw over the soil, will reduce the loss of water by surface evaporation and is a common practice for promoting seed germination and seedling establishment by maintaining a moist soil surface.

C. Percolation

Water continues to percolate through the soil in the absence of pans, and it may reach ground water and remain there. Or it may percolate through cracks in the bed rock to deeper levels, later to reappear as seepage. Seepage moves downhill until it either joins a water surface (e.g. lake or stream), forms a spring, or joins subterranean water.

D. The upward movement of water

Water may rise above the ground water level in the capillary spaces of the soil. Soil with fine capillary spaces may permit a capillary rise of 1 m or more. Some deep rooted tree species tap this continually moist zone as their primary water source.

Water that rises to the surface from perched water tables may cause the soil to become saline in arid climates. Solutes accumulate after evaporation because in arid climates the evaporation potential exceeds precipitation, preventing the solutes from being leached through the soil to ground water.

VI. Measurement of Soil Water

A. Water Content.

1. Soil water content is measured by drying a known volume or weight of soil at 105 degrees, then re-weighing in order to determine the amount of water evaporated.

2. The water content of soils in the field can be determined by a neutron probe. This technique is especially useful in watershed management. A thin aluminum pipe is driven into the ground (neutrons pass through aluminum) and a probe containing a fast neutron source is lowered down the pipe. When fast neutrons collide with hydrogen atoms they are deflected, slowed, and measured when they rebound back toward the probe which also contains a slow neutron detector. Since water is the primary source of hydrogen atoms, measurement of the slow neutrons created by fast neutron collisions with hydrogen can be used to estimate water content. (Fig. 4.3)

The probe allows measurements to be made at several soil depths.

3. Soil water content can be measured by lysimeters. Soil and plants are placed in containers than can be weighed. Precipitation, evapotranspiration, and soil water can be measured by periodic weight measurements of the lysimeter. (Fig.4.2)

B. Field Capacity (FC)

1. The ability of the soil to retain water against the force of gravity can be measured by weighing a saturated soil that has been allowed to drain for 24 hours.

2. FC is more commonly estimated in soils laboratories by placing a sample in a pressure membrane apparatus, and extracting all the water held in a saturated soil at a tension less than 0.03 MPa. This approximates the force of gravity. The soil is then weighed, dried, and re-weighed in order to determine its water content (Fig. 3.19).

C. Permanent Wilting Percentage (PWP)

1. The classic method of determining PWP is to place a plant, generally a sunflower, in a pot of soil, allow it to grow so that its roots thoroughly penetrate the soil. The plant is then allowed to withdraw water from the soil until it wilts.

Permanent wilting is determined when the plant does not recover turgor overnight when placed in a humid environment (e.g. under a bell jar). The soil is then removed, weighed, dried, and reweighed to determine the amount of water left after plant extraction.

2. Since the classic method requires several days, a more convenient laboratory method is used, again with the pressure membrane apparatus. In this case water is removed at 1.5 MPa pressure, the approximate value that most crop plants can extract soil. The water remaining after pressure extraction at 1.5 MPa is determined by weighing, drying, and reweighing the soil, and this is expressed as the PWP. (Fig. 3.5, 3.19)

D. Available water.

Available water is computed as the difference between FC and PWP. It also may be crudely estimated on the basis of the texture of the soil. (Fig. 3.9)

E. Soil Moisture Tension or Water Potential Ψ

1. Soil Ψ may be measured by a tensiometer. These have a porous clay or ceramic water-filled bulb attached to a water filled stem connected to a mercury manometer or other means of measuring tension. Water is withdrawn from the porous bulb into the soil under increased tension as mercury rises in the manometer. Measurement is made at equilibrium and expressed in MPa. (Fig.3.7, 3.7)

2. Soil Ψ may also be measured by porous (often gypsum) blocks in which electrodes have been inserted. The blocks are placed into the soil, and the moisture in them allowed to come into equilibrium with the soil moisture. The more water absorbed by the block, the less resistance to the flow of electricity from one electrode to the other. The blocks are calibrated to relate resistance units to soil Ψ. (Fig. 4.4)

3. Neither of the above methods of measuring soil Ψ takes into account of contribution solutes in the soil solution. These are usually negligible in soils, but may be substantial if soils approach saline conditions. In such cases soil Ψ can be measured using a colligative properties of water; the change in vapor pressure with change in Ψ (Fig. 3.2).

In this method the soil sample is placed in a temperature controlled chamber with a thermocouple. Current is applied to the thermocouple, which causes it to cool (Pelter effect). When it cools to the dew point of the atmosphere in the chamber, which is controlled by the soil Ψ, a droplet condenses on the thermocouple, liberating heat of condensation, which is measured. Soil Ψ is computed from the vapor pressure of water in the sample chamber caused by water in the soil.

F. Soil Salinity

The most common method of measurement for salinity is conductivity, using the relationship that the greater soil solute concentration, the greater soil conductivity since salts are charged ions.

Additional Reading:

Kimmins, J. P. 1987. Forest Ecology. pp.270-272
Kramer, P.J. 1983. Water Relations of Plants. pp.73-82
Slavik, B. 1974. Methods of Studying Plant Water Relations. pp.157-190.

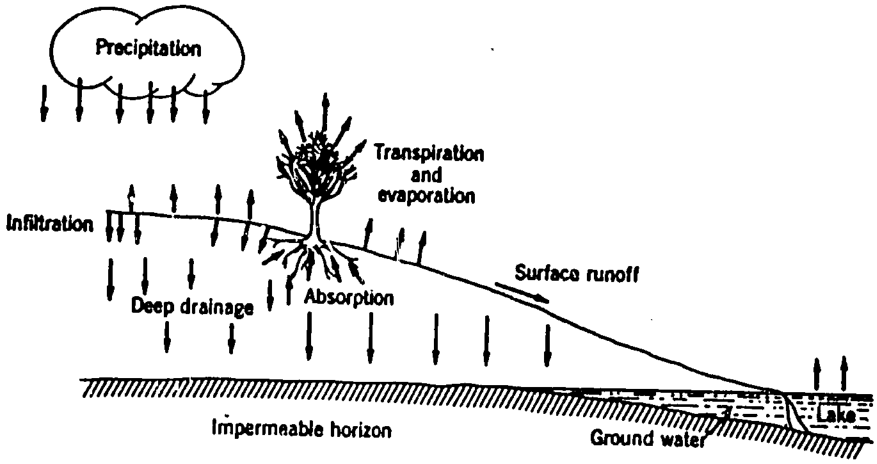


Fig. 4.1. The hydrologic cycle, showing disposition of precipitation by surface runoff, infiltration, and deep drainage, and its removal from the soil by evaporation and transpiration.

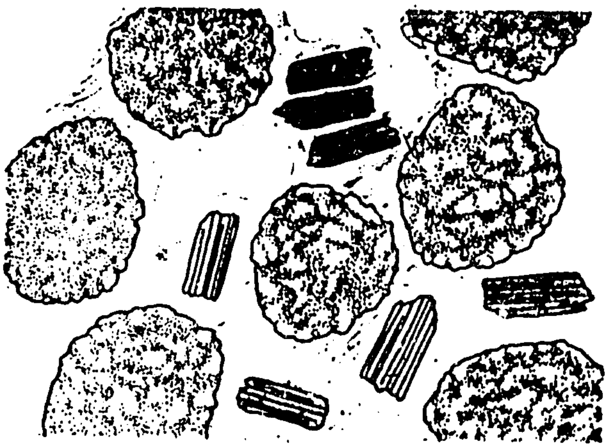


Figure 4-11 Diagram illustrating the concept of capillary water in soil, in which the large particles represent silt or sand and the smaller particles represent clay. Water is adsorbed to the particle surfaces by hydrogen bonding, hydrating the particles. Forces of hydration extend farther from the more highly charged clay surfaces. Curved surfaces are the menisci that appear in the capillary pores of the soil; they result from surface tension in the water. (Compare Figure 4-3.) (From W. A. Jensen and F. B. Salisbury, 1984, *Botany*, p. 253.)

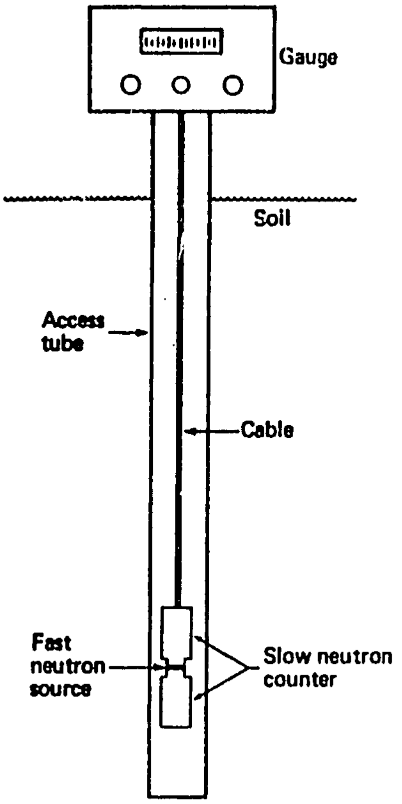


Fig. 4.3. Diagram showing essential features of a neutron meter. A source of fast neutrons and a counter for slow neutrons are lowered to any desired depth in the access tube installed in the soil. The slow neutrons reflected by the hydrogen in soil water are counted and the results indicated on the attached gauge. The water content of a spherical mass of soil surrounding the counter is measured, the size of the mass increasing with decreasing soil water content. A special model is available to measure water in the surface soil.

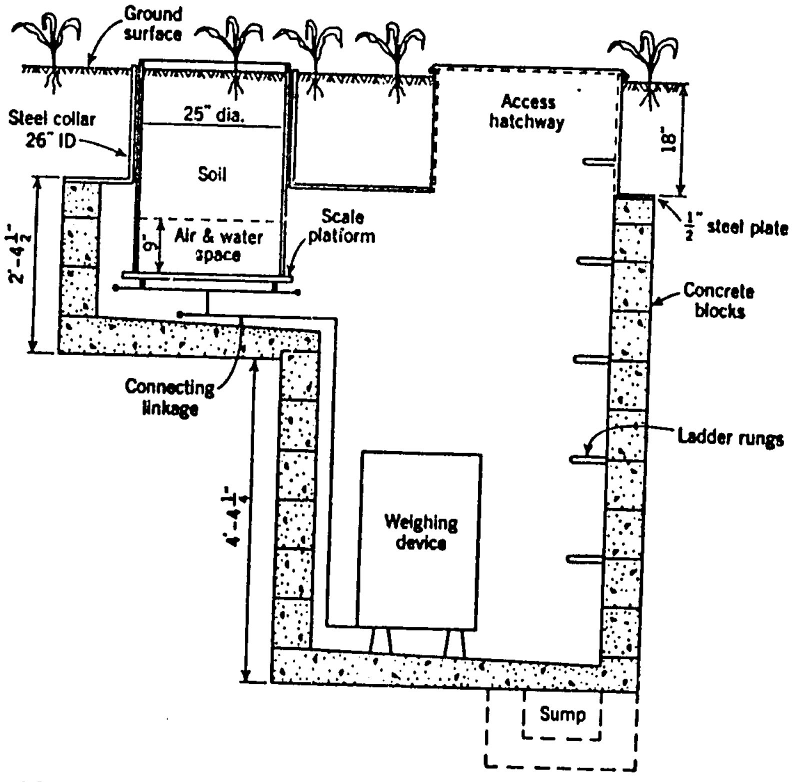


Fig. 4.2. Diagram showing the principle of a weighing lysimeter, modified from England and Lesesne (1962). It consists of a large container filled with soil, mounted on a weighing device. Electronic weighing mechanisms are often used. The lysimeter must be surrounded by a border of similar vegetation if the results are to be applicable to crops or stands of plants. Some lysimetry problems are discussed by Hagan *et al.* (1967, pp. 536–544).

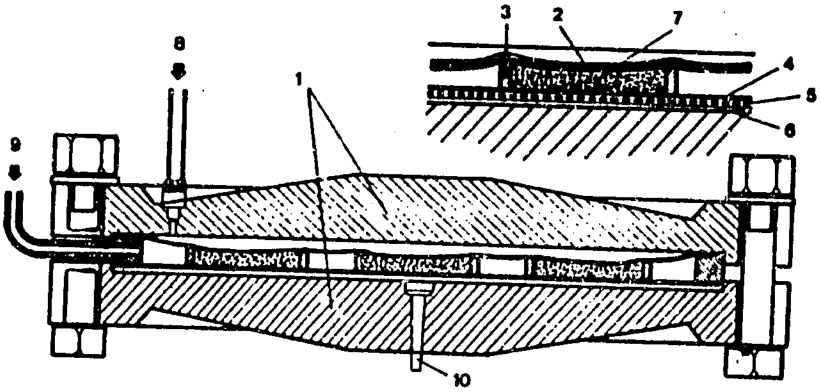


Fig. 3.19 Cross section of the RICHARDS' pressure membrane apparatus (RICHARDS 1947). Two brass halves (1) of the pressure chamber containing (see also detail on right upper part of the figure) soil samples (2) which are placed in metal rings (3) on cellophane visking film (4) lying on metal mesh (5) and a brass plate (6). The samples are covered with a sheet of rubber (7) which is pressurised through an inlet (8). The pressure is controlled through the inlet (9). Excess water is expressed from the samples through the cellophane visking film, brass mesh and water outlet (10).

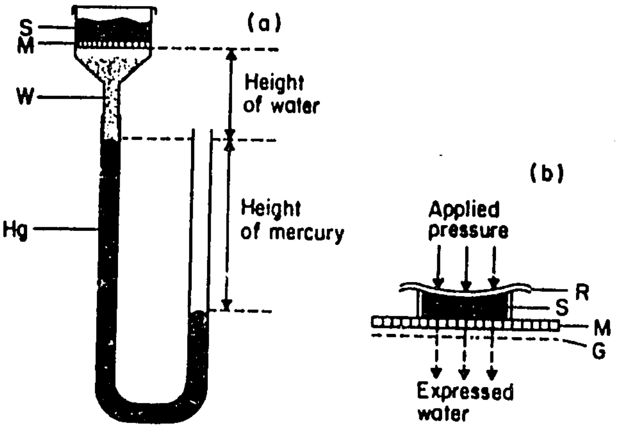


Figure 3.5 Determination of soil water content by (a) the suction plate method and (b) the pressure membrane. S, soil sample; M, membrane permeable to water; U, water; Hg, mercury; R, rubber sheet; G, metal grille. In (a) the applied tension is the equivalent height (in m of water) of the water and mercury columns and is, at equilibrium, a measure of the soil water (matric) potential. In (b) the samples are contained in a pressurized container and the applied pressure provides a measure of soil water (matric) potential. In both cases the soil water content can be detennined at equilibrium.

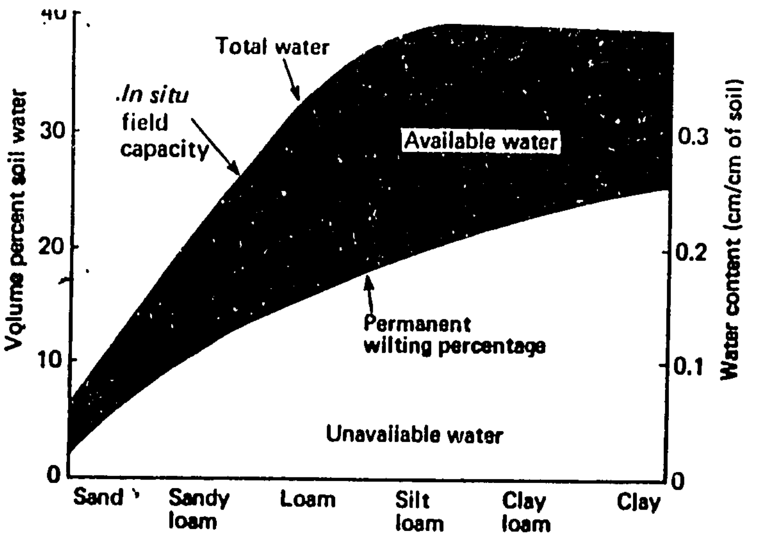


Fig. 3.9. Diagram showing the relative amounts of available and unavailable water in soils ranging from sand to clay. Amounts are expressed as percentages of soil volume and as centimeters of water per centimeter of soil. (From Cassell, 1983.)

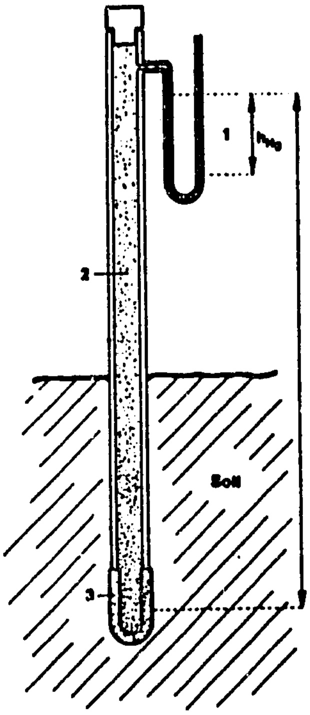


Fig. 3.7 Diagram of a soil tensiometer. 1 — mercury manometer, 2 — tensiometer tube, 3 — porous cup.

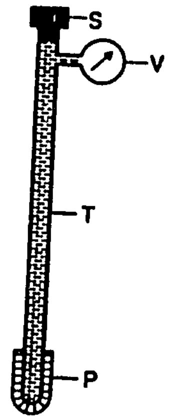


Figure 3.7 Soil tensiometer (diagrammatic). S, air-tight stopper; T, tube filled with water (no air); V, vacuum gauge (or manometer) to measure water tension; P, porous pot.

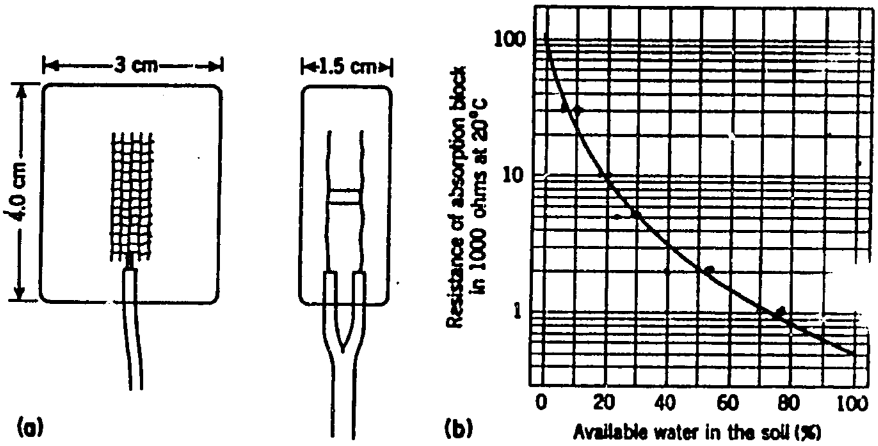


Fig. 4.4. (a) Surface and edge views showing location of electrodes in a plaster of paris block designed to measured changes in soil water content by changes in resistance. The electrodes are pieces of stainless steel screen separated by a plastic spacer and enclosed in plaster of paris. (b) Resistance in ohms of a plaster of paris resistance block plotted over available soil water content of a silt loam soil. (After Bouyoucos, 1954.)

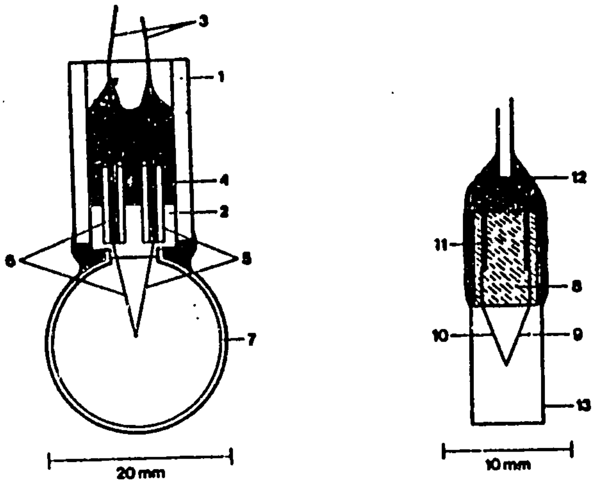


Fig. 3.2 Left: A cross section of the thermocouple psychrometer (type A) for measuring soil water potential (Rawlins and Dalton 1967). 1 - acrylic tubing, 2 — Teflon insert, 3 — copper lead wires soldered with cadmium-tin "low thermal" solder using stainless steel solder flux, 4 — copper heat sinks, 5 — chromel-p wire 0.025 mm, 6 — constantan wire 0.025 mm, 7 — porous ceramic bulb 2 cm in diameter.

Right: Screen thermocouple psychrometer constructed by Brown (1970). 8 — Teflon insert, 9 — chromel wire (25 μm diameter), 10 — constantan wire (25 μm diameter), 11 — copper lead wires, 12 — epoxy resin, 13 — screen cage made of fine-mesh stainless-steel wire.

LESSON EIGHT

ROOT GROWTH AND ENVIRONMENTAL FACTORS AFFECTING ROOT GROWTH

By the end of this lesson you should be able to:

....Describe the difference in origin of primary, lateral, secondary, and adventitious roots
....Be able to identify tap, fibrous, flat, pneumatophore and heart root systems
....Diagram the cross section of a primary root, including root hairs, epidermis, cortex, endodermis, pericycle, phloem, cambium, and xylem
....Diagram the primary root in longitudinal section including the root cap, meristematic, elongation, and maturation regions, and location of root hairs
....Describe the origin and importance of mycorrhizae
....Describe three methods of inducing adventitious roots
....Describe the effect of gravity, soil texture and structure, moisture, aeration, flooding, temperature, and minerals (including salts and Ph) on root growth

ROOT GROWTH AND THE ENVIRONMENTAL FACTORS THAT AFFECT ROOT GROWTH

I. Origin and Anatomy of Roots

A. Primary roots develop from meristematic cells at the root tip. Meristematic cells are capable of cell division.

The embryo in plant seeds consists of a plumule, the embryonic stem and leaves, and a radicle, the embryonic root. During germination the cells at the tip of the radicle divide and elongate, and eventually break through the seed coat. After emergence from the seed coat the radicle becomes the first primary root. The cells at the tip of the new primary root may continue to divide and elongate, forming a tap root. (Fig.2.1)

B. Lateral roots develop from the division of cells in the pericycle of a primary root. The dividing cells first form a bulge that grows through the cortex of the primary root, and then penetrates the epidermis. This is followed by organization of the cells into tissues such as xylem and phloem. Continued cell division at the tip of the lateral root forms a new primary root, since cell division is now taking place in the meristematic region at the root tip. (Fig. 15.2)

If lateral root development replaces taproot development, a fibrous root system develops.

Plants may emphasize tap root development at one phase of their life cycle, and lateral development at another. In the important cottonwood, *Populus deltoides,* radicle growth continues as a single, primary, taproot that may extend a meter or more into the soil, where it eventually reaches the capillary fringe. At the capillary fringe lateral root development replaces taproot growth so this moist soil zone becomes fully utilized.

C. Secondary root development creates the woody roots so important in the anchorage of most trees. Cell division again occurs in the pericycle of the primary root as it did in lateral root development, but in secondary growth division occurs around the root cylinder rather than in just one spot. Division in this region develops into the bark tissues of the root. This causes the endodermis, cortex, and epidermis of the primary root to eventually sluff off.

Plants that develop secondary roots must have an active cambium to develop woody tissue. The cambium is located between the phloem and xylem of the root, just as it is in woody stems. Cell division in the cambium develops into water and mineral conducting xylem cells on the inside, and sugar and nutrient conducting phloem cells on the outside of the cambium. Secondary development may occur in both tap and lateral primary roots.

D. Continued primary root growth is crucial for the plant, even though in some species older primary roots may develop into secondary roots. Secondary development of bark tissue, and even suberin deposits in the tissues of primary roots, restricts the absorption of water and minerals, as well as insect and disease organisms from entering the root. Water and minerals already absorbed are kept inside the root by suberization and secondary development, but continued absorption requires the presence of young, primary roots.

The developing region of the primary root contains a root cap, where gravity affects root growth, a meristematic region where cell division occurs, a region of elongation where the cell expansion occurs that drives the root tip deeper into the soil, and a region of maturation where the root hairs, xylem, phloem, and pericycle cells develop, and later, the epidermal cells become suberized. The majority of water and mineral absorption occurs in the elongation and early maturation regions, where water is then swept into the developing xylem. The development of suberin reduces the permeability of the root in the older portion of the maturation region (Fig. 15.2).

If primary root growth becomes restricted, maturation continues. This includes the development of suberized cells. This truncates the region of elongation, reducing the ability of the root to absorb water and minerals.

E. Adventitious roots develop from stem tissue. Some of these may be aerial roots. The prop roots that develop near the base of corn stocks, and the roots that originate on the branches of the banyan tree *(Ficus bengalensis)* are examples.

Adventitious roots also form on underground stems such as rhizomes and bulbs, and at the points where runners such as those of strawberry touch the ground.

The development of adventitious roots is an important technique of plant propagation. Foresters may obtain stem cuttings from the small twigs of woody plants. These are often treated with a hormone to accelerate the development of adventitious roots, and then the cuttings are placed in moist soil and protected from excess transpiration to encourage rooting. Adventitious roots develop from that portion of the stem buried in the soil.

Another technique of developing adventitious roots, especially in plants that are slow to root, is layering. A lower branch, e.g. juniper, can be bent downward, and the bend held down, covered with soil, and kept moist. This allows slow adventitious root development while the shoot can still provide photosynthate, and the stem can still obtain water from the parent plant. After the roots have developed, the branch can be severed from its parent, the new sapling trimmed back for better root/shoot balance, and then transplanted.

A modification of layering is to wrap a portion of an aerial branch with moist soil or peat, then wrap the soil with black plastic and seal it. After roots grow into the soil containing bag, the twig may be cut free and planted. This works well with *Ficus spp.*

E. Mycorrhizae are fungal infections that develop in the roots of many perennial species. There are two types of mycorrhizae, endomorphic, where the fungal hyphae invade the cells of the root cortex, and ectomorphic, where the hyphae replace the cortex with a fungal sheath (Fig. 15.3).

Each host species is generally infected by a specific fungus, and many of these are mushroom forming species. The fungus obtains carbohydrates, amino acids, vitamins, and other nutrients from the host plant. The mycelia of fungi are much finer than roots or root hairs, and they have a much higher metabolic rate. Because of this the mycelia intensively tap large soil volumes and absorb minerals more effectively than roots, especially in infertile soils.

The excess minerals absorbed by mycorrhizae are transferred to the host. Nutrient enrichment of the host increases its photosynthetic capabilities, which in turn provides more carbohydrates, etc., to the mycorrhizae, which absorbs more minerals for the host, etc., and both partners benefit from this *symbiotic* relationship. (Fig.5.13, Table 10.3)

F. Roots may develop into many forms The root systems of different species of uncultivated plants are stratified in different soil layers. The plant community can fully utilize soil resources and avoid competition by root stratification. The form of forest tree roots is affected by heredity and the environment (Figs. 6.1, 6.6, 3.21, 10.10).

II. Environmental Factors Affecting Root Growth

A. Gravity is detected by the root cap. If a root is placed horizontally a hormone is liberated by the root cap that migrates to the lower surface of the root, inhibiting elongation on that side. Normal elongation occurs on the upper side, causing the root to bend downward.

B. Soil Texture may affect root growth because it controls the availability of soil water and aeration. (Fig.3.9)

C. Soil Structure may affect root growth. Good crumb structure promotes root growth, whereas compaction, impermeable layers such as those that develop from hard pans or cultivation, and rock layers all inhibit root growth. Roots may grow several meters in deep, well aerated loess soils. (Fig. 6.9)

D. Soil Moisture affects root growth because roots grow more rapidly in moist soils than dry soils. This is the origin of the layman belief that roots can "seek out" water at a distance and grow to it, such as leaky pipes and tube wells. Roots grow randomly in all directions. When these randomly growing roots encounter moisture they branch profusely.

E. Soil Aeration affects root growth when the soil oxygen concentration drops to less than 10%, and/or the CO_2 concentration rises. Flooding the soil reduces soil oxygen by restricting exchange with the atmosphere, but microbial respiration continues anaerobically, liberating CO_2. These conditions not only reduce plant growth, but may make the root less permeable to water and eliminate mineral absorption, causing the plant to wilt, even though flooded, and develop nutrient

Some species adapt to flooding by the development of tissues that help deliver oxygen internally to the root tip. The air spaces in the stems of some marsh plants and the pneumatophores of mangroves are examples.

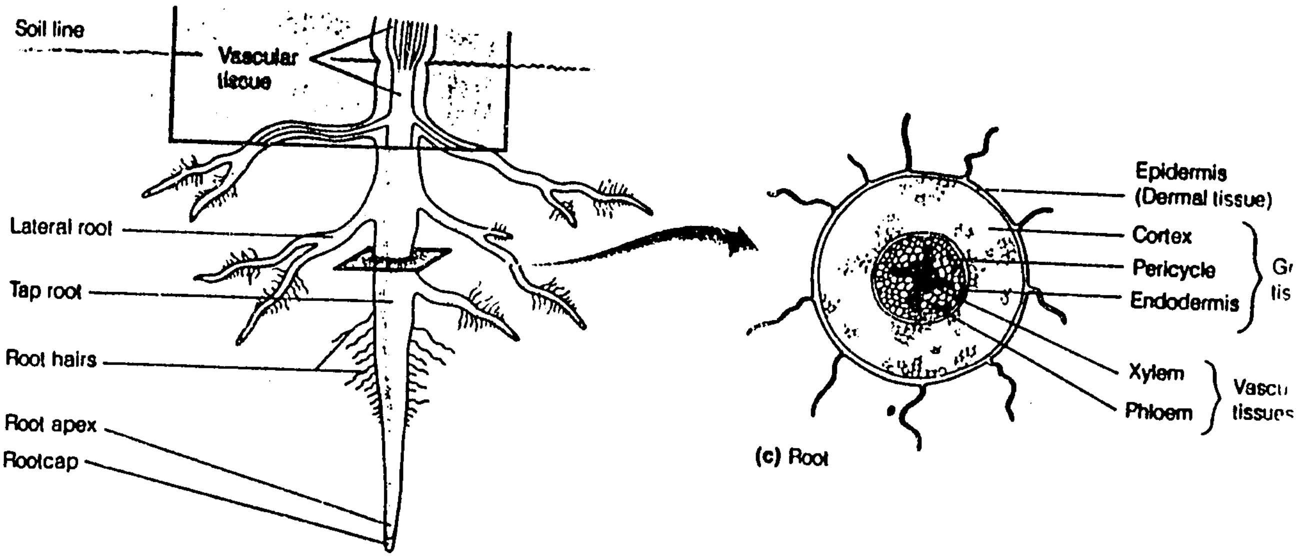
F. Soil Temperature affects root growth by slowing or stopping growth at low and high temperature extremes. The temperature of best root function varies with species. Species of warm climates adapt to higher soil temperatures than those of cool climates, whereas they may not grow in the cold soils ideal for plants from cool climates.

G. Minerals, Salt Concentration, and pH also affect roots. Roots grow more rapidly in soils supplied with nitrogen and phosphorous. High concentrations of salt tends to slow down or stop root growth, but there are considerable differences in the tolerance of different species to saline conditions.

H. Allelopathy refers to substances released by plants that affect the growth of other plants, either favorably or unfavorably. Terpene excreted by *Artemisia* and *Eucalyptus*, root exudates, leachates from the decay of plant materials, may be sources of allelopathic chemicals that may inhibit root growth

Additional Reading:

Kimmins, J. P. 1987. Forest Ecology. pp. 239-242
Kramer, P. J. 1983. Water Relations of Plants. pp. 120-186.



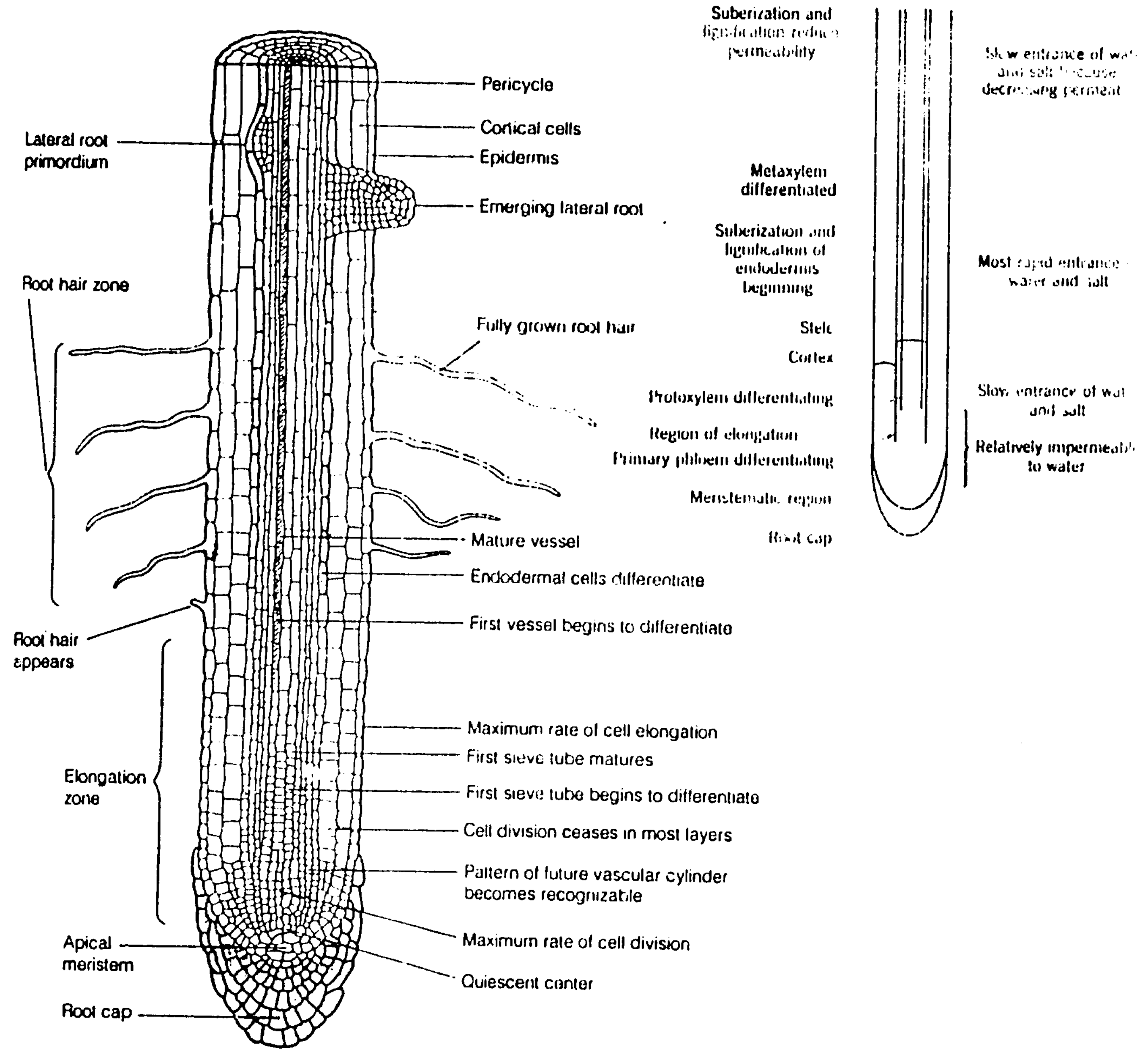


FIGURE 15.2. Primary root growth.

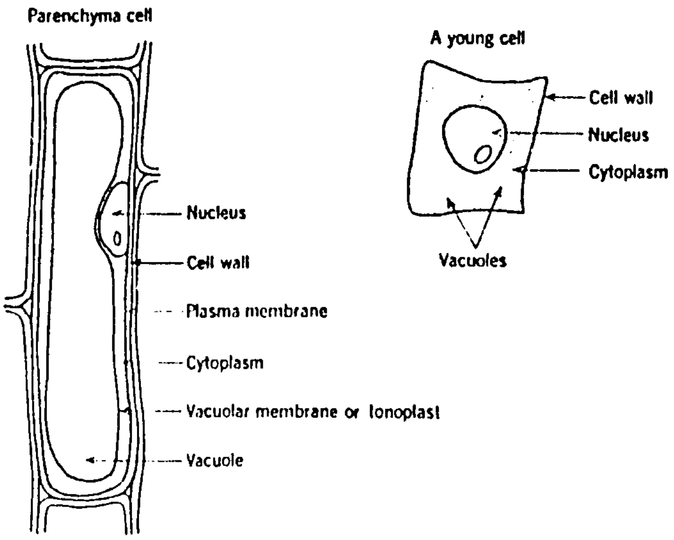


Fig. 2.1. Diagrams of a meristematic cell and a mature vacuolated parenchyma cell. The layer of cytoplasm in mature cells is usually much thinner than shown in this diagram.

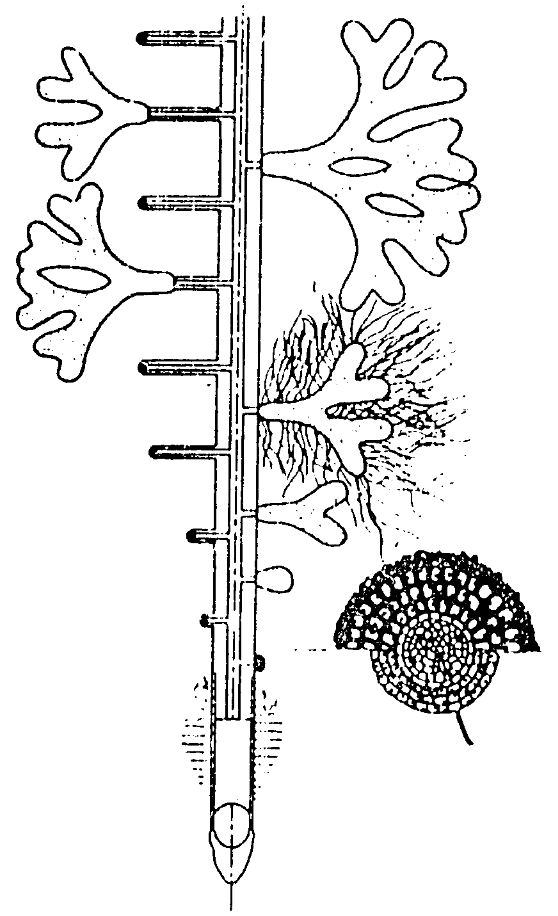


Fig. 5.13. Development of mycorrhizae on a pine root. The long root bears a normal root cap and root hairs, but mycorrhizal branches, similar to those shown in Fig. 5.14 are developing from the branches (short roots). The upper part of the cross section represents a mycorrhizal root, the lower part an uninfected root. (From Hatch, 1937.)

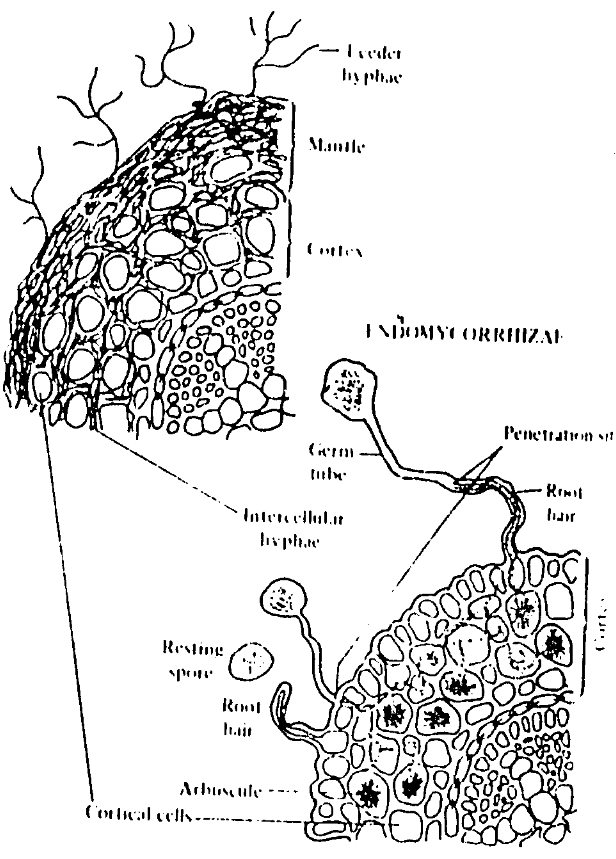


Table 10.3 Growth of Seedlings of Three Species With and Without Incorporation of *Pisolithus tinctorius* Inoculum into the Nursery Soil Mix in Which the Seedlings Were Grown

Species and Treatment	Weight at 16 Weeks after Seeding, mg: Shoot	Root	Total	Shoot/root Ratio
Douglas-fir[a]				
Inoculated	354 (51)[b]	151 (35)	505 (40)	2.36
Control	235	112	347	2.11
Lodgepole pine[a]				
Inoculated	129 (55)	120 (48)	249 (52)	1.08
Control	83	81	164	1.03

	Wt. in g. of 7 Month Seedling: Shoot	Root	Total	Shoot/root Ratio	Ht. (cm)	Stem diam. (mm)
Loblolly pine[c]						
Inoculated	8.9 (112)	2.6 (86)	11.5 (105)	3.42	36 (38)	8.2 (37)
Control	4.2	1.4	5.6	3.00	26	6.0

[a] Data from J. A. Dangerfield (unpublished).
[b] Percent increase attributable to inoculation.
[c] Data from Marx and Bryan (1976).

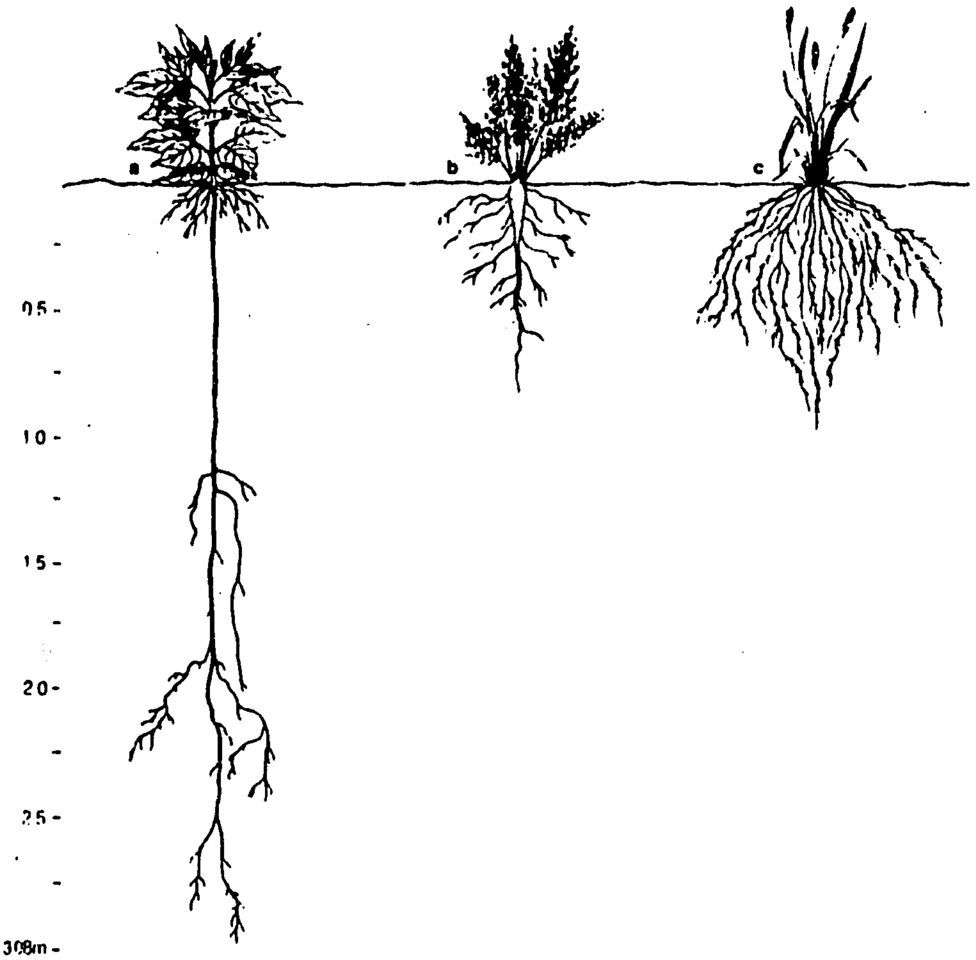


Figure 6-1 Types of root systems: **(a)** In poison ivy, the taproot is adapted to reach moisture deep in the ground. **(b)** The carrot taproot system is adapted to store food. **(c)** The fibrous root system of blue grama grass is adapted to absorb surface water. (From W. A. Jensen, et al.

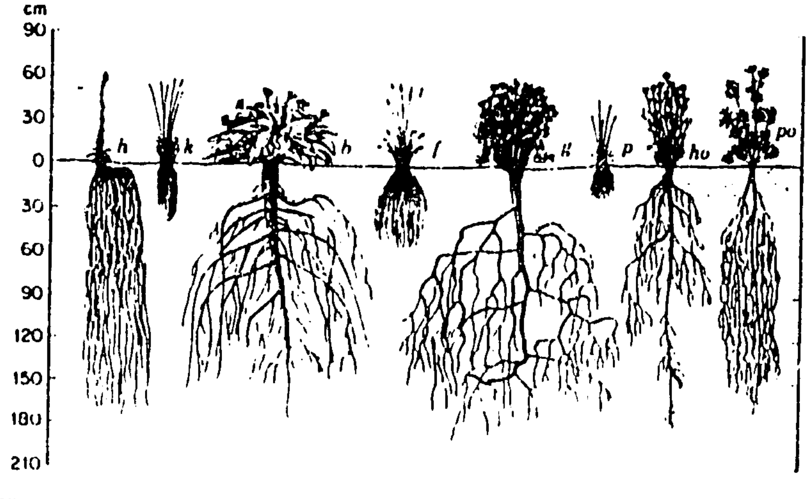


Fig. 6.6. Differences in spread and depth of root systems of various species of prairie plants growing in a deep, well aerated soil. *h*, *Hieracium scouleri*; *k*, *Koeleria cristata*; *b*, *Balsamina sagittata*; *f*, *Festuca ovina ingrata*; *g*, *Geranium viscosissimum*; *p*, *Poa sandbergii*; *ho*, *Hoorebekia racemosa*; *po*, *Potentilla blaschkeana*. (From Weaver, 1919.)

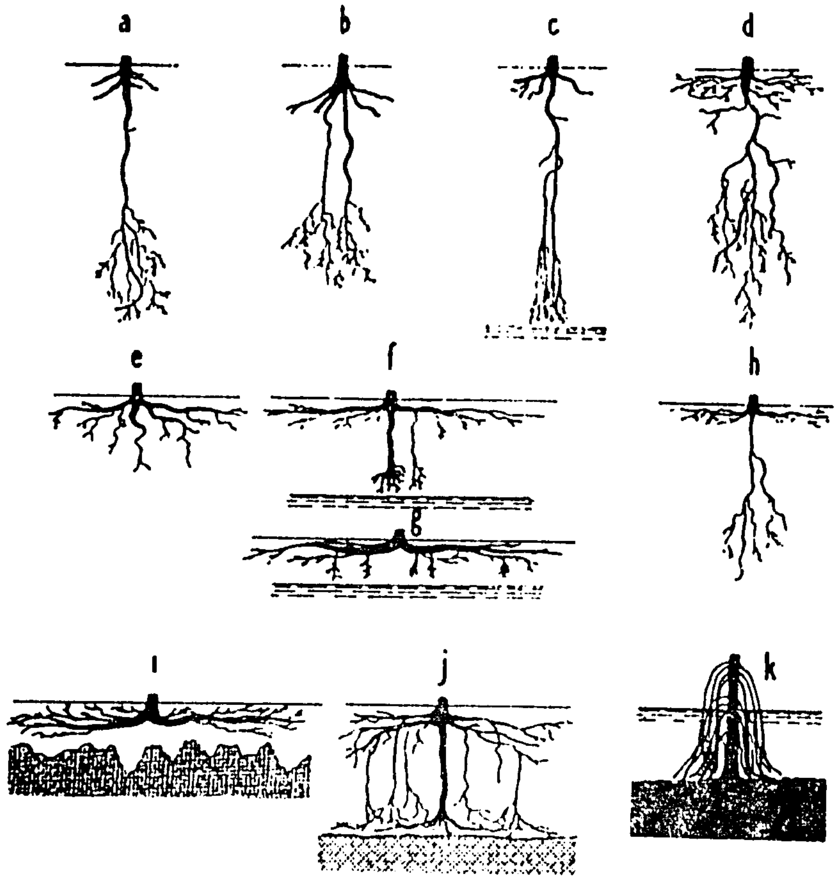


Figure 3.21. Modification of root systems of forest trees by site. *(a,b)* Taproots and heartroots with reduced upper laterals: patterns found in coarse sandy soils underlain by fine-textured substrata. *(c)* Taproot with long tassels, a structure induced by extended capillary fringe. *(d)* Superficial laterals and deep network of fibrous roots outlining an interlayer of porous materials. *(e)* Flattened heartroot formed in lacustrine clay over a sand bed. *(f)* Plate-shaped root developed in a soil with a reasonably deep ground water table. *(g)* Plate-shaped root formed in organic soils with shallow ground water table. *(h)* Bimorphic system of platelike crown and heartroot or taproot, found in leached soils with a surface rich in organic matter. *(i)* Flatroot of angiosperms in strongly leached soils with raw humus. *(j)* Two parallel plate-roots connected by vertical joiners in a hardpan spodosol. *(k)* Pneumatophores of mangrove trees in tidal lands. (After S. A. Wilde, *Forest Soils*, 1958, The Ronald Press Company.)

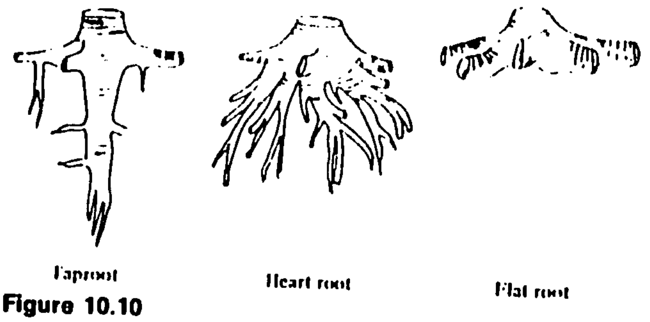


Figure 10.10

The three major types of root system commonly found in trees. In some tree species the form of the root is under strong genetic control, whereas in others the root form is more a reflection of the soil conditions under which the tree is growing. Intermediates between these three main types are common. (After Armson, 1977. Used by permission of the University of Toronto press and the author.)

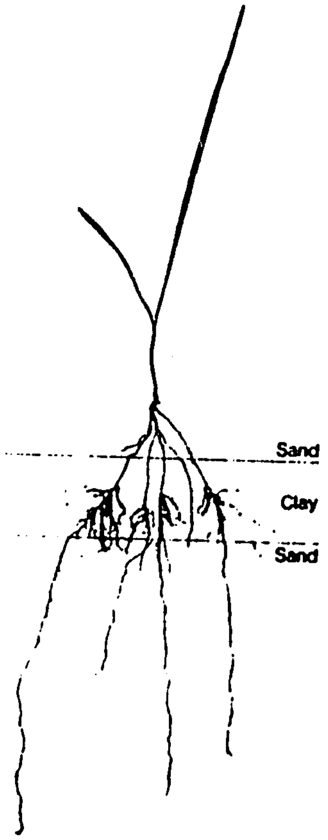


Figure 3.9. The root system developed by a plant of wheat grown through a sandy soil containing a layer of clay. Note the responsiveness of root development to the localized environment that it encounters. (Courtesy of J.V. Lake.)

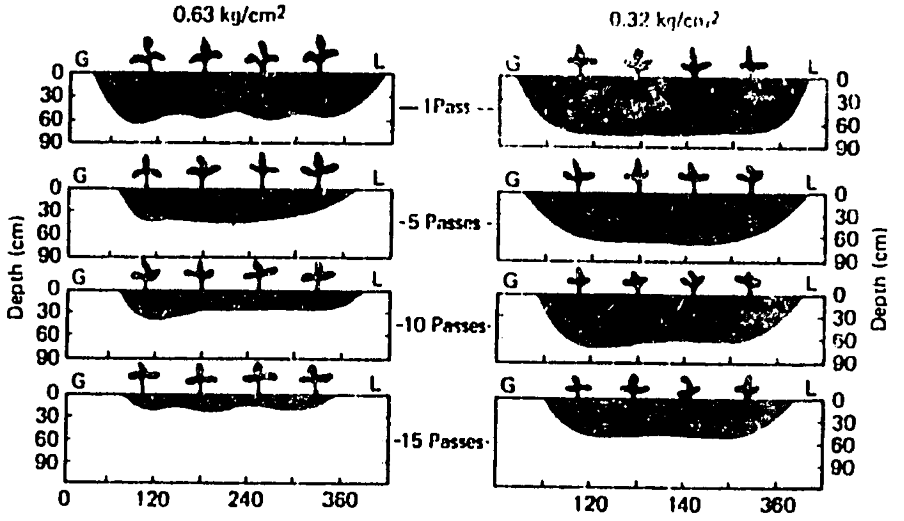


Fig. 6.9. Effect on root penetration of soil compaction at 0.63 kg cm^{-2} and 0.32 kg cm^{-2} for 1, 5, 10, or 15 passes over the soil prior to seeding. (From Cassell, 1983).

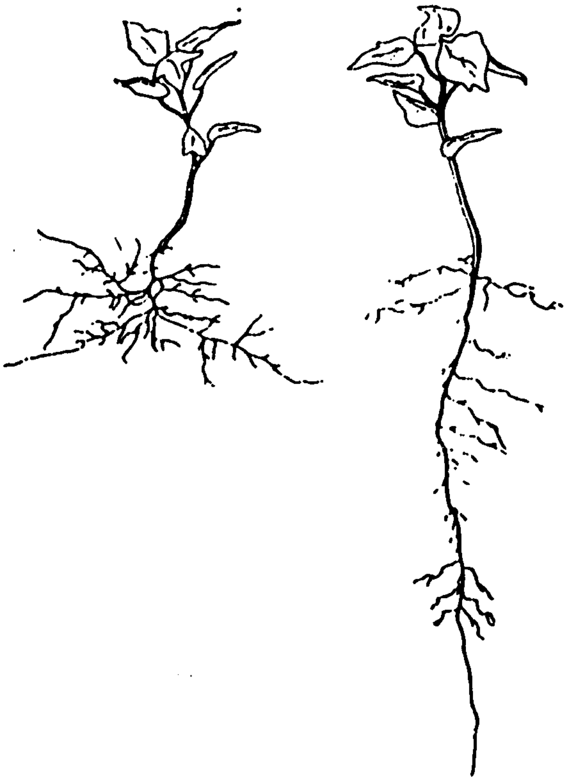


Fig. 6.7. Effects of soil conditions on development of the adaptable root systems of red maple (*Acer rubrum*) seedlings. (Left) A typical seedling from a swamp. (Right) A seedling from a well-drained upland site. (After Toumey, 1929.)

LESSON NINE

ROOT FUNCTION AND ROOT/SHOOT RELATIONS

By the end of this lesson you should be able to:

....List four functions of roots
....List four effects roots have on shoots
....Estimate the portion of the biomass of a typical forest that is composed of roots and mycorrhizae
....Define net primary productivity NPP
....Estimate the portion of NPP allocated to root growth
....Discuss the variations in NPP allocation to roots caused by site and age differences
....List the major effect shoots have on roots
....Discuss the effects of herbivory and shade on root growth

ROOT FUNCTION AND ROOT/SHOOT RELATIONS

I. Root Function

A. Anchorage Roots keep the plant upright, but both species differences and the environment affect how well roots function as anchors. For example, spruces can often adapt to swampy areas by forming a relatively deep and spreading root system for anchorage. Most pines, although better adapted for drier sites, and subject to windthrow in marshy areas because they do not form spreading root systems.

B. Food Storage Secondary roots often function as food storage reservoirs. Most trees store foods in roots toward the end of summer, and many nutrients recovered from deciduous leaves before abscission are also stored in roots. At the time of dormancy release in the spring these food reservoirs are redistributed to the expanding buds and leaves.

Biennials such as beet and carrot are also examples of root storage systems, but the plant anatomist will distinguish between them and food storage in underground stems (e.g. potato, ginger).

C. Synthesis The conversion of inorganic nitrogen to organic nitrogen (e.g. amino acids) takes place in the roots of most species, and the nitrogen is translocated to the shoot in the organic form. Roots also synthesize several growth regulators such as the hormones cytokinnin, gibberellic acid, and abscissic acid. acid, as well as the vitamins niacin and thiamine. Shoots are dependent on roots for these vitamins and cytokinnin. Other substances such as nicotine are synthesized in the root and accumulate in the shoot.

D. Absorption Roots are crucial for the absorption of water and mineral nutrients.

E. Soil Channels Dead and decayed roots provide channels for soil aeration and water movement.

F. Root excretion Root tips excrete substances, e.g. sugars, that stimulate microbial activity. The zone of this effect is termed the *rhizosphere*. Microbial activity in the rhizosphere may be twenty-fold that in the rest of the soil, and it includes microorganisms that fix nitrogen, decompose organic matter, and release slowly available soil nutrients.

II. Allocation of Net Primary Production to Root Growth

Net Primary Production is the photosynthate that remains after deduction for leaf respiration:

Net Primary Production = Gross Primary Production - Respiration

Root growth in corn is 5-6 cm day^{-1}, and in pine at 2.5 mm day^{-1}. Root growth must remain continuous throughout the growing season because only young roots absorp water and minerals.

Root biomass is the fraction of total biomass in an ecosystem allocated to roots. In polar regions root comprise 20 - 45% of the total biomass, whereas in tropical rain forests roots account for only 10 - 20% of the biomass. In tropical rain forests much of the mineral component of the ecosystem is maintained in the stem and leaves, and dependable precipitation reduces the need for extensive root systems for water absorption.

Root replacement requires a substantial allocation of NPP. In scotch pine 50% of NPP is required for root growth.

A study of biomass allocation and NPP in Pacific silver fir disclosed that in infertile sites 30% NPP was allocated to root growth, whereas on good sites only 8% NPP went to root growth. On good sites much more NPP could be used for above-ground production. This study also disclosed an NPP root allocation of 35% in young (23 year old), but 66% in mature (180 year old) stands. Mycorrhiza comprised 0.7% and 0.3% of the biomass in these stands respectively, but they required 14% and 15% of NPP.

These studies disclosed that a substantial portion of forest NPP goes to root growth, and that even though mycorrhizae are a minor biomass component, they require a substantial component of the energy allocation of forests for their maintenance.

III. Effect of Roots on Shoots

Many of the effects of roots on shoots were discussed in Section I, Root Function. Roots supply water, mineral nutrients, and growth regulators to the stem. The supply of the growth regulator cytokinin affects the allocation of NPP, such as into fruit development at one period and bud development at another.

Ci[illegible] and apple root stocks can affect fruit quality, as demons[illegible] grafting studies. And root stocks have also been shown to affect the disease resistance of the scion or grafted shoots, especially of grape and apple.

Damage to the root threatens the life of the plant. A classic case in forestry occurs when a root system becomes damaged during road construction, permitting disease organisms to breech the root's defenses and enter it. Such trees may turn yellow in a few years, and die some years later; often so much time passes that the cause of death (mechanical damage to the root) becomes forgotten.

IV. Affect of Shoots on Roots

The major shoot effect on roots is the supply of carbohydrates to the root.

Many species are intolerant to shade because when shaded NPP, is allocated to stem growth at the expense of root growth. If this strategy is successful the stem may grow through the shading canopy. If it is not, the plant will suffer, especially during drought, from a poor root/shoot ratio, as it becomes more susceptible to drought-induced mortality.

Herbivory may benefit the plant by reduction of self-shading, but too much grazing or browsing will reduce the ability of the plant to supply sufficient carbohydrate to the roots for proper growth, once again exposing the plant to increased mortality from drought or nutrient deficiencies.

Additional Reading:

Kimmins, J. P. 1987. Forest Ecology. pp. 46 - 48, 239
Kramer, P. J. 1983. Water Relations of Plants. pp. 121 - 123, 161 - 164

LESSON TEN

WATER ABSORPTION MECHANISMS
ROOT AND STEM PRESSURE

By the end of this lesson you should be able to:

- ....Describe the path of water across the root
- ....Describe the difference in origin of the water potential gradient between slowly and rapidly transpiring plants
- ....List the physiological requirements for osmotic (active) water absorption
- ....List the reasons osmotic water absorption is not adequate for rapidly transpiring, tall trees
- ....Associate stem, root, or phloem pressures with exudation in maple, birch, and palms
- ....List the properties of water that allow it to be under negative pressure or tension
- ....Explain how passive water absorption occurs

WATER ABSORPTION MECHANISMS

All mechanisms of water absorption require a free energy gradient from soil water to the water transporting tissue of the root, the xylem. In order for water absorption to continue, that free energy gradient must extend through the leaf to the atmosphere. This gradient is referred to as the soil-plant-atmosphere system.

The free energy gradient is expressed as water potential Ψ, and the gradient must be increasingly negative from water in the soil to that in the xylem for absorption to occur. In order to resupply water being lost from even a slowly transpiring plant, most water flow across the root must be by bulk flow rather than by diffusion. Bulk flow occurs under a pressure gradient. The pressure gradient is the primary Ψ component that determines bulk flow across the root. Gradients may be induced either by osmotic potential or negative pressure (tension) in the water column.

II. Path of Water Movement Across the Root

Water is absorbed through the epidermis of the root, especially the root hairs which greatly expand the root's absorbing surface. Water may also be absorbed by mycorrhizae (Fig. 4.1)

Water crosses the cortex of the root in the cell walls and intercellular spaces, not passing through the membranes of cortical cells. However, when the water encounters the endodermis it is forced to go through the cell membrane rather than around it because the radial walls of endodermal cells are filled with waxy suberin.

The endodermis serves the important function of regulating the traffic of minerals into the stele, or the core of the root containing the phloem and xylem. Minerals that pass into the stele are prevented from leaking back out by the endodermis. It is this feature that permits osmotic water absorption. (Fig. 4.3)

II. Osmotic (Active) Water Absorption

The forces that create pressure gradients are very different between slowly and rapidly transpiring plants. In slowly transpiring plants, osmotic absorption may occur because minerals accumulate in the stele making the Ψ_{xylem} more negative than Ψ_{soil}. An example of osmotic water absorption is as follows:

Assume $\Psi_{soil} = -0.05$ MPa, indicating a moist soil, and that the xylem has accumulated solutes so that $\pi_{xylem} = -0.15$ MPa. Using the water potential equation (Lesson Four) it can be seen that the water in the xylem will be under pressure when it reaches equilibrium with soil water.

$$\Psi_{soil} = -0.05 \text{ MPa} = \Psi_{xylem} \text{ at equilibrium}$$

$$\Psi_{xylem} = \pi_{xylem} + P_{xylem}$$
$$-0.05 \text{ MPa} = -0.15 \text{ MPa} + 0.10 \text{ MPa}$$

In this example, water in a moist soil held with little tension, e.g. $\Psi_{soil} = -0.05$ MPa, would be drawn into the xylem because of its osmotic potential π. A pressure would be created in the xylem as a result of the osmotic absorption of water.

Osmotic water absorption occurs in warm, moist, well-aerated, fertile soils, the factors that enable the root to absorb minerals. It is sometimes called *active water absorption*, because active, respiring cells are required for mineral absorption. Under such conditions π, the measure of the osmotic potential of the root xylem, may reach -0.1 to -0.2 MPa.

After the osmotic gradient has been established, water moves from soil to the xylem until the gradient disappears, e.g. by a drying soil or by pressure in the xylem. Soil water is essentially being sucked into the root by the high mineral concentration (osmotic concentration) in the stele, and then forced up the stem to the leaves under pressure. Review that relationship by study of Fig.8.2.

C. Effects of Osmotic Water Absorption

1. Water Balance Osmotic water absorption can maintain water balance in a slowly transpiring plant that is not very tall. A root xylem with $\pi = 0.1$ MPa has sufficient osmotic potential under ideal circumstances to raise a water column to a height of 10 meters. This is sufficient for many shrubs and herbs, but not for trees. In addition, related phenomena to this have not been observed in conifers, the tallest trees.

2. Guttation Osmotic water absorption may cause xylem sap to leak from special pores, *hydrothodes*, in leaves. Hydrothodes are common at the tips of grass leaves. This is called guttation and it occurs under conditions of very low transpiration when the root acts as an osmometer. Salts accumulate in the stele, soil water flows into the stele in response to the Ψ gradient created by the minerals in the stele, and continues to do so even as pressure develops inside the root. This pressure forces xylem sap through the hydrothodes. If the water of guttation dries, the remaining xylem salts and may cause tip burn of the leaf. (Fig. 8.5).

3. Root Pressure. If the top of a plant using osmotic water absorption is detached, and a pressure gage such as a mercury manometer attached to the root stump, pressure may be measured. This is called root pressure, and it is a plant expression of osmotic pressure. Root pressure may reach as much 0.15 MPa under unusual circumstances. Root pressure has not been detected in many tree species. However, root pressure may be demonstrated by tying a portion of a child's balloon on the stump of grape in the spring, and watching the balloon swell with exuded sap until it bursts.

4. Exudation. Many cuttings exude xylem sap from the root stump. Volumes of sap from 20-100 l during spring in birch stumps, 1 l per week in sugar cane, and 100 ml per day in corn have been measured. Exudation is similar to guttation, but it occurs from the cut stump rather than through hydrothodes. There

may or may not be measurable root pressure in exuding stumps, but the cause is once again the accumulation of minerals in the stele, and soil water being drawn into the root in response to the osmotic Ψ gradient created. However, even the most rapid rate of exudation does not approach the transpiration rates that occurred before shoot removal (Table 8.2).

Maple also exudes sap, but this is not caused by osmotic water absorption. Maple stems alternatively expand and contract on bright sunny days followed by cold winter nights. The expansion and contraction of the stem pumps sap from the stem, which, like birch, may be evaporated to produce a syrup.

Coconut, date, and Palmyra palms can produce 6 - 20 l day^{-1} of exudate from a cut inflorescence. This sugary exudate is from the phloem, which is also under pressure, and it is not related to osmotic water absorption.

IV. The Role of Osmotic Water Absorption

Although osmotic water absorption may induce guttation, root pressure, exudation, and maintain the water balance of slowly transpiring plants, it has many limitations that prevent it from being the sole, or even major mechanism of water absorption.

Root pressure has not been observed in many tree and other plants. Root pressure is necessary if water is to be moved from the root to the shoot by osmotic water absorption. Even in species that demonstrate root pressure, the pressure observed under the best conditions would only support of hydrostatic head of about ten meters, much less than ordinary tree height.

Under rapid transpiration the mineral concentration of the stele will be diluted, destroying the π gradient from soil to stele. (This is illustrated in Table 8.1). The low Ψ gradient associated with osmotic water absorption does not allow a sufficient pressure difference for rapid absorption.

Osmotic water absorption may be able to maintain water balance in short, slowly transpiring plants, but another mechanism is responsible for absorption in trees and most plants.

V. Passive Water Absorption

When transpiration exceeds the rate of water absorption, the water in the xylem is placed under tension. Turgor is maintained in leaf cells because they have high concentrations of solutes. Water flows from the xylem cells, which have low solute concentrations, into the leaf cells to maintain turgor, and on through mesophyll cell walls to replace water lost by transpiration.

Examination of Fig. 8.1 discloses a rapid increase in transpiration in the morning, exceeding absorption, thus developing tension in the water column. Absorption continues late into the night after transpiration has ceased. This will relieve water stress induced by rapid transpiration during the day.

Water can exist under tension in the xylem cells because of its high *adhesion* (attraction for the cellulose walls of xylem cells) and *cohesion* (attraction of water molecules for each other) (Fig. 4-14). Only under exceptional circumstances (e.g.hard freezing) is the cohesive and/or adhesive forces of water exceeded by tension. If this happens water turns to vapor, a bubble forms, and cavitation occurs (Fig. 4.6). The construction of xylem cells restricts this bubble to just one cell, and water in adjacent cells is able to flow around the cavitated cell unhindered.

As water is lost from the surface of a leaf cell it is replaced by pulling water through adjacent cell walls, from cell to cell, until it is pulled from the water in the cavity of a xylem cell. As water continues to be pulled out of the xylem tension is created, and this tension is relayed from xylem cell to xylem cell down t the root. (Fig. 4-13).

An illustration of water potential equation of xylem root cells is:

$$\Psi_{root\ xylem} = \pi + P$$

$$-10\ \text{MPa} = -0.1\ \text{MPa} + (-9.9\ \text{MPa})$$

In this equation the osmotic potential π is a minor component of the root Ψ. The major component is the tension or negative pressure. At this tension the Ψ_{root} would be able to extract soil water at a tension of -10 MPa or less, and if Ψ_{soil} was near field capacity, e.g. -0.5 MPa, rapid water absorption could occur because of the large Ψ gradient. Compare this equation with that used to illustrate osmotic water absorption and to Table 8.1.

The path of liquid water is continuous from the surfaces of mesophyll cell walls in the substomatal cavity of the leaf, through the space in and between cell walls, across the cell wall of the xylem into its interior cavity, from one xylem cell to the next all the way down the stem to the root. This allows water to be pulled from the soil to the leaf, and this process is sometimes referred to as *transpirational pull*. It is also called *passive water absorption* because the root acts passively as an absorbing surface, and will function if anaesthetized, or even dead or removed. It has also been referred to as the *cohesion theory* because of the property of water crucial for passive absorption.

The process of passive water absorption can continue in the absence of roots as illustrated by cut flowers in a vase. It is best to re-cut the flower stems under water to remove xylem cells cavitated during the first cutting and thus insure improved water supply to the flowers.

F. Measurement of Xylem Water Potential

The Ψ_{xylem} can be measured by a pressure bomb. When a stem using passive water absorption is cut, xylem water retracts from the cut in both directions because it is under tension. The cut branch (or leaf) is then be placed in a cylinder with the stump (or petiole) projecting from it. Pressure is applied to the

VI. Measurement of Xylem Water Potential

The Ψ_{xylem} can be measured by a pressure bomb. When a stem using passive water absorption is cut, xylem water retracts from the cut in both directions because it is under tension. The cut branch (or leaf) is then be placed in a cylinder with the stump (or petiole) projecting from it. Pressure is applied to the cylinder, and the cut examined for the reappearance of xylem sap. The pressure required to force re-wetting of the cut by sap is equal to the sap tension before cutting. (Fig. 3.F).

<u>Additional Readings</u>:

Kramer, P. J. 1983. Water Relations of Plants. pp.215-234.
Salisbury, F., and C. Ross. 1985. Plant Physiology. pp. 75-95
Taiz, L., and E. Zeiger. 1991. Plant Physiology. pp. 84-89

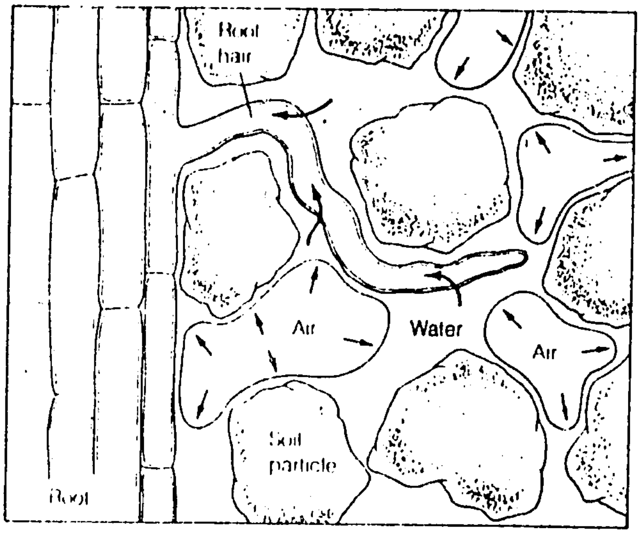


FIGURE 4.1. Root hairs make intimate contact with soil particles and amplify the surface area needed for water absorption by the plant. The soil is a mixture of particles (both mineral and organic), water, dissolved solutes, and air. As water is absorbed by the plant, the soil solution recedes into smaller pockets, channels, and crevices between the soil particles. This recession causes the surface of the soil solution to develop concave menisci (curved interfaces between air and water), which brings the solution into tension, or negative pressure, by surface tension. As more water is removed from the soil, more acute menisci are formed, resulting in greater tensions (more negative pressures).

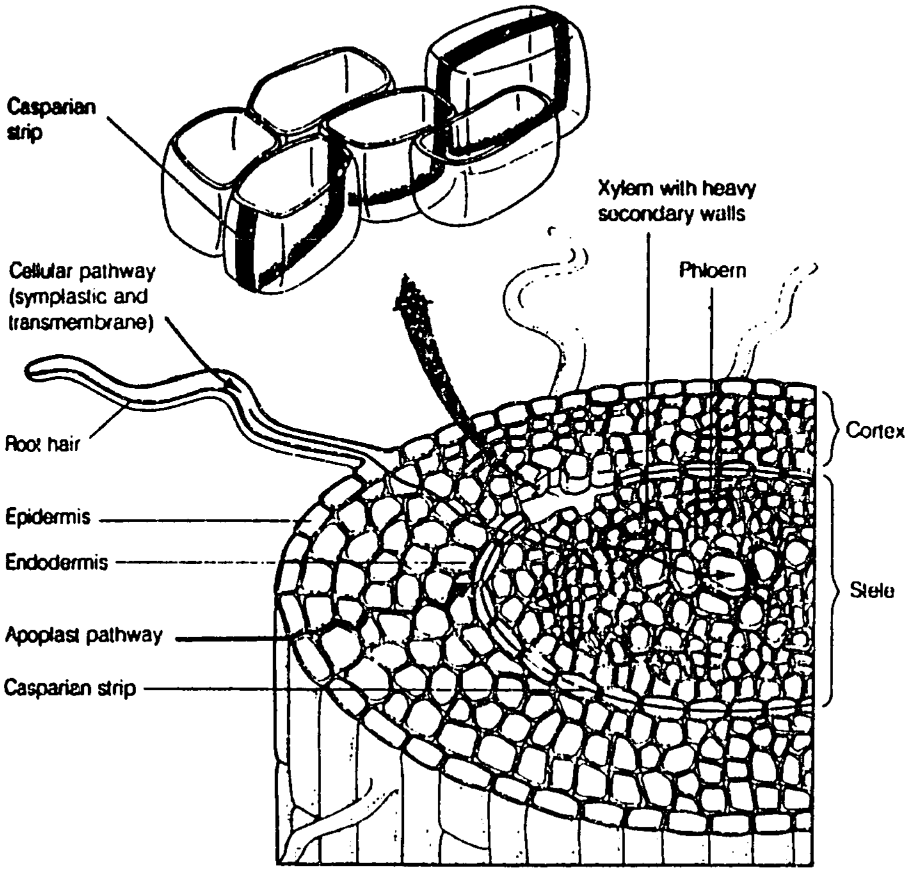
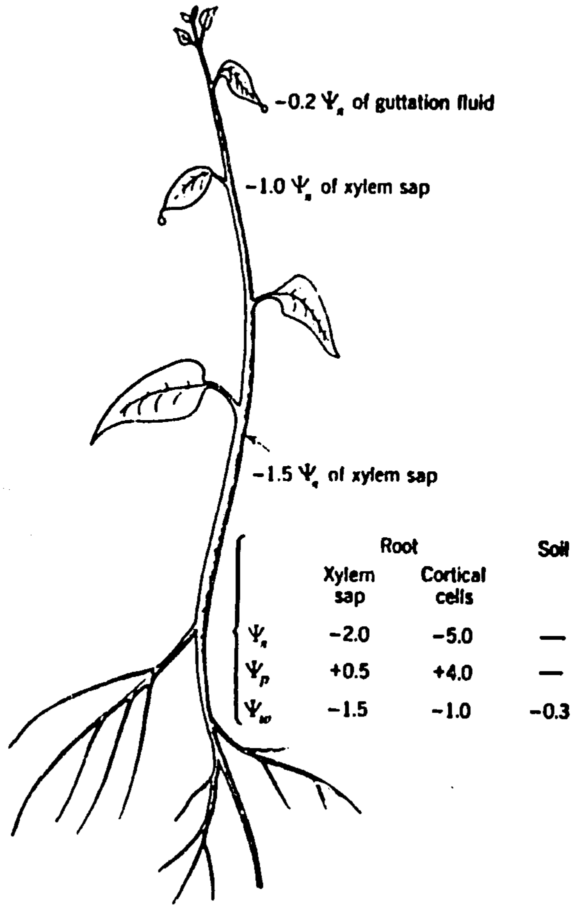


FIGURE 4.3. Pathways for water uptake by the root. Through the cortex, water may travel via the apoplast pathway or the cellular pathway, which includes the transmembrane and symplast pathways. In the symplast pathway, water flows between cells through the plasmodesmata without crossin the plasma membrane. In the transmembrane pathway, water moves across the plasma membranes, with a short visit to the cell wall space. At the endodermis, the apoplast is blocked by the Casparian strip. Water entering the root's vascular system must cross the plasma membrane of the endodermis.



	Root		Soil
	Xylem sap	Cortical cells	
Ψ_s	−2.0	−5.0	—
Ψ_p	+0.5	+4.0	—
Ψ_w	−1.5	−1.0	−0.3

Fig. 8.2. Decrease in osmotic potential, Ψ_s, of xylem sap as it moves upward, caused by transfer of salt to living cells adjacent to the xylem. The amount of decrease is based on data from Klepper and Kaufmann (1966) and Oertli (1966). The tabular data illustrate how, in slowly transpiring plants, a gradient in water potential can occur from moist soil to root xylem across the root cortex, which has a much lower osmotic potential than either soil or root xylem but an intermediate water potential. (From Kramer, 1969.)

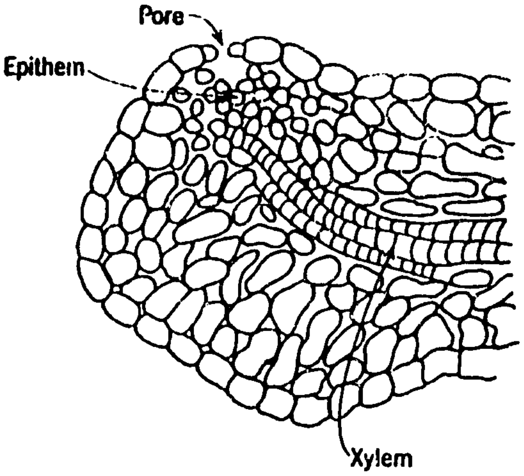


Fig. 8.5. Diagram of a hydathode showing a pore, the underlying epithem, and termination of xylem. The epithem is merely a mass of thin-walled parenchyma with large intercellular spaces through which water can move readily. Hydathodes often resemble incompletely differentiated stomata with nonfunctional guard cells. They usually occur at the tips and along the margins of leaves. (Adapted from several sources.)

TABLE 8.2 A Comparison of Exudation with the Rate of Transpiration prior to Removal of the Tops[a,b]

Species	Number of plants	Transpiration, milliliters of water per plant per hour First hour	 Second hour		Exudation, milliliters of water per plant per hour[c] First hour	 Second hour	Exudation as percent of transpiration[d]
Coleus	6	8.6	8.7		0.30	0.28	3.2
Hibiscus	5	5.8	6.7		−0.01	0.05	0.7
Impatiens	6	2.1	1.9	Tops	−0.22	−0.06	
Helianthus	8	4.3	5.0	removed	0.02	0.02	0.4
Tomato (1)	6	10.0	11.0		−0.62	0.07	0.6
Tomato (2)	6	7.5	8.7		0.14	0.27	3.1

[a] Rapidly transpiring plants usually show absorption of water through the stumps during at least the first half hour after the tops are removed, exudation beginning only after the water deficit in the root system is eliminated.

[b] From Kramer (1939).

[c] A minus sign indicates absorption of water by the stump instead of exudation.

[d] Percentage relations are based on transpiration and exudation rates for the second hour.

TABLE 8.1 Relative Water Potentials in Soil, Root Cortex, and Xylem Sap of Slowly and Rapidly Transpiring Plants in Soil at Approximately Field Capacity[a]

Soil	Slowly transpiring plant, osmotic absorption Cortex	 Xylem sap	Rapidly transpiring plant, passive absorption Cortex	 Xylem sap
Ψ_s − 0.01	−0.5	−0.2	−0.05	−0.05
Ψ_m − 0.02	—	—	—	—
Ψ_p —	−0.4	−0.05	0.10	−0.5
Ψ_w − 0.03	−0.1	−0.15	−0.4	−0.55

[a] Values are estimates in megapascals. The positive pressure in the xylem of the slowly transpiring plant often results in guttation.

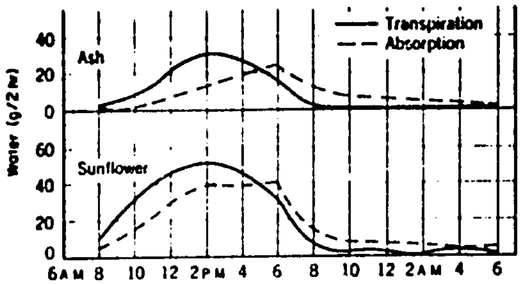
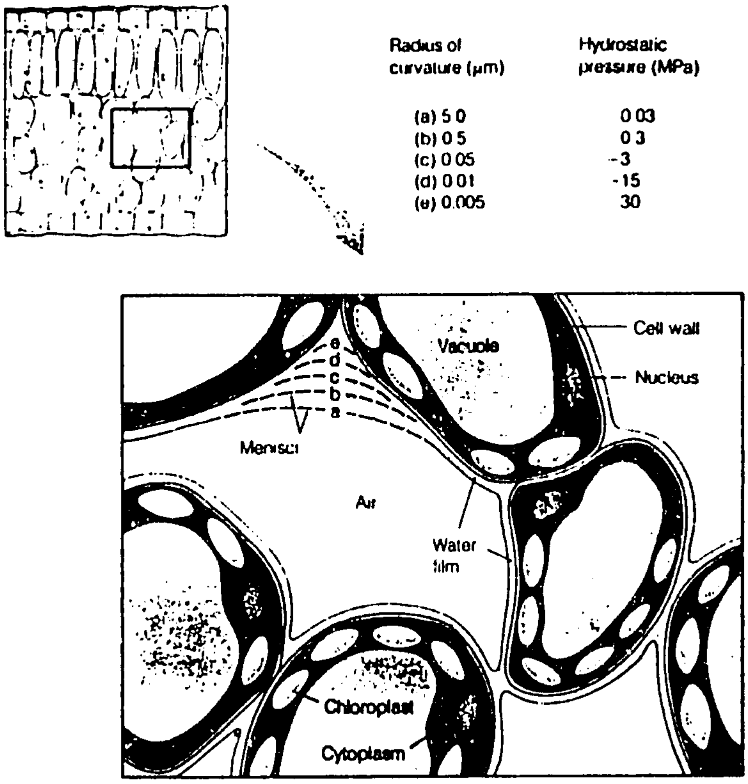


Fig. 8.1. Rate of transpiration and absorption of a woody and an herbaceous species on a bright, hot summer day. The plants were rooted in autoirrigated pots, similar to that shown in Fig. 4.10. (From Kramer, 1937.)



Radius of curvature (μm)	Hydrostatic pressure (MPa)
(a) 5.0	0.03
(b) 0.5	0.3
(c) 0.05	-3
(d) 0.01	-15
(e) 0.005	30

FIGURE 4.8. The origin of tensions or negative pressures in cell wall water of the leaf. As water evaporates from the surface film covering the cell walls of the mesophyll, water withdraws farther into the interstices between neighboring cells, and surface tension effects result in a negative pressure in the liquid phase. As the water potential decreases, liquid water remains only in the smaller cracks and crevices in and between cell walls, and the radius of curvature of the meniscus progressively decreases. As the radius of curvature decreases (dashed lines), the pressure decreases (becomes more negative), as calculated from the equation $P = -2T/r$, where T is the surface tension of water and r is the radius.

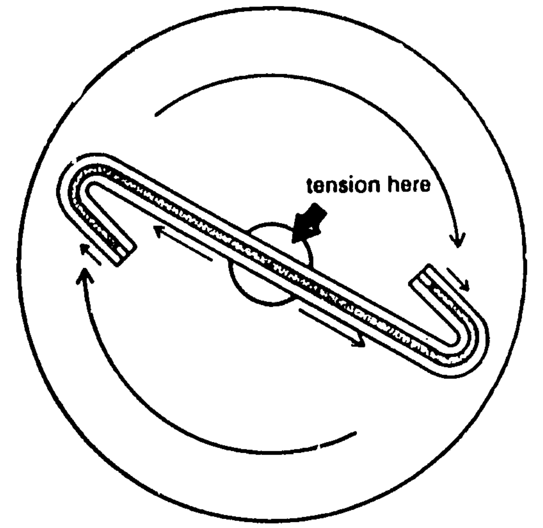


Figure 4-14 Method of measuring the cohesive properties of water utilizing a centrifuged Z-tube. Small arrows indicate the direction of centrifugal force and the principle of balancing. The shape of the Z-tube prevents water from flying out either end of the tube.

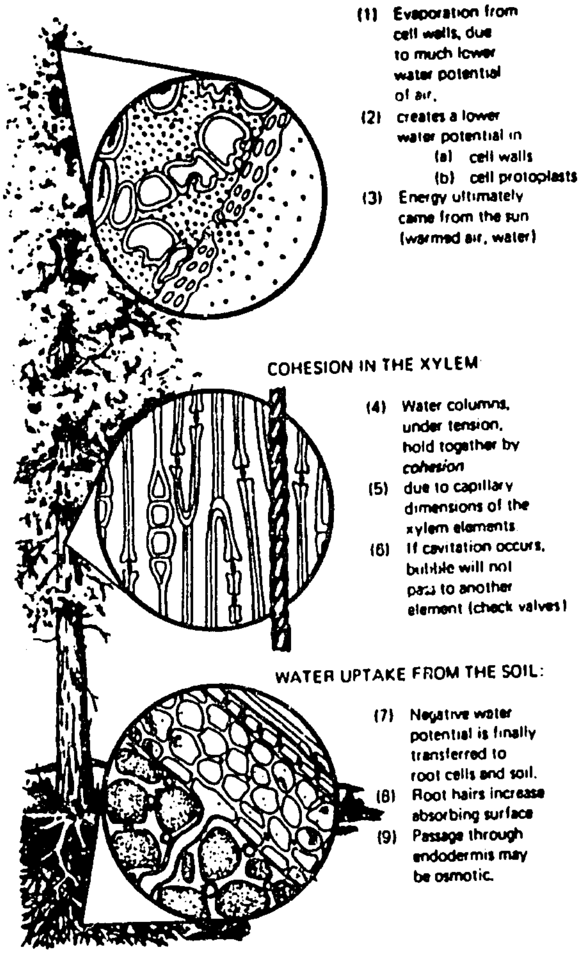


Figure 4-13 A summary of the cohesion theory of the ascent of sap

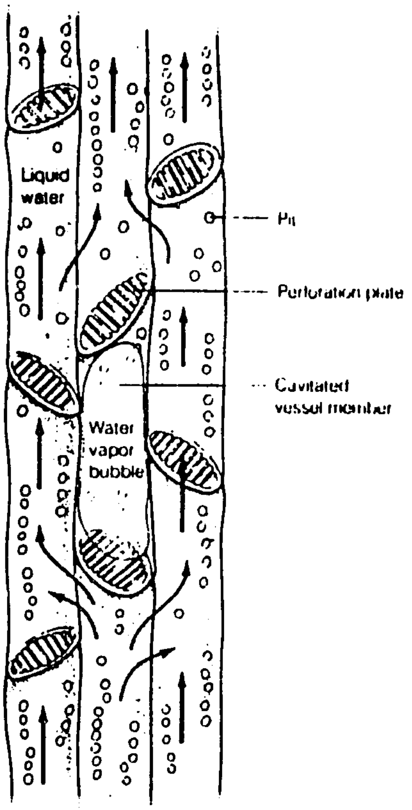


FIGURE 4.6. Detours around a vapor-locked vessel member. Tracheids and vessels constitute multiple, parallel, interconnected pathways for water movement. Cavitation in this example blocks water movement within the cavitated vessel member. However, because these water conduits are interconnected through wall pits, cavitation of a vessel or tracheid does not completely stop water movement in the cell file. Water can detour around the block by moving through adjacent tracheary elements. The spread of the vapor bubble throughout the xylem is eventually stopped by an imperforate end wall.

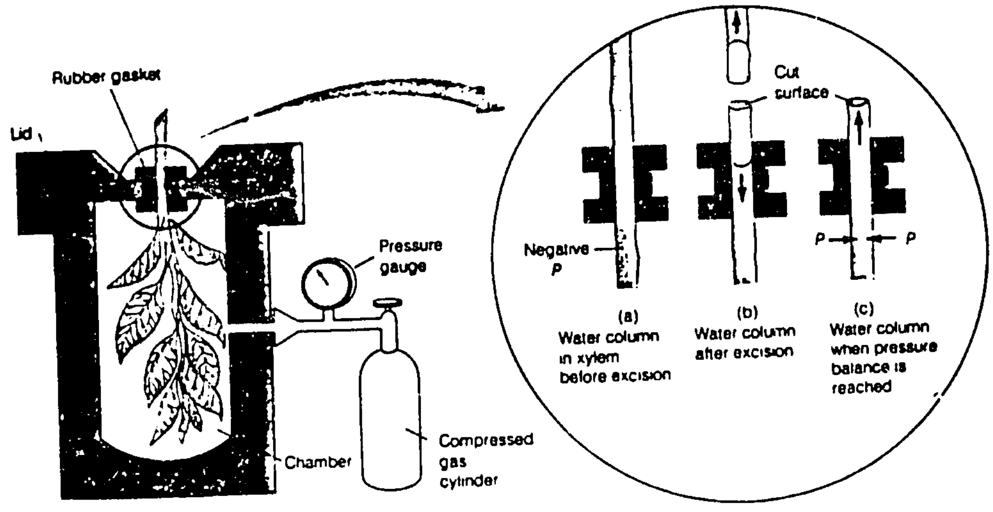


FIGURE 3.F. The pressure chamber method for measuring plant water potential. The diagram at the left shows a shoot sealed into a chamber, which may be pressurized with compressed gas. The diagrams at right show the state of the water columns within the xylem at three points in time. In (a), the xylem is uncut and under a negative pressure, or tension. In (b), the shoot is cut, causing the water to pull back into the tissue, away from the cut surface, in response to the tension in the xylem. In (c), the chamber is pressurized, bringing the xylem sap back to the cut surface.

LESSON ELEVEN

FACTORS AFFECTING WATER ABSORPTION

By the end of this lesson you should be able to:

....Express water absorption in terms of Ohm's law
....Describe the effect of transpiration on water absorption
....List the factors that affect root resistance to water
....Describe the relationship between soil moisture stress and water absorption
....Describe the effects of salinity, soil temperature, and aeration on water absorption

FACTORS AFFECTING WATER ABSORPTION

I. Ohm's Law and Water Absorption

The absorption of water is analogous to Ohm's law in that it is affected by the driving force, i.e. the difference between the water potential of the soil and that of the root xylem (or the Ψ gradient), and the resistance of the root to water.

$$Absorption=\frac{(WP_{soil})-(WP_{xylem})}{resistance_{roots}}$$

In moist, warm, well-aerated soils absorption is controlled by transpiration. Increased transpiration causes $\Psi_{root\ xylem}$ to become more negative by increasing the tension (negative pressure) in the xylem. This increases the difference between $\Psi_{soil} - \Psi_{root\ xylem}$, and that will increase the rate of absorption by increasing the Ψ gradient.

The efficiency of the root in extracting soil water depends upon the extent of the root system (i.e. how well roots have permeated the soil), and the resistance of the root to water, or the permeability of the root.

II. Root Resistance or Permeability to Water

A. Plant Factors

The effect of age and maturation on root permeability was discussed in Lesson Eight. In review, it is the region just behind the root tip that is most permeable to water. Beyond these first few mm the root begins to mature, and in doing so the outer layers become less permeable because of suberization. Still farther back from the tip cork development begins in secondary roots. If conditions are unfavorable for root growth, maturation continues, reducing the region available for favorable water absorption.

B. Soil Factors

1. Available Soil Water. As available water is removed from the soil, that which remains is bound more tightly, and it is less available than the initial soil water. Fig. 9.5 illustrates that in Indio sandy loam, 75% of the total soil water available was held with a tension less than -0.1 MPa, not much more than field capacity. The tension holding the remaining 25% increased markedly, requiring that the $\Psi_{root\ xylem}$ be even more negative in order for absorption to occur. If Ψ_{root} becomes as negative as Ψ_{soil} the plant will incur moisture stress. This may induce stomatal closure, which will in turn reduce transpiration. Since transpirational pull is the driving force for water absorption, absorption is reduced. Thus an increase in soil moisture stress may reduced water absorption.

2. Soil Solution - Salinity. In arid lands, where evapotranspiration potential exceeds precipitation, there is a

tendency for the soil solution to become saline. This process may be accelerated by irrigation. When the π_{soil} increases to 0.35 - 0.4 MPa, growth and yield are seriously depressed in most crops. Recall that the standard permanent wilting point is a soil moisture stress of -1.5 MPa, illustrating that the effect of salinity is more than its osmotic effect on water availability.

Plants vary in their tolerance to salinity, with crops such as cotton and sugar beet being much more tolerant than bean, tomato, and deciduous fruits. Excessive use of fertilizers can induce soil salinity in these agricultural crops.

Many plants adjust to salinity by absorbing salt into the cell vacuole in order to counter balance that in the soil solution. Other species may synthesize substances such as proline to provide osmotic adjustment.

High solute concentrations in the vacuole can affect the hydration of proteins (enzymes) and enzyme activity in the cell, disrupting cellular metabolism, and by this means reducing the permeability of the cell to water, or reducing root growth. The decreased root permeability may reduce water absorption, thus placing the plant under water stress (Fig. 9.10). Plants may adjust to some salinity if salinity increases gradually.

Succulence is a common characteristic of halophytes (saline adapted species).

3. Soil Temperature. Chilling the soil causes an increase in the viscosity of water, and a decrease in root permeability, growth, and salt accumulation. All these factors combine to reduce water absorption. Species from warm climates are more adversely affected by root chilling than species from cold climates. Roots are also damaged at high temperatures, generally above 30 degrees. (Figs. 9.4, 9.13)

4. Soil Aeration. A common cause of poor soil aeration is flooding. Flooding causes the soil to become anaerobic, and continued microbial activity in such soils may liberate CO_2 as well as toxins such as methane and H_2S, which can kill roots. Soil compaction also reduces soil aeration.

A decrease of soil oxygen to 17% adversely affects mycorrhizae. At 10% soil oxygen root growth slows, and at 3% mineral absorption is affected in most roots. When soil oxygen falls to 0% the permeability of the root to water is reduced so much that some flooded plants may actually wilt. CO_2 accumulation inhances the depressing effect of lack of oxygen on the permeability of the roots to water, and at 10% soil CO_2 many roots are killed.

Species that adapt to flooded soils, e.g. rice, mangrove, cypress, appear to do so by transferring oxygen to the root internally from the stem.

<u>Additional Reading:</u>

Kozlowski, T.T. et al. 1991. Physiological Ecology of Woody Plants. pp. 308-336.
Kramer, P. J. 1983. Water Relations of Plants. pp.235-261
Taiz, L., and E. Zeiger. 1991. Plant Physiology. pp.362-367.

Additional Reading:

Kozlowski, T.T. et al. 1991. Physiological Ecology of Woody Plants. pp. 308-336.

Kramer, P. J. 1983. Water Relations of Plants. pp.235-261

Taiz, L., and E. Zeiger. 1991. Plant Physiology. pp.362-367.

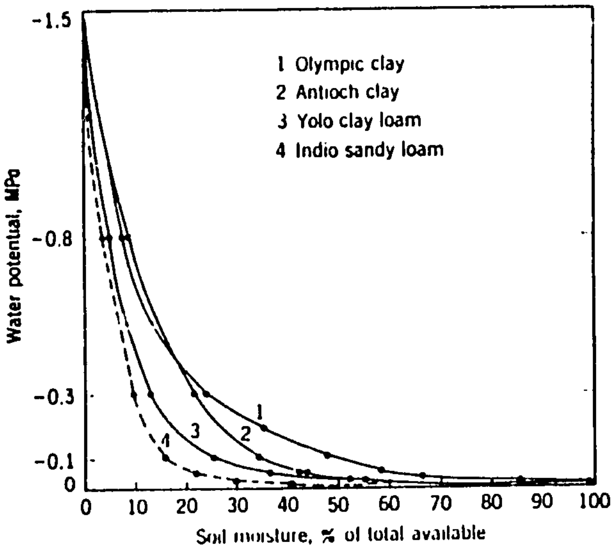


Fig. 9.5. Percentages of readily available water remaining in four soils at various soil water potentials. Curves were constructed from data for soil water potential over soil water content by assuming that available water occurs in the range from - 0.015 to - 1.5 MPa. (After Richards and Wadleigh, 1952.)

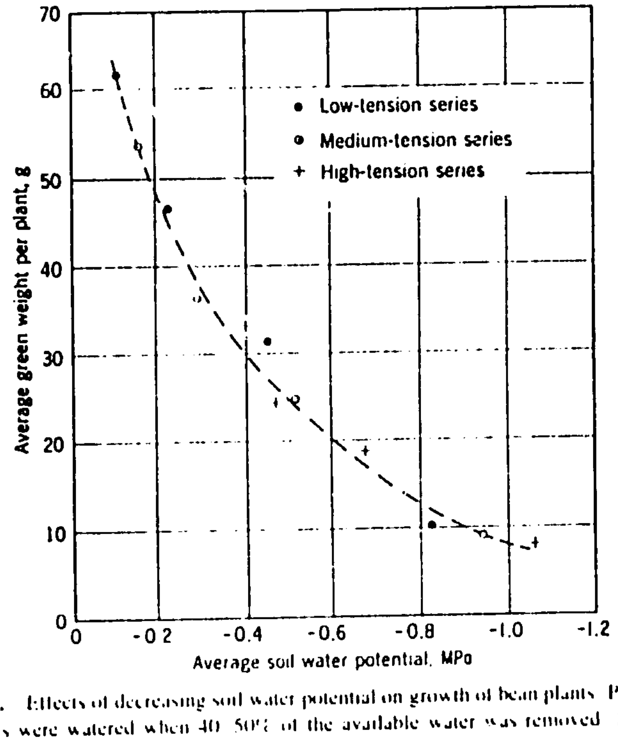


Fig. 9.10. Effects of decreasing soil water potential on growth of bean plants. Plants in the low-tension series were watered when 40–50% of the available water was removed. Medium-tension plants were watered when 60–65% of the available water was removed, and high-tension plants were not watered until 90–100% was removed. Each moisture series was subdivided into four groups which received no salt, 0.1%, 0.2%, or 0.3% salt. Reduction in yield was proportional to decrease in average water potential, whether the decrease was caused by low soil water content, high salt, or a combination of the two. For example, the highest yield was in low-tension soil containing no salt, and the lowest yield was in high-tension soil containing 0.3% salt. (From Wadleigh and Ayers, 1945.)

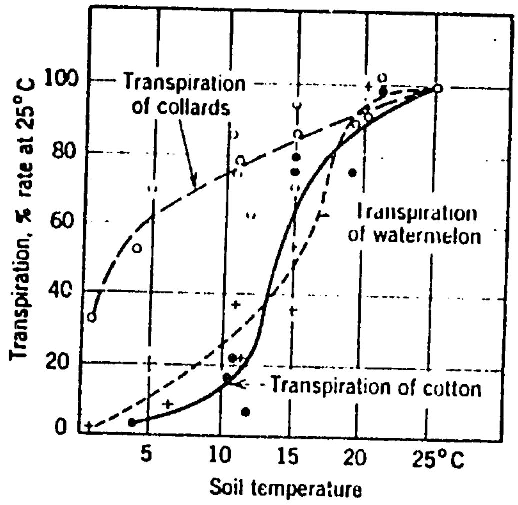


Fig. 9.4. Effects of low temperature on water absorption by plants of 3 species, measured by rates of transpiration. (From Kramer, 1942.)

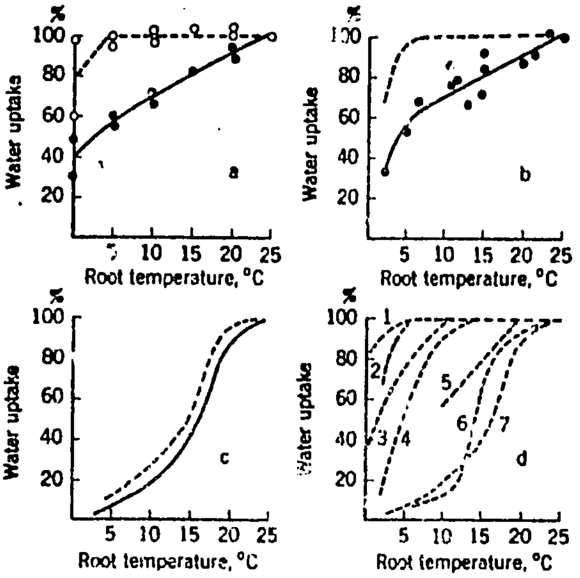


Fig. 9.13. The effect of temperature on water uptake through roots of white pine (a), cabbage (b), and watermelon (c). The solid curves are after Kramer (1942), and the dashed lines are corrected for differences in the viscosity of water at various temperatures. Graph (d) combines corrected curves from various sources: white pine (1), cabbage (2), citrus (3), sunflower (4), loblolly pine (5), cotton (6), and watermelon (7). The rate at 25°C was set as 100%. The critical temperature for reduction in root permeability is much lower in white pine (1) and cabbage (2) than in cotton (6) and watermelon (7). (From Kuiper, 1961.)

LESSON TWELVE

MINERAL ABSORPTION
THE RELATIONSHIP BETWEEN WATER AND MINERAL ABSORPTION

By the end of this lesson you should be able to:

....Compare the pathways of water with that of mineral nutrients from the soil solution, across the root, into the root xylem
....List the characteristics of active mineral absorption
....Describe the role of mineral accumulation on cell growth
....Describe the importance of mycorrhiza on the nutrition and water relations of forest plants
....Describe the source of the minerals accumulated by leaves

MINERAL ABSORPTION; THE RELATIONSHIP BETWEEN WATER AND MINERAL ABSORPTION

I. Absorption of minerals by roots

A. Root Growth. Root growth taps new soil reservoirs of water and minerals by growing into them. Any factor that affects root growth will affect water and mineral absorption.

B. Path of water and nutrients across the root. Nearly all of the mineral nutrients absorbed by plants are ions dissolved in the soil solution. Soil water is swept across the root in response to osmotic or transpirational pressure gradients and it carries the ions with it. Since most soil water travels through the *apoplast* (cell walls and intercellular spaces), each cortical cell is essentially bathed in an extension of the soil solution. This markedly increases the root surface area available for ion absorption.

When water reaches the endodermis it is forced through cell membranes. Although the membrane offers resistance to the passage of water, it is fairly water permeable. There are generally some unsuberized cells in the endodermis, and during rapid transpiration, water, along with its dissolved solutes, may be swept into the stele through these open, unsuberized windows, without being forced through a membrane. (Fig.6-8)

C. Characteristics of Mineral Absorption. Membranes are impermeable to ions. It requires metabolic energy to pull ions across the membrane into the cytoplasm of the cell, but once they are inside the cell, ions do not readily leak back out because of membrane impermeability.

Cells use metabolic energy to absorb ions. Much of the energy is used by ion carriers that pull ions across the membrane barrier. Ion carriers are special molecules that are specific, that is, one carrier is designed for K^+, another for Ca^{++}, etc. This allows the root to be selective, absorbing some ions more than others, and even excluding some ions, depending upon the presence and abundance of specific carriers. For example, most plants absorb far more K^+ than Na^+ even though there may be more Na^+ in the soil solution.

Cells accumulate ions in concentrations far above that of the soil solution. Accumulations of 100-fold are common.

All of the metabolically active cortical cells participate in ion absorption, and once ions are absorbed they enter the *symplast*. Recall that cytoplasmic strands pass from cell to cell through pores in the cell walls (*plasmodesmata*), and that this multicellular system of the cytoplasm is referred to as the symplast. See Fig. 6-8, 6-23.

Absorbed ions move in the symplast from cell to cell, eventually crossing the endodermis, also in the symplast. Once inside the stele, ions are secreted back across the membrane to the apoplast. In the apoplast (inside the stele) the ions are swept into the xylem, and transported to the leaf.

If transpiration is slow, the ions may accumulate in the root, increasing π_{root}, the osmotic concentration of the root. If the soil is moist this may result in the osmotic absorption of water (Lesson Ten), which in turn may induce exudation, root pressure, and other phenomena related to osmotic absorption.

When transpiration is rapid the absorbed ions are swept up the xylem stream to the leaf, where the leaf absorbs ions back into the symplast by the same process that occurred in the cortical cells of the root.

II. Ion absorption and Cell Growth

The vacuoles of newly divided cells are small and scattered. Soon after division the new cell begins to absorb ions, concentrating them in dispersed, small vacuoles. This lowers the Ψ_{cell} by an increase in π, and soil water enters the cell in response to the Ψ gradient. This increases turgor pressure P, and in young cells with thin, elastic cell walls, the vacuole expands and the cell grows.

During cell development additional cellulose is laid down in the cell wall, and the wall becomes less and less elastic, until sufficient wall material accumulates that it becomes rigid. At this point cell growth is complete, and the water potential component P becomes more significant because P cannot be dissipated by cell expansion. Compare the young and mature cells depicted in Fig. 2.1.

III. Mineral Absorption by Mycotrophy

Most forest plants do not absorb minerals directly from the soil solution, but from mycorrhizae. The strands of ectotrophic mycorrhizae (hyphae) form a mantle around the young root and penetrate the outer layers, growing to form a network (Hartig net) through the remaining root cells (Lesson Eight). The hyphae also penetrate the soil

Because hyphae are smaller in diameter and much more extensive than roots, they occupy the soil more intensively, exposing much more absorbing surface area than roots. Mycorrhizae are also more metabolically active than roots, and they liberate organic acids that dissolve soil minerals for absorption. For these reasons mycorrhizae absorb ions, as well as water, more efficiently than roots.

The minerals absorbed by the mycorrhizae are carried to the root by its hyphae, and then made available for root absorption but in a higher concentration than in the soil solution.

The efficient mineral and water absorption system provided by mycorrhizae permits tree growth especially in soils of low fertility. Today most forests are restricted to infertile soils because forests that occurred on fertile soils in the past have been removed, and the soil converted to agricultural use. For this reason, mycorrhizae are especially important.

Additional Reading:

Kozlowski, T. T. et al. 1991. Physiological Ecology of Woody Plants. pp. 240, 227-231

Salisbury, F., and C. Ross. 1985. Plant Physiology. pp.114-134.

Taiz, L. and E. Zeiger. 1991. Plant Physiology. 100-107

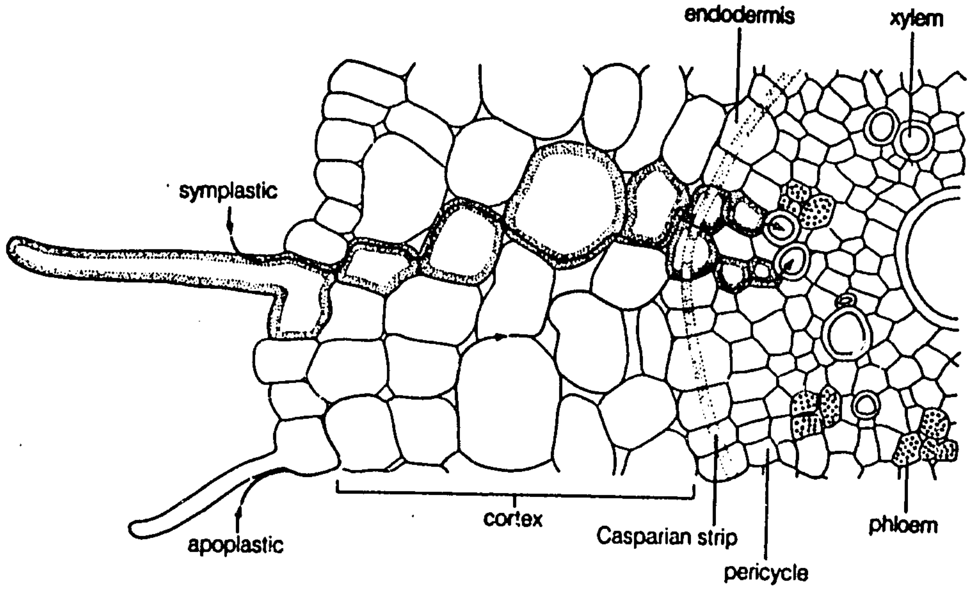


Figure 6-8 Anatomical aspects of symplastic and apoplastic pathways of ion absorption in the root-hair region. The symplastic pathway involves transport through the cytosol (stippled) of each cell all the way to nonliving xylem. The apoplastic pathway involves movement through the cell wall network as far as the Casparian strip, then movement through the symplasm. Casparian strip of endodermis is shown only as it would appear in end walls. (Redrawn from K. Esau, 1971.)

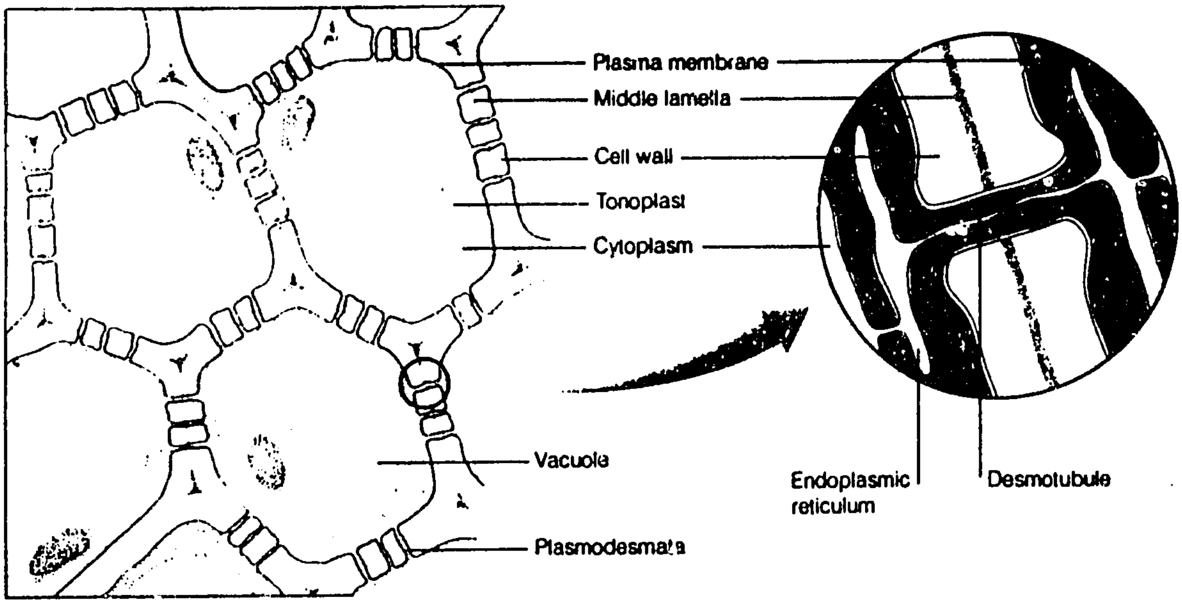


FIGURE 8.23. Diagram illustrating how plasmodesmata connect the cytoplasm of neighboring cells. Plasmodesmata are about 40 nm in diameter and allow free diffusion of water and small molecules from one cell to the next. Desmotubules provide a direct connection between endoplasmic reticula of adjacent cells.

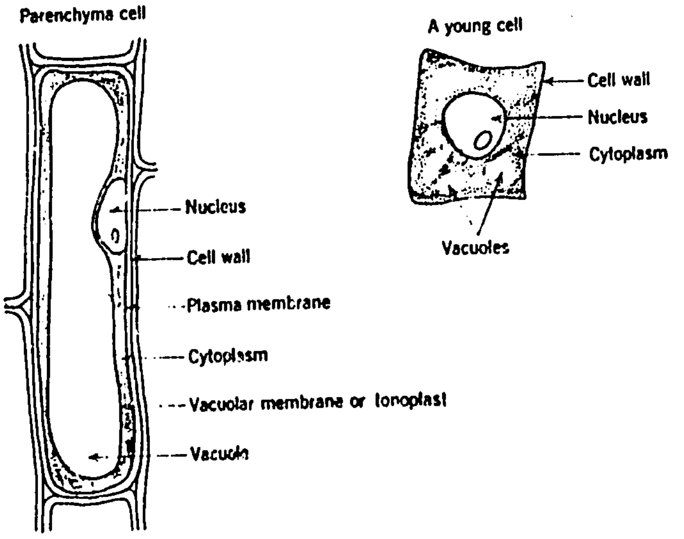


Fig. 2.1. Diagrams of a meristematic cell and a mature vacuolated parenchyma cell. The layer of cytoplasm in mature cells is usually much thinner than shown in this diagram.

LESSON THIRTEEN

THE ASCENT OF SAP

By the end of this lesson you should be able to:

....Describe the role of matrix potential in the flow of water from leaf vein xylem to the mesophyll cell surface
....Define the factor that limits mesophyll cells to remain turgid during water stress
....Distinguish between the advantages and disadvantages of the water conducting systems of angiosperms and gymnosperms
....Provide evidence for the lateral movement of sap
....Relate maximum Ψ_{xylem} and species habitat
....Explain the relationship between Ψ_{xylem}, tree height, and time of day
....Explain the ascent of sap in a mangrove growing in sea water
....Identify the source of the Ψ gradient that permits sap to be raised to the top of the tallest trees

THE ASCENT OF SAP

Sap ascends in response to transpirational pull, and that force originates in the leaf. Transpiration is the consequence of the exchange of gas between leaf and air that is essential for photosynthesis. As CO_2 diffuses into the leaf, H_2O diffuses out (Fig. 4.9).

I. Role of Matrix Potential

Water evaporates from mesophyll cell walls to replace that lost through the stomates by transpiration. The matrix potential by which each layer of water is held on the cell wall increases on layers of water closer to the wall (Fig. 4.8). If the matrix potential of the cell wall exceeds -1.5 MPa (equivalent to a radius of curvature <0.01 μm in Fig. 4.8), it will exceed Ψ_{cell} of most crops. In that case water will be drawn from the vacuole into the cell wall, causing the cell to loose turgor P and perhaps wilt. Species of arid climates compensate by an increase in π_{cell}. This decreases Ψ_{cell} and thus a more negative cell wall matrix potential must occur before loss of turgor.

The matrix potential of the cell wall causes sap to flow in the intercellular spaces, on the surface of cells, and between the fibrils of the cell wall, much like water flows across filter paper. As water evaporates from the surface of the cell into the substomatal cavity, sap flows from the xylem in the leaf vein to replace it, and in response to the matrix potential gradient. Xylem sap is placed under tension as a result. This tension is relayed down the xylem column to the root.

II. Design of Xylem Cells

Xylem cells have an almost fool-proof design, but the specific pattern varies between species adapted to different environments. The water conducting cells are of two major types: vessels and tracheids. (Fig. 4.5)

Vessels are larger in diameter (80 - 200 μm), and they have endwalls that may be perforated, or absent, so that a string of vessels may join in one long tube. Vessels may be from a few cm to several m in length, and they conduct water rapidly and at high velocity. The longest vessels are in ring porous wood and in vines. Vessels also have pits that permit the lateral movement of sap from one column to another.

Tracheids are much smaller in diameter, and they do not have end walls, but their walls contain abundant pits. Water passes from one tracheid to the next through pits. The pits are small enough to permit the passage of water, but too small to permit a vapor bubble to pass through. Surface tension at the vapor-liquid interface of the bubble is too great to permit passage through such a narrow opening. The velocity of sap movement in vessels is from 5 to 40 m hr^{-1}, whereas in tracheids velocity ranges from 0.5 - 1.2 m hr^{-1}.

Vessels are prominent in broadleaf angiosperms. These trees are found in regions with a dependable water supply during the growing season, either from precipitation or ground water. Their large leaf surfaces capture light for rapid photosynthesis (and growth), but the leaf transpires heavily as a consequence. This requires an efficient water conducting system, and vessels provide it. However, the large diameter of vessels makes them more susceptible to cavitation. Vessels with end walls can confine the cavitation to a single vessel while water moves laterally around it (Fig. 4.6). But the long vessels that transport sap so efficiently are seriously compromised by cavitation because the conduit becomes blocked for a substantial distance.

Gymnosperms such as conifers do not have vessels. Because their tracheids are quite narrow and without end walls, cavitation is confined to a single tracheid. In addition, the vapor is more likely to be reabsorbed than in large diameter vessels. Conifers are more likely to be able to tolerate high water stress conditions that cause cavitation in angiosperms, but as importantly, they are able to survive the consequence of cold winters that freeze the sap. Gases are not soluble in ice, so any gas dissolved in the sap that is frozen will form a bubble, and cause cavitation. In the spring bubbles in tracieds dissolve in the thawed, moving sap. The larger bubbles in vessels may not dissovle, maintaining cavitation, and compromising the water conduction capabilities of the vessel.

Neither vessels nor tracheids remain efficient water conducting systems indefinitely. In time, cavitation accumulates, xylem elements become plugged with gums and other chemicals, and tyloses (special cells in the wood) grow into xylem cells, plugging them. It is by this process that the non-conducting heartwood is formed. Heartwood is not useless; it may store chemicals used in defense or nutrients, and water that may be withdrawn from heartwood in times of stress. But nearly all ascent of sap takes place in sapwood. There is an excellent correlation between cross-sectional sapwood area of a stem and dependent characteristics such as total leaf area or weight in the crown.

The pits in vessels and tracheids permit water to move laterally in the stem. This can be demonstrated by making crosscuts partially across the stem, and then attaching a cup to the stem using modeling clay below the crosscuts. A dye, e.g. acid fuscin, can be placed in the cup, and then a whole drilled though the dye into the wood. The dye will be drawn into the xylem stream in a transpiring plant, marking the path of transport. Using this technique lateral paths around the crosscuts can be visualized (Fig. 10.5)

Rapid transpiration can place so much negative tension on xylem cells that they are pulled inward, and when this happens all across the stem, the diameter of the stem decreases. Tracings of this may be seen in Fig. 7.10.

III. Xylem Water Potential

Water tension in the xylem is measured with a pressure bomb and expressed as Ψ_{xylem}. There is a relationship between the magnitude of Ψ_{xylem} developed by a species and its ecological distribution. Fig. 4.15 illustrates that the Ψ_{xylem} of hydrophytes is about -1.0 MPa, of forest plants -1.5 MPa, of desert plants up to -8.0 MPa, and about -5.0 MPa for sea shore plants that must compensate for the salinity of the sea.

There is also a relationship between the magnitude Ψ_{xylem} and the height of the tree. Fig. 10.11 illustrates Ψ_{xylem} measured at 30 m and 79 m up the stem, and throughout the day. These trees had a pre-dawn Ψ_{xylem} of -0.5 and -1.0 MPa for the lower and upper branches respectively, indicating the requirement for a more negative Ψ to compensate for gravity in the taller tree. The Ψ_{xylem} became progressively more negative during the day, reaching -1.6 and -2.25 MPa respectively by noon. After noon Ψ_{xylem} became less negative, indicating water stress caused stomatal closure. The reduction of transpiration caused by stomatal closure with the same rate of water absorption should relieve moisture stress in time. However, photosynthesis is also restricted following stomatal closure. For this reason some trees may photosynthize more on cloudy days (reduced moisture stress and open stomates) than on sunny days.

IV. Magnitude of the Drying Power of the Air

A summary of forces involved in the ascent of sap is given in Figs. 4-13 and 4.15. The ultimate driving force is the sun, which provides the energy required to evaporate sap in the leaf, and to warm the air. Note that at 50% relative humidity the Ψ_{air} was -94 MPa. In would require a pressure of 1 ton cm^{-2} on the water in the atmosphere to raise its free energy equal to that of the water vapor at 100% inside the leaf! This Ψ gradient from soil-root-stem-leaf-air (as illustrated in Fig. 4.15) is far more than enough to pull water in large volume and velocity to the tops of the tallest trees, providing there is a proper conducting system. The design of the xylem and the adhesive and cohesive properties of water provides that system.

The special case of the ascent of sap in mangrove is illustrated in Fig. 4-17. Mangrove must compensate for the salinity of the sea which bathes its roots, and it does so by increasing π_{root} and π_{leaf}. Follow the Ψ from sea through tree to air in this illustration. Also note that a downward flow is depicted in the phloem. This will be the topic of the next lesson on the circulatory system of plants.

Additional Reading:

Kramer, P. J. 1983. Water relations of Plants. pp. 262-284
Salisbury, F. and C. Ross. Plant Physiology. pp. 75-94
Taiz, L., and E. Zeiger. 1991. Plant Physiology. pp. 84-92

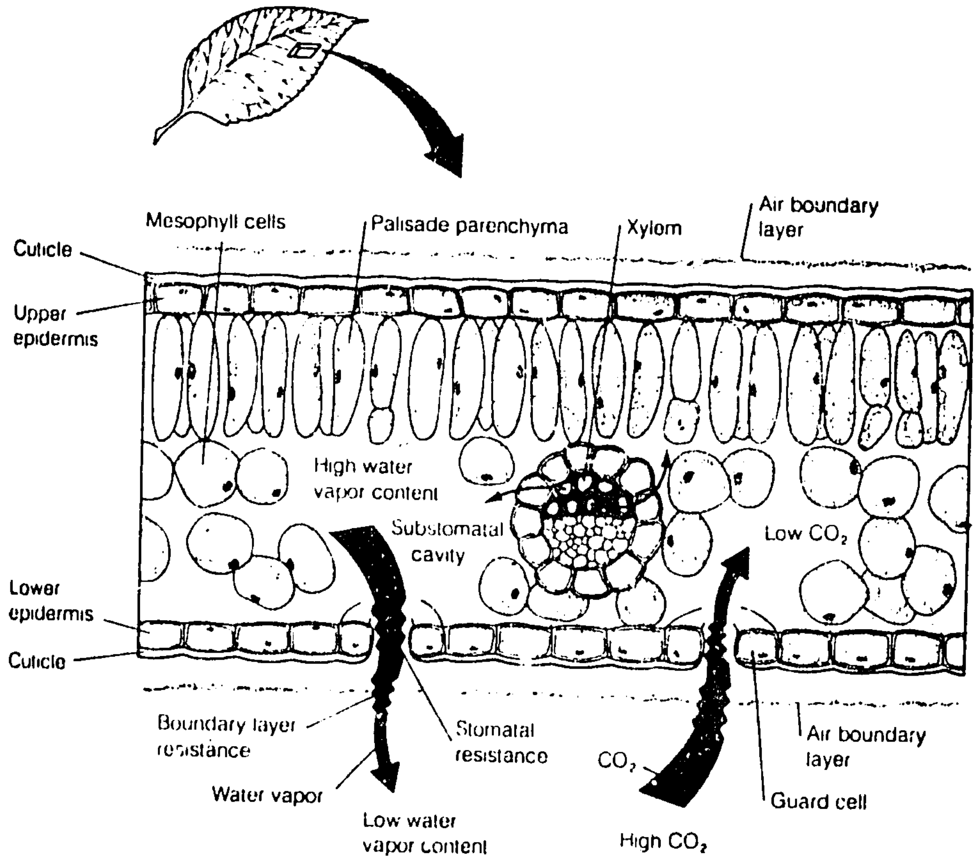
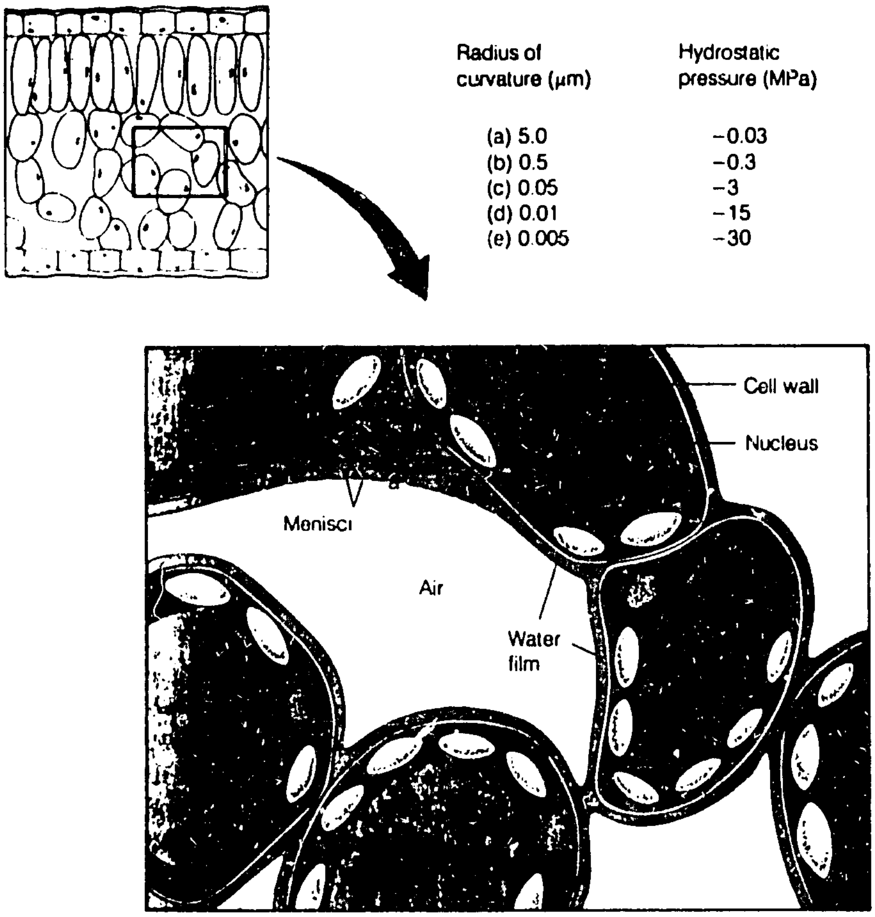


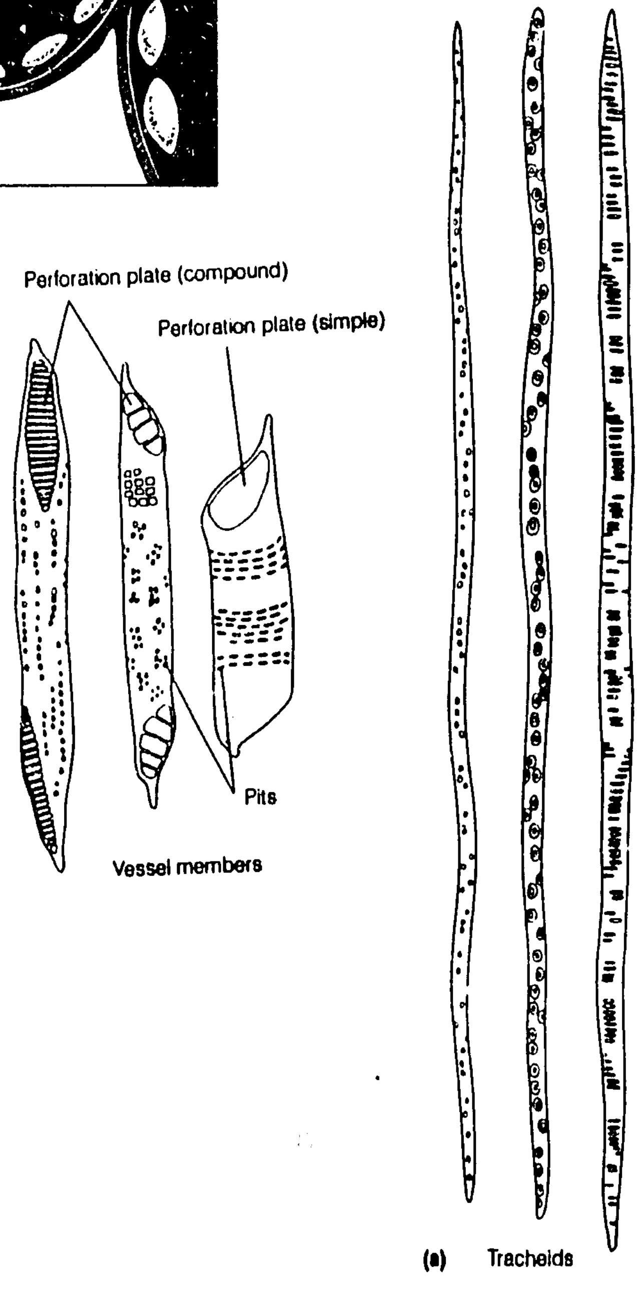
FIGURE 4.8. The water pathway through the leaf. Water is drawn from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces within the leaf. By diffusion, water vapor then moves through the leaf air space, through the stomatal pore, and across the boundary layer of still air that adheres to the outer leaf surface. CO_2 also diffuses into the leaf through stomata along a concentration gradient.

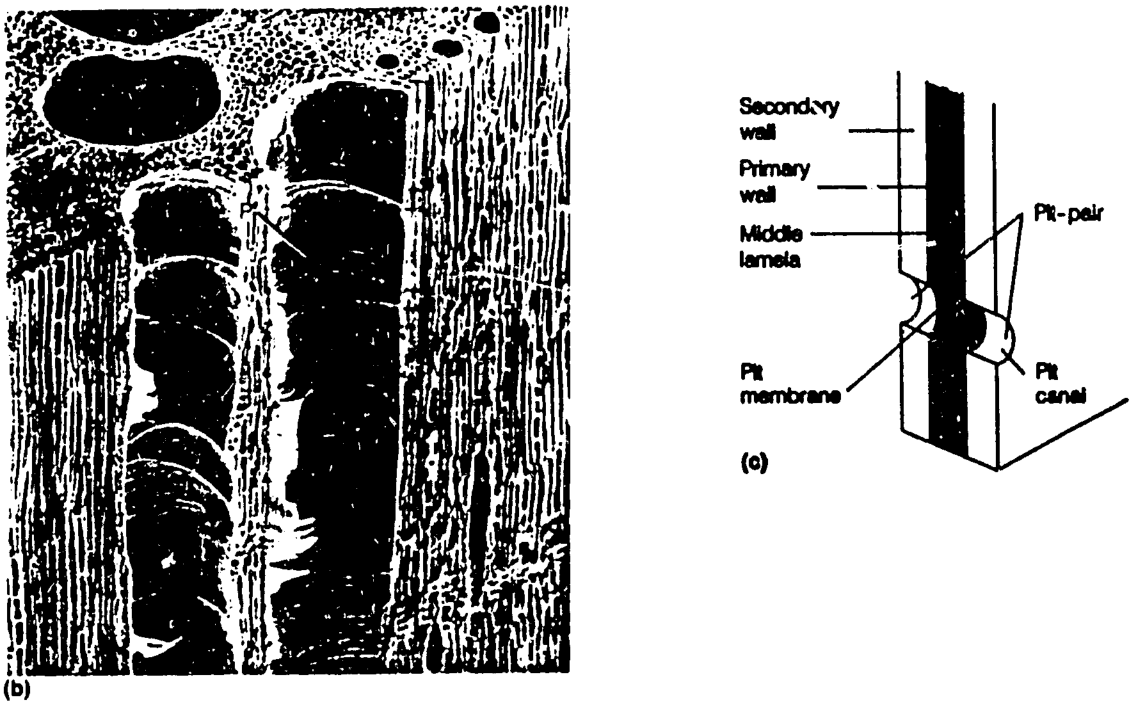


Radius of curvature (μm)	Hydrostatic pressure (MPa)
(a) 5.0	−0.03
(b) 0.5	−0.3
(c) 0.05	−3
(d) 0.01	−15
(e) 0.005	−30

FIGURE 4.4. The origin of tensions or negative pressures in cell wall water of the leaf. As water evaporates from the surface film covering the cell walls of the mesophyll, water withdraws farther into the interstices between neighboring cells, and surface tension effects result in a negative pressure in the liquid phase. As the water potential decreases, liquid water remains only in the smaller cracks and crevices in and between cell walls, and the radius of curvature of the meniscus progressively decreases. As the radius of curvature decreases (dashed lines), the pressure decreases (becomes more negative), as calculated from the equation $P = -2T/r$, where T is the surface tension of water and r is the radius.

FIGURE 4.5. (a) Structural comparison of tracheids and vessel members, two classes of tracheary elements involved in xylem transport of water. Tracheids (left) are elongate, hollow, dead cells with highly lignified walls. The walls contain numerous pits—regions where secondary wall is absent but primary wall remains. The shape and pattern of wall pitting vary with species and organ type. Tracheids are present in all vascular plants. Vessels consist of a stack of two or more vessel members (right). Vessel members are also dead cells and are connected to one another through perforation plates—regions of the wall where a pore or hole in the wall has developed. Vessels are connected to other vessels and to tracheids through pits. Vessels are found in most angiosperms and are lacking in most gymnosperms.
(b) Scanning electron micrograph of red oak wood showing stacks of individual vessel members (VM) comprising a portion of a vessel. Large pits (P) are visible on the side walls (100 ×). (Photograph courtesy of W. A. Côté.) (c) Diagram of a simple pit pair.





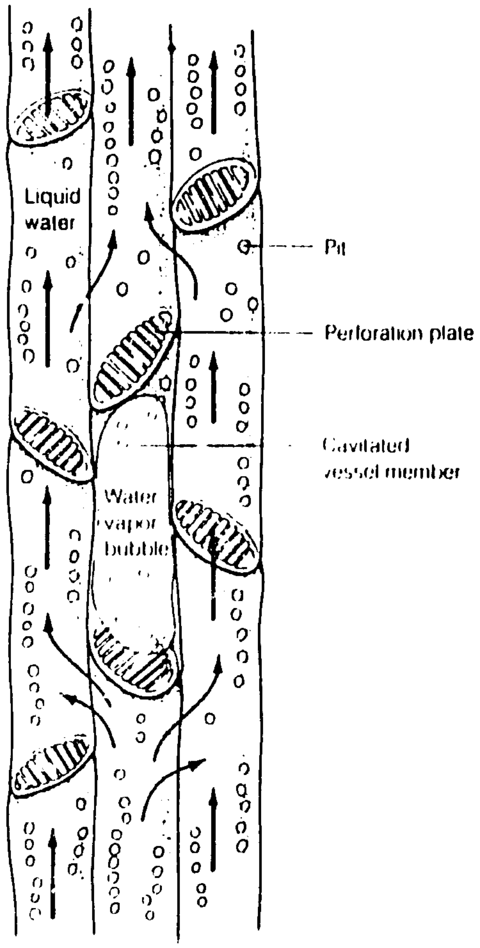


FIGURE 4.6 Detours around a vapor-locked vessel member Tracheids and vessels constitute multiple, parallel, interconnected pathways for water movement Cavitation in this example blocks water movement within the cavitated vessel member However, because these water conduits are interconnected through wall pits, cavitation of a vessel or tracheid does not completely stop water movement in the cell file. Water can detour around the block by moving through adjacent tracheary elements The spread of the vapor bubble throughout the xylem is eventually stopped by an imperforate end wall.

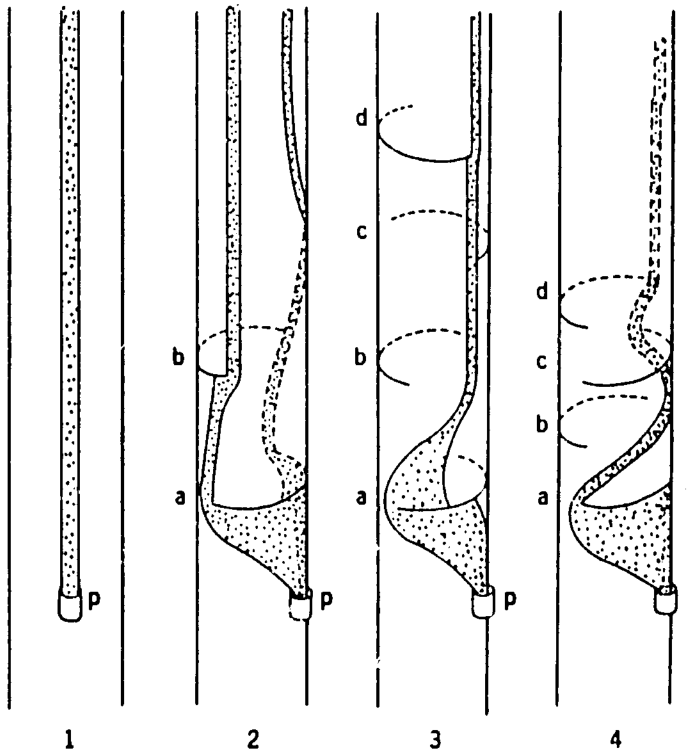


Fig. 10.5. Diagrams showing movement of ^{32}P around cuts in trunks of pine trees. The cuts are designated as a, b, c, and d. ^{32}P was supplied at point p, and the stippled areas indicate the path followed by the isotope. (After Postlethwait and Rogers, 1958; from Kramer and Kozlowski, 1979, by permission of Academic Press.)

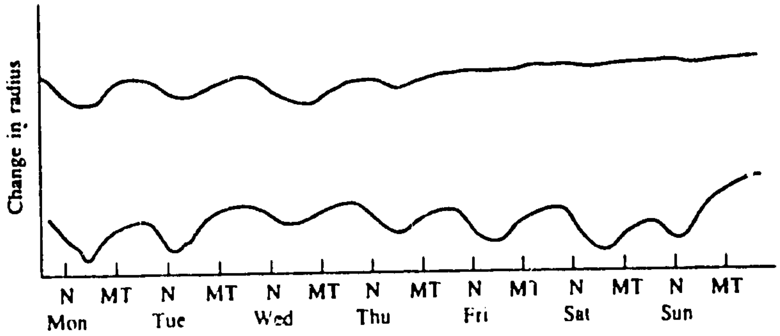


Figure 7.10 Dendrograph traces showing afternoon shrinkage and night swelling of red pine stems during the summer. The upper tracing (July 10–17) shows no daily shrinking and swelling during the latter part of the week, but only continuous diameter growth because cloudy, rainy weather reduced transpiration. The lower trace is for a week of sunny weather, August 21–28. (From Kozlowski, 1968c.)

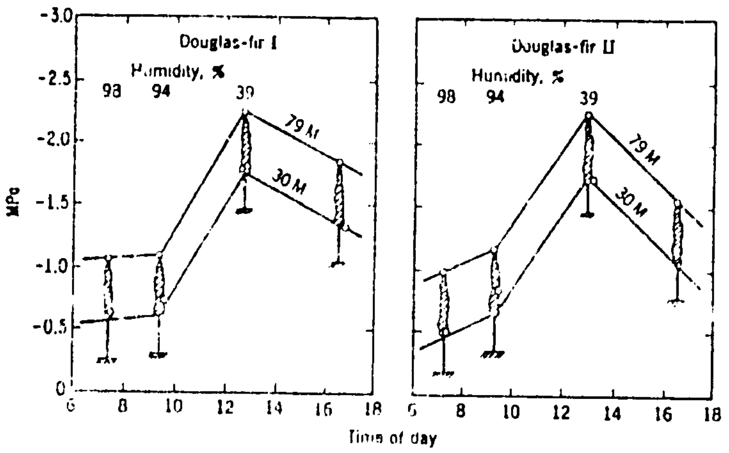


Fig. 10.11. Differences in xylem water potentials, measured with a pressure chamber, of twigs from upper and lower parts of crowns of Douglas-fir trees. (From Scholander *et al.*, 1965.)

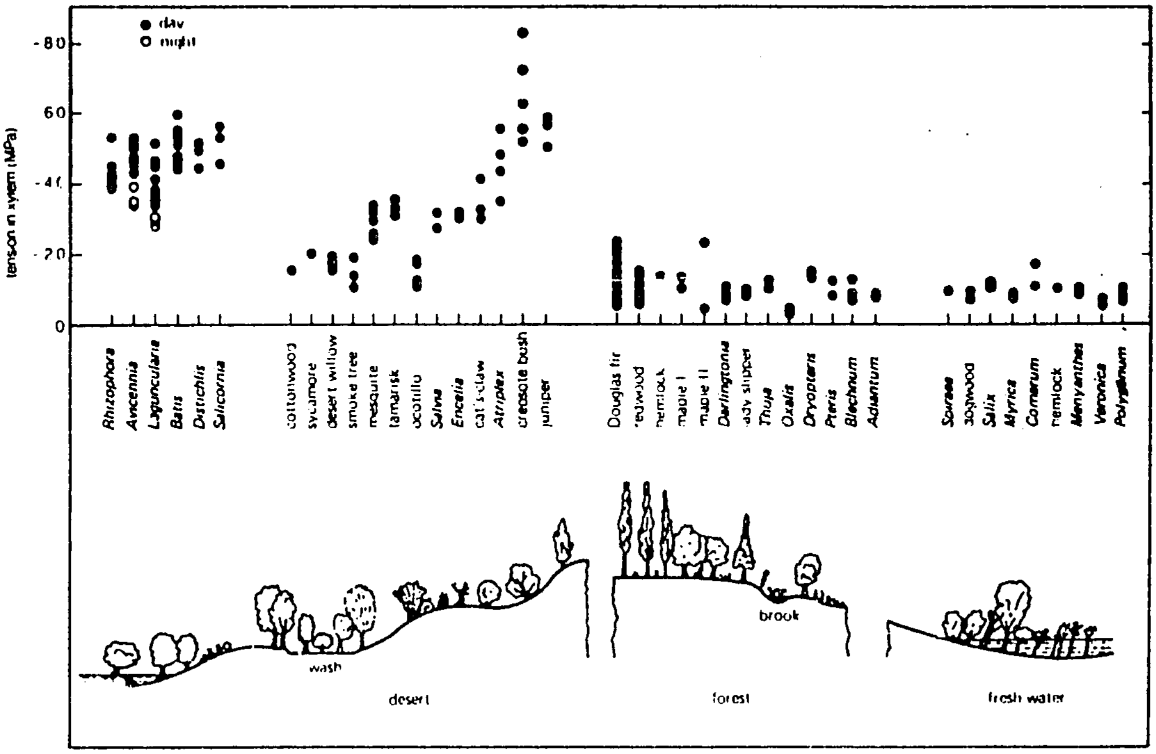


Figure 4-15 Negative sap pressures in a variety of flowering plants, conifers, and ferns. Most measurements were taken with a pressure bomb during the daytime in strong sunlight. Night values in all cases are likely to be several tenths of megapascals higher (less negative). (From Scholander et al., 1965; used by permission.)

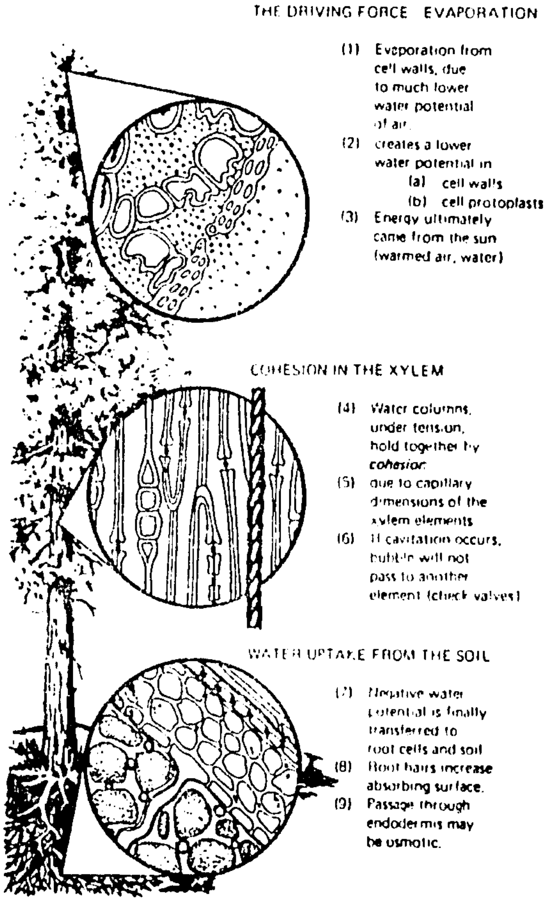
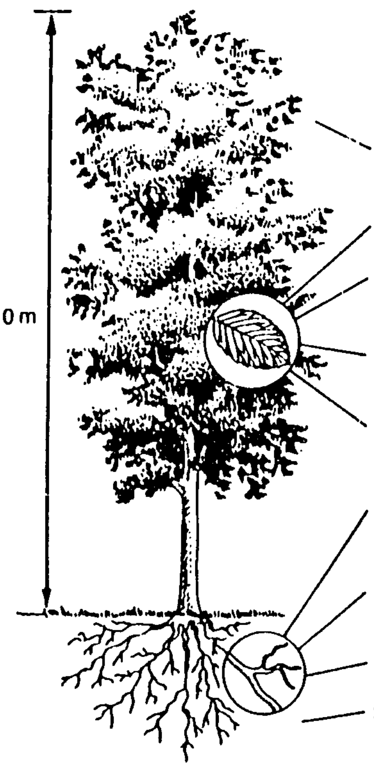


Figure 4-13 A summary of the cohesion theory of the ascent of sap.



LOCATION	Water Potential and Its Components (in MPa)				
	ψ	P	$-\pi$	$\rho_w gh$	$\frac{RT}{\bar{V}_w}\ln(\mathrm{RH})$
Outside air (relative humidity=50%)	−95.1			0.1	−95.2
Leaf internal air space	−0.8			0.1	−0.9
Cell wall of mesophyll (at 10 m)	−0.8	−0.7	−0.3	0.1	
Vacuole of mesophyll (at 10 m)	−0.8	0.2	−1.1	0.1	
Leaf xylem (at 10 m)	−0.8	−0.8	−0.1	0.1	
Root xylem (near surface)	−0.6	−0.5	−0.1	0.0	
Root cell vacuole (near surface)	−0.6	0.5	−1.1	0.0	
Soil adjacent to root	−0.5	−0.4	−0.1	0.0	
Soil 10 mm from root	−0.3	−0.2	−0.1	0.0	

FIGURE 4.15. Representative overview of water potential and its components at various points in the transport pathway from the soil through the plant to the atmosphere. Water potential ψ can be measured through this continuum, but the components vary. In the liquid part of the pathway, pressure (P), osmotic pressure (π), and gravity ($\rho_w gh$) determine ψ, whereas in the air, only the effects of gravity and relative humidity—$RT\ln(\mathrm{RH})/\bar{V}_w$—are important. Note that although the water potential is the same in the vacuole of a mesophyll cell and in the surrounding cell wall, the components of ψ can differ greatly (e.g., in this example P inside the mesophyll cell is 0.2 MPa and outside the cells is −0.7 MPa). (After Nobel, 1983.)

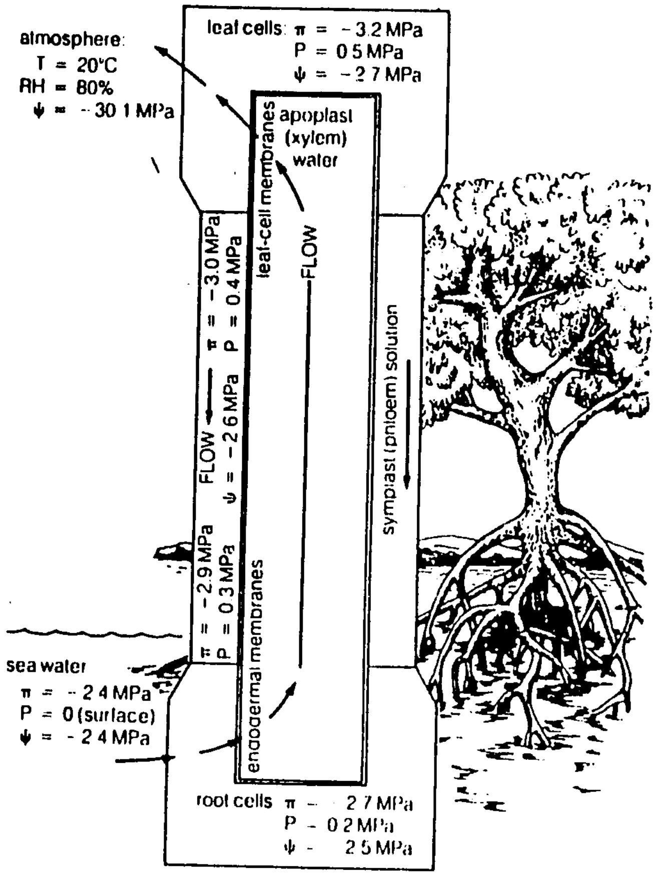


Figure 4-17 Water relations of a mangrove tree growing with its roots immersed in sea water. The diagram indicates the "essential" parts of the mangrove tree in this context. The endodermal membrane keeps salt out of the xylem (except for negligible amounts), and the leaf-cell membranes maintain a high solute concentration in the cells. The result is that water in the xylem must be under considerable tension both day and night to remain in equilibrium with sea water, and leaf cells have such a negative osmotic potential that they absorb water from the xylem in spite of its tension and low water potential. Only osmosis keeps the leaf cells from collapsing. (Data based on Scholander et al., 1965, but the hypothetical numbers have been modified to better match the discussions in this chapter and in Chapter 7.)

LESSON FOURTEEN

THE CIRCULATORY SYSTEM OF PLANTS

By the end of this lesson you should be able to :

....Describe the Munch hypothesis of phloem transport, including the identification of sugar source and sinks, how phloem pressure gradients develop, and how water flows from xylem to phloem at the sugar source, and from phloem to xylem at the sink

THE CIRCULATORY SYSTEM OF PLANTS

Water and minerals are transported upward from the root in the xylem. Sugars are created by photosynthesis in the leaf, and transported to the tissues where they are used (e.g. developing fruits, cambium, the roots) in the phloem.

The transporting cells of the phloem are sieve tubes. Sieve tubes react quickly to injury by forming a plug (callous) that prevents leakage from the injured cell. The formation of callous made studies of the phloem difficult until it was noticed that aphids insert their stylet into sieve tubes without inducing the callous-forming response. Aphid activity allowed the contents of sieve tubes to be sampled and studied.

I. Sugar Source and Sinks

Fluid in the sieve tube is under pressure. This phenomenon can be confirmed by aphid observations. After inserting its stylet into a sieve tube the aphid is force fed as phloem sap is forced under pressure through its body, forming a droplet at its anus. These droplets often fall to the ground creating a sticky surface. Phloem sap continues to flow through the stylet after the aphid body has been cut free from it.

Analysis of phloem sap collected from detached aphid stylets disclosed that the major solutes are sugars, usually di- and trisaccarides. The concentration of sugars decreased the further down the stem from the leaf the sap was collected. This gave rise to the terminology of the leaf as the *source* (of sugars), and the tissues where sugars are used as *sinks*.

Figure 7-24 illustrates the change in sugar (osmotic) concentration determined in the phloem sap of *Salix* collected from aphid stylet extracts. Analyses disclosed $\pi_{\text{upper stem}}$ = 1.344 MPa, and $\pi_{\text{lower stem}}$ = 1.053 MPa. Using the water potential equation (Lesson Three), assumming that $\Psi_{\text{xylem}} = \Psi_{\text{phloem}}$ at their respective upper and lower sampling points, and that the Ψ_{xylem} is more negative (-0.400 MPa) at the upper stem than the lower stem -(0.223 MPa, also see Fig. 10.11 in Lesson Thirteen), the phloem pressure gradient can be determined:

	Ψ	=	π	+	P
Upper Stem:	-0.400	=	-1.344	+	0.944
Lower Stem:	-0.223	=	-1.053	+	0.830

The phloem pressure gradient of 0.114 MPa converts to 0.073 MPa m^{-1}, and since 1 MPa = 10 kg cm^{-2}, the pressure gradient converts to 0.73 kg cm^{-2} m^{-1}. It is this pressure gradient that transports the sugars created in photosynthesis to sinks throughout the plant.

II. The Münch Hypothesis

Fig. 7-5 shows a laboratory model of the Münch Hypothesis of phloem transport. When sugar is placed into a bag permeable to water but not sugar, and then the bag placed into water, water flows into the bag by osmosis and creates pressure. If the bag is attached to another bag containing a less concentrated sugar solution, the pressure created in the second bag will not be as great as the first with its more concentrated solution. This creates a pressure gradient. Water carrying the concentrated sugar solution will flow from the first bag to the second in response to the pressure gradient. The first bag containing the concentrated sugar solution represents the source, or leaf, and the second, the sink, or roots, cambium, etc.

Fig. 7.20 illustrates upward xylem sap transport under Ψ gradient of -0.8 MPa - (-0.6 MPa) = 0.2 MPa. At the leaf source sugars are being loaded into the sieve cell creating $\Psi_{phloem\text{-}source} = -1.1$ MPa. Xylem sap ($\Psi = -0.8$ MPa) should flow to the sieve tube at the source, creating $P_{phloem} = 0.6$ MPa.

As sugars are consumed by sink cells the π_{phloem} is reduced from 1.7 MPa at the source to 0.7 MPa at the sink, creating a pressure gradient of 0.3 MPa that can induce pressure flow in the phloem.

Water leaves the phloem sink cell for the xylem in response to a Ψ gradient of 0.2 MPa, completing the circulatory system.

Demonstrate to yourself that this circulatory system can operate without transpiration (e.g. during the night), but not without photosynthesis (e.g. after leaf drop in the autumn).

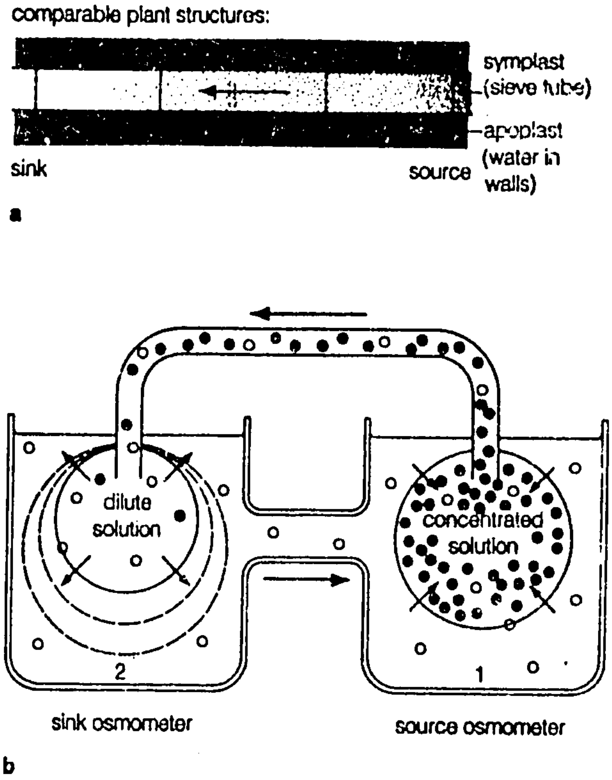


Figure 7-5 Bottom: A laboratory model consisting of two osmometers and illustrating the pressure-flow theory of solute translocation as proposed by Münch. Note that the concentration of the solute present in the largest amount (represented by black circles) will control the rate and direction of flow, while more dilute solutes (open circles) will move along in the resulting stream. Dashed lines on the left imply that flow will occur if pressure is relieved by expansion of the osmometer as well as by outward movement of water. Top: A schematic suggestion of how the model might apply to the concentrated solutions in the phloem system (symplast) surrounded by the dilute solutions of the surrounding apoplast. Solute concentration is maintained high at the source end of the system as sugars and other solutes are moved into the sieve tubes there; concentrations are low at the sink end as solutes are moved out, which also occurs to some extent along the route from source to sink. Lowered concentration of solutes at the sink end allows water to move out in response to the pressure transmitted from the source end (or in response to even higher concentrations of solutes in the apoplast at the sink.) Sieve tubes do not expand in analogy to the expanding osmometer of the laboratory model, but growth of storage cells at the sink will cause absorption of water from the apoplast, lowering its water potential and thus facilitating exit of water from sieve tubes there.

<u>Additional Reading</u>:

Salisbury, F., and C. Ross. 1985. Plant Physiology. pp.135-160.

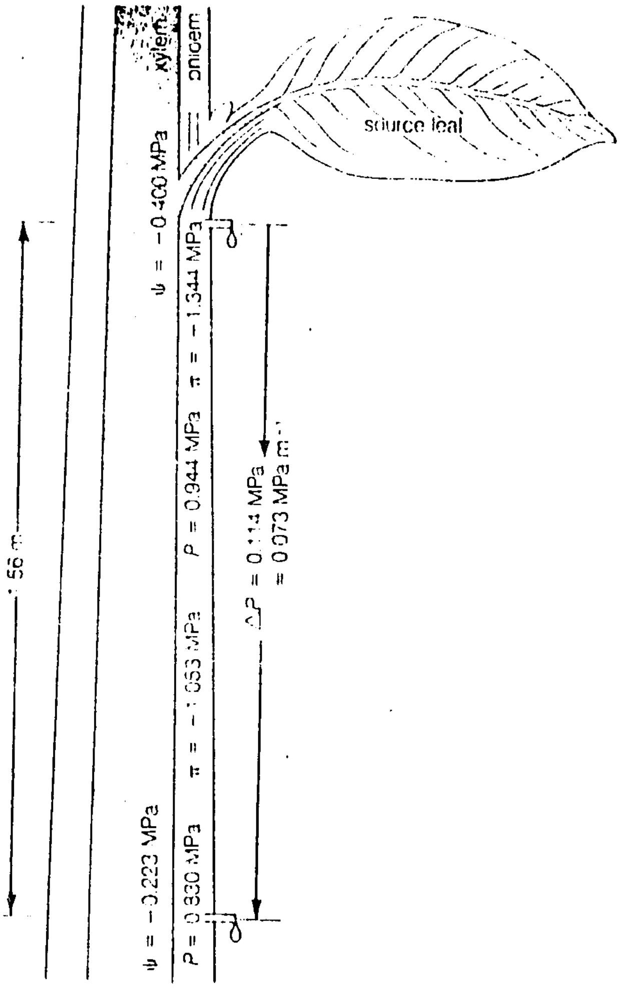


Figure 7-24 The osmotic quantities in phloem sieve tubes and xylem (apoplast) of a young willow *(Salix viminalis)* sapling. The osmotic potentials (π) were determined on phloem sap exuded from aphid stylets, water potentials (ψ) of the apoplast (bark samples) were determined with a vapor psychrometer system (see Figs. 2-5 and 2-9), and pressures (P) in the sieve tubes were calculated by assuming that water potential of the phloem sap was in equilibrium with that of the surrounding tissues ($P = \psi - \pi$) including xylem. Note that there is a positive pressure gradient (ΔP) in the sieve tubes from the apex toward the base, even though there is an opposite gradient in the water potential of the apoplast (caused by tension in the xylem plus matric forces). The pressure gradient of about 0.07 MPa m^{-1} is ample to drive a pressure flow of sap through sieve tubes. (Data are averages from several experiments of S. Rogers and A. J. Peel, 1975.)

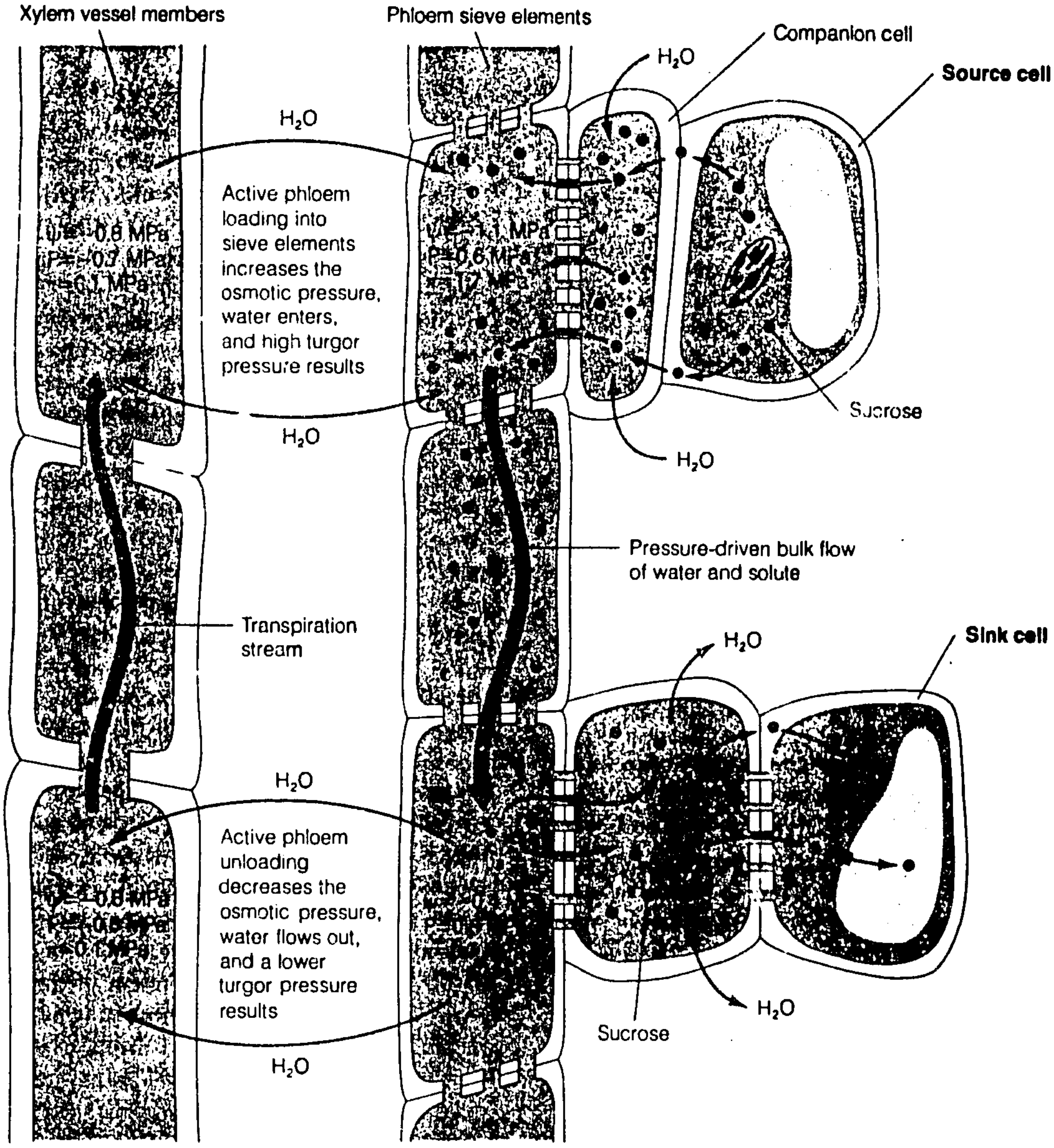


FIGURE 7.20. Schematic diagram showing the pressure-flow model. In the source, sugar is actively loaded into the sieve element–companion cell complex. Water enters the phloem cells osmotically, building up a high turgor pressure. At the sink, as sugars are unloaded, water leaves the phloem cells and a lower pressure results. Water and its dissolved solutes move by bulk flow from the area of high pressure (source) to the area of low pressure (sink). Possible values for ψ, P, and π in the xylem and phloem are illustrated. (From P. S. Nobel.)

LESSON FIFTEEN

TRANSPIRATION

By the end of this lesson you should be able to:

....List the sources from which water vapor may be lost from plants

....Define absolute humidity, relative humidity, vapor pressure, vapor pressure deficit

....List the factors that affect C_{leaf} - C_{air} in the transpiration equation

....List the factors that affect r_{leaf} in the transpiration equation

....List the factors that affect r_{air} in the transpiration equation

....Describe the role of energy in transpiration

....List three ways of measuring transpiration

I. The Process of Transpiration

Transpiration is a special form of evaporation. Evaporation can be described by a simple formula:

$$Evaporation = \frac{C_{source} - C_{air}}{r_{air}}$$

or

$$Evaporation = \frac{e_{source} - e_{air}}{r_{air}}$$

where:
C = absolute humidity in g m^{-3}; r = resistance in seconds cm^{-1}; and e = water vapor pressure in KPa, kilopascals

The driving force for evaporation is the difference in water potential across a boundary, expressed in the above formulas as the difference in the concentration of water at the source (e.g. lake surface or soil), with that of the air. Concentration can be expressed as the difference in the water vapor content of the air C, or as the difference in vapor pressure e.

The rate of evaporation is determined by the resistance to the flux of water across that boundary.

Similarly, transpiration may be described as:

$$Transpiration = \frac{C_{leaf} - Cair}{r_{leaf} + r_{air}}$$

or

$$Transpiration = \frac{e_{leaf} - e_{air}}{r_{leaf} + r_{air}}$$

Transpiration is defined as the loss of water vapor from plants. Water vapor can be lost from lenticels in the bark, and through the cuticle of the leaf, but most vapor passes through leaf stomata. There is a continuous gradient of water potential, from the leaf cell to the air in the transpiring plant, and that gradient can be expressed either in terms of concentration or vapor pressure differences (Table 4.3).

The potential force for both evaporation and transpiration is similar; i.e. the water potential at the surface of the cell or body of water, and the air into which water vapor will diffuse. The flux of water vapor in evaporation crosses one resistance, that imposed by the water surface-air boundary layer. But the flux of water vapor from leaf to air crosses two boundaries, that imposed internally by the leaf, and that across the boundary between the leaf surface and the air beyond.

This pathway is illustrated in Fig. 4.9. Water first evaporates from cell wall surfaces into the substomatal cavity, and may then diffuse through the cuticle, then across the air boundary layer, and finally into the air beyond. More commonly, water vapor will diffuse through the open stomate, then across the air boundary layer. The air boundary layer is thicker over open stomates than the rest of the leaf.

The water potential difference between leaf and air is determined by the environment, principally the humidity of the air (or its water vapor pressure), and the temperature. The magnitude of Ψ_{air} is given in Table 4.2, which illustrates the drying power of the air; at Relative Humidity (RH)of 75% the Ψ_{air} ≈ -89.4 Mpa! Fig. 11.3 illustrates the increase in vapor pressure deficit Δe(the vapor pressure in the leaf - vapor pressure in the air) as a function of temperature. Note the difference in Δe at 60% RH at different temperatures.

Leaf and air resistances are determined by the geometry and physiology of plants.

II. Energy Relations of Transpiration

A. Definitions: In the formulas given above, C, *absolute humidity*, is the weight of water vapor in the air in g H_2O m^{-3}. The capacity of the air to hold water increases with temperature.

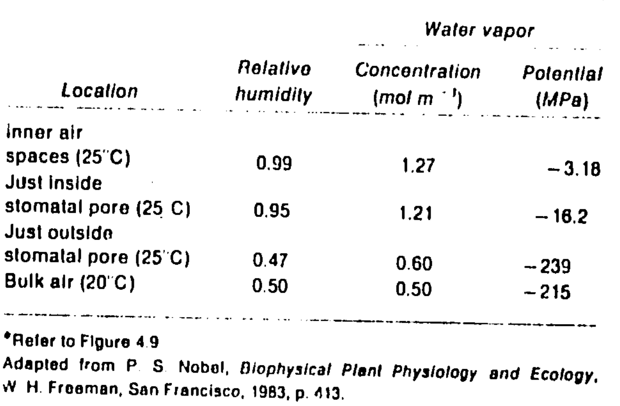
Another measure of the water content of the air is *vapor pressure*. Water vapor in the air exerts a pressure in addition to atmospheric pressure, and in relation to the amount of water vapor present. VP is expressed kPa (Table 11.5)

Absolute humidity and vapor pressure at saturation can be determined from tables in the *Handbook of Physics and Chemistry* and other sources.

Relative humidity (RH) is the vapor pressure or absolute humidity as a portion of that which would be present at saturation. For example at 20 degrees the vapor pressure at saturation is 2.34 KPa, and at 70% RH the vapor pressure at 20 degrees is 70% of that, or 1.64 KPa.

The difference between the vapor pressure at saturation and that of measurement is called the *vapor pressure deficit* Δe. In the example above of 70% RH and 20 degrees, the VPD is 0.70 KPa. The Δe constitutes the potential for evaporation or transpiration, and resistances determine the rate of water loss.

B. Solar energy is required in evapotranspiration to supply the large number of calories required for vaporization.



Location	Relative humidity	Water vapor Concentration (mol m^{-3})	Water vapor Potential (MPa)
Inner air spaces (25°C)	0.99	1.27	−3.18
Just inside stomatal pore (25°C)	0.95	1.21	−16.2
Just outside stomatal pore (25°C)	0.47	0.60	−239
Bulk air (20°C)	0.50	0.50	−215

*Refer to Figure 4.9

Adapted from P. S. Nobel, *Biophysical Plant Physiology and Ecology*, W. H. Freeman, San Francisco, 1983, p. 413.

TABLE 4.3. Representative values for relative humidity, absolute water vapor concentration, and water potential for four points in the pathway of water loss from a leaf.*

III. Factors Affecting Transpiration

A. Factors affecting Vapor Pressure Deficit

$$(e_{leaf} - e_{air}) = \Delta e$$

The major factors that affect Δe are air and leaf temperature and the humidity of the air. Table 11.5 lists the effect of temperature on Δe at 70% RH. Note that at 20 degrees and 70% RH Δe is 0.701 KPa, but at 30 degrees and 70% RH the Δe is 1.273. Given equal resistances at both temperatures, transpiration should occur nearly twice as fast at 30 degrees than at 20 degrees.

The effect of temperature on Δe is further illustrated in Fig. 11.3. In this illustration it is assumed that leaf and air temperatures are the same, and that the interior leaf atmosphere is at water saturation. In natural, leaves may exceed ambient air temperatures if they absorb energy more rapidly than it can dissipated by latent heat of vaporization or convection. Leaves may be cooler than air if dissipation of heat by vaporization exceeds energy absorption. In other words, plants can regulate to some extent leaf temperature by control of transpiration. This phenomena is significant in alpine and desert plants.

B. Factors that affect resistance of the air r_{air}

The rate of diffusion of gases, including water vapor, is controlled by the steepness of the diffusion gradient, i.e. the depth of the boundary over which diffusion occurs. Fig. 4.9 illustrates the boundary layer, and Fig. 3-14 compares the depth of the boundary layer as affected by wind. Wind velocities of 1 - 5 km hr^{-1} have the greatest effect on transpiration because at these relatively low velocities the humid zone above the leaf is removed, making the boundary layer thinner, and steepening the diffusion gradient (Fig. 11.4). However, the relationship between wind and transpiration in sunflowers (Fig. 11.4) may not occur in other species (Fig.11.6) because wind may cause stomatal closure.

Leaf size and shape also affects r_{air}. Large leaves retain a thicker boundary layer than small leaves. Leaves may also change shape to maintain a boundary layer, such as the curling or rolling of grass blades during drought.

C. Factors that affect leaf resistance r_{leaf}

Leaf resistance r_{leaf} can be divided into subcategories of mesophyll resistance, cuticular resistance, intercellular resistance, and stomatal resistance (Fig. 11.1).

Mesophyll resistance is affected by mesophyll cell π and the Ψ_{matrix} of the cell wall. This resistance is very low (Table. 11.4). Intercellular resistance is the resistance to diffusion of water vapor from the cell wall to the epidermis, and that too is low. However, the internal anatomy leaves adapted to xeric environments, and between sun and shade leaves on the same plant, have decreased intercellular space by decreased spongy mesophyll and increased palisade layers. These anatomical changes increase intercellular resistance, thus reducing the flux of water vapor from the leaf. (Fig. 11.12).

Cuticular resistance varies over 1,000 fold between species, with those adapted to hydric and mesic environments generally the least, and those with xeric environments the greatest. (Table 11.3). The differences are due to the thickness of the waxy cuticle layer over the epidermis of the leaf.

Stomates control the majority of r_{leaf}. The number, size, position, and degree of opening control most transpiration. These factors will be discussed in Lesson Sixteen.

A comparison of the boundary, cuticle, and stomatal resistance for several species is presented in Table 11.3.

Leaf anatomy, size, shape, and orientation determine energy absorbed by the leaf, and subsequently leaf temperature, the availability of energy available for vaporization, and the Δe. For example, the leaves of some desert species are orientated vertically, minimizing absorption of solar radiation, and thus solar heating of the leaf. Many desert species have compound leaves dissected into small leaflets (e.g. *Acacia* species). Small leaves or leaflets can dissipate heat by convection better than large leaves, thus maintaining the leaf at ambient temperature instead of above air temperature from solar absorption. If the leaf becomes warmer than air Δe increases accordingly. Maximizing convective heat loss is a common adaptive strategy to xeric environments, and small leaves increase the effectiveness of convection.

Root/Shoot ratios can also affect transpiration (Fig. 11.7). Decreased root growth increases resistance of water absorption which results in partial stomatal closure.

IV. Magnitude of transpiration

On an annual basis a corn plant loses over 200 liters or 100 times its weight in water during the growing season. Deciduous forests transpire 25-35% of annual precipitation.

There are marked seasonal differences in transpiration caused by either leaf fall during winter or drought, and/or colder temperatures. Fig.11.24 compares the annual transpiration pattern for evergreen and deciduous trees.

Diurnal variations in transpiration also occur (Fig. 11.23). Sunflower transpiration rates track changes in VPD, stomatal closure at night (because of darkness), and late afternoon water stress. The cactus shows an increase in transpiration at night because its stomates open in darkness to absorb CO_2 during that period of less water stress. This is an adaptive mechanism to the xeric environment.

V. Measurement of Transpiration

A. Gravimetric. Transpiration may be measured by weight loss, including monitoring the weight loss of a potted plant or in the more complex lysimeters previously illustrated (Lesson Seven, Fig. 4.2).

B. Volumetric. The volume of water transpired can be measured from cut shoots, or whole plants in a container in which input and output of liquid water can be measured.

C. Water Vapor. Plants can be enclosed in a chamber, and the water vapor content of air going into the chamber and leaving it measured. The increased water vapor in exhaust is from transpiration. Methods of measuring water vapor range from absorbing water vapor in a desiccant, e.,g. $CaCl_2$, to using electronic humidity sensors.

D. Determination of measuring leaf resistance r_{leaf}. If a cup containing a humidity sensor is clamped to a leaf, the increase in water vapor content of the cup over time can be determined, and this value converted to r_{leaf} in sec cm^{-2}. Assuming the water on the surface of leaf cells is at saturation, and C or e of the air is measured, transpiration can be computed from the above equation. If leaf area is measured the result can be expressed in mg H_2O cm^{-2} hr^{-1}.

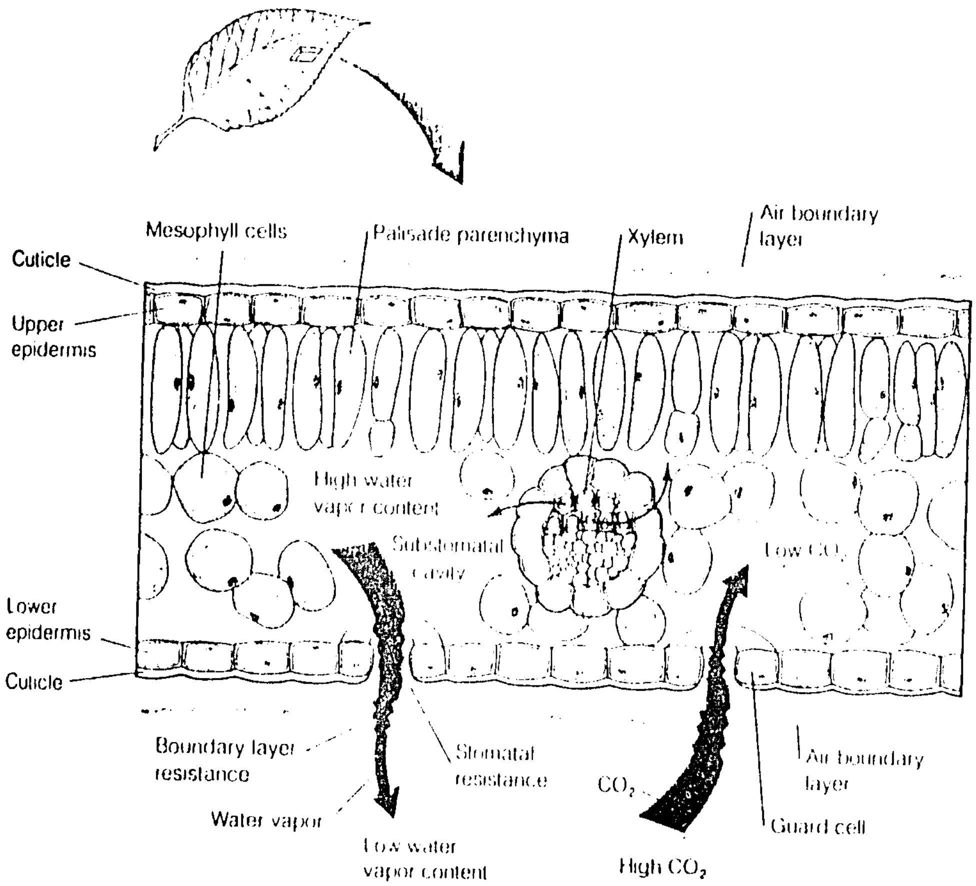


FIGURE 4.9. The water pathway through the leaf. Water is drawn from the xylem into the cell walls of the mesophyll, where it evaporates into the air spaces within the leaf. By diffusion, water vapor then moves through the leaf air space, through the stomatal pore, and across the boundary layer of still air that adheres to the outer leaf surface. CO_2 also diffuses into the leaf through stomata along a concentration gradient.

Additional Reading:

Kramer, P.J. 1983. Water Relations of Plants. pp. 291-340.
Taiz, L., and E. Zeiger. Plant Physiology. pp. 90-93

TABLE 4.2. Relation between relative humidity and water potential of air, calculated from Equation 4.4*

Relative humidity	Water potential (MPa)
1.0	0
0.999	−0.31
0.995	−1.56
0.990	−3.12
0.980	−6.28
0.950	−15.95
0.900	−32.8
0.750	−89.4
0.500	−215.5
0.200	−500
0.100	−718

*Assuming a temperature of 20°C (293 °K); at which $RT/\bar{V}_w$ = 135 MPa.

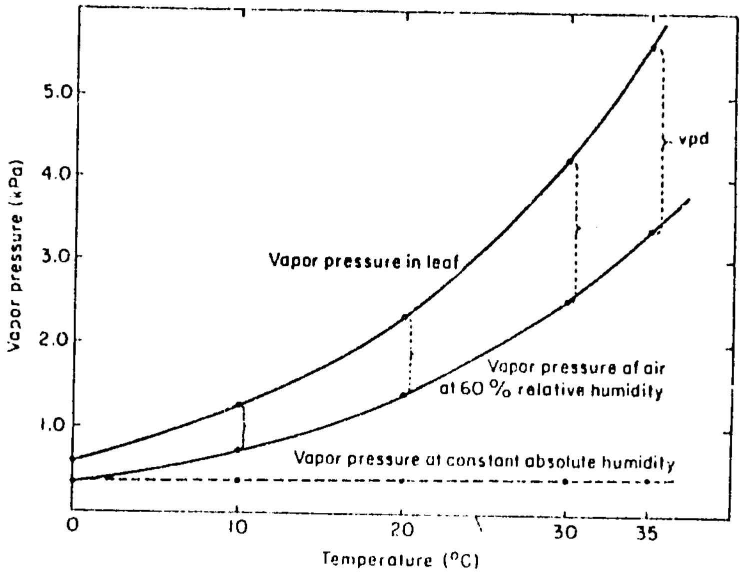


Fig. 11.3. Effect of increasing temperature on the vapor pressure difference (vpd) between leaf and air if the air in the leaf is assumed to be saturated, leaf and air temperatures are similar, and the external air is at 60% relative humidity at each temperature. The dashed line shows water vapor pressure in the atmosphere if the absolute humidity is kept the same at all temperatures.

TABLE 11.5 Effect of Temperature on the Saturation Vapor Pressure of Water, on the Vapor Pressure of Air at 70% Relative Humidity, and on the Vapor Pressure Gradient (Δe) from Water Surface to Air

Temperature (°C)	Vapor pressure at saturation (kPa)	Vapor pressure of air at 70% relative humidity (kPa)	Δe (kPa)
0	0.610	0.427	0.183
10	1.227	0.858	0.369
20	2.337	1.635	0.701
30	4.243	2.970	1.273
40	7.377	5.163	2.214

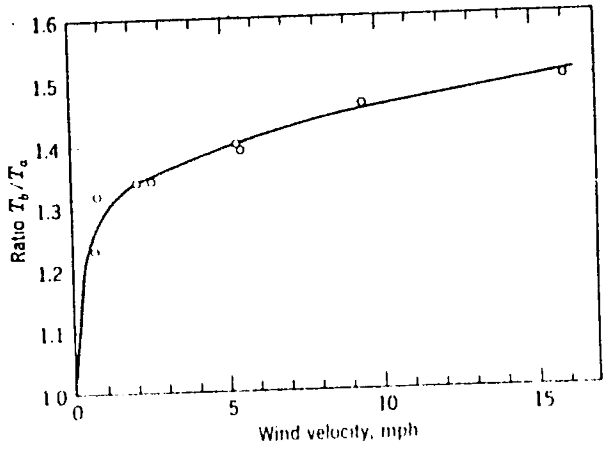


Fig. 11.4. Effect of increasing velocity of air movement on the transpiration rate of potted sunflowers growing in a sunny greenhouse. Ordinate is the ratio of rate of plants exposed to wind (T_b) to the rate of plants in quiet air (T_a). Most of the effect occurs at velocities of less than 2 mph. A velocity of 1 mph equals 44.69 cm/s. (After Martin and Clements, 1935, from Kramer and Kozlowski, 1979, by permission of Academic Press.)

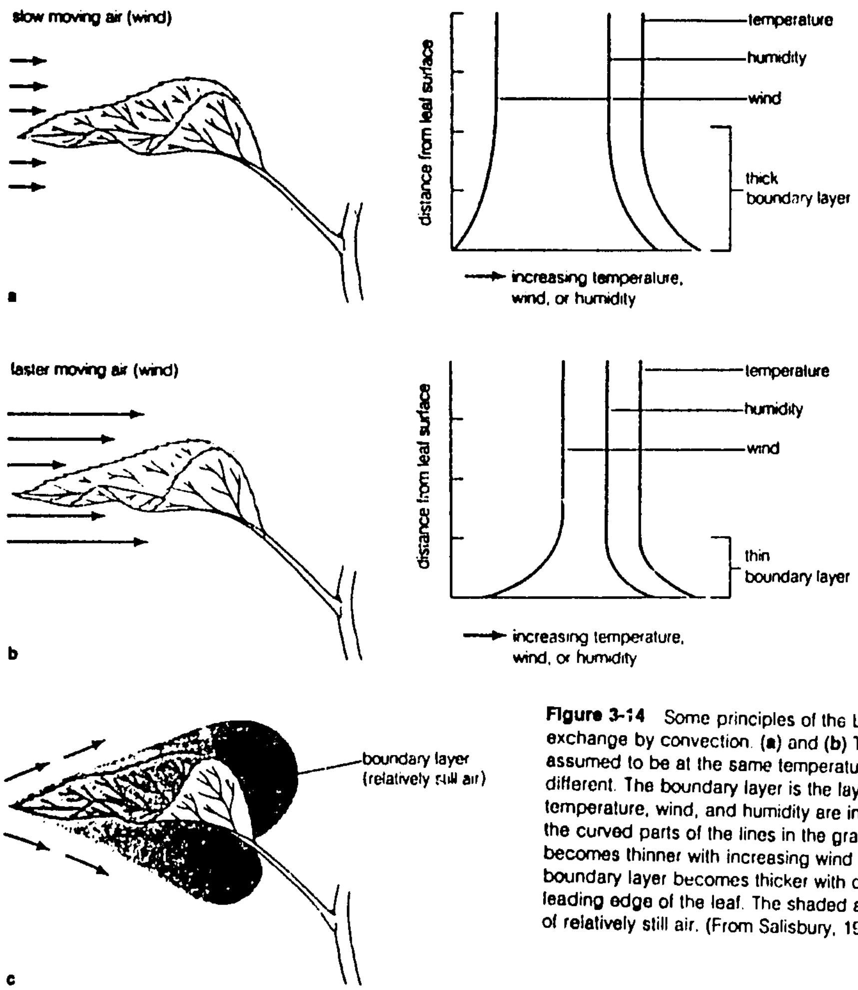


Figure 3-14 Some principles of the boundary layer and heat exchange by convection. (**a**) and (**b**) The two leaves are assumed to be at the same temperature; only wind velocity is different. The boundary layer is the layer of air in which temperature, wind, and humidity are influenced by the leaf: the curved parts of the lines in the graphs. The boundary layer becomes thinner with increasing wind speed. (**c**) The boundary layer becomes thicker with distance from the leading edge of the leaf. The shaded area represents a layer of relatively still air. (From Salisbury, 1979.)

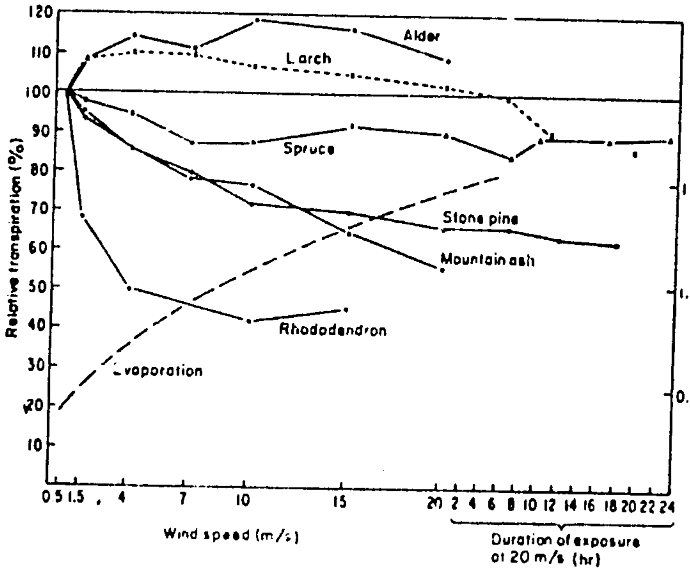


Fig. 11.6. Effect of wind velocity on transpiration of young potted subalpine plants in a wind tunnel at air temperature of 20°C, soil temperature of 15°C, and light intensity of 30,000 lux. Evaporation was measured with a green Piche atmometer. Although evaporation increased steadily with increasing wind speed, transpiration of most species decreased. Alder is *Alnus viridis*; larch is *Larix decidua*; spruce, *Picea abies*; stone pine, *Pinus cembra*; mountain ash, *Sorbus aucuparia*; rhododendron, *Rhododendron ferrugineum*. (After Tranquillini, 1969; from Kramer and Kozlowski, 1979, by permission of Academic Press.)

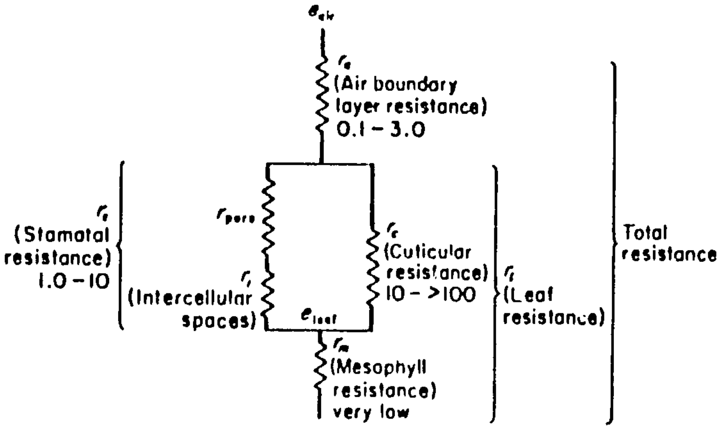


Fig. 11.1. Diagram showing resistances in seconds per centimeter to diffusion of water vapor from a leaf. Stomatal and cuticular resistances vary widely among species and with leaf hydration and atmospheric humidity. The rate of transpiration or transpiration flux density is proportional to Δe, the water vapor pressure gradient, e_{leaf} to e_{air}, and inversely proportional to the resistances in the pathway. (From Kramer and Kozlowski, 1979, by permission of Academic Press.)

TABLE 11.4 The Vapor Pressure of Water (e), the Vapor Pressure at Cell Surfaces at Three Cell Water Potentials, and the Difference in Vapor Pressure (Δe) between Cells and Air at Relative Humidities of 80 and 50%[a]

Ψ_w of water and of mesophyll cells (MPa)	e at cell surfaces (kPa)	Δe at 80% relative humidity (kPa)	Δe at 50% relative humidity (kPa)
0.0	4.243	0.849	2.121
−1.5	4.200	0.806	2.079
−3.0	4.158	0.764	2.037
6.0	4.073	0.679	1.952

[a] The relative effect of a low Ψ_w diminishes as the relative humidity decreases. All vapor pressures are for 30°C.

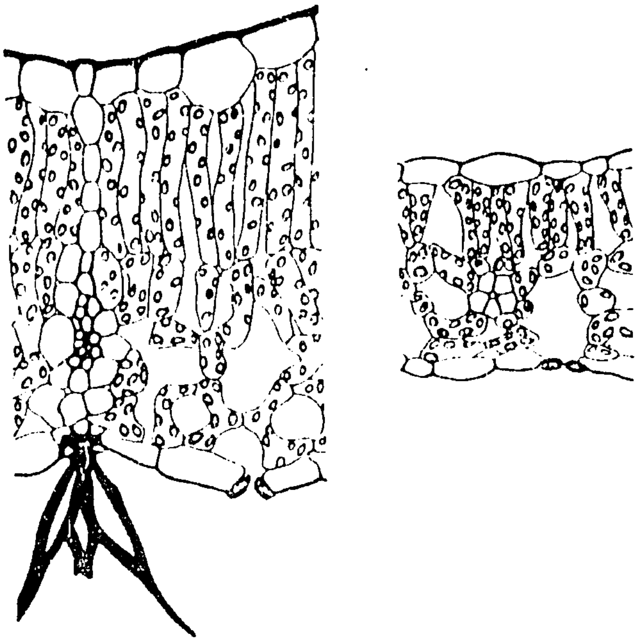


Fig. 11.12. Cross sections through leaves of post oak (left) and American beech (right). Post oak (*Quercus stellata*) leaves are representative of the xeromorphic type, with thick cutin, a double layer of palisade cells, bundle sheath extension, and a high ratio of internal to external surface. Beech (*Fagus grandifolia*) leaves are typical of the mesomorphic type, being thinner, with a thinner cutin, a single layer of palisade cells, and a lower ratio of internal to external surfaces. (Drawings courtesy of J. Philpott.)

TABLE 11.3 Resistances to Movement of Water Vapor through the Boundary Layer (r_a), Cuticle (r_c), and Stomata (r_s) in Leaves of Several Species[a]

Species	Resistances to water vapor (s cm^{-2})		
	r_a	r_s	
Betula verrucosa	0.80	0.92	83
Quercus robur	0.69	6.7	380
Acer platanoides	0.69	4.7	85
Circaea lutetiana	0.61	16.1	90
Lamium galeobdolon	0.73	10.6	37
Helianthus annuus	0.55	0.38	.

[a] From Holmgren *et al.* (1965).

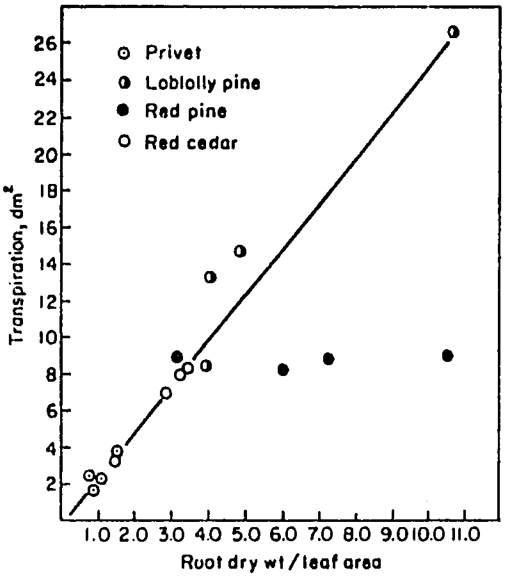


Fig. 11.23. Daily course of transpiration of sunflower and *Opuntia* plants in soil at field capacity on a hot summer day. Note the midday decrease in transpiration of sunflower the first day, probably caused by loss of turgor and partial closure of stomata. Also, note that the maximum rate of transpiration of *Opuntia* came at night, a characteristic of plants with Crassulacean acid metabolism. (After Kramer, 1937.)

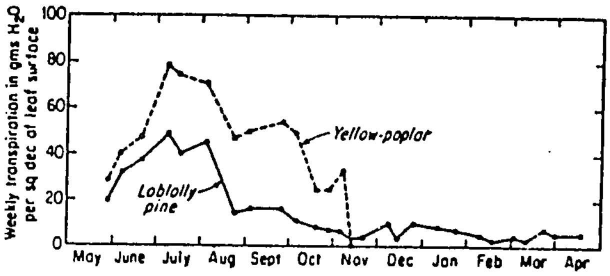


Fig. 11.24. Seasonal course of transpiration of potted seedlings of an evergreen and a deciduous species growing outdoors in Durham, North Carolina. (From Kramer and Kozlowski, 1979.)

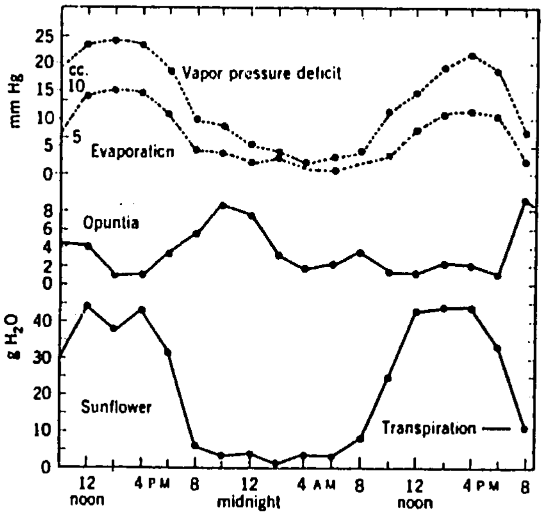


Fig. 11.7. Transpiration plotted over ratio of roots to leaf area (root dry weight in grams over leaf area in square decimeters) for four species of tree seedlings. An increase in ratio of roots to leaf area was accompanied by an increase in rate of transpiration per unit of leaf area for three species. The exception, red pine, had an extensively branched root system and densely clustered needles. (After Parker, 1949; from Kramer and Kozlowski, 1979, by permission of Academic Press.)

LESSON SIXTEEN

STOMATAL CONTROL OF TRANSPIRATION

By the end of this lesson you should be able to:

....Describe the anatomical features of guard cells that permit them to open and close
....Describe the physiological mechanism of stomatal opening
....Describe how light, wind, CO_2, and water stress affect stomatal opening
....Explain the adaptive significance of species variation of stomatal position and sensitivity to environmental factors

STOMATAL CONTROL OF TRANSPIRATION

I. Occurrence of Stomata

Fig. 3-3 shows that the stomata occur mostly or exclusively on the lower leaf surface of most plants. Stomata occur on both surfaces of grasses, and in conifers they may be arranged in distinctive lines on either side of the midvein of the needle (e.g. *Abies spectabalis*), or on one of more facets of a multi-sided pine needle. Hydrophytes (e.g. water lily) have stomata on the upper surface.

There is a greater likelihood that the boundary layer will be thicker on the lower leaf surface because the layer is not so likely to be disrupted by convection. Concentrating stomata on the lower surface conserves water by taking advantage of the thicker boundary layer and thus lower transpiration.

Another water conservation strategy is stomata sunken below the epidermal surface (Fig. 3-3 b,d). The vapor cap above sunken stomata is likely to stay in place even with wind, thus maintaining a thick boundary layer and reducing transpiration.

II. Factors Affecting Stomatal Opening

A. Light. Most stomata open in the light. Fig. 6.14 illustrates how closely stomatal opening (and the photosynthesis that results from it) track solar radiation. The degree of opening was measured by stomatal conductance.

B. CO_2. Most stomata open in CO_2 free air, and close at high CO_2 concentrations (e.g. >1,000 ppm). The mechanism of CO_2 action on stomata is not well understood.

C. Water Stress overrides all other factors. Water stress may be induced if transpiration exceeds water absorption because of high transpiration rates, or slow water absorption because of inadequate root growth or dry soil. Water stress often occurs at midday, and this may be accompanied by partial stomatal closure.

If water stress is severe the leaf liberates abscissic acid (ABA) which will keep stomata closed for several days even after water stress has been relieved. The ABA response occurs in some crop plants with as little as Ψ_{leaf} = -1.0 Mpa, thus it is prudent for the farmer with irrigation available to water crops well before wilting.

Fig. 3-8 shows the daily course of stomatal opening. Succulents are a special case because during water stress some keep their stomata closed during the daylight, but open them at night to absorb and store CO_2 (as an organic acid) for photosynthesis conducted without gas exchange during the day.

In summary, darkness, high CO_2, and most of all, water stress close the stomata of most plants, conserving water until a time more favorable for photosynthesis.

III. Stomatal Anatomy

Stomata are composed of two, opposing, guard cells which are surrounded by the accessory cells. All of these cells are a part of the leaf epidermis.

Guard cells are unique among epidermal cells in that they contain chloroplasts - not as many as mesophyll cells, but enough to sense light and perform some photosynthesis (Fig. 6.15). They are also unique in having radially arranged cellulose microfibrils in their cell walls (*radial micellation*). The concentration of radial microfibrils is much greater on the inner, concave cell wall (because of its decreased radius of curvature) than on the outer, convex cell wall. This causes the inner cell wall to be thicker (Fig. 6.15, 4.14).

When turgor pressure increases in a guard cell the outer, thin wall expands, pushing into its accessory cell. The radially arranged microfibrils pull the thicker, inner wall toward the bulging outer wall. Since this happens to both of the paired guard cells, their touching walls pull apart and the pore opens.

In summary, when a pair of guard cells becomes turgid their outer walls expand and bulge into accessory cells. Radial microfibril pull the inner wall toward the outer wall, opening the stomatal pore. Stomatal opening depends upon turgor changes in the guard cells.

IV. Turgor Changes in Guard Cells

The energy of photosynthesis in guard cells is used to pump K^+ into the guard cells from the accessory cells. This increases $\pi_{\text{guard cell}}$ and makes $\Psi_{\text{guard cell}}$ more negative. Water then flows into the guard cell from accessory cells, increasing their turgor, causing the pore to open. This is the mechanism of stomatal opening in the light. In darkness, K^+ leaves the guard cell, reducing $\Psi_{\text{guard cell}}$, and as water leaves the guard cell in response to increased Ψ, the cells loose turgor, and the pore closes.

Any factor that increases water stress may also cause the guard cells to loose turgor and close. The $\pi_{\text{guard cell}}$ is less than $\pi_{\text{mesophyll cell}}$. Thus, the same negative Ψ which causes the guard cells to loose turgor and close should not cause a loss of turgor in the mesophyll cells. This should protect the mesophyll from serious water stress, but the mechanism is not perfect because drought is the major cause of plant death in the world.

Water stress occurs in guard cells when transpiration is more rapid than the cells can absorb water. This may be caused by high soil moisture stress (i.e. dry soil), high resistance to the movement of water up the stem, or an excessively dry air in which the flow of water from vein to accessory cell to guard cell is slower than guard cell transpiration. This commonly occurs at midday, even in well-watered soils. Midday stress causes partial stomatal closure and reduced photosynthesis until the evapotranspiration potential is lowered by decreased temperature in the late afternoon. Fig. 5.27 illustrates midday closure with increasing soil moisture tension, and Fig. 5.28 shows the effect of progressive soil moisture stress on transpiration (stomatal closure) in *Pinus radiata*.

V. Variation in Stomatal Sensitivity

Stomata vary considerably in their sensitivity to water stress, and this variation reflects adaptive strategies to different environments.

The π_{leaf} varies between species (Fig. 5.16), and $\pi_{stomata}$ varies in concert with that of the rest of the leaf. This means that some species adapted to arid conditions may keep stomata open at higher levels of soil moisture stress than species found in moist environments. Note that succulents, generally considered well adapted to xeric environments, have very low π_{leaf}. Succulents are very sensitive to soil or atmospheric moisture stress, and quickly close their stomata at the slightest stress. They save water with their thick cuticles from one favorable time for photosynthesis to the next, but are not very productive because of the long intervals with closed stomata (and thus little photosynthesis). For this reason succulents are generally restricted to habitats too harsh for most plants, and thus compensate for low photosynthetic capacity by avoidance of competition.

Species vary in conductance of water vapor (Fig. 11.16). Conifers generally have low conductance regardless of the humidity of the air, thus conserving water. The other species shown in Figure 11.16 close stomates with varying sensitivity as the relative humidity decreases, even though they are well-watered.

Some desert species can maintain open stomata (and thus maintain photosynthesis) because of very negative Ψ_{leaf} (Fig.3.46). *Larrea* and *Olea* are desert shrubs that exhibit this. Other desert plants close stomata with slight water stress similar to succulents, conserving water at the expense of photosynthesis during drought. Many phreatophytes, e.g. some *Populus* species, maintain open stomata even during hot, dry days, but compensate by having root systems that tap the dependable soil water of the capillary fringe above ground water, and have low resistance conducting system in the stem.

Stomata may also become less sensitive with age. Stomata in the older needles of many conifer species become so plugged with cutin that they no longer function. Stomata in aging grass leaves accumulate silicon, which reduces and eventually eliminates cell wall elasticity. Such stomata in mature grass leaves remain open, "curing" or drying the leaf as a part of senescence. This has the ecological advantage of also reducing the moisture content of the grain, helping to insure its long term viability.

Additional Reading:
Larcher, W. 1980. Physiological Plant Ecology. pp. 90-93
Salisbury, F, and C. Ross. 1985. Plant Physiology. pp.56-62
Taiz, L. and E. Zeiger. 1991. Plant Physiology. pp. 94-97

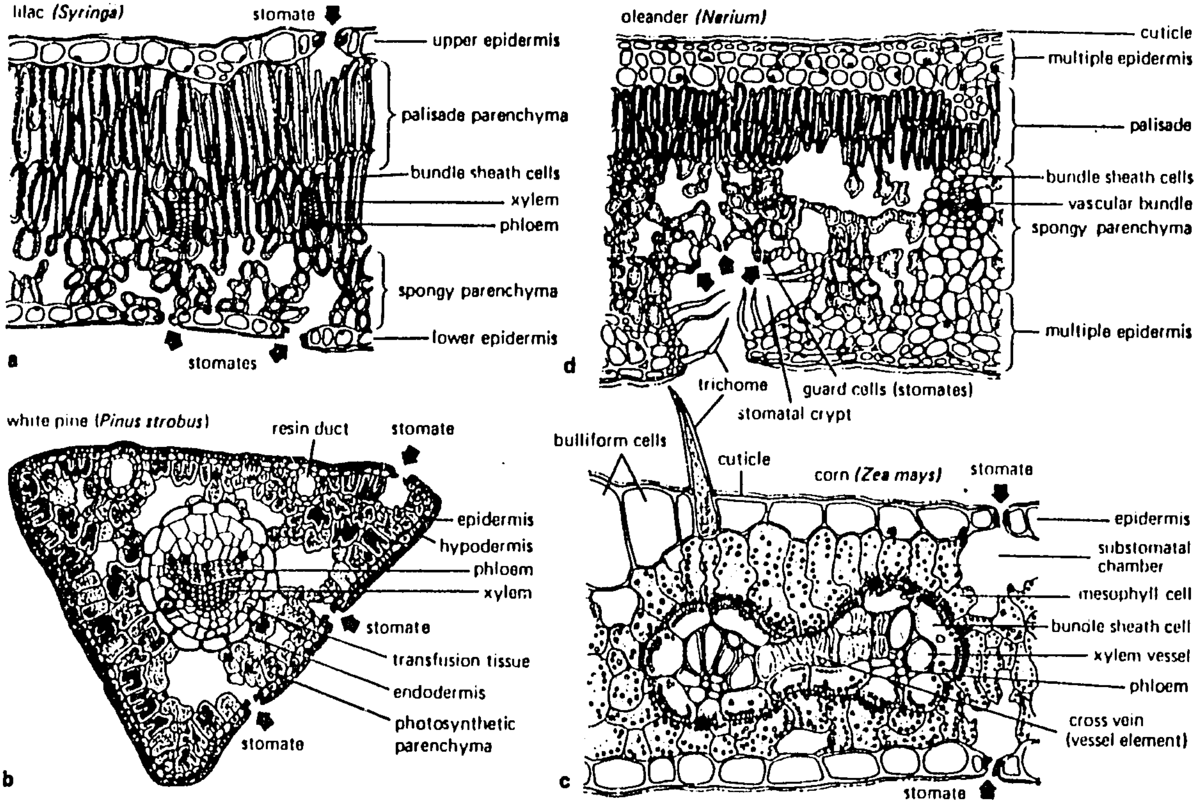


Figure 3-3 Cross sections through four representative leaves, one with "normal" stomates (**a**), one with slightly sunken stomates (**b**), one a grass with stomates about equal on both surfaces (**c**), and one with stomates deeply sunken in a substomatal cavity (**d**). Note other details of differing leaf anatomy. Pine leaves do not have a palisade layer, for example.

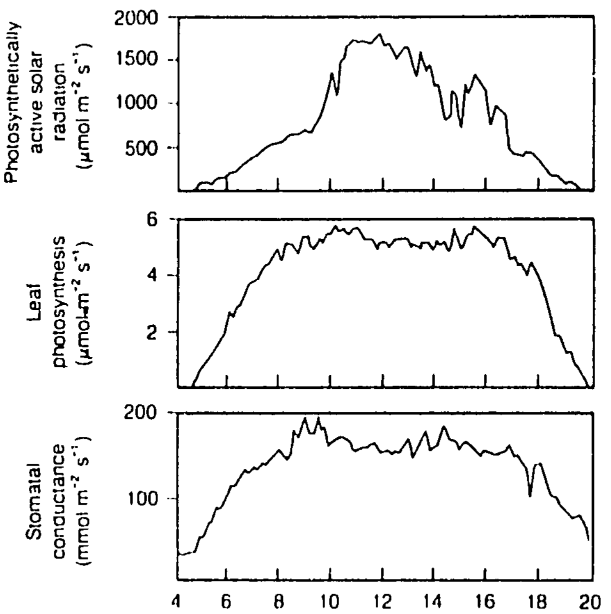


FIGURE 6.14. Photosynthetically active solar radiation, leaf photosynthesis, and stomatal conductance in a leaf of the tree *Fagus sylvatica*. Measurements of solar radiation (moles of photons per square meter of leaf per second, that is, mol m^{-2} s^{-1}) were made with a photometer, photosynthesis and stomatal conductance were measured in an intact attached leaf that was enclosed in a gas exchange chamber through which air of known CO_2 concentration and relative humidity was circulated. Photosynthesis and stomatal conductance increase in parallel with the amount of light reaching the leaf surface and decrease later in the day as the solar radiation declines. (From Schulze, 1970.)

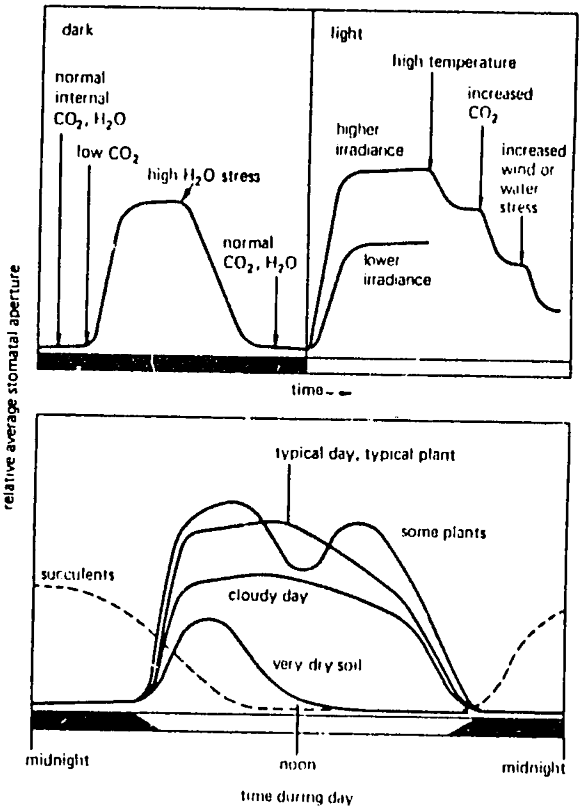


Figure 3-8 A summary diagram of stomatal response to several environmental conditions. In the top graph, arrows point to times when some environmental parameter was changed as indicated by the label.

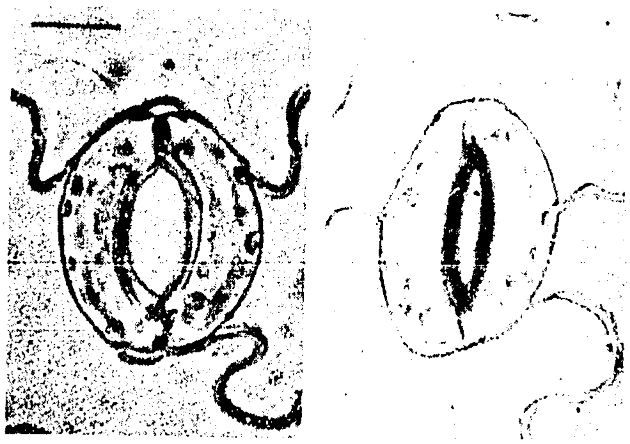


FIGURE 6.15. Stomata in detached epidermis of the broad bean *Vicia faba*, showing a wide-open stomatal pore (a) and a nearly closed pore (b). Stomatal apertures are measured under a microscope by recording aperture widths. Measurements of the change in aperture as a function of experimental conditions allow characterization of stomatal responses to different environmental stimuli. Bar = 20 μm. (Photos courtesy of G. Tallman and E. Zeiger.)

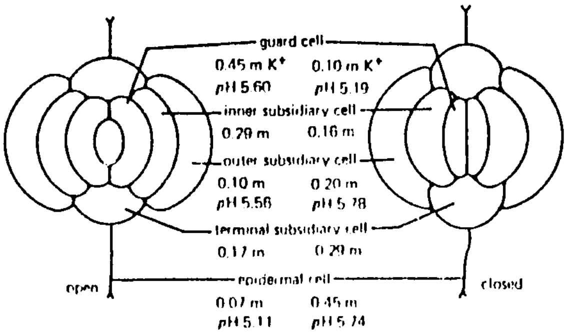


Figure 3-9 Quantitative changes in K^+ concentrations and *p*H values of the vacuoles in several cells making up the stomatal complex of *Commelina communis*. Values are given for the open and closed conditions of the stomatal pore. (Data of Penny and Bowling, 1974 and 1975.)

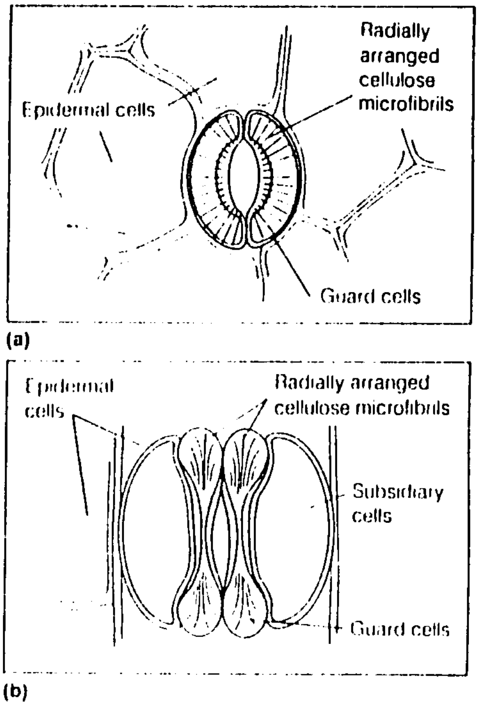


FIGURE 4.14. The radial alignment of the cellulose microfibrils in guard cells and epidermal cells of a kidney-shaped stoma (a) and a grass-like stoma (b). (From Meidner and Mansfield, 1968.)

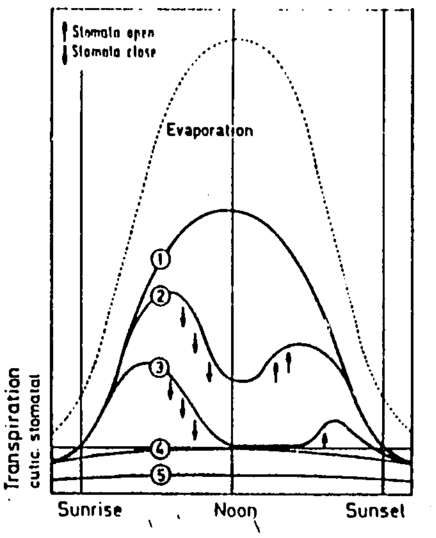


Fig. 5.27

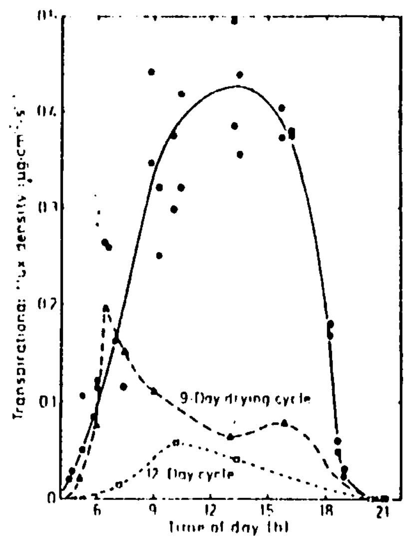


Fig. 5.28

Fig. 5.27. Diagram of daily changes in transpiration as it becomes progressively more difficult (curves *1*–*5*) to maintain the water supply. The *arrows* indicate the stomatal movements elicited by changes in the water balance. The stippled area shows the range in which transpiration is exclusively cuticular. *1*, unrestricted transpiration; *2*, limitation of transpiration at noon as the stomata begin to close; *3*, full closure of the stomata at midday; *4*, complete cessation of stomatal transpiration by permanent closure of the stomata (only cuticular transpiration continues); *5*, considerably reduced cuticular transpiration as a result of membrane shrinkage. After Stocker (1956)

Fig. 5.28. Diurnal changes in transpiration of two-year-old seedlings of *Pinus radiata* during progressive drying of the soil. From Kaufmann (1977).

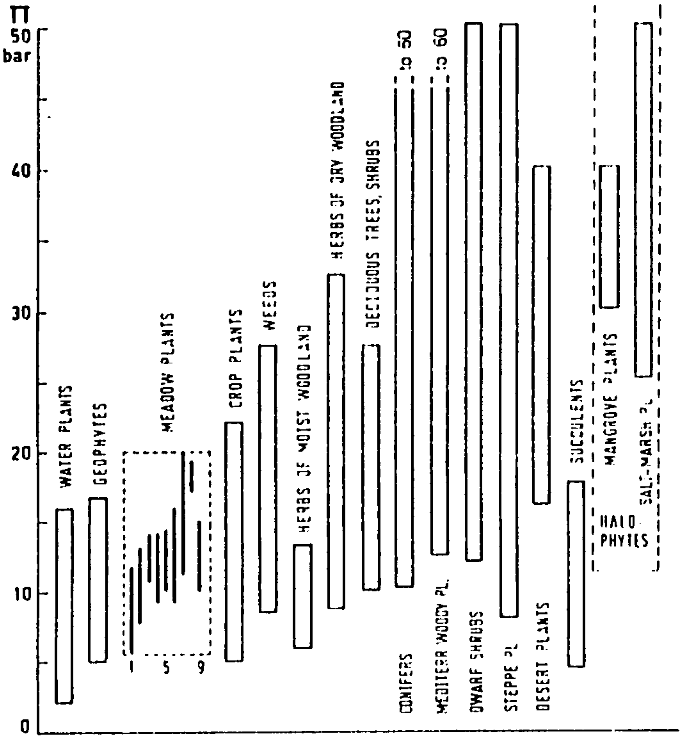


Fig. 5.16. Ranges for the values of osmotic pressure of leaves of ecologically different types of plants (the osmotic spectrum). The sub-ranges (*black bars*) shown for the meadow plants illustrate how to interpret the osmotic range given for each plant group; that is, it is derived from the difference between the lowest and the highest osmotic pressures found among all plants studied in the ecological group. *1*, *Polygonum bistorta*; *2*, *Taraxacum officinale*; *3*, *Galium mollugo* and *Campanula rotundifolia*; *4*, *Achillea millefolium*; *5*, *Tragopogon pratensis*; *6*, *Poa pratensis*; *7*, *Melandrium album*; *8*, *Cynodon dactylon* and *Lilium perenne*; *9*, *Arrhenatherum elatius*. After Walter (1960)

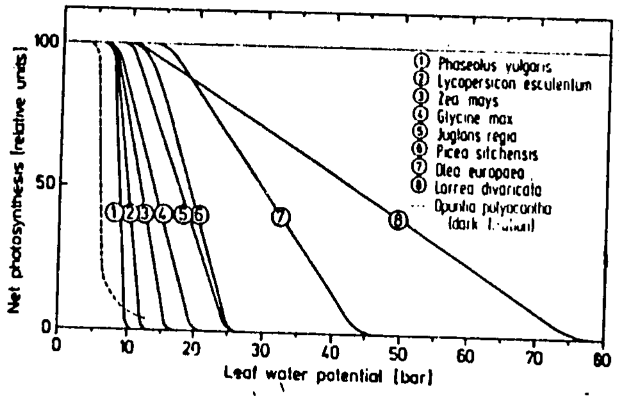


Fig. 3.46. Restriction of photosynthetic CO_2 uptake with increasing water stress in leaves. *1*, from Pospišilová et al. (1978); *2*, Brix (1962); *3* and *4*, Boyer (1970b); *5*, Davies and Kozlowski (1977); *6*, Beadle and Jarvis (1977); *7*, Moraes et al. (1980); *8*, Odening et al. (1974); *Opuntia* (*stippled*), Gerwick and Williams (1978). Data on the dependence of net photosynthesis on water saturation deficit are given by Larcher (1969a)

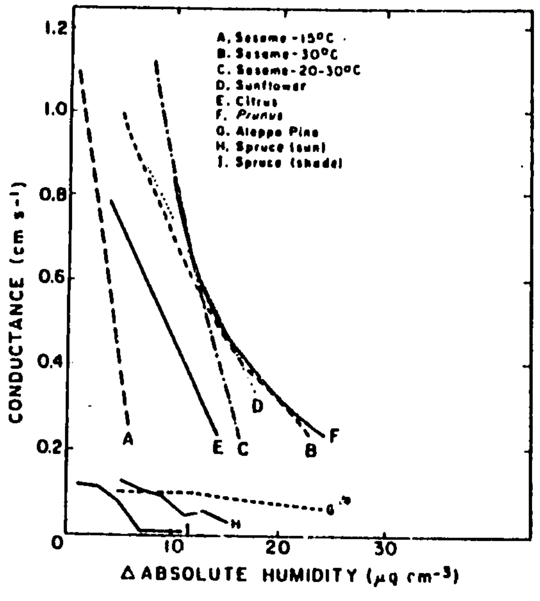


Fig. 11.16. Relationship between stomatal conductance and the difference in absolute humidity between leaves and air. Conductances for conifers are much lower than those for other species studied. (After Kaufmann, 1976.)

LESSON SEVENTEEN

TRANSPIRATION FROM PLANT COMMUNITIES

By the end of this lesson you should be able to:

....List the factors that determine the maximum rates of community transpiration
....Describe the factors that generally prevent maximum transpiration rates from being achieved
....Describe seasonal patterns of community transpiration
....Explain the effects of leaf area index and solar radiation on community transpiration
....List two methods of measuring community transpiration
....Describe the role of models in predicting community transpiration and in forest hydrology

TRANSPIRATION FROM PLANT COMMUNITIES

Transpiration from plant communities differs from that of individual plants, primarily because of the effect surrounding plants have on each other. An illustration of this is the "oasis" effect depicted in Fig. 11.2. In this study transpiration rates of sudan grass growing in a lysimeter were measured, first when surrounded by other grasses, and next after removal of the grasses surrounding the lysimeter. Transpiration increased markedly after removal of the surrounding grass, primarily because of increased wind and the advective transfer of heat into the remaining stand.

Wind is also reduced in forests, tending to flow over forests rather than through them. This increases humidity in the stand, and helps maintain boundary layer resistance, both of which tend to reduce transpiration.

I. Magnitude of Plant Community Transpiration

Community transpiration is of interest because it represents a major loss of water from watersheds. Computations of watershed yield for purposes such as irrigation, hydroelectric generation, and public water systems include not just precipitation measurements, but loses of water by evapotranspiration.

Stands of trees stocked at 250 trees ha^{-1} may transpire as much as 40,000 liters ha^{-1}.

A more useful unit of expression for transpiration is mm of soil water per day. An average soil 1 m deep at field capacity holds about 20 cm of water. Energy is required for evapotranspiration, and this energy comes from the sun. Solar radiation in temperate climates is about 350 calories cm^2 day^{-1}. Water requires 570 calories cm^3 at 20 degrees for vaporization. The maximum rate of transpiration is:
(350 cal cm^2 day^{-1} available energy)/(570 cal required cm^3 water) or 0.6 cm^3 water cm^2 day^{-1}, providing all solar radiation is used for evapo- transpiration. This theoretical maximum is seldom reached because not all radiation is absorbed, plus leaf and air-boundary resistance.

A soil moisture depletion rate of 0.5 cm^3 water cm_2 day^{-1} is a reasonable maximum estimate. Given the 20 cm water in 1 m soil depth at field capacity described above, maximum transpiration could be sustained for about 40 days. This means that maximum transpiration rates cannot be maintained for the full growing season. Transpiration may be reduced because of increased stomatal resistance, perhaps stomatal closure, reduced solar radiation (i.e. cool, cloudy days), or summer rainfall. Summer rainfall usually does not supply enough water to maintain maximum summer transpiration in high latitudes because so much precipitation is lost by interception and litter storage and evaporation; however, it may prolong the period of water stress avoidance. Summer rain is very significant in monsoon climates.

A watershed study area in North America covered by mixed hardwoods disclosed that of an annual precipitation of 2,000 mm, 500 mm were transpired from the forest, and 50 mm from understory plants. This rate approximates the reasonable maximum estimate of 5 mm day^{-1} given above for the 100+ day growing season.

Transpiration losses from forest trees are given in Table 11.4. Note that annual transpiration remains about the same regardless of leaf biomass. Trees with little leaf biomass transpire more per leaf than tress with large leaf biomass. Table 11.5 lists water utilization by forests in various parts of the world. Forests generally use far less water than falls during the year, but some forests may suffer severe water deficits during the growing season. At San Dimas there is little or no water to transpire in the summer, and most transpiration occurs when rains return in winter.

Transpiration increases with crown coverage and leaf area index (LAI). It is also affected by vegetation type. The transpiration rates in different vegetation types are in order: wet meadow>open water>forest>grasslands>vegetable crops>bare soil. The high rate of transpiration in forests is due to more complete absorption of energy, and rooting at several soil depths.

II. Seasonal Patterns of Transpiration

Transpiration closely follows available soil moisture. An extreme example is pine forests that occur on deep sand dunes which transpire only after rains for as long as soil moisture lasts. Similar information concerning the water economy of Pakistan's *Juniperus excelsa* forests would be valuable.

North America , Europe, and much of Russia are characterized by winter precipitation during the period of dormancy. Melting snowfall causes soils to become "recharged" with moisture to field capacity to the depth of the soil. Transpiration in these forests is greatest during the period of soil moisture availability, i.e. May, June, and early July. As a rule midseason storms do not add greatly to soil moisture because so much of the precipitation is lost from interception and litter storage and evaporation. Transpiration slows during the late summer months, but in evergreens may resume if sufficient rains occur in the fall. This cycle is depicted in Fig. 10.3.

III. Leaf Area and Transpiration

Transpiration increases as LAI increases up to about 4, but even at LAI = 4+, transpiration in forests is less than that of moist soils or open water. This is due to stomatal resistance and the lack of wind within the forest, which increases the relative humidity inside the canopy.

Transpiration rates are similar over a wide variety of vegetation types with LAI >3. Large, widely spaced trees transpire greater than smaller, closely spaced trees, reminiscent of the oasis effect discussed earlier (Fig. 11.2).

IV. Measurement of Transpiration from Plant Communities

A. Evapotranspiration (ET) potential may be measured by monitoring water loss from standard open pans, and estimated from meteorological data such as temperature, wind, and the saturation vapor deficient Δe. The ET potential is generally not achieved because of lack of available water and stomatal resistance.

B. Infra-red gas analysis. It is possible to measure the upward flow of water vapor using infra-red absorption techniques.

C. Determination of water balance in watershed has been used to estimate transpiration. Watersheds selected have impermeable rock parent material (to minimize deep seepage). Precipitation and streamflow leaving the watershed is monitored, and the balance attributed to evapotranspiration and soil moisture storage. This can be done on a micro scale by lysimeters (Lesson Seven).

D. Soil moisture storage can be monitored by means of the neutron probe (Lesson Seven). Withdrawal of soil moisture is an index of transpiration. See Fig. 5.8.

E. Transpiration. An elegant technique for determining plant community transpiration is determination of the variables in the water balance model illustrated in Fig. 4.11. This requires knowledge of solar radiation, temperature, relative humidity, Δe, precipitation, storage and storage capacity of water in soil, stem, and leaf, and hydraulic conductivity of soil and stems. With known initial conditions (e.g. after winter recharge) the model should help keep track of soil water at various depths, seepage, runoff, stomatal conductance, transpiration, and such things as the mm of precipitation required to recharge the soil to the point where additional seepage and runoff could be expected. The Penman-Monteith equation (see Waring and Schlesinger, 1985) is used in the solution of this model, and its use illustrated in Fig. 5.9.

F. Another elegant method of measuring the transpiration of conifers is the solution of the following equation:

$$T = \frac{k_2 k_3}{k_1 k_4} D r_{leaf} LAI$$

Where: K_1 - the latent heat of vaporization; K_2 - specific heat of air; K_3 - density of air; K_4 - psychrometric constant. (These values can be obtain from standard tables; see references in Waring and Schlesinger); T - Transpiration; D - saturation vapor pressure deficit Δe; r_{leaf} - leaf resistance; and LAI - leaf area index. This equation can be modified for broadleaf trees by incorporation r_{air}. The surface area of conifer needles is so small r_{air} becomes negligible.

Leaf area index can be determined by using the relationship between sapwood cross-sectional area and LAI ((Fig. 2.17, Table 2.4), which must be determined for each species of interest.

Stomatal resistance can be determined using the relationship between pre-dawn plant moisture stress (measured with the pressure bomb, Lesson Ten) as illustrated for Douglas fir in Fig. 4.9. This relationship must also be determined for each species.

Additional Reading:

Kramer, P. J. 1983. Water Relations of Plants. pp. 337-339
Spurr, S. H. and B. V. Barnes. 1992. Forest Ecology.pp.257-260
Waring, R. H.and W. Schlesinger.1985. Forest Ecosystems.pp.88-113

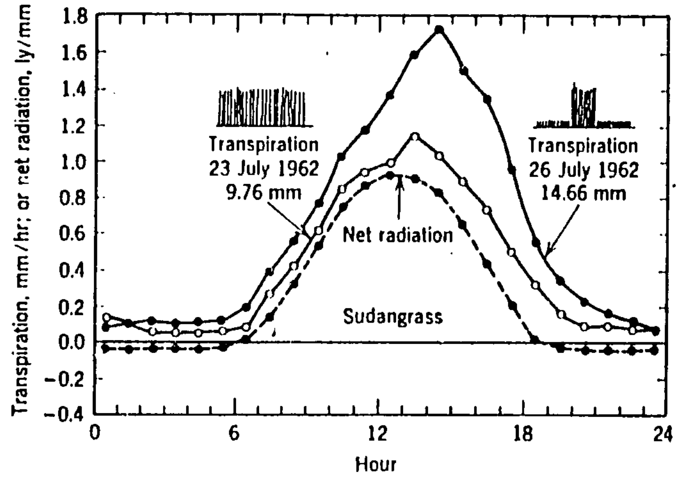


Fig. 11.2. Transpiration from a lysimeter in a closed stand of Sudangrass and from the same lysimeter 3 days later after the surrounding crop had been removed, exposing the plants in the lysimeter. Radiation was essentially the same on the 2 days, but additional energy supplied by advection caused much higher transpiration after the plot was exposed. (From van Bavel *et al.*, 1963.)

Table 11.4 Variation in Transpiration Losses of Water from Forest Trees

Species	Biomass of Foliage, kg ha^{-1}	Daily Transpiration of Leaves, g H_2O (g green leaves)$^{-1}$	Annual Transpiration of 40-50-yr-old Stands cm H_2O[a]
Birch	4,940	9.5	17
Beech	7,900	4.8	14
Larch	13,950	3.2	17
Pine	12,550	1.9	8.6
Spruce	31,000	1.4	16
Douglas-fir	40,000	1.3	19

Source: Data from Rutter, 1968. Copyright Academic Press. Used with permission.
[a] Water loss expressed in terms of cm H_2O per unit area.

Table 11.5 Utilization of Water by Forests in Various Parts of the World (After Rutter, 1968)

Forest Type	Annual Precipitation, cm	Annual Evapotranspiration Loss cm	Annual Evapotranspiration Loss %	Growing Season Soil Water Deficit
Northern taiga conifer forest, USSR	52.5	28.6	54	Negligible
Southern taiga conifer forest, USSR	60.0	32.9	55	Negligible
Spruce stand, Great Britain	135.0	80.0	59	Negligible
Mixed conifer and deciduous stand, Switzerland	165.0	86.1	52	Negligible
Mixed conifer and deciduous stand, N. Japan	261.7	54.2	21	Negligible
Evergreen rain forest, Kenya	195.0	157.0	81	Small
Deciduous forest, European USSR	45.7	42.4	93	Moderate
Coulter pine, California	123.0	63.7	52	Severe
Ponderosa pine, California	126.0	58.0	46	Severe
Coulter pine, San Dimas, Calif.	52.5	63.7	75	Extreme

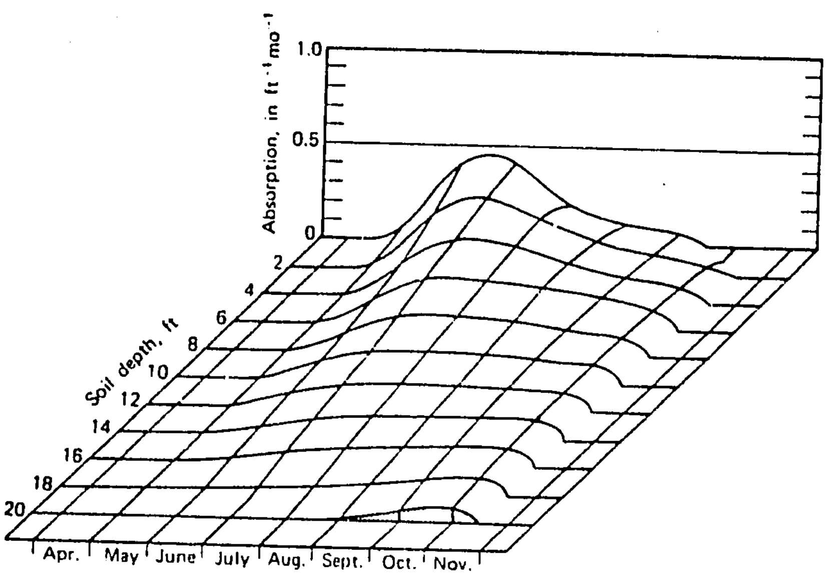


Figure 10.3. The pattern of water absorption from the upper 20 feet (6 m) of soil at a southern Appalachian mountain site. Total absorption peaks in June and thereafter extraction of water comes more and more uniformly from the entire profile. (After Patric et al., 1965. Reproduced from *Soil Science Society of America Proceedings*, Vol. 29, p. 305, 1965, by permission of the Soil Science Society of America.)

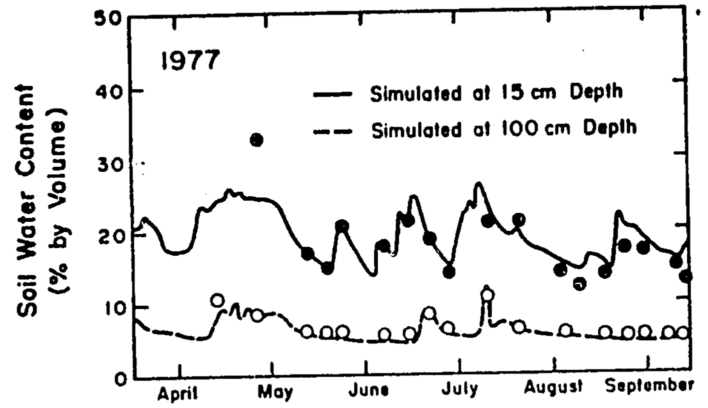


Fig. 5.8. Recharge or withdrawal of soil moisture from various depths were predicted by combining models for estimating water flux through the canopy, litter, and soil. Soil water contents were independently assessed (○, ●) with a neutron probe at four access tubes installed in the sandy soil under a 120-yr-old Scots pine forest in central Sweden. (After Jansson and Halldin, 1979.)

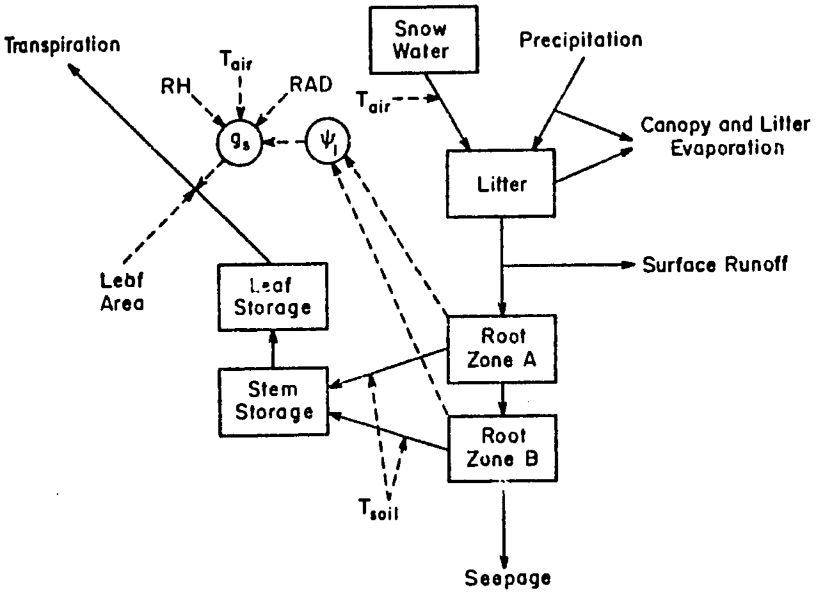


Fig. 4.11. General structure of a tree water balance model that accounts for precipitation entering into the litter or soil root zones [upper (A) or lower (B)] and its eventual loss from the system through transpiration, evaporation, runoff, or seepage. Within the tree, water may be stored temporarily in the sapwood or leaves. Transpiration depends on the potential evaporation, a function of air temperature (T_{air}), relative humidity (RH), and net radiation (RAD). Actual transpiration is less than potential, being constrained by the amount of leaf area and stomata conductance (g_s). Stomatal conductance in turn is constrained by cold soil temperatures (T_{soil}) that affect leaf water potential (ψ_l). In addition, T_a, RH, and RAD may affect stomatal conductance. Such a model may be expanded to a stand of trees and have a variable time resolution. (After Running, 1984.)

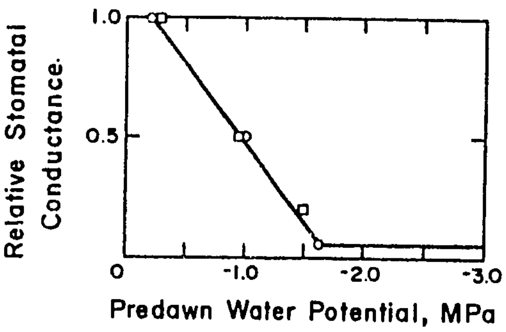


Fig. 4.9. As soils dry, the predawn water potentials of both Douglas fir (□) and tulip poplar (*Liriodendron*) (○) decrease. Maximum relative stomatal conductance during the day also decreases until complete closure is attained (−1.6 MPa here). (From Waring *et al.*, 1981b.)

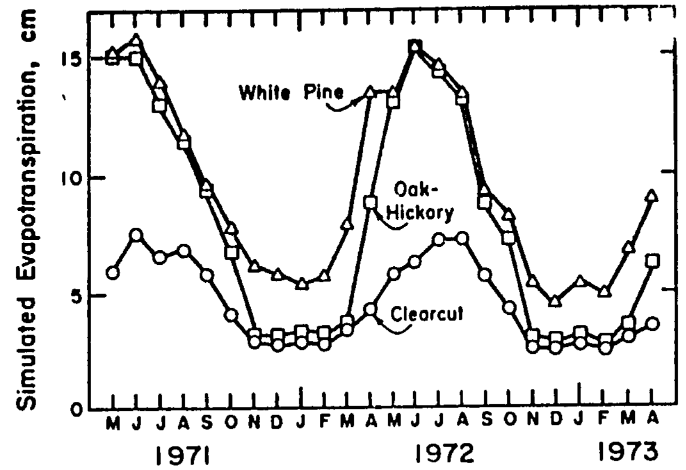


Fig. 5.9. Using the Penman–Monteith equation, evapotranspiration was simulated for forests of white pine (*Pinus strobus*), oak–hickory (*Quercus–Carya*), and vegetation reestablished on a recent clearcut. The predictions take into account seasonal changes in canopy LAI and climate.

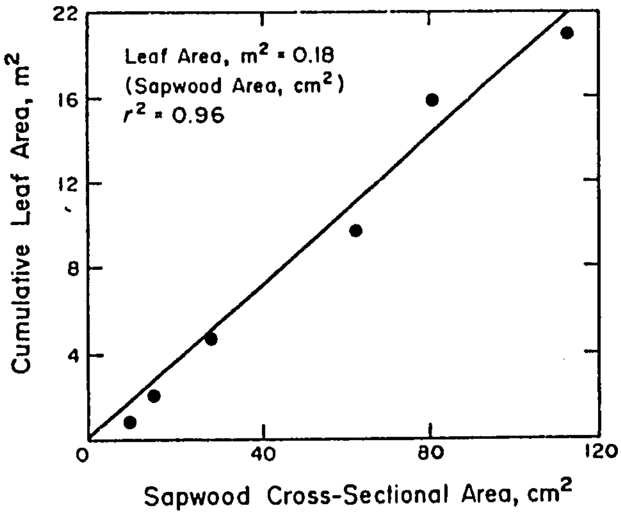


Fig. 2.17. The amount of leaf area above any level in a tree's crown is directly related to the sapwood area at that cross section. Data are from a single 12.4-cm diameter Scots pine showing this relationship from near the top to the bottom of the crown. (Unpublished data from B. Axelsson and R. Waring, Swedish University of Agricultural Sciences, Uppsala, Sweden.)

TABLE 2.4 Ratio of Projected Leaf Area to Sapwood Cross-Sectional Area for Selected Tree Species

Leaf area/sapwood area	m²/cm²	Reference
A. Conifers		
Abies lasiocarpa	0.75	Kaufmann and Troendle (1981)
Abies procera	0.27	Grier and Waring (1974)
Picea engelmannii	0.35	Waring *et al.* (1982)
Pinus contorta	0.15	Waring *et al.* (1982)
Pinus ponderosa	0.25	Waring *et al.* (1982)
Pinus sylvestris	0.14	Whitehead (1978)
Pseudotsuga menziesii var. *menziesii*	0.54	Waring *et al.* (1982)
Pseudotsuga menziesii var. *glauca*	0.25	Snell and Brown (1978)
Tsuga heterophylla	0.46	Waring *et al.* (1982)
Tsuga mertensiana	0.16	Waring *et al.* (1982)
B. Hardwoods		
Acer macrophyllum	0.21	Waring *et al.* (1977)
Castanopsis chrysophylla	0.46	Waring *et al.* (1977)
Nothofagus solandri (montane)	0.12	Benecke and Nordmeyer (1982)
Nothofagus solandri (subalpine)	0.07	Benecke and Nordmeyer (1982)
Populus tremuloides	0.10	Kaufmann and Troendle (1981)
Quercus alba	0.40	Rogers and Hinckley (1979)
Tectona grandis	0.65	Whitehead *et al.* (1981)

LESSON EIGHTEEN

CAUSES OF WATER DEFICITS AND STRESS

By the end of this lesson you should be able to:

....List the factors that induce water deficits
....Explain how trees may supplement soil water storage by stem water storage
....Diagram the daily cycle of induction and reduction of water deficits in a well-watered soil
....Define water stress in plants

THE CAUSES OF WATER DEFICITS AND STRESS

The development of water deficits is similar to a bank savings account. Plants loose water by transpiration (withdrawals), and water is made available to plants by precipitation (deposits). Soil depth and texture determine the soil capacity for moisture storage. The amount of available soil water is analogous to the current account balance. Such factors as root growth and salinity determine how easy it is to make withdrawals, and the hydraulic conductivity of roots, stem, and leaves determine how rapidly transfers can be made from one account (e.g. the soil) to another (e.g. the leaf). Water deficits develop whenever withdrawals (transpiration) exceed the rate at which transfers can be made to keep the leaf account with a current, positive balance.

I. Transpiration

Transpiration often exceeds water absorption during the day. Fig. 4.4 illustrates the common course of water absorption and transpiration in Scots pine. Transpiration began at sunrise, and soon exceeded water absorption. By 9:00 am a water deficit had accumulated sufficient to increase water absorption by increasing the Ψ gradient at the root-soil water interface. At 10:00 am the accumulated water deficit had been sufficient to cause partial stomatal closure as evidenced by decreased transpiration. Transpiration decreased more toward sunset, but water absorption continued into the night until the deficit was removed. The water deficit developed in the morning was removed at night.

II. Conductance

The conductance to the movement of water through the stem is regulated by several factors (Lesson Thirteen), including xylem anatomy and age. As previously discussed, water transport encounters less resistance in xylem composed of vessels than of trachieds. Fig. 4.14 illustrates decreased water conductance of Scots pine wood with age. Water deficits can be induced in leaves even with adequate soil moisture if stem or root conductance is not sufficient to supply the transpiration demand.

III. Water Absorption

The ability of the roots to absorb water is also affected by several factors (Lesson Eleven), including soil temperature, salinity, water content, and any factor that affects root growth. Poor soil aeration causes the resistance of the root to the passage of water to increase, and plants often wilt because of this, even though flooded. During later stages of poor soil aeration (e.g. by flooding) roots may die, and become quite resistant to water flux, or roots may cease growth, causing the prime root region for water absorption to diminish because of tissue maturation. All of these can induce water deficit

Salinity affects both the permeability of the root to water and increases π_{soil}, thus reducing the potential for water absorption. Restricted absorption may induce a water deficit.

IV. Soil Drying Cycle

Fig. 7.5 illustrates water potential changes during a soil drying cycle. Water deficits accumulate over time. The dashed line depicts the increasingly negative Ψ_{soil} over six days, until Ψ_{soil} reaches the permanent wilting point at day six at -1.5 MPa. Note that Ψ_{leaf} (solid line) goes though a diurnal cycle, becoming very negative during the day, but overnight Ψ_{leaf} becomes less negative, equaling Ψ_{soil} by dawn. Pre-dawn measurements of plant moisture stress (using the pressure bomb, Lesson Nine) are used to measure soil moisture stress based upon this relationship.

On day four in Fig. 7.5 Ψ_{leaf} dropped below -1.5 MPa. Recall that the solute or osmotic concentrations of most leaves is about 1.5 MPa. When $\Psi_{leaf} = -1.5$ MPa, turgor = 0 ($\Psi = \pi + T$, Lesson Three), and the leaf wilts. On days five and six the leaf continues to absorb water, as evidenced by less negative Ψ_{leaf} during the night, but the Ψ remained more negative than -1.5MPa, and the plant has entered the permanent wilting point. In contrast, on day three the leaf wilted in the late afternoon, but recovered by the following morning.

The daily leaf water potential of pine in three soil moisture regions is shown in Fig. 7.6. When grown in moist soil, Ψ_{leaf} dropped to -1.3 MPa, and in dry soil to -1.8 MPa, but no lower, indicating stomatal closure in dry soil.

V. Stem Storage

Trees have a tremendous capacity for stem storage of water, as much as 300 t ha^{-1}, or the amount that may be transpired over 5-10 days. In some cases stem water may be recharged quickly following rainstorms, but in others, as illustrated in Fig. 4.3, the stems may not recharge water lost during the summer until autumn or winter. The ability to store and use water to replace transpirational losses can significantly delay the onset of water deficits in large trees. Stem water storage actually supplements soil water storage in large trees.

Water stored in the stem may also be used during the day by trees as illustrated in Fig. 7.4. The use of stored water is reflected in diameter changes of the stem. Diurnal fluctuations in stem diameter are common in trees.

VI. Water Stress

As can be seen from the above discussion, the development of water deficits is a near daily occurrence in plants. *Water stress* develops whenever: ".. water loss exceeds absorption long enough to cause a decrease in cell enlargement and perturbation of various essential physiological processes" (Kozlowski, et.al. 1991). The usual cause for water stress is drought, but any situation of excess transpiration, inadequate absorption, insufficient water storage in stem and/or soil, or insufficient rate of transfer, if severe enough and prolonged enough, can cause water stress.

Additional Reading:

Kramer, P. J. 1983. Water relations of plants. pp. 344-351
Kozlowski, T, P. Kramer, and S. Pallardy. 1991. Physiological Ecology of woody plants. pp.250-254
Waring, R. and W. Schlesinger. Forest Ecosystems. 1985. pp.77-80.

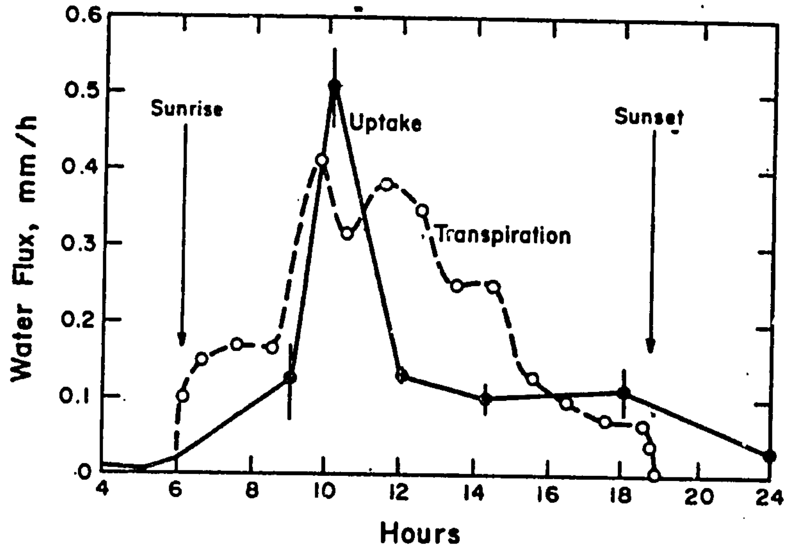


Fig. 4.4. In a 36-yr-old Scots pine forest, uptake of water over the daylight hours lagged behind transpiration by a third. Over a 24-h period, however, uptake balanced transpiration within 7%. Data derived from a study where uptake was estimated by radioisotope tracers injected into trees and transpiration were calculated from knowledge of canopy leaf area, stomatal conductance, and meteorological conditions. (After Waring *et al.*, 1980.)

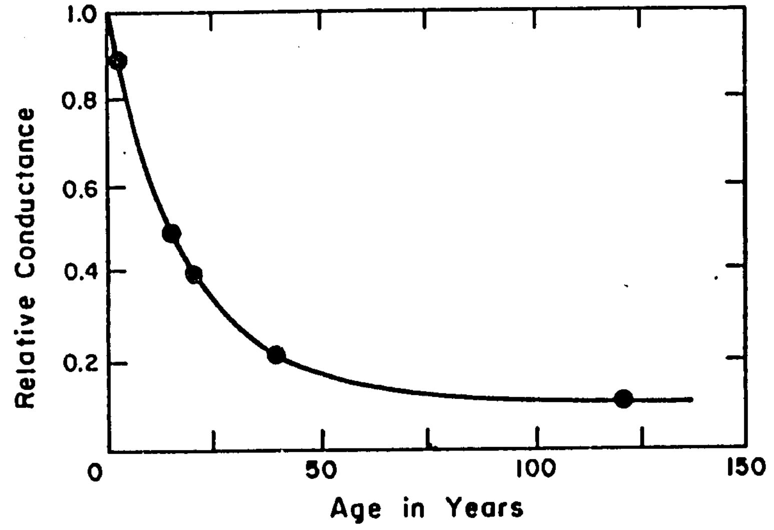


Fig. 4.14. As trees grow larger, the ability to conduct water through sapwood decreases and may eventually limit height growth. The relative conductance of Scots pine trees 5 yr old and 0.2 m high was 90% greater than that observed in 125-yr-old, 18-m tall trees on a sandy soil in central Sweden. (After Mattson-Djos, 1981.)

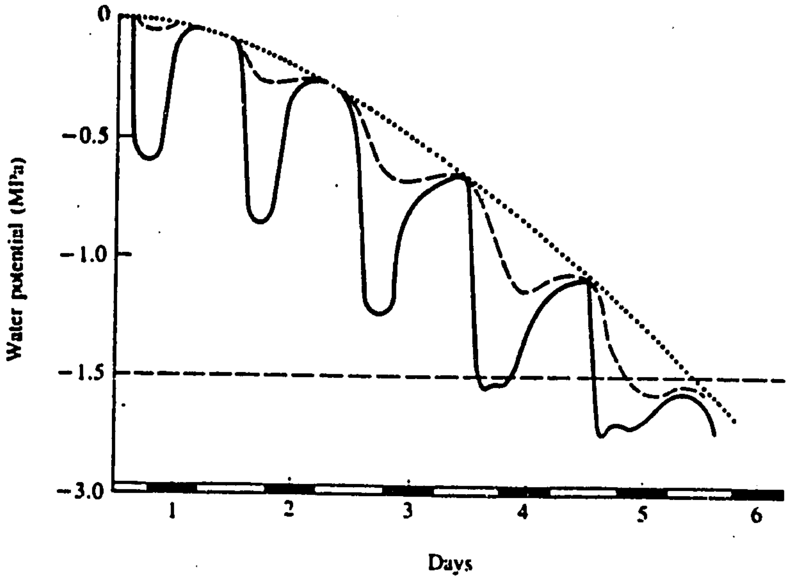


Figure 7.5 Diagram showing probable daily changes in leaf (——) and root (– –) water potential of a transpiring plant rooted in drying soil (····). The dark bars indicate darkness. (After Slatyer, 1967; from Kramer, 1983.)

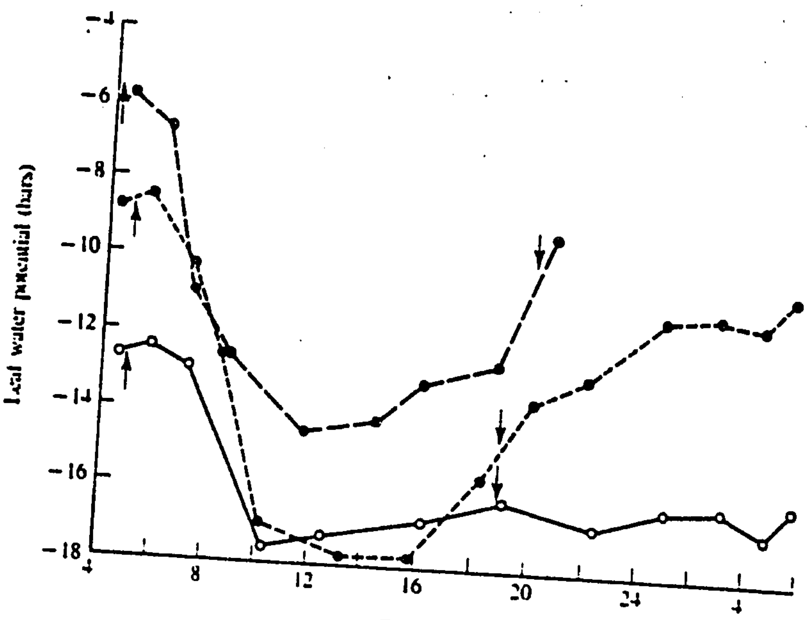


Figure 7.6 Daily cycle in leaf water potential of red pine trees showing slowing recovery with decreasing soil moisture during a drought. Tree W, July 1 (– –), was in moist soil; tree R, August 20 (---), was in intermediate soil; tree W, August 20 (——), was in dry soil. Arrows denote sunrise (*left*) and sunset (*right*). (See Sucoff, 1972, for more details.)

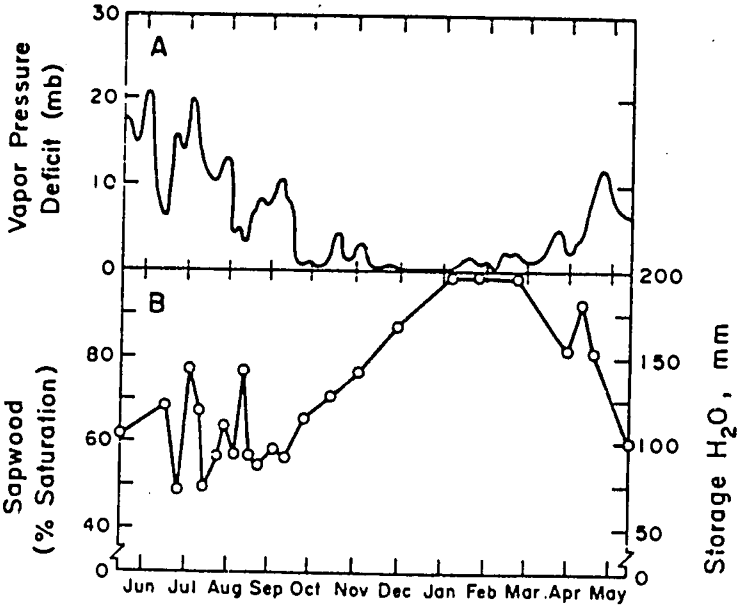


Fig. 4.3. Withdrawal of water from the sapwood of 500-yr-old Douglas fir growing in the Pacific Northwest (B) began when the water vapor gradient in the atmosphere averaged less than 5 mb for the day (A). During summer rains in June and late August, partial recharge of the sapwood began but was not completed until January, following extended periods of precipitation. Maximum daily rates of transpiration did not exceed 5 mm/day. (From Waring and Running, 1978.)

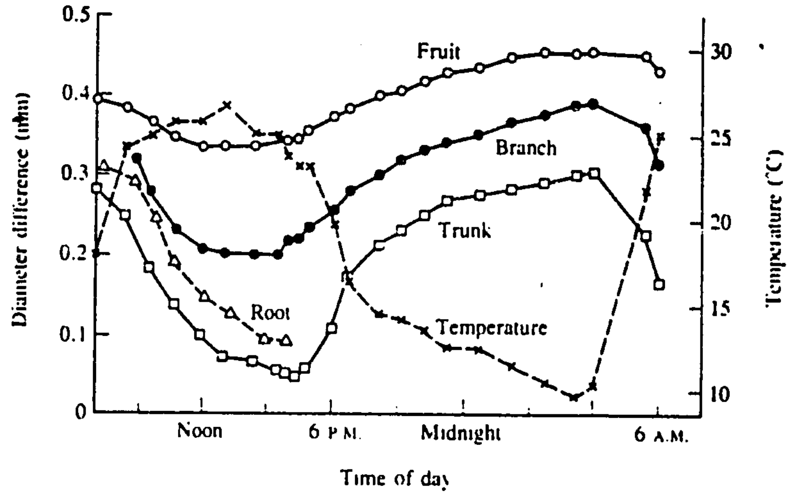


Figure 7.4 Midday shrinkage of various parts of an avocado tree caused by water deficits produced by rapid transpiration. (After Schroeder and Wieland, 1956; from Kramer, 1983.)

LESSON NINETEEN

THE EFFECTS OF WATER STRESS

By the end of this lesson you should be able to:

....Define water stress
....Describe the effect of water stress on cell elongation and tissue enlargement
....Compare the effect of water stress on cell elongation with its effect on photosynthesis
....Describe the mechanism by which some plants and seeds resist water stress
....Define osmotic adjustment
....Describe the cause of water stress induced in winter
....Describe how water stress may be measured

THE EFFECTS OF WATER STRESS

I. Water Stress

Water stress occurs when turgor pressure becomes so low that cell enlargement, or other physiological processes are adversely affected.

II. Avoidance of Water Stress

Turgor pressure develops in cells with a central vacuole. Cells form a central vacuole after cell division when scattered small vacuoles coalesce into one large vacuole, and that vacuole expands. Vacuolar expansion causes cell enlargement.

Not all plant cells form a central vacuole, and those without them avoid water stress. Examples include the mosses and lichens, which can be desiccated, but regain function upon rehydration. But the cells of mosses and lichens do not expand either, and thus they are limited to very short stature because no conduction tissue (e.g. xylem cells) are formed.

The embryo and endosperm cells of most seeds also do not have a central vacuole, and thus seeds avoid water stress. When the seed germinates the emerging root expands by formation and enlargement of the central vacuoles of its cells, and the developing root is then subject to water stress.

III. Effects of Water Stress on Cells

The effects of water stress are summarized in Table 24-1. Cell growth and wall synthesis is affected at Ψ = -0.7 MPa, which is less negative than required to induce stomatal closure in most species. This means that photosynthesis can still occur in plants under water stress (Figs. 12.10, 24-6). Note that ABA (abscissic acid) accumulation begins under a water stress of about -10 MPa. ABA causes stomates to close and remain closed even for some time after stress is relieved.

Proline and sugar accumulation occur at about the same stress level as ABA accumulation. Both proline and sugar accumulation increase π_{cell}, permitting the cell to maintain turgor against increasingly negative Ψ_{cell}. This is *osmotic adjustment* by which plants acclimate to increased water stress.

Sudden water stress is generally more damaging than stress that develops gradually. Gradual induction allows the plant to acclimate by osmotic adjustment, formation of additional leaf cutin, and improved root/shoot ratios

Water stress affects diameter growth in trees by reduced cell expansion. Fig. 7.8 compares trachied growth in irrigated and drought grown red pine. Water was not limiting in initial early wood growth, but under drought conditions the large cells of earlywood growth ended sooner. Both the number and the size of latewood cells were reduced in drought.

IV. Effect of Water Stress on Tissues and Whole Plants

The reduction in trachied number and size is reflected in diameter growth as shown in Fig. 10.5. Thinning this pine stand increased the amount of water available to the remaining trees. Thinned trees responded by increased diameter growth.

Water stress can also reduce height growth in trees. In Fig. 7.11 water stress was measured as pre-dawn water potential during summer drought in different habitats. Height growth of Douglas fir decreased as water potential became more negative. Species distribution is related to maximum pre-dawn water potentials during summer drought. *Abies* has a similar distribution to *Abies spectabolis* in Pakistan, preferring cool, moist habitats. The distribution of *Pinus ponderosa* is similar to *Pinus roxburgii*, occupying more xeric habitats; and the distribution of the *Quercus* species in both areas is similar by being found in the most xeric forest habitats.

The effect of water stress in reducing cell size is not uniform throughout plant tissues. In general, the effect of cell size and number reduction is most severe in leaf expansion. Leaf area deceases, but leaf thickness may increases. Water stress may also induce leaf senescence and leaf shedding.

Shoots are generally more reduced by water stress than roots, resulting in an improved root/shoot ratio for drought.

V. The Cause of Water Stress Induced Cell Death

The vacuole shrinks as turgor becomes increasingly negative. Eventually this shrinkage causes the cytoplasmic membrane to be torn as the cytoplasm is pulled away from the cell wall. This causes cell death.

VI. Effect of Water Stress on Insect Damage

Pine engraver beetles require tree Ψ = -1.5 MPa or less for successful penetration, and widespread infestations of pine bark beetles occur after prolonged drought.

VI. Winter Water Stress

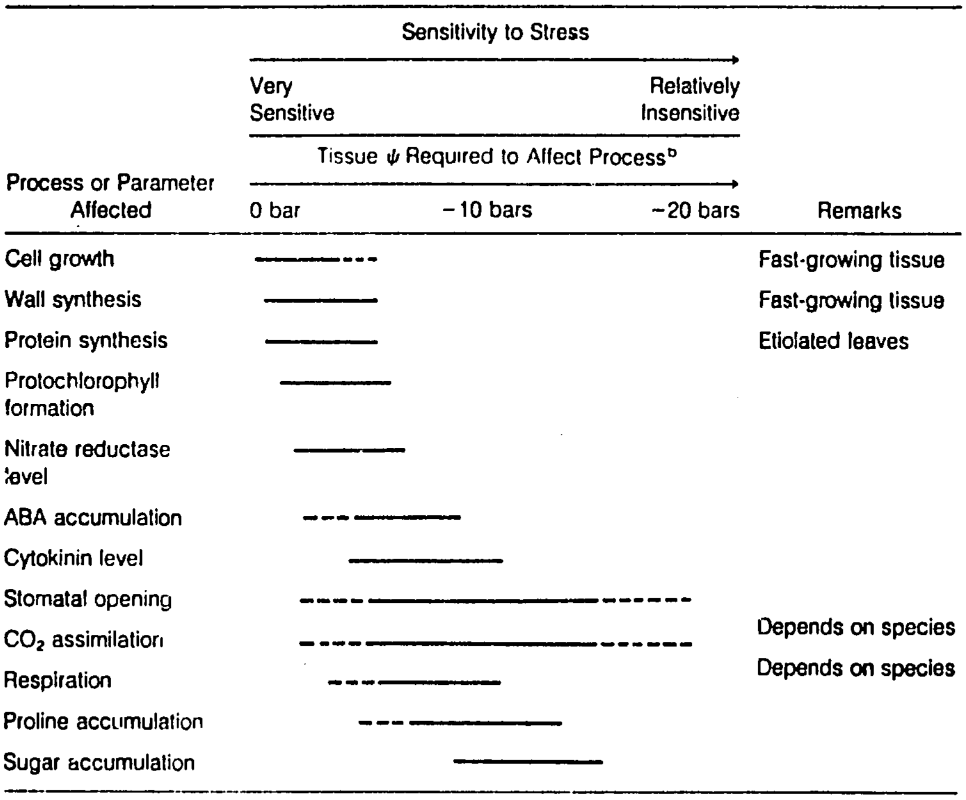
Water stress developing in winter may kill buds and leaves. The hardening process during autumn increases the amount of bound water and solutes in leaves, and protective, water retaining tissues are formed around buds to protect them. But water can be lost from these tissues during the dry winter. If the stem and/or ground is frozen, preventing replacement, injury may occur.

VII. Measurement of Water Stress

Water stress may be measured by relative water content. A leaf or leaf disk is weighed, floated on water, and weighed again. Weight gained during hydration indicates water content below saturation at the time the sample was taken. Most plants suffer water stress when the relative water content is less than 92% of saturation.

Additional Reading:
Kramer, P. J. 1983. Water relations of plants. pp. 352-380
Landsberg, J. J. 1986. Physiological ecology of forest production. pp. 156-159.
Slavik, B. 1974. Methods of study of plant water relationships. pp.136-145
Spurr, S. and B. Barnes. 1992. Forest ecology. pp. 264-268.

Table 24-1 Generalized Sensitivity to Water Stress of Plant Processes or Parameters[a]



Process or Parameter Affected	Sensitivity to Stress → Very Sensitive … Relatively Insensitive Tissue ψ Required to Affect Process[b] → 0 bar … −10 bars … −20 bars	Remarks
Cell growth	———---	Fast-growing tissue
Wall synthesis	———	Fast-growing tissue
Protein synthesis	———	Etiolated leaves
Protochlorophyll formation	———	
Nitrate reductase level	———	
ABA accumulation	---———	
Cytokinin level	———	
Stomatal opening	----————------	
CO_2 assimilation	----————------	Depends on species
Respiration	---———	Depends on species
Proline accumulation	---———	
Sugar accumulation	———	

[a] Length of the horizontal lines represents the range of stress levels within which a process first becomes affected. Dashed lines signify deductions based on more tenuous data.

[b] With ψ of well-watered plants under mild evaporative demand as the reference point.

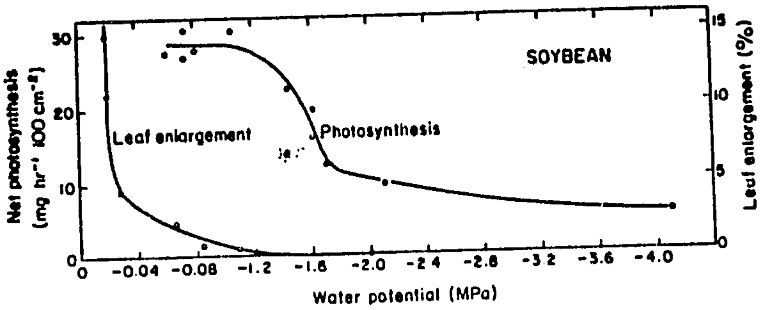


Fig. 12.10. The relationship between leaf water potential, leaf elongation, and photosynthesis in soybean. Leaf elongation practically ceased before there was much reduction in photosynthesis. See also Fig. 1.4. (From Boyer, 1970a.)

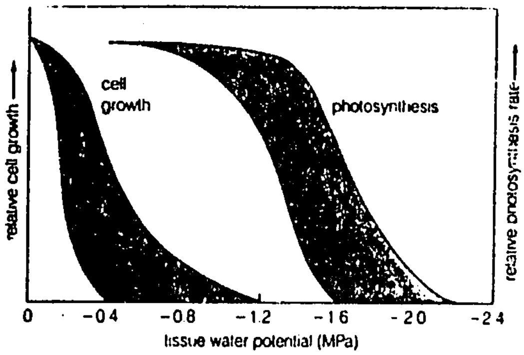


Figure 24-6 Cell growth and photosynthesis as a function of decreasing tissue water potentials. Shaded areas include ranges of response as observed with several species in different experiments. Cell growth (leaf enlargement, for example) is much more sensitive to decreasing water potential than is photosynthesis. (See Boyer, 1970, and Acevedo et al 1971.)

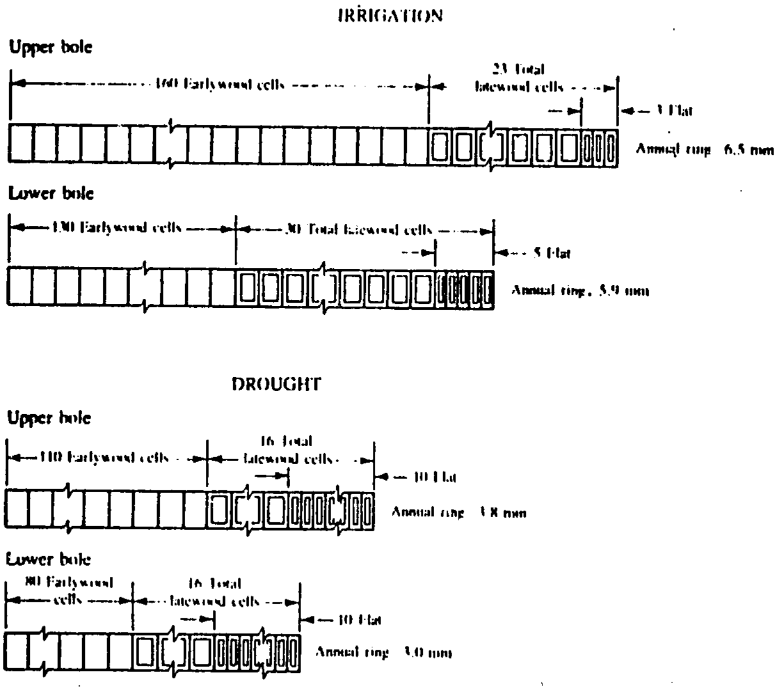


Figure 7.8 Difference in width of tracheids and in proportion of latewood in xylem rings of red pine grown with irrigation and under water stress. Also note differences between upper and lower bole. (From Zahner, 1968.)

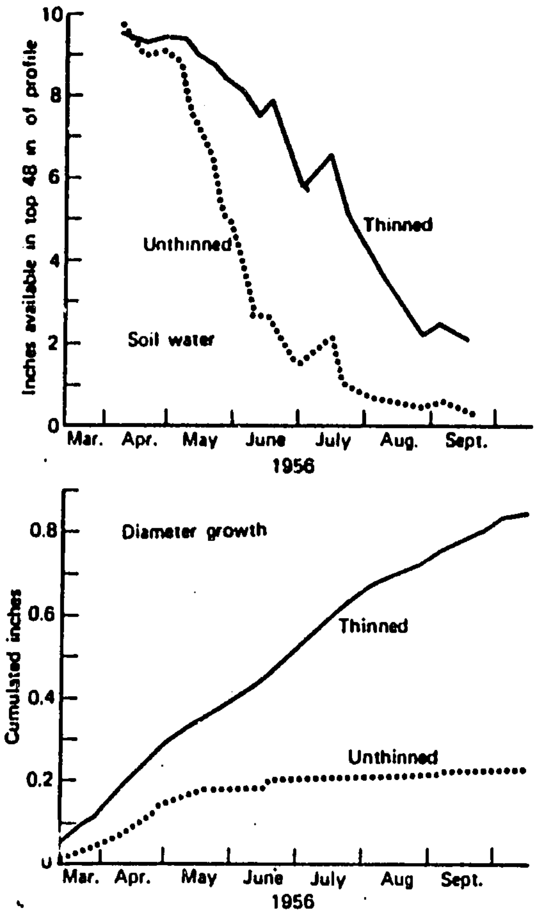


Figure 10.5. **Trends of soil water depletion and diameter increment per tree for average dominant loblolly pine during one growing season, thinned plots and unthinned plots. (Redrawn from Zahner and Whitmore,**

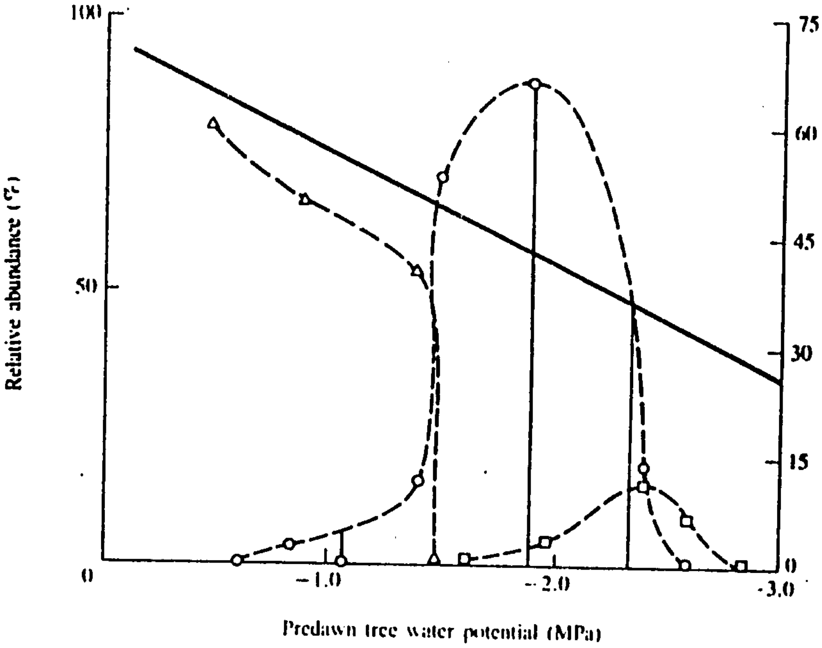


Figure 7.11 Relationship between predawn water stress of seedlings during summer drought and maximum height of Douglas-fir trees in southwestern Oregon (bold line). Also shown is the relative abundance of trees of three other species: *Abies concolor* (△), *Pinus ponderosa* (○), and *Quercus garryana* (□). (After Waring, 1970; from Waring and Schlesinger, 1985, by permission of Academic

LESSON TWENTY

WATER USE EFFICIENCY

By the time you complete this lesson you should be able to:

....Define water use efficiency WUE
....Identify the factors that affect the rate of diffusion, and describe the effect these factors have on transpiration, photosynthesis, and WUE
....Explain the effects of changes in mesophyll, stomatal, and boundary layer resistances on WUE
....Describe the effect of internal leaf surface area on WUE
....Explain variation in leaf form as an adaptive response to the environment

I. Water Use Efficiency

Water use efficiency WUE is the ratio of water transpired to dry matter, crop yield, or CO_2 fixed. Although WUE is related to plant distribution, it is not equivalent to drought tolerance.

The loss of water vapor by transpiration, and the absorption of CO_2 by photosynthesis, are both diffusion processes. The rate of diffusion is controlled by the diffusion gradient and by resistances to diffusion. In Lesson Fifteen the relationship for transpiration was expressed as follows:

$$T = \frac{(H_2O_{ins} - H_2O_{ext})\,(diffusivity)}{r_a + r_s}$$

In this equation (H_2O_{ins} - H_2O_{ext}) expresses the concentration of water vapor in the air (ext) and in the leaf (ins) respectively, or the diffusion gradient. Resistances r_s and r_a are stomatal and air-boundary layer resistances respectively. These resistances are illustrated in Fig. 18-6. Diffusivity is the diffusion coefficient of water vapor in still air.

The diffusion of CO_2 in photosynthesis can be expressed as:

$$Ps = \frac{(CO_{2_{ins}} - CO_{2_{ext}})\,(diffusivity)}{r_m + r_s + r_a}$$

In this equation ($CO_{2\,ins}$ - $CO_{2\,ext}$) represents the diffusion gradient. Diffusivity is the diffusion coefficient of CO_2 in still air, and r_m has been added to account for the resistance of CO_2 diffusion into mesophyll cells. Although water vapor originates from evaporation from the mesophyll cell surface, CO_2 must diffuse through cell walls into the mesophyll.

These two equations can be combined to give an expression for WUE:

$$WUE = \frac{(0.64\,Diffusivity\ H_2O)\,(conc.diff.CO_2)}{conc.diff.H_2O}\ \frac{(r_a + r_s)}{(r_a + r_s + r_m)}$$

CO_2 diffuses more slowly than H_2O because diffusion is proportional to molecular weight; MW $CO_2 = 44$ and MW $H_2O = 18$. The value 0.64 in the equation accounts for the differences between the diffusivity of water and CO_2 caused by molecular weight. *Conc.diff.* refers to the diffusion gradients of H_2O and CO_2 from inside to the exterior of the leaf.

An examination of the WUE equation discloses that there are three ways in which the diffusion of H_2O can be altered in relation to CO_2: changes of r_m which only affect CO_2; a differential effect of $r_s + r_a$ on the two gases; and changes in the diffusion gradient, mostly of CO_2 since that of H_2O is fixed by environmental conditions.

II. Differences in WUE

WUE varies more than ten fold between plant groups, including notable differences between C3, C4, and CAM (Crassulacean Acid Metabolism) plants (Table 5.5). C3, C4, and CAM refer to different pathways of carbon fixation in photosynthesis. The WUE of C3 plants is about 500:1, of C4 plants about 250:1, and CAM plants about 50:1.

III. Differences in WUE based upon mesophyll resistance r_m

A. C3 and C4 Plants

The differences in WUE of C3 and C4 plants is illustrated in Fig. 13.2. Sorghum is a C4 species, whereas soybean is C3.

The initial CO_2 acceptor in C3 photosynthesis is ribulose biphosphate carboxylase-oxidase (rubisco). This enzyme has a relatively low affinity of CO_2, and as its name implies, it reacts with oxygen as well as CO_2. When rubisco reacts with oxygen, carbon is lost by photorespiration. Carbon loss by photorespiration increases with temperature, and net photosynthesis (or yield) decreases when it occurs.

In initial acceptor in C4 photosynthesis is phosphoenol pyruvic acid carboxylase (PPC). It has a very high affinity for CO_2 and does not react with oxygen, thus does not lose fixed carbon by photorespiration. The C4 process has a higher potential for net photosynthesis. Many of the most productive crops are C4 species (e.g. corn, sugar cane), especially in hot climates because the increased carbon loss by photorespiration by C3 plants in warm climates does not occur in C4 plants.

Plants which possess C4 photosynthesis have a greater WUE because PPC has a higher affinity for CO_2, thus lowering mesophyll resistance r_m. C4 plants also maintain a steeper diffusion gradient because no CO_2 is lost back into the substomatal cavity by photorespiration. Because of this C4 plants can reduce the internal CO_2 concentration to near zero, whereas C3 plants can only reduce the internal CO_2 concentration to 80-120 ppm (atmospheric CO_2 is about 340 ppm). The combined properties of a steep CO_2 diffusion gradient and low r_m account for the high WUE of C4 plants.

B. CAM plants

CAM plants are succulents such as cactus. They have the highest WUE. These plants are adapted to arid conditions. Their stomata open at night and close during the day, just the reverse of most plants. CAM plants absorb CO_2 during the cool, humid night, minimizing water loss. CO_2 is stored as an organic acid, and undergoes photosynthesis the following day. CAM plants also have a low r_m. Although CAM photosynthesis utilizes the less efficient C3 pathway, they have high WUE because, in addition to night time CO_2 absorption, these succulents expose a large, internal surface area of mesophyll cells through which absorption can take place, reducing r_m by increased surface area.

IV. WUE differences based upon internal surface area

A large ratio of internal leaf (mesophyll) surface area to exterior surface area is a general characteristic of plants with high WUE. Xerophytes have a ratio of internal/external leaf area of 17-31, sun leaves of mesophytes 12-19, and shade leaves 7-10. Xerophytes have the highest WUE, and shade leaves the least.

The greater the internal mesophyll area of the leaf the greater surface offered for CO_2 absorption, and the lower r_m.

V. Differences Based upon Differential r_s and r_a to CO_2 and H_2O

The major resistance to CO_2 diffusion is r_m. In order to enter the cell CO_2 must first dissolve in the water-filled cell walls. The rate of diffusion in liquids is about one thousand times slower than in gas, thus diffusion of CO_2 is much more affected by r_m than by r_s and r_a.

Since the major source of resistance to CO_2 diffusion is r_m, any factor that increases r_s and r_a will affect transpiration more than photosynthesis, and thus improve WUE. Partial stomatal closure improves WUE for this reason. This is the reason that WUE may increase in midday as excess transpiration over water absorption causes partial stomatal closure.

VI. Differences in WUE based upon CO_2 diffusion gradients

WUE efficiency increases with increasing external CO_2 concentrations. Fig. 10.6 illustrates that the effect of increased CO_2 is greater in C3 soybean than in the C4 corn. Increased external CO_2 has a greater effect on low CO_2 affinity rubisco than high CO_2 affinity PPC.

The effects of CO_2 on photosynthesis, leaf conductance and transpiration of cottonwood is illustrated in Fig. 10.4. WUE increased with increasing CO_2 because of increased photosynthesis and decreased transpiration. This was caused by partial stomatal closure, as evidenced by decreased leaf conductance (to water vapor) with increased CO_2.

The effects of partial stomatal closure on conductance (the reciprocal of resistance) on CO_2 and H_2O diffusion is given in Tab. 10.2. Note that stomatal closure reduced water conductance by 50%, but CO_2 conductance by only 27%.

VII. Ideal Leaf Form

Fig. 18.8 illustrates the relationships between leaf size (expressed as cm of width), stomatal resistance (sec cm^{-1}) on photosynthesis and WUE at two temperatures. Large leaves at high temperatures, especially those with high stomatal resistance, exhibit poor photosynthetic rates. Large leaves maintain temperature by evaporative cooling since the alternative, convectional cooling, is not efficient over large surfaces. Such leaves tend to overheat in hot climates, close stomata, and reduce photosynthesis.

One alternative for large leaves in hot climates is to maintain very low transpiration resistance, and this is the strategy of some phreatophytes and related plants with poor WUE. These species must have a dependable water supply for their roots, but they maintain high levels of photosynthesis because their large leaves can be kept cool by rapid transpiration. *Populus deltoides*, an exotic widely planted in Pakistan, utilizes this strategy.

A poor WUE is not always a disadvantage. In areas with water tables near the surface with danger of surface evaporation and subsequent salinization, plantings of species such as *Populus* may lower the water table by rapid transpiration rates, thus reducing the likelihood of salinization by reduced evaporation from the soil surface.

Fig. 18-8 also discloses the reason why small leaves are common in hot, dry climates. This includes the world-wide distribution of legumes with pinnately compound leaves. These small leaflets are effectively cooled by convection, transpiring water only as needed during CO_2 exchange. Water is not needed for cooling small leaves.

In contrast, in cool, moist climates, large leaves are more photosynthetically efficient. Those with high leaf resistance have high WUE.

The factors that affect transpiration and photosynthesis are summarized in Fig. 19-10. Leaf characters such as pubescence are included in this figure because of effects on solar absorbance, with resultant effects on transpiration and photosynthesis, thus WUE.

VII. Global CO_2 increase, global warming, and WUE

Fig. 10.6 discloses the effect of increased CO_2 on WUE, illustrating the effect is greatest on the C3 soybean, and least on the C4 corn. WUE increases with CO_2 to 1900 ppm, or about six-fold current atmospheric concentrations.

This trend is further illustrated in Fig. 10.4 in which the photosynthetic rate of cottonwood increased to about 900 ppm CO_2, whereas leaf conductance (to water vapor) and transpiration decreased, giving an improved WUE.

These data suggest that as global CO_2 concentration increases, photosynthesis, especially in C3 plants should increase, causing an increase in WUE. But this is confounded by the fact that CO_2 enrichment of the atmosphere will cause global warming and thus photorespiration in C3 plants, causing a decrease in WUE. This conflict allows only speculation and not prediction of the effect of global warming on plant productivity or WUE.

<u>Additional Reading</u>:

Barbour, M. G., et al. 1987. Terrestrial Plant Ecology. pp. 372, 445-447.

Kozlowski, T. T. 1991. Physiological ecology of woody plants. pp. 382-385, 391.

Kramer, P. J. 1983. Water relations of plants. pp. 405-415.

Table 5.5. Average transpiration ratios for productivity ($1/\omega_{\mathrm{p}}$, in liters of transpired water per kg dry matter produced). Data taken from Maximov (1923), Shantz and Piemeisel (1927), Ringoet (1952), Joshi et al. (1965), Polster (1950, 1967), Black (1971), Nobel (1977a), Caldwell et al. (1977), and André et al. (1978)

Herbaceous C_3 plants	
Grain	500–650
Legumes	700–800
Potatoes and beets	400–650
Sunflowers (young)	280
Sunflowers (flowering)	670
Woody plants	
Tropical foliage trees (crop plants)	600–900
Temperate-zone foliage trees	200–350
Conifers	200–300
Oil palms	ca. 300
C_4 plants	220–350
Maize species in field experiments:	
INRA 260 (early variety)	320
Pioneer 3567 (late variety)	266
Maize in growth chamber:	
INRA F7 × F2	136
CAM plants	50–100

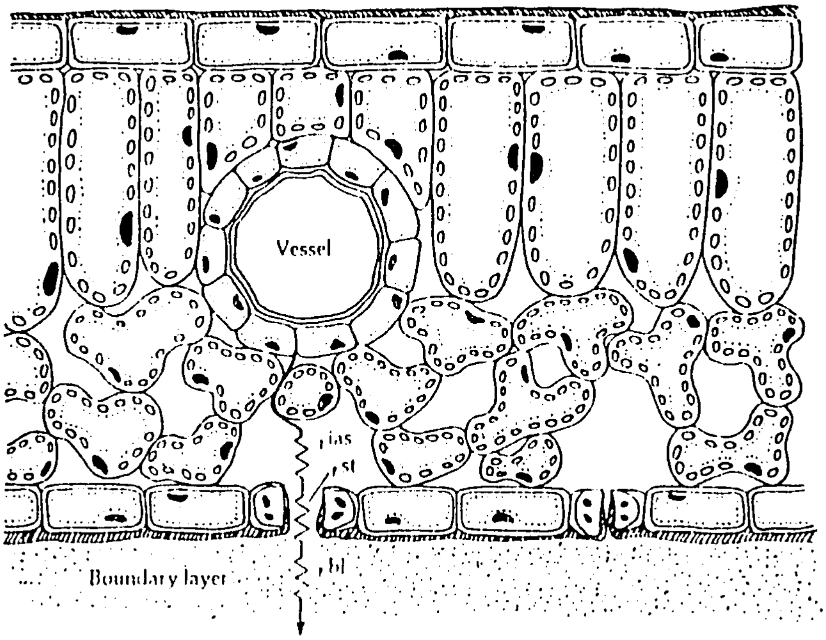


Figure 18-6 Cross section of a leaf showing the resistances associated with water loss. r^{ias} is the resistance to vapor movement in the substomatal cavity, r^{st} is the resistance offered by the stomatal pore and guard cells, and r^{bl} is the resistance offered by the boundary layer on the leaf surface.

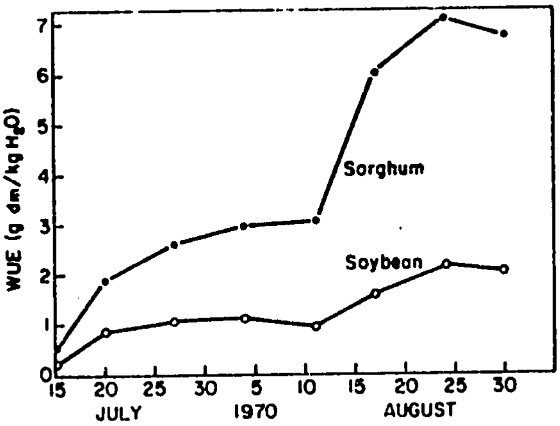


Fig. 13.2. Differences in water use efficiency (WUE) of soybean and sorghum. (From Teare *et al.*, 1973.)

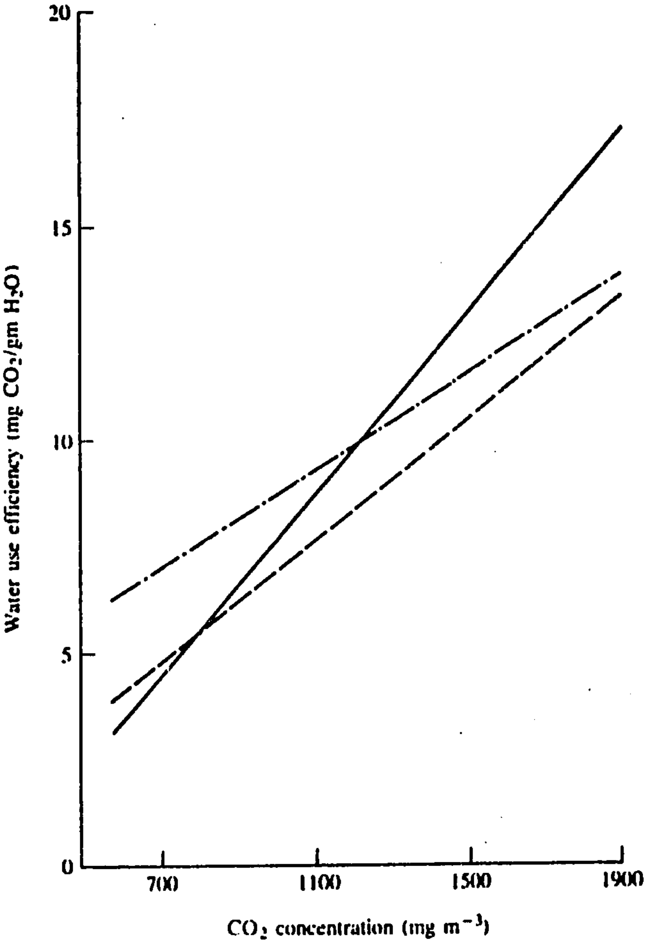


Figure 10.6 Water use efficiencies of sweet gum (– –), corn (–·–), and soybean (——) with increasing CO_2 concentration. (After Rogers *et al.*, 1983.)

Table 10.2

Approximate Effects of Partial Closure of Stomata on Conductances for Water Vapor and CO_2[a]

	Air and stomatal conductance (cm sec⁻¹)	Internal or mesophyll conductance (cm sec⁻¹)	Total conductance (cm sec⁻¹)	Reduction in total conductance
Water vapor				
Stomata open	0.43	0	0.43	
Stomata closed	0.22	0	0.22	50%
CO_2				
Stomata open	0.27	0.16	0.102	
Stomata closed	0.14	0.16	0.074	27%

[a] From data of Cooke and Rand (1980).

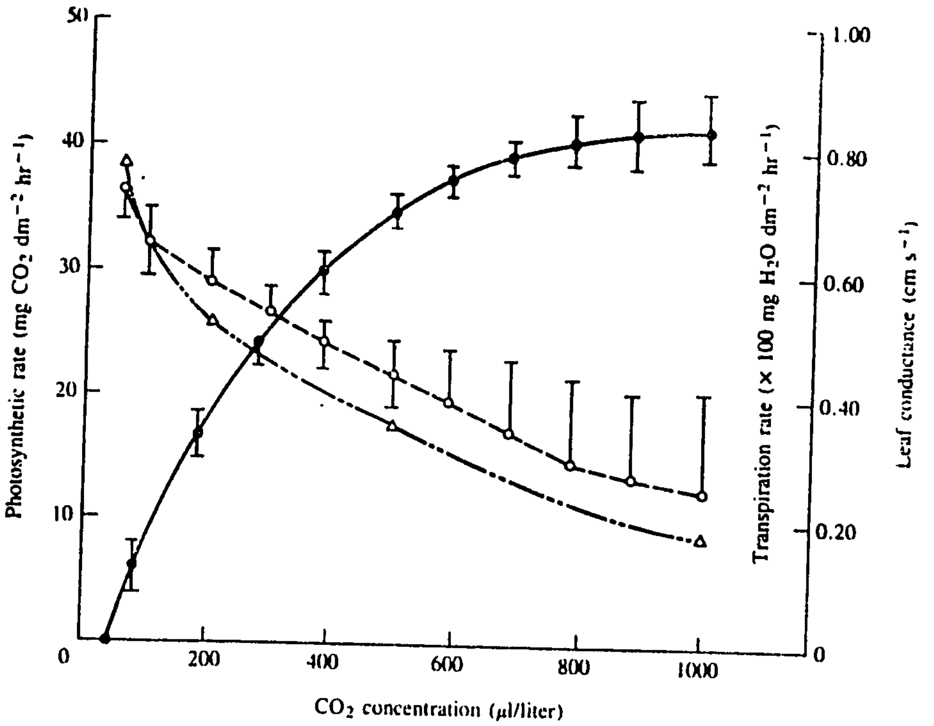


Figure 10.4 Effects of increasing CO_2 concentration on net photosynthesis (●), leaf conductance (△), and transpiration (○) of eastern cottonwood. (Adapted from Regehr *et al.*, 1975; from Sionit and Kramer, 1986; reprinted with permission from "Carbon Dioxide Enrichment of Greenhouse Crops," Volume II. Copyright © 1986 by CRC Press, Inc., Boca Raton, FL.)

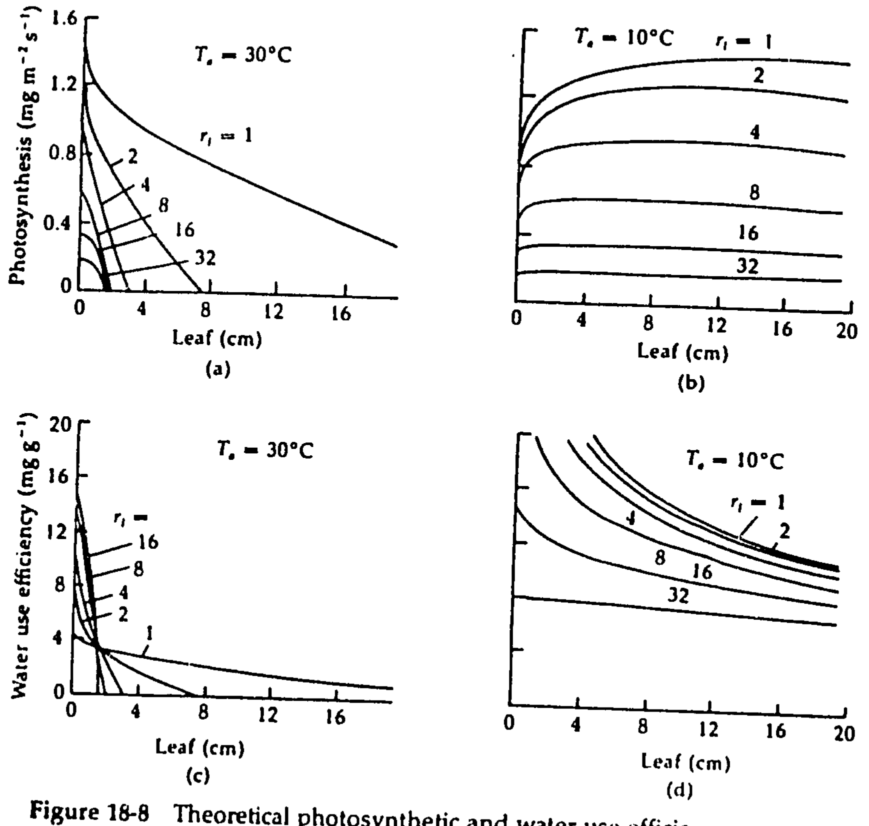


Figure 18-8 Theoretical photosynthetic and water use efficiency responses for leaves of different sizes and for different levels of resistance (r_l) when exposed to ambient temperatures (T_a) of 30°C and 10°C. (From Campbell, G. S. 1977. *An Introduction to Environmental Biophysics.* By permission of Springer-Verlag, New York.) WUE = mgCO_2 fixed per g H_2O transpired.

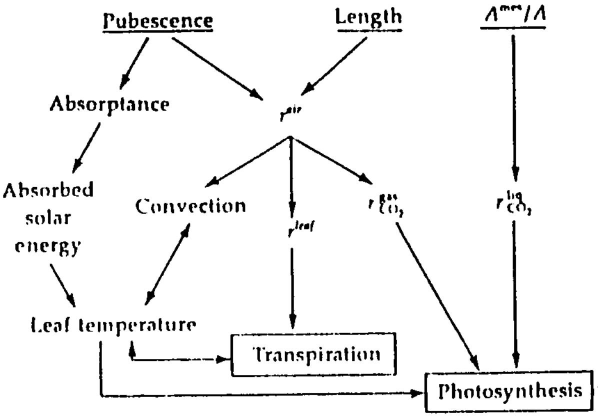


Figure 19-10 Schematic of the influences of pubescence, leaf length, and A^{mes}/A on transpiration and photosynthesis. (From "Influences of seasonal changes in leaf morphology on water use efficiency for three desert broadleaf shrubs" by W. K. Smith and P. S. Nobel, 1977. Ecology 58: 1033-1043. Copyright © 1977 by the Ecological Society of America. Reprinted by permission.)

LESSON TWENTY-ONE

DROUGHT TOLERANCE

When you finish your study of this lesson you should be able to:

....Describe the major causes of deserts
....Describe the characteristics of drought avoiders
....List two characteristics of water spenders
....Describe four ways plants may postpone dehydration
....List three ways in which plants may reduce water loss in response to drought
....Define dehydration tolerance

DROUGHT TOLERANCE

I. Drought

Drought is a meteorological event defined as a period without precipitation of sufficient duration that soil moisture is depleted and injury to plants may result. It is permanent in arid regions, seasonal in regions with well-defined wet and dry seasons, and unpredictable or random in many humid regions.

The response of plants to water stress is more appropriately termed dehydration tolerance, and that term will be used throughout the rest of this lesson.

II. The Causes of Arid Regions and Deserts

Arid regions have an evaporation potential EP that is greater than precipitation P, and this includes about one-third of the earth's land surface. Deserts receive <25 cm yr^{-1} precipitation and have a P/EP ratio of about 0.25.

The major deserts of the world occur in the horse latitudes, or between 15-30 degrees north and south of the equator. The horse latitudes are an around-the-world band of arid regions. They are called the horse latitudes because of the historic abundance of these animals on the plains, grasslands and deserts that occur in these regions. Grasses prosper in arid regions because they can endure long periods of drought in dormancy, yet grow quickly when water is available.

Air that ascended in other latitudes descends in the horse latitudes, and in so doing it becomes warmer because of compression. Warm air holds more moisture than cool air, and thus precipitation does not occur with descending air masses.

The arid effect of the horse latitudes shifts northward in summer and southward in winter. In the northern hemisphere this causes summer drought in the higher latitudes, and increased summer precipitation in the lower latitudes.

The other major cause of arid regions is mountain ranges. When air masses encounter mountain ranges the air is forced to ascend; it cools during ascension and precipitation may occur. The air mass descends on the lee side, warms, thus preventing precipitation in the "rain shadow" of mountain ranges.

Because there is little water vapor in desert air, little incoming short-wave radiation or long-wave outgoing radiation is absorbed. For this reason deserts tend to be hot in the daytime and cold at night. Hot air rises up slopes and canyons during the day, and when cooled at night the air descends, causing winds that may, in the proper circumstances, build sand dunes. More commonly, "desert pavement" develops because the fine particles on the soil surface are blown away leaving larger stones on the surface.

The stress of drought has induced a number of adaptive mechanisms in plants, and these are similar around the world. The same mechanism has evolved in very different plant groups (convergent evolution). For example the succulent form and appearance of some *Cactaceae* are very similar to the *Euphoriaceae* even though these families are unrelated.

Desert soils are often saline because there is insufficient precipitation to wash the salts that have accumulated as a result of weathering away from the soil surface into ground water.

III. Adaptation to Drought by Drought Avoidance

Desert ephemerals and geophytes are included in this group. Many desert annuals avoid drought by passing through the dry period in dormancy as a seed. After precipitation these annuals germinate, display photosynthetically active leaves, flower, and set seed very quickly, utilizing the water stored in the soil before it drys out.

Geophytes, those plants that pass through the dormant season as in the soil as bulbs, rhizomes, corms, tubers, or similar organs, are also common in deserts. Because of their long vegetative life cycles, few if any trees are drought avoiders.

Drought avoiders such as desert annuals and geophytes seldom have xerophytic characteristics such as extra wax layers on their leaves. The environment is mesic during the period of their vegetative and floral development, and there is adequate soil water because of the recent rain that induced their growth.

Many drought avoiders have characteristics that prevent them from breaking dormancy or germinating until sufficient precipitation has occurred. A common characteristic is a germination inhibitor on the seed coat which must be washed away by the percolation of soil water past it. These seeds will not germinate if simply kept moist. This biological rain gauge often requires the passage of about 25 cm of water before the inhibitor is removed. This is sufficient precipitation to wet the soil to a depth of about 15 cm, enough soil water to assure that the seed can germinate and complete its life cycle.

IV. Adaptation to Drought by Dehydration Postponement

There are two general strategies of dehydration postponement: the water savers and the water spenders. Both categories may have a few features in common, but differ in others.

A. Water Spenders

This category includes the phraeatophytes such as *Prosopis* and some *Populus* species. They are common as riparian vegetation along water courses, and the roots of some may extend fifty meters into the soil to tap deep ground water sources. Some, such as *Prosopis* are so efficient at extracting soil water that the growth of more desirable species such as grasses are inhibited.

The stomata of water spenders remain fairly open, and transpirational water may be used for evaporative cooling of their leaves. In order to supply large volumes of transpiration water these plants develop extensive root systems, both in depth and in spread. They also maintain favorable root to shoot ratios. The water conduction system of water spenders is efficient, having more vessels in the xylem, dense leaf venation, shorter internodes, and more sapwood.

B. Water Savers

These plants may also have extensive root systems and efficient conduction systems, but may also have water storage capacities as well as characteristics designed to reduce water loss.

1. Water Storage

Succulents such as cactus and manyh euphorbes store water, often enough to supply plant needs for several months. The succulent stems of many of these species are pleated, allowing the stem to expand when absorbing water, and to contract as water is used. The π of these succulents is generally low. After precipitation, roots develop to tap soil water, and then as the soil dries out the roots abscess and scar tissue forms sealing the succulent stem from the dry soil.

The African baobab (*Adamsonia digitata*) is the best example of water storage in the tree form. The tree grows to a diameter of several meters, and is used as a water (and food) source by the African elephant. Douglas fir sapwood can supply several days of the trees water needs, that of Scotch pine about one-third of the daily requirement, and 24% of the daily requirement of spruce. Current investigations indicate that a substantial portion of the water withdrawn from storage in trees comes from the bark.

2. Reduced Water Loss

Many species reduce water loss during water stress. *Olea europea* reduces its water loss by 28% after acclimatization, *Quercus ilex* by 11%, and many desert species by 30-70%. Sclerophyllous trees and shrubs may reduce their water loss to 10-20% the rates before water stress.

This reduction is accomplished in a number of ways. Leaf hairs and additional waxy layers may develop, Some leaves fold or roll to reduce water loss. There is generally a reduction in leaf size during water stress, and there may be a change in leaf orientation to reduce radiation absorption.

Leaves may also be shed during drought. *Aesculus california*, *Prunus persica*, and *Quercus* species are known to shed leaves during drought. Leaf abscission reduces water loss, and preserves the buds and cambium for a longer period.

Low humidity induces stomatal closure in some species even if soil water is adequate. This characteristic has been shown to vary among province collections in species such as *Populus,* and *Juglan nigra*, the black walnut.

V. Adaptation to Drought by Dehydration Tolerance

Dehydration tolerance is the capacity of the protoplasm to endure dehydration without damage to its fine structure. There are very few examples of dehydration tolerance among higher plants, but many thallophytes are remarkably dehydration tolerant. These include some fungi, algae, and the lichens which can resume photosynthesis within an hour after rehydration from an air-dry condition. The resurrection plant, *Seleginella*, a few ferns, mosses, and a few grasses can also tolerate air-dry dehydration.

Among higher plants such dehydration is tolerated at one stage of the life cycle, the seed. Indeed, seed preservation depends upon, in part, maintenance in a dry condition.

Dehydration tolerance can be determined by measurement of the relative water content RWC which is lethal to 50% of the cells or tissue. Cells generally die if allowed to equilibrate with air at a relative humidity of 92 - 96%. This corresponds to Ψ -5.5 to -11 MPa. The organs of most species (e.g. leaves) are fatally damaged if the relative water content falls to 50-75%, but there are some exceptions. The desert shrub creosote bush (*Larrea divaricata*) of North and South America, and *Acacia aneura* of the Australian desert can withstand reductions of RWC to 30%.

VI Winter Drought

Trees may be damaged by drought in late winter in regions where the soil and/or stem is frozen, but air temperature and humidity is conducive to evaporation. Water loss from buds, even though covered with protective bud scales, may cause damage, as well as the excessive dehydration of evergreen leaves.

Additional Reading:

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