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MANUAL DEL CURSO
RELACIÓN SUELO-AGUA-PLANTA (SAP)
PARA INGENIERÍA AGRONÓMICA

DR. FRANCISCO A. SQUEO

**MANUAL DEL CURSO
RELACIÓN SUELO-AGUA-PLANTA (SAP)
PARA INGENIERÍA AGRONÓMICA**

© Francisco A. Squeo

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PRESENTACIÓN

“Donde quiera que alguien cultive plantas, desde un simple geranio en un macetero o cientos de hectáreas de maíz o algodón, conoce la importancia del agua para el éxito del crecimiento. La disponibilidad de agua no sólo afecta la productividad en jardines y campos de cultivo, sino que también controla la distribución de las plantas sobre la superficie de la tierra, desde los desiertos y pastizales hasta los bosque lluviosos, dependiendo de la cantidad y estacionalidad de las precipitaciones”

(Kramer y Boyer, 1995)

En el año 1997 preparé una primera versión de este Manual, con la intención de apoyar el estudio de mis alumnos. El éxito fue notorio, el rendimiento del curso aumento aún por sobre mis expectativa, demostrando que el tiempo que se invierte en el desarrollo de herramientas pedagógicas tiene su recompensa en el corto plazo. De la primera edición quedan sólo unas copias muy borrosas producto del uso y del re-fotocopiado. Considerando que los contenidos de este curso han evolucionado con el tiempo, puesto que he incorporando nuevos elementos que lo han enriquecido, se hizo necesaria esta segunda edición del manual.

Pocas personas entienden completamente porque el agua es tan importante para el crecimiento vegetal. En este curso trataremos de explicar su importancia a través de mostrar como el agua afecta los procesos fisiológicos que controlan la cantidad y calidad del crecimiento y productividad.

El estudio profundo de las relaciones hídricas en los vegetales es muy relevante en la formación del Ingeniero Agrónomo de la Universidad de La Serena, dado que su futuro campo laboral está centrado en zonas áridas. La necesidad de un enfoque científico en la enseñanza de la agronomía en Chile ya fue planteado a mediados del siglo pasado. Según R. A. Philippi (1868) en su libro de Botánica, *“la fisiología vegetal es la base de la agricultura, horticultura y selvicultura racionales. ¡Ojalá llegue pronto el tiempo en que se enseñe también en Chile la agricultura racional!”*.

Este Manual del Curso Relación Suelo-Agua-Planta (SAP) para Ingeniería Agronómica resume la visión moderna de las relaciones hídricas en plantas, y fue diseñado para servir de apoyo a las actividades de la asignatura. Del momento que en cada tema sólo se entrega un punteo de la materia tratada, de ninguna manera reemplaza la asistencia a clases. Junto con el punteo de temas, en cada capítulo se reunieron las figuras y tablas que son utilizadas durante las clases, con la finalidad de apoyar su posterior estudio. En la segunda sección se encuentran las actividades prácticas a desarrollar durante el curso.

El texto guía de este curso es el libro Relaciones Hídricas en Plantas y Suelo (Kramer y Boyer, 1995), el cual debe ser utilizado por el estudiante. Adicionalmente, en cada capítulo se indica otra lectura recomendada.

Este Manual está dedicado al Dr. Paul J. Kramer (8 de Mayo de 1904 - 24 de Mayo de 1995), por su invaluable contribución al desarrollo de la Fisiología Vegetal moderna.

Francisco A. Squeo

La Serena, Marzo de 2003.-

PROGRAMA DE LA ASIGNATURA

RELACIÓN SUELO-AGUA-PLANTA PARA INGENIERÍA AGRONÓMICA

PROFESOR: Dr. Francisco A. Squeo

TEL: 302 PRE-REQUISITO: Edafología, Fisiología Vegetal.

TEORÍA: Jueves 10:30 - 13:00

LABORATORIO: Jueves 14:30 - 16:00 (Grupo 1), 16:15-17:45 (Grupo 2)

SEMINARIOS: Jueves 14:30 - 17:45

DESCRIPCIÓN Y OBJETIVOS DE LA ASIGNATURA

Curso teórico-práctico orientado al análisis de los principios fisiológicos involucrados en la absorción, transporte y re-distribución de agua y nutrientes de los vegetales. El estudiante será capaz de comprender las relaciones que se producen entre el suelo, el agua y las plantas, entre las que destacan: movimiento del agua en el suelo, absorción de agua y nutrientes por las plantas, transporte de elementos, transpiración, relación entre el balance hídrico y la nutrición mineral, efectos de la falta de agua.

CONTENIDOS DEL CURSO

UNIDAD I. El agua

- 1.- Funciones y propiedades del agua.
- 2.- Relaciones hídricas a nivel celular.
- 3.- Retención y liberación de agua en el suelo.

UNIDAD II. El agua en la Planta

- 4.- Crecimiento y desarrollo del sistema radicular.
- 5.- La absorción del agua y los potenciales hídricos de la raíz y el tallo.
- 6.- La transpiración y la subida de la savia.
- 7.- Estomas e intercambio de gases.
- 8.- Transporte de iones y metabolismo del nitrógeno.

UNIDAD III. El agua y la productividad vegetal

- 9.- Fotosíntesis y respiración - crecimiento.
- 10.- Estrés hídrico.
- 11.- Uso del agua a nivel evolutivo y agronómico.

LABORATORIOS Y SEMINARIOS

Sistema Radicular 1 (preparación)
Sistema Radicular 2 (montaje)
Seminario I
Sistema Radicular 3 (Fin de exp. Botellas)
Seminario II
Conductancia por xilema
Transpiración
Caracterización hídrica (curvas PV)
Seminario III-a
Eficiencia en el uso del agua / Sistema Radicular (Fin exp. en tubos)
Salida a Terreno
Discusión salida a Terreno
Seminario III-b

FORMA DE EVALUACIÓN

Se realizarán tres Pruebas Parciales que incluirán los temas tratados en las clases teóricas, pasos prácticos y seminarios precedentes (24% cada una). Al iniciar cada sesión de laboratorio se realizarán interrogaciones escritas u orales del objetivo y actividad a desarrollar, lo que sumado a los informes de laboratorio y terreno tendrá una ponderación final de 16%.

Seminario: Cada alumno tendrá por responsabilidad desarrollar un tema de investigación bibliográfica durante el curso, el cuál será evaluado de acuerdo a la calidad de la exposición y la presentación de un resumen escrito del tema, nota que valdrá un 12%.

WEB del curso.

En el sitio WEB del Departamento de Biología (<http://www.biouls.cl>), todas las asignaturas tienen una pagina web. Luego de ingresar a la pag. Principal, entrar a Docencia, Ingeniería Agronómica y SAP. El programa del curso y otros antecedentes de interés para los alumnos se encontrarán en esta dirección.

BIBLIOGRAFÍA DEL CURSO

Textos Guía:

Kramer P.J. y JS Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego.

Jones H.G. (1992) Plant and Microclimate. Cambridge.

Fernández G. y M. Johnston (1986) Fisiología Vegetal Experimental. Instituto Interamericano de Cooperación para la Agricultura.

Fitter A.H. y R.K.M. Hay (1981) Environmental Physiology of Plants. Academic Press.

Textos de Apoyo:

Banner J. y A. Galston (1970) Principios de Fisiología Vegetal.

Bewley J.D. y M. Black (1978) Physiology and Biochemistry of Seeds in relation to Germination. Spring-Verlag.

Bidwell, R.G.S. (1993) Fisiología Vegetal. AGT Editor S.A., México.

Coleman, D.C. y B Fry (1991) Carbon Isotope Techniques. Academic Press.

Glass A.D.M. Plant Nutrition: An Introduction to Current Concepts. Jones and Bartlett Publ.

Givnish T.J. (1990) On the Economy of Plant Form and Function. Cambridge.

Grace J. (1983) Plant- Atmosphere Relationships. Outline Studies in Ecology. Chapman and Hall.

Jensen W.A. y F.B. Salisbury (1988) Botánica. Mc Graw Hill.

- Kramer P.J. (1983) Water Relations of Plants. Academic Press, Inc.
- Lange O.L., L. Kappen y E.D. Schulze (1976) Water and Plant Life - Problems and Modern Approaches. Springer-Verlag.
- Larcher W. (1977) Ecofisiología Vegetal. Omega.
- Larcher W. (1995) Physiological Plant Ecology. Springer, Berlin.
- Marschner H. (1995) Mineral Nutrition of Higher Plants. Academic Press, London.
- Medina E. (1977) Introducción a la Ecofisiología Vegetal. Monografía O.E.A.
- Marschner H. (1995) Mineral Nutrition of Higher Plants. Academic Press, London.
- Milburn J.A. (1979) Water flow in Plants. Longman.
- Mooney H.A. , E.R. Fuentes y B.I. Kronberg (1993) Earth System Responses to Global Change. Academic Press.
- Nobel P.S. (1991) Physicochemical and Environmental Plant Physiology. Academic Press.
- Pearcey R.W., J. Ehleringer, H.A. Mooney y P.W. Rundel (1990) Plant Physiological Ecology: Field Methods and Instrumentation. Chapman and Hall.
- Poljakof-Mayber A. y J. Gale (1975) Plants in Saline Environments. Springer-Verlag.
- Salisbury F.B. y C.W. Ross (1979) Plant Physiology. Wadsworth Publ. Co. Inc.
- Salisbury F.B. y C.W. Ross (1994) Fisiología Vegetal. Grupo Editorial Iberoamérica, S.A., México.
- San Pietro A. (1974) Experimental Plant Physiology. Mosby Company.
- Turner N.C. y P.J. Kramer (1980) Adaptation of Plants to Water and High Temperature Stress. John Wiley & Sons.
- Yaron B., E. Danfors y Y. Vaadia (1973) Arid Zone Irrigation. Springer-Verlag.

ASIGNATURA

RELACIÓN SUELO - AGUA - PLANTA

ACTIVIDADES TEÓRICAS

Unidad I: EL AGUA

Capítulo 1: FUNCIONES Y PROPIEDADES DEL AGUA

A) FUNCIONES DEL AGUA

- a) Importancia ecológica del agua
- b) Importancia fisiológica del agua
 - funciones: constituyente, solvente, reactante, mantención del turgor.

B) PROPIEDADES DEL AGUA

1. Propiedades moleculares del agua

a. **Isótopos en el agua** (^1H = abundante (99.9844%); ^2H (deuterio)= 0.0156%, estable; ^3H (tritio)= muy raro, radiactivo (vida media= 12,5 años); ^{16}O = abundante (99.763%); ^{17}O = muy raro (0.0375%), ^{18}O = 0.1995%).

- $\delta^2\text{H} = ((R_{\text{muestra}}/R_{\text{estándar}}) - 1) * 1000\text{‰}$, donde el R_{muestra} y el $R_{\text{estándar}}$ son los cuocientes molares de $^2\text{H}/^1\text{H}$ (ó $^{18}\text{O}/^{16}\text{O}$ para $\delta^{18}\text{O}$) de la muestra y el estándar

* $\delta^2\text{H}$ = la proporción de Isótopos estables de hidrógeno ^1H y ^2H relativo al estándar SMOW (Standard Mean Ocean Water), varía entre +100 y -400‰.

* $\delta^{18}\text{O}$ = proporción de Isótopos estables de oxígeno relativo al estándar PDB (Pee Dee Belemnite, CaCO_3 fósil de Carolina del Sur, USA), varía entre +50 a -50‰.

- Proporción de Isótopos se mide con un espectrómetro de masa.

- $\delta^2\text{H}$ en neblina (0‰), lluvia (-40‰), nieve y agua subterránea de nieve (-90‰).

b. Estructura del agua: H_2O (D_2O)

- Puente de hidrógeno y fuerzas de van der Waals (alta tensión superficial, cohesión entre moléculas de agua y adhesión del agua a sólidos). Angulo = $104,5^\circ$, molécula bipolar.

- Alto calor específico (cantidad de calor requerida para elevar la temperatura de 1 g de la sustancia en 1°C) (agua líquida= $4.18 \text{ J}/(\text{K g})$) y alta capacidad calórica volumétrica (CCV= densidad * calor específico). Sólo el amonio tiene mayor CCV que el agua.

- Alto calor latente de vaporización (568 cal/g = 2256.0 J/g) y fusión (80 cal/g = 334.8 J/g), y sólo 1 cal. para elevar la temperatura de 1 g agua en 1°C .

- Empaque de moléculas de agua (hielo: 1 molécula esta rodeada por otras 4; agua líquida: 1 a 5). Menor volumen relativo se observa a $+4^\circ\text{C}$.

- Viscosidad $\propto 1/\text{Flujo}$. Altamente dependiente de la temperatura: $0.0179 \text{ g}/(\text{cm s})$ a 0°C , 0.01 a 20°C , 0.0055 a 50°C .

- Viscosidad en solución con líquidos polares (p.e., etil alcohol-agua)

- Gran conductor de calor (salvo por metales)

- Transparencia a radiación visible (390 - 760 nm) y opaca en rojo lejano (absorbe calor).

- Baja ionización: $1: 5.55 \times 10^8$

- Alta constante dieléctrica (abilidad para neutralizar la atracción entre cargas eléctricas).

** Explicación: puentes de hidrógeno

- t° de evaporación es $+100^\circ\text{C}$, cuando le corresponde menor a -100°C por su masa; Metano (CH_4 , no polar y sin puentes de H) tiene una t° de evaporación -

161°C.

- % puentes de hidrógeno: hielo= 100%, agua a 0°C= 85%, agua a 100°C= 70%.

- Agua unida a macromoléculas (p.e., proteínas): no se congela hasta -20°C a -25°C

2. Propiedades de las soluciones acuosas

a. **Presión de vapor** (presión ejercida cuando un sólido o líquido está en equilibrio con su propio gas; función(sustancia, temperatura). Presión de vapor a saturación (atmósfera saturada con agua) es altamente dependiente de la temperatura: 4.58 mm Hg a 0°C; 92,5 mm Hg a 50°C; 760 mm Hg a 100°C.

- Humedad relativa (HR)= $100 \cdot p/p^\circ$, donde p y p° son la presión de vapor de agua actual y saturada, respectivamente.

- Déficit de presión de vapor (DPV): $p^\circ - p$

- Temperatura de punto de rocío (Dew point): temperatura a la que el aire insaturado debe ser enfriada para producir condensación.

b. **Presión de vapor** de soluciones salinas

- Ley de Raoult (1887): $p = p^\circ \cdot X$, donde X es la fracción molar del solvente (moles solvente / (moles soluto + solvente)). Válido para soluciones diluidas.

c. **Osmosis**: difusión de solvente a través de una membrana que mantiene diferencias de concentración de soluto y presión (membrana semipermeable o con permeabilidad diferencial). La presión que debe ser aplicada a la solución para evitar el movimiento de agua se conoce como presión osmótica (π).

- Ecuación de Van't Hoff $\pi V = n_s i R T$, donde V es el volumen del solvente (m^3), n_s los moles del soluto, i = cte. de ionización, R = cte. gases ($8.32 \times 10^{-6} \text{ MPa } m^3 \text{ mol}^{-1} \text{ K}^{-1}$), T = t° absoluta (K). Para un mol de soluto no ionizable (p.e., sacarosa) en un litro de solvente a 273 K (=0°C), $\pi = 2.27 \text{ MPa}$; para NaCl $\pi = 4.32 \text{ MPa}$.

d. **Tensión superficial - Efecto capilaridad.**

-Altura de la columna (h) = $(2s \cos \alpha) / (D g r)$; donde s = tensión superficial del líquido, $\cos \alpha$ = coseno del ángulo de contacto, D = densidad del líquido, g = aceleración debido a la gravedad, r = radio del capilar. Para el agua a 20°C $h = 0.1485/r$, ó $r = 0.15/h$ (cm).

e. **Absorción de agua en la superficie de sólidos.** Resultado de fuerzas electrostáticas, hidratación es proceso exotérmico por lo que se libera calor (p.e., hidratación de la arcilla)

C) REPASO DE CONCEPTOS BÁSICOS

- Teoría termodinámica

1º Ley: conservación de la energía, la energía no se crea ni se destruye, solo se transforma de una forma en otra.

Energía Interna (E) = Energía cinética + Energía potencial

Entalpía (H) = $E + PV$

2º Ley: En cualquier conversión de energía, algo de ella se transfiere como calor al ambiente (todo sistema y su medio tiende espontáneamente al desorden; ningún proceso de transferencia de energía es 100% eficiente).

- Entropía (S): medida del desorden de un sistema
- Energía libre de Gibbs: $\Delta G = \Delta E + \Delta PV - T\Delta S$,
donde ΔE = energía interna, ΔPV = producto presión-volumen, $T\Delta S$ = factor de desorden (S= entropía).
 - Potencial químico (PQ)= G/M
 - PQ_{agua} = potencial hídrico= $\Psi = PQ_w - PQ_w^\circ$
 - difusión ocurre en respuesta a gradientes G ó PQ: concentración, temperatura, presión, hidratación.
 - velocidad de difusión: gradiente de PQ por unidad de distancia, permeabilidad del medio, temperatura.

LEER:

Kramer P.J. y J.S. Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego. Capítulos 1 y 2.

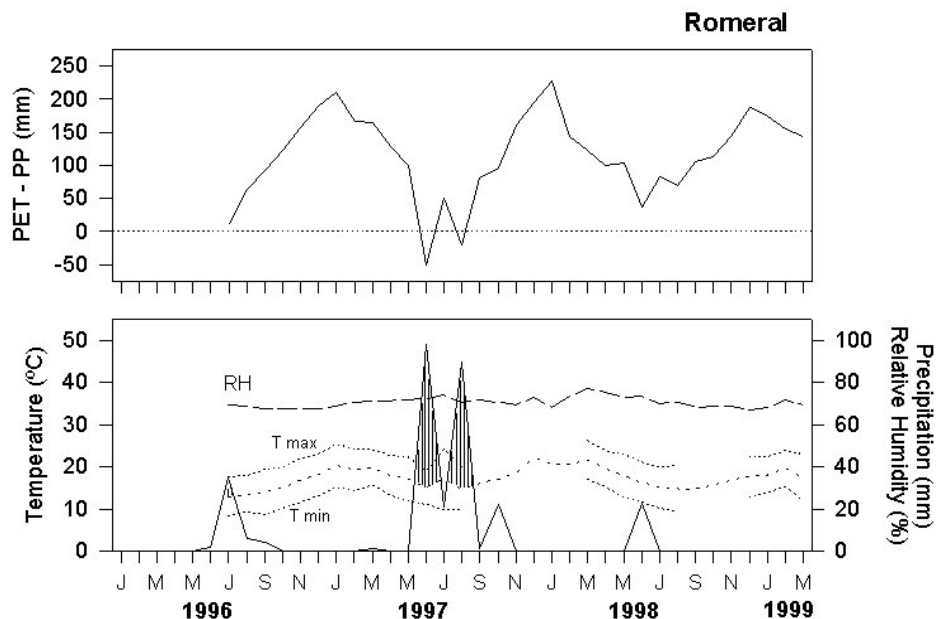
Kramer, P.J. (1983) Water Relations of Plants. Academic Press, Inc. Capítulo 1.

Squeo F.A. y J.R. Ehleringer (2003) Isótopos Estables: una Herramienta Común para la Ecofisiología Vegetal y Animal. En (F Bozinovic y HM Cabrera, eds): Fisiología Ecológica y Evolutiva en Animales y Plantas.

Salisbury F. y C. Ross (1994) Fisiología Vegetal. Grupo Editorial Iberoamérica, México. ISBN 970-625-024-7. Capítulo 1 y 2.

Jensen W.A. y F.B. Salisbury (1988) Botánica. Mc Graw Hill. Capítulo 1. p.16-19.

Nobel P.S. (1991) Physicochemical and Environmental Plant Physiology. Academic Press. Capítulo 2. p.47-77



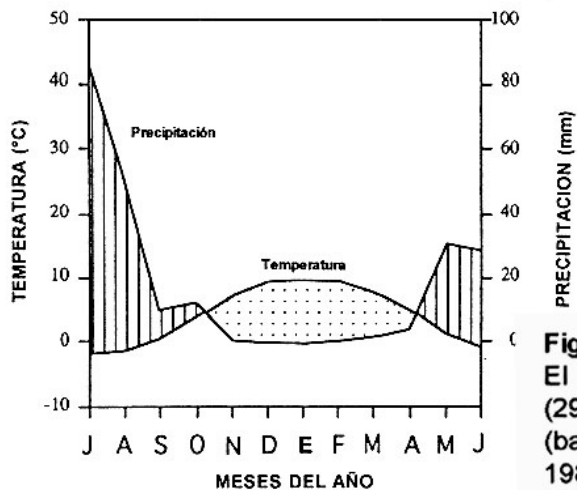


Fig. 2.: Diagrama ombrotérmico de El Indio, Cordillera de Doña Ana (29° 45' S, 69° 59' O, 3.750 m) (basado en datos de Ojeda et al. 1989).

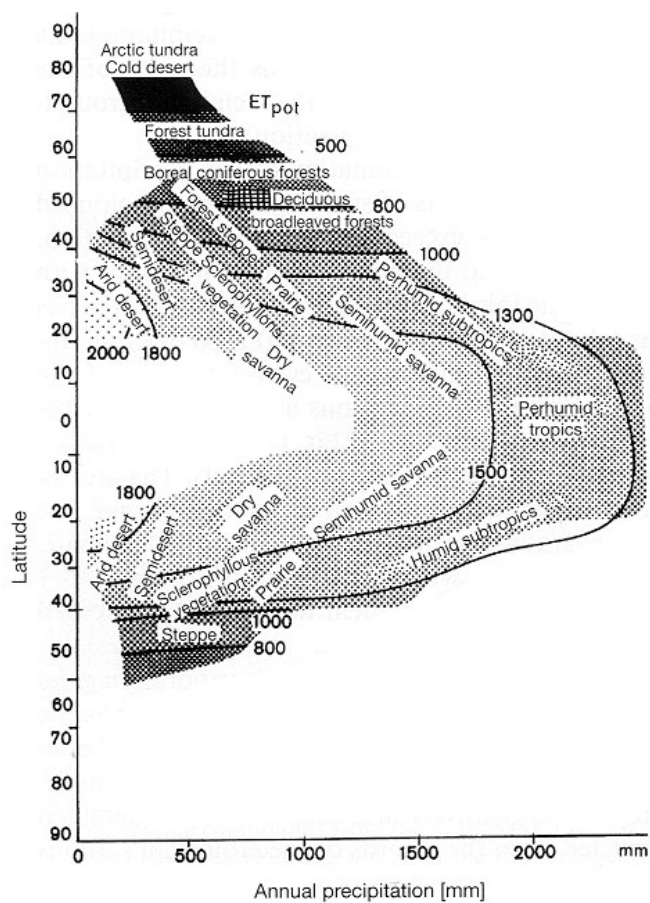


Fig. 6.55. Latitudinal distribution of annual precipitation and potential evapotranspiration (ET_{pot} in mm a^{-1}), and of characteristic plant formations. (After Schultz 1988)

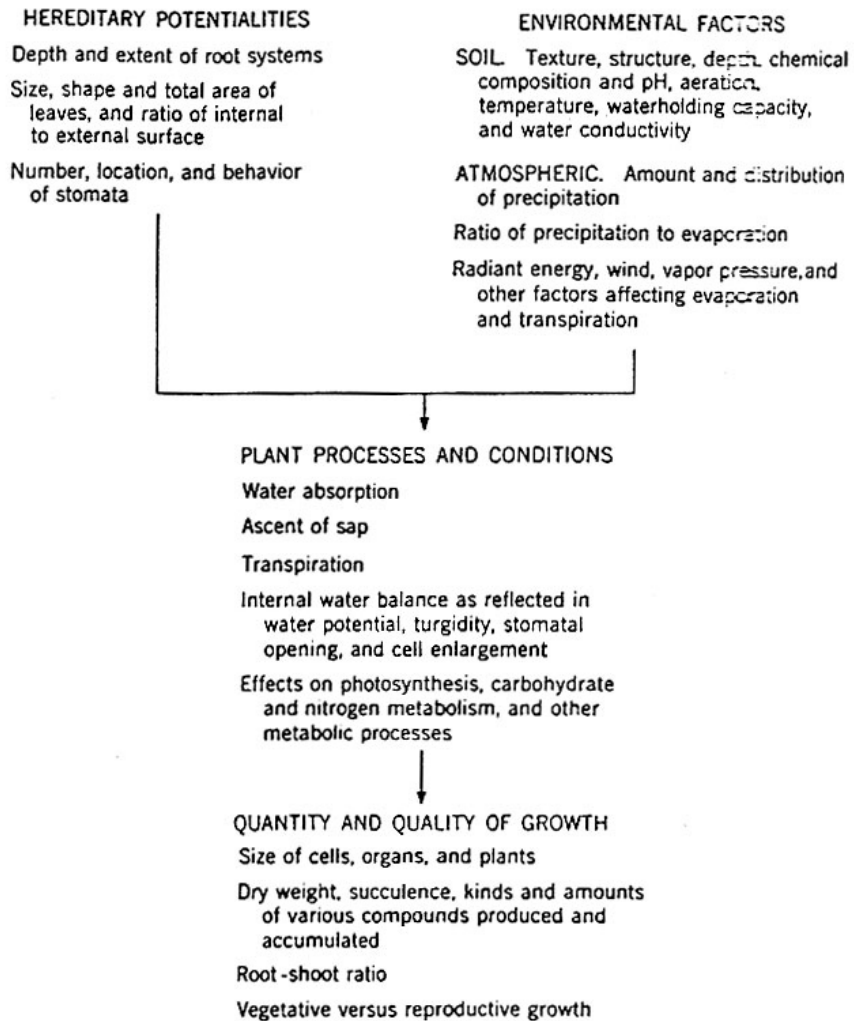


Fig. 1.1. Diagram showing how the quantity and quality of plant growth are controlled by hereditary potentialities and environmental factors operating through the internal processes and conditions of plants. Special attention is given to factors and conditions affected by water relations.

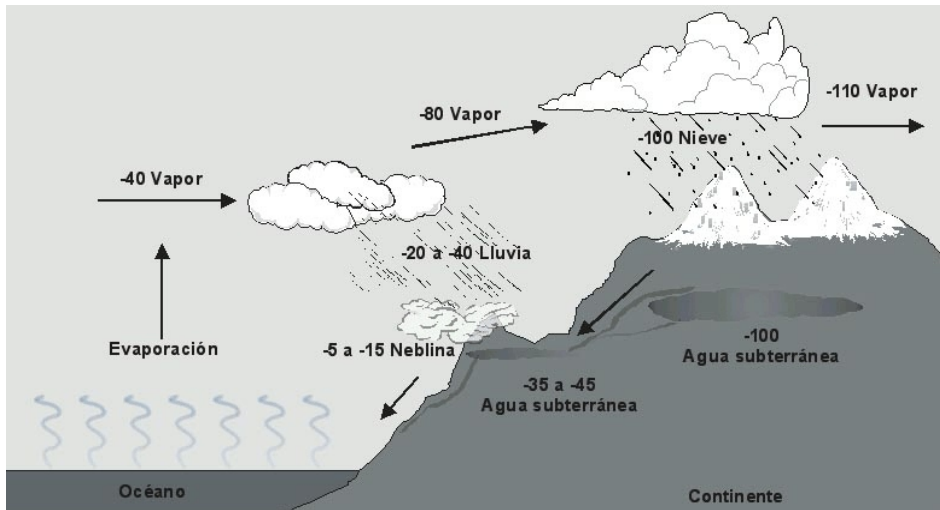


Fig. $\delta^2\text{H}$ en el Ciclo del agua (a los 30°S) (tomado de Squeo & Ehleringer 2003)

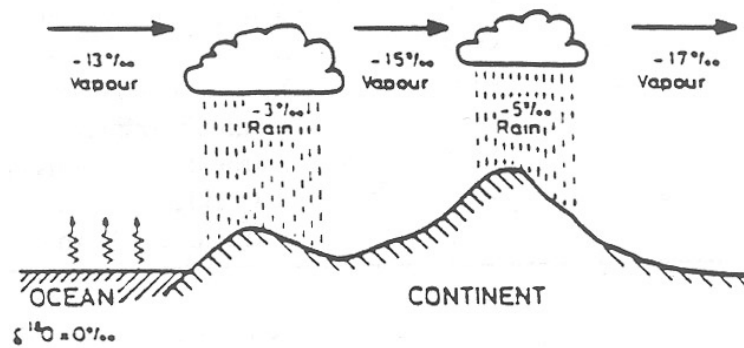
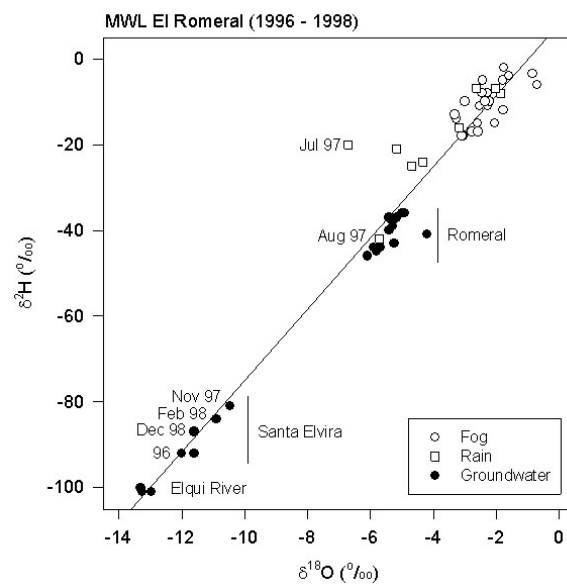


Fig. $\delta^{18}\text{O}$ en el Ciclo del agua (USA)



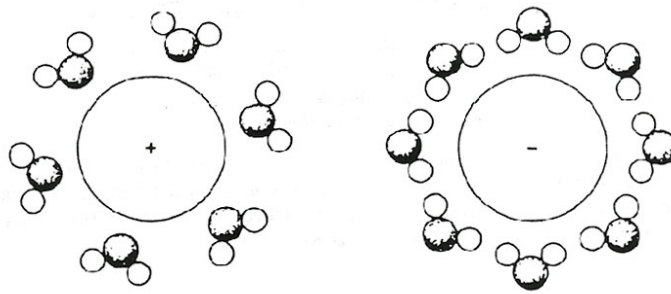


Figure 2.6 Diagram showing approximate arrangement of water molecules in shells oriented around ions. These shells tend to separate ions of opposite charge and enable them to exist in solution. They also disrupt the normal structure of water and slightly increase the volume. From Kramer (1983), after Buswell and Rodebush (1956).

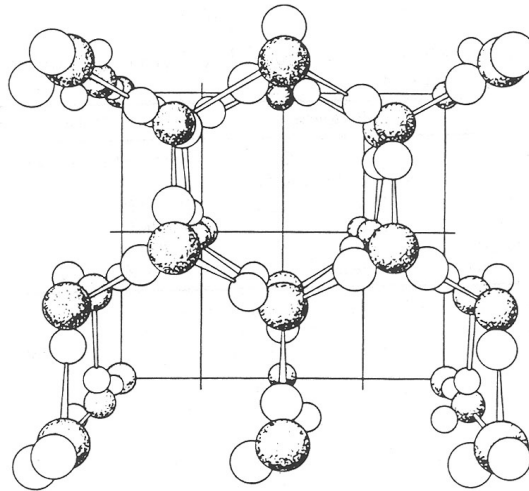
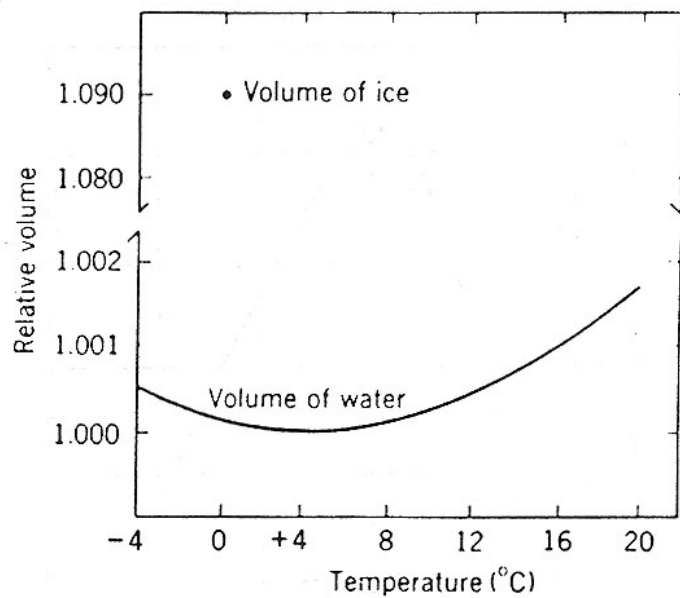


Figure 2.7 Diagram showing approximately how water molecules are bound together in a lattice structure in ice by hydrogen bonds. The dark spheres are oxygen atoms, and the light spheres are hydrogen atoms. From Kramer (1983), after Buswell and Rodebush (1956).



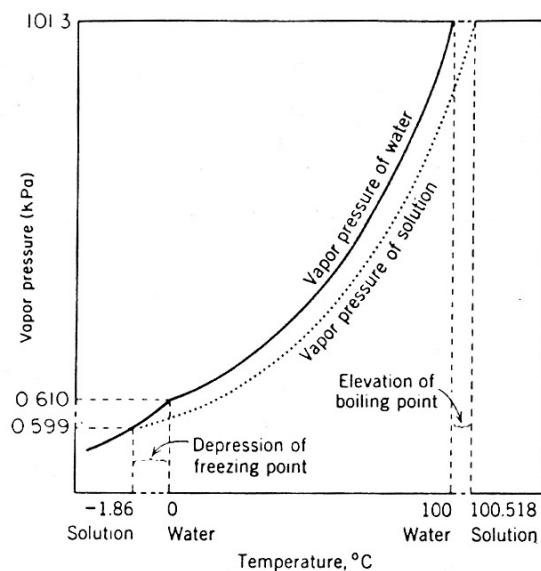


Figure 2.9 Effects of 1 mol of nonelectrolyte per 1000 g of water (a 1 molal solution) on the freezing and boiling points and vapor pressure of the solution. Note that this diagram is not drawn to scale. From Kramer (1983).

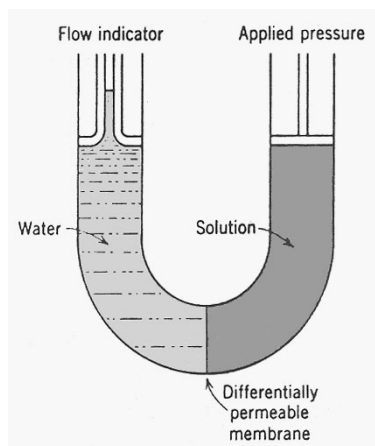
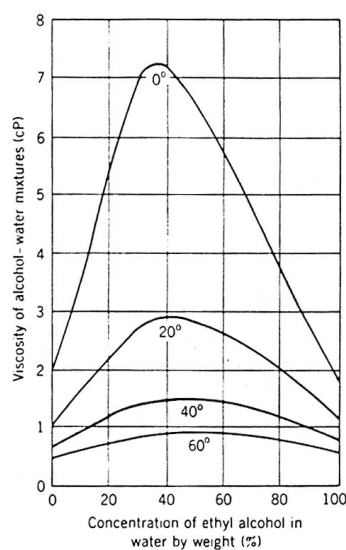


Table 2.2 Colligative Properties of a Molal Solution of a Nonelectrolyte Compared with Water

	Pure water	Molal solution
Vapor pressure	0.61 kPa at 0°C 101.3 kPa at 100°C	Decreased according to Raoult's law
Boiling point	100°C	100.518°C
Freezing point	0°C	-1.86°C
Osmotic pressure	0	2.27 MPa at 0°C
Chemical potential	Reference	2.27 MPa below reference at 0°C

Unidad I: EL AGUA

Capítulo 2: RELACIONES HÍDRICAS A NIVEL CELULAR

A) Relaciones entre la Pared celular, Citoplasma y Vacuolas

- Pared: estructura, crecimiento plástico y elástico, diagrama de Höfler, propiedades físicas y químicas, contenido de agua y elasticidad (módulo de elasticidad).
- Citoplasma
- Vacuolas: ventajas de una vacuola grande (máx. superficie mín proteínas, mantención de la forma).

B) Distribución del agua en la célula

- apoplasto y simplasto
- pared (5-40%): citoplasma (5-10%): vacuola (50-80%)
- 50% del volumen en la pared contiene agua
- hidratación de proteínas (relación con estructura)

C) Membranas celulares

- acumulación de sustancias requiere membrana con permeabilidad diferencial y transporte activo de solutos.
- Modelo de Singer y Nicolson (1974): Mosaico fluido.
- conductancia hidráulica (L_p) = Flujo de volumen (J_v) / (Fuerza conductora).
- factores que afectan el transporte a través de membrana: inhibidores metabólicos, solventes lipofílicos, Ca^{++} , Concentración de CO_2 , temperatura, ABA, presión, hidratación.

D) Movimiento de Agua y solutos.

* Movimiento pasivo: a favor de un gradiente de Potencial hídrico.

- Flujo de masa: movimiento de agua y solutos en una dirección debido a diferencia de potencial de presión o gravitacional. Hipótesis de flujo por presión (Münch).
- Difusión: movimiento al azar de las moléculas causado por su propia energía cinética. Evaporación de líquidos, osmosis, imbibición.

$$\text{Difusión:} \quad x = a \sqrt{t} \quad t = x^2 / a$$

- + Primera Ley de Fick (1855) $dm/dt = -DA \, dc/dx$, donde dm/dt es la cantidad de sustancia que difunde por unidad de tiempo, D = coef. de difusión ($m^2 \, s^{-1}$), A = área por donde ocurre la difusión, dc/dx = diferencia de concentración por unidad de distancia.
- Otra forma de la Primera Ley de Fick: $J_v = -D \, dc/dx$, donde J_v se conoce como la densidad de flujo (cantidad de sustancia que cruza una cierta área por unidad de tiempo, $mol \, m^2 \, s^{-1}$), (dc/dx) = gradiente de concentración en la dirección del flujo ($mol \, m^{-4}$).

+ El movimiento de agua entre protoplasto (p) y apoplasto (a):

$J_v = L_p (\Psi_{m(a)} - \Psi_{p(p)} + \sigma (\Psi_{s(a)} - \Psi_{s(p)}))$, donde J_v = volumen de agua que cruza la membrana por unidad de membrana ($m^3 \, m^{-2} \, s^{-1}$), L_p = conductividad hidráulica de la

membrana ($\text{m s}^{-1} \text{MPa}^{-1}$), $(\Psi_{m(a)} - \Psi_{p(p)})$ = diferencia de presión a través de la membrana (potencial mátrico apoplástico - potencial de presión protoplástico, en MPa), σ = coeficiente de reflexión de la membrana, $(\Psi_{s(a)} - \Psi_{s(p)})$ = gradiente de potencial osmótico a través de la membrana (MPa).

- para membranas ideales ($\sigma = 1$), $J_v = L_p \Delta \Psi_w$.

- respuesta para $\sigma = 1$ (e.g., sacarosa) o $\sigma < 1$ (e.g., etanol).

+ Ley de Poiseuille: el volumen de fluido que se mueve por unidad de tiempo a través de un cilindro es proporcional al cuarto poder del radio (r^4):

Tasa de flujo de un Volumen por un tubo = $-(\pi r^4/8\eta)(d\Psi_p/dx)$
y expresado como flujo volumétrico (J_v)= $-(r^4/8\eta)(d\Psi_p/dx)$, donde r = radio del cilindro,
 η = viscosidad de la solución, $-(d\Psi_p/dx)$ = gradiente negativo de presión hidrostática.
+ efecto temperatura sobre la difusión.

* Absorción activa (no osmótica) de agua

- electro osmosis (Fensom 1957 - Spanner 1958).

- Movimiento polar del agua

- Secreción de agua

E) Temperatura y Movimiento del agua: termo osmosis

F) Potencial hídrico y sus componentes.

- Potencial hídrico (Ψ)= energía/masa= $(RT/mV) \ln(p/p^\circ)$, donde m = peso molecular de agua (18 gr/mol), V = volumen específico del agua (1 g/mol), R = cte. gases (8.31 J/(K mol)), T = t° (K).

- Potencial de presión o de turgor (Ψ_p , + a -) + Potencial osmótico (Ψ_π ó Ψ_s , ≤ 0) + Potencial mátrico (Ψ_m , ≤ 0) + Potencial gravitacional (Ψ_g , ≤ 0).

$$\Psi = \Psi_p + \Psi_\pi + \Psi_m + \Psi_g$$

G) Métodos de medición de los componentes del potencial hídrico. +

H) Capacitancia (Fig. 3.11)

$$dV/d\Psi_{w(p)} = V / (\xi - d\Psi_{s(p)})$$

LEER:

Kramer P.J. y J.S. Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego. Capítulo 3.

Kramer P.J. 1983. Water Relations of Plants. Academic Press. Capítulo 2.

Nobel P.S. (1991) Physicochemical and Environmental Plant Physiology. Academic Press. Pág. 10-12, 508-509.

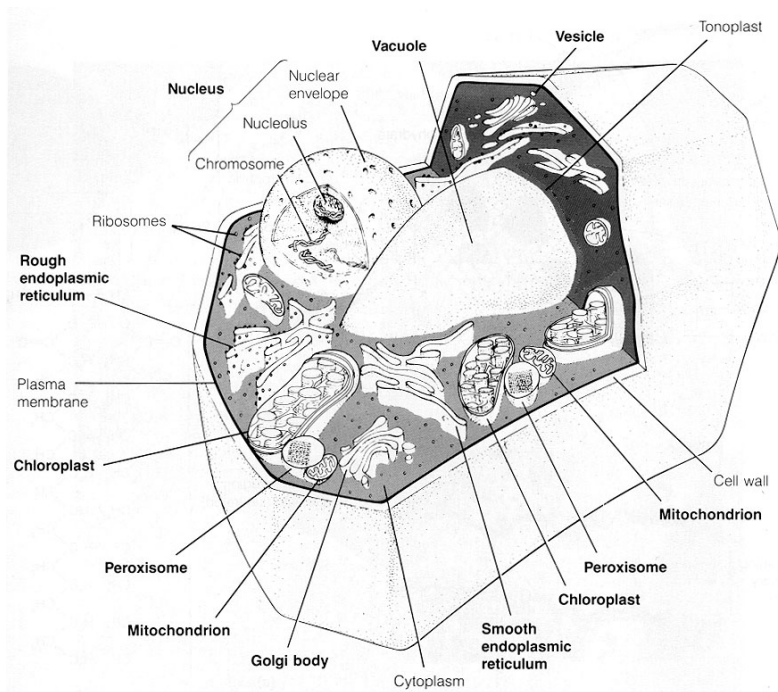


FIGURE 1.7. Diagrammatic representation of a plant cell. Note the intracellular compartments defined by the tonoplast, the nuclear envelope, and the membranes of the other organelles, labeled in boldface type.

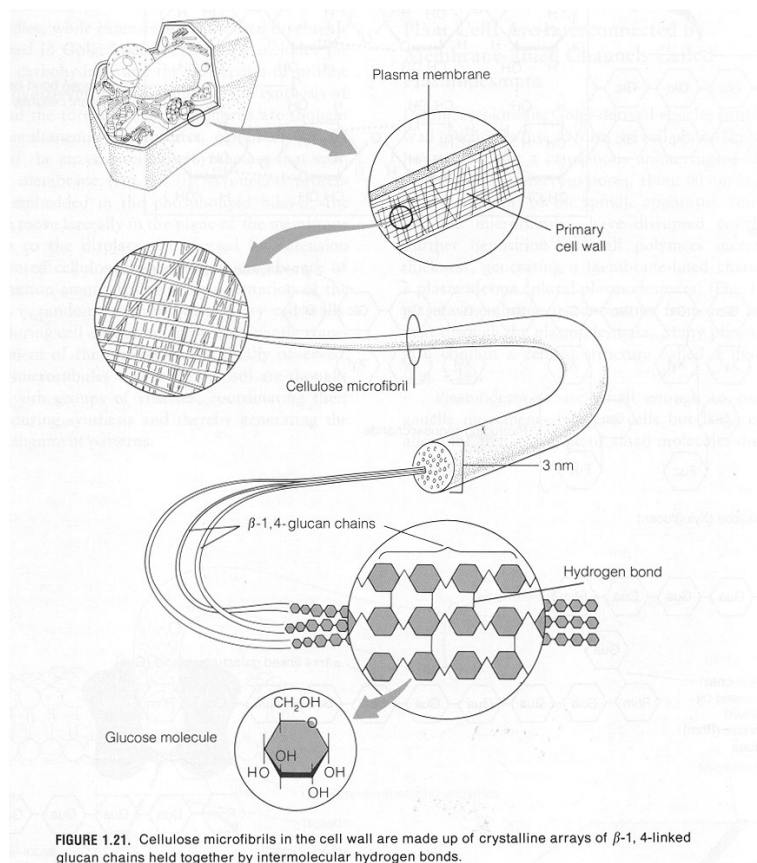


FIGURE 1.21. Cellulose microfibrils in the cell wall are made up of crystalline arrays of β -1, 4-linked glucan chains held together by intermolecular hydrogen bonds.

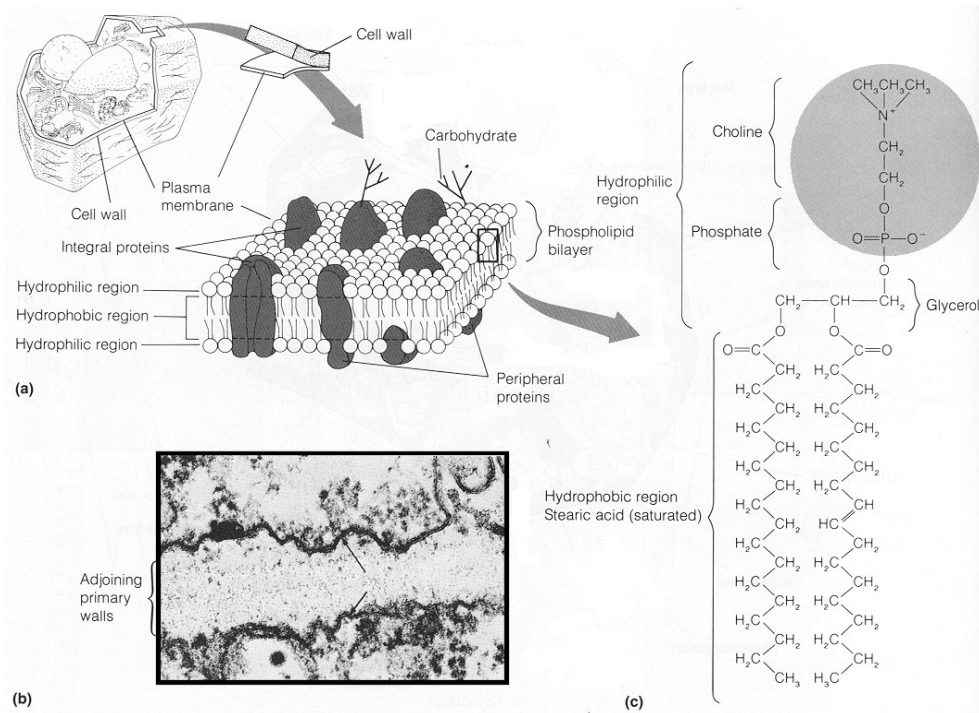


FIGURE 1.8. (a) The plasma membrane of plant cells consists of proteins embedded in a phospholipid bilayer. (b) The transmission electron micrograph shows plasma membranes (arrows) in a parenchyma cell from wheat. The overall thickness of the plasma membrane, viewed as two dense lines and an intervening space, is 8 nanometers. (From Ledbetter and Porter, 1970.) (c) Chemical structure of a typical phospholipid, phosphatidylcholine.

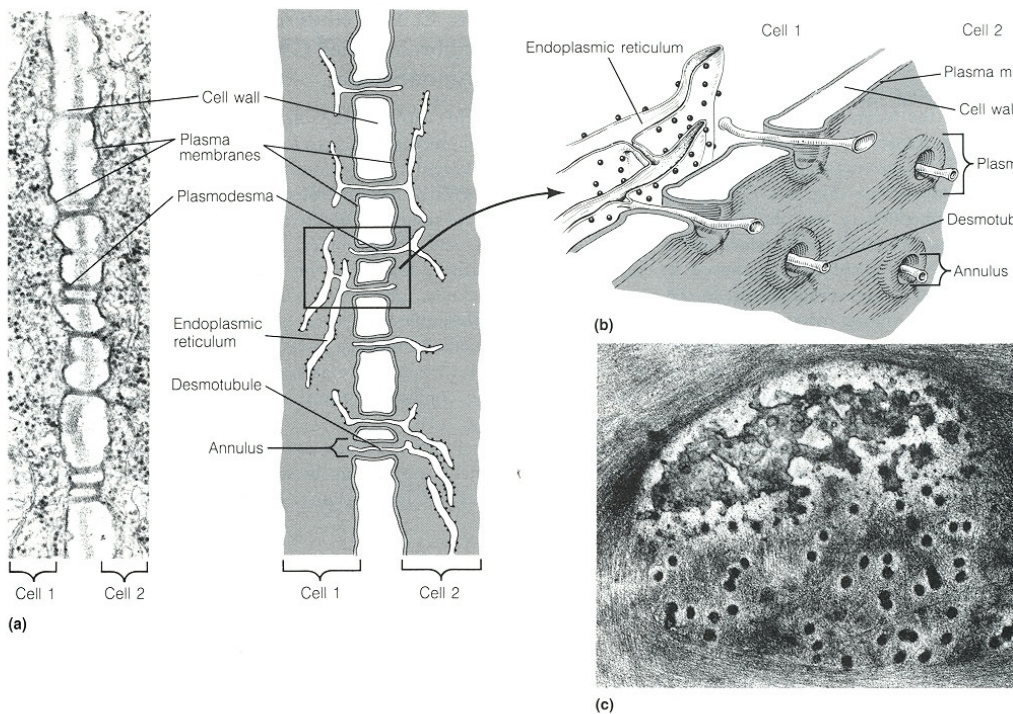
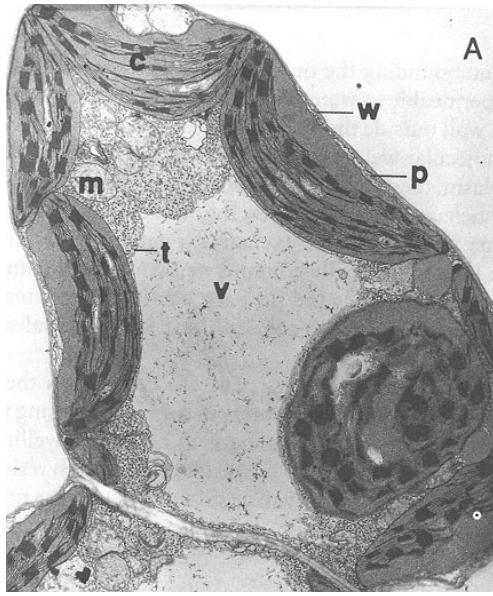
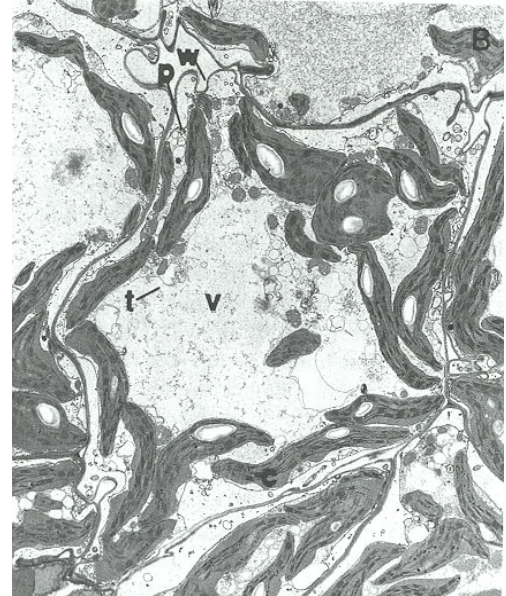


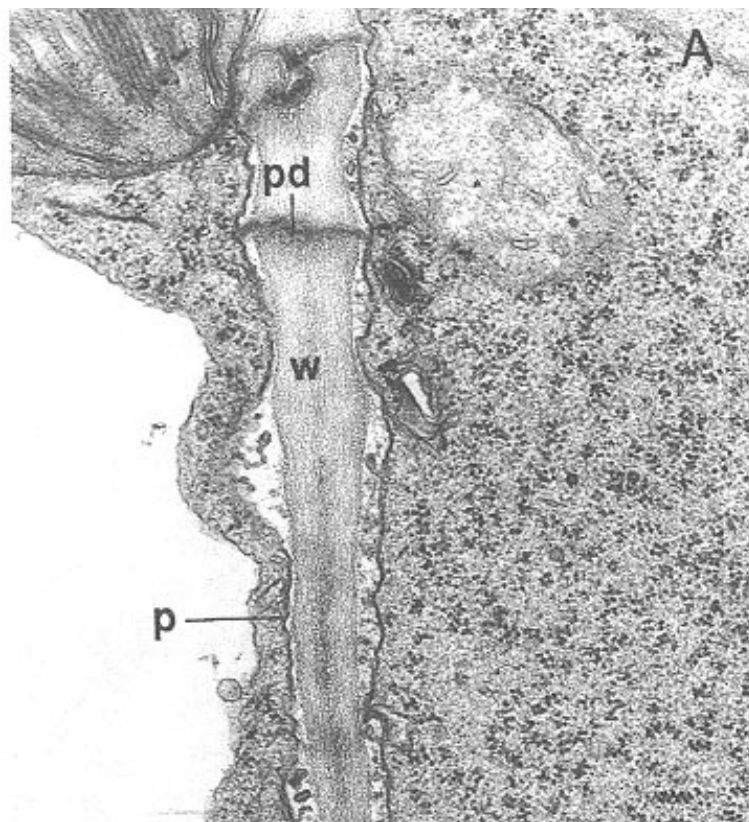
FIGURE 1.24. Plasmodesmata between cells. (a) Electron micrograph of a wall separating two adjacent cells of a timothy grass root, showing the plasmodesmata, schematically depicted on the right. (Micrograph by W. P. Wergin; photo provided by E. H. Newcomb.) (b) Schematic view of a cell wall with plasmodesmata. (c) Electron micrograph showing plasmodesmata in cross section (25,400 ×). (Courtesy of E. H. Newcomb.)



Célula de mesófilo de girasol
 $\Psi = -0,44$ MPa, CRA = 99%



Célula de mesófilo de girasol
 $\Psi = -2,11$ MPa, CRA = 35%



p = memb. plamática, w = pared celular, pd = plasmodesm

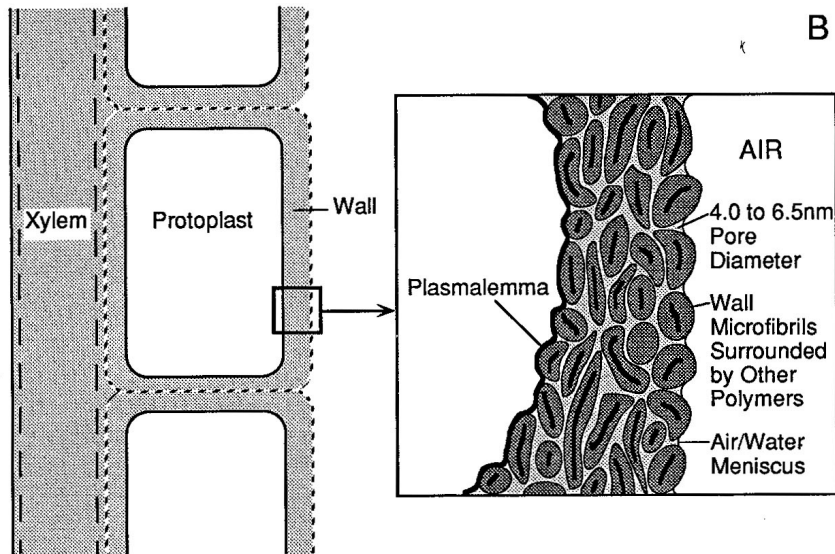
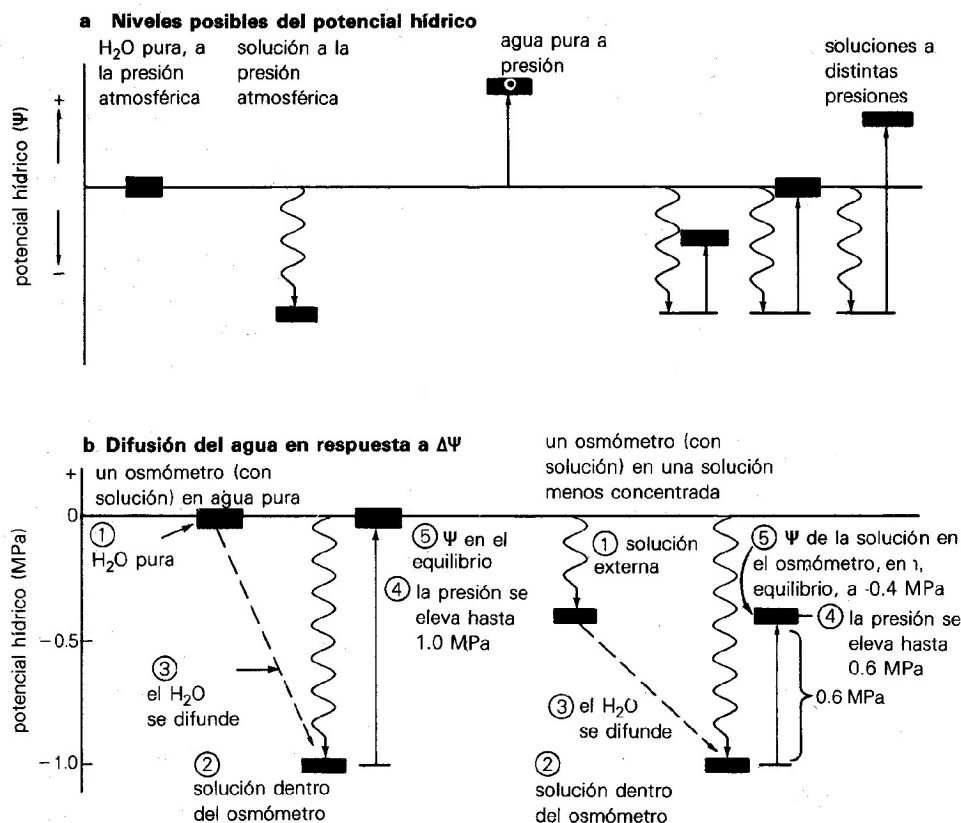


Figure 3.2 (A) Enlarged view of the cell wall (w) and plasmalemma (p) of a mesophyll cell in a sunflower leaf ($37,400\times$). Note the plasmodesma (pd) extending through the wall to form a symplast between the adjacent protoplasts (R. J. Fellows and J. S. Boyer, unpublished). The microfibrillar structure of the wall is also apparent. (B) Diagrammatic representation of the apoplast (shaded). The microfibrillar structure of the wall is shown in the enlarged inset together with the air/water menisci between the microfibrils and matrix polymers. Not shown are cross links between the polymers. The plasmalemma is pressed against the wall substructure by the pressure inside and tension outside. The tension in the wall passes into the xylem through the 4 to 6.5 nm pores distributed throughout the wall.



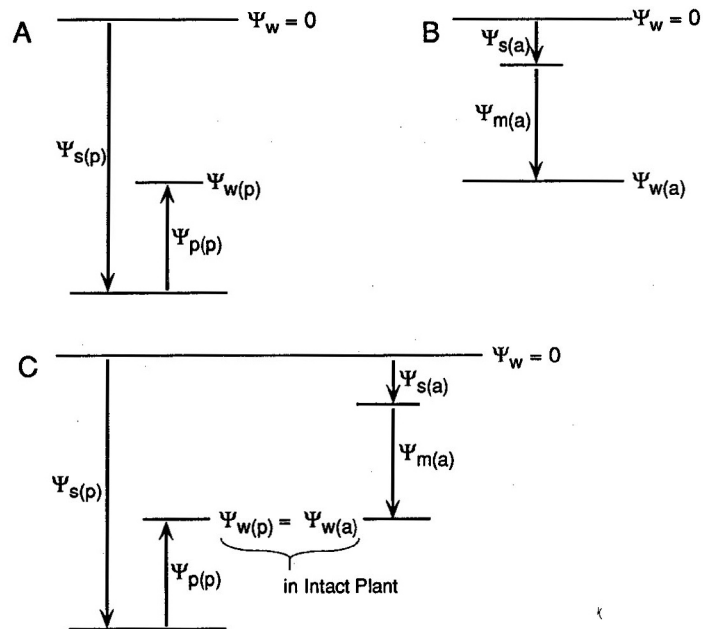
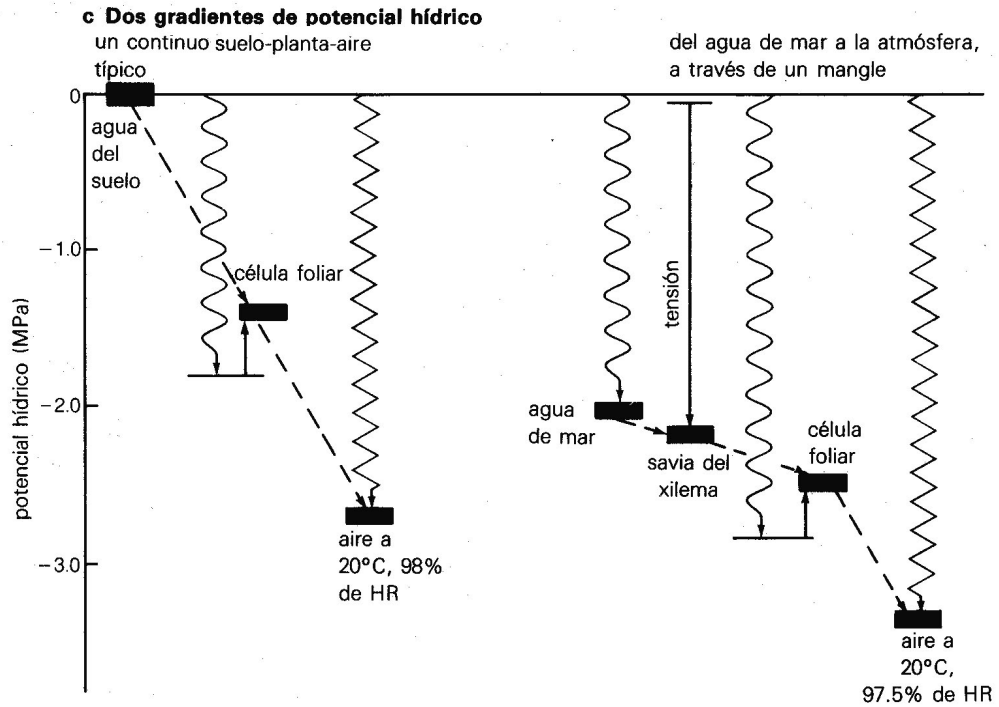


Figure 3.4 Water potentials in plant cells with component potentials shown by arrows (decreasing potentials are downward pointing, increasing potentials are upward pointing). The water potential of zero is shown by upper horizontal bar. (A) Protoplast (symplast) water potential consisting of the osmotic potential ($\Psi_{s(p)}$) and the turgor pressure ($\Psi_{p(p)}$), (B) cell wall (apoplast) water potential consisting of the osmotic potential ($\Psi_{s(a)}$) and matric potential ($\Psi_{m(a)}$), (C) equilibrium between the protoplast and apoplast water potentials. Note that the difference in osmotic potential is large across the plasmalemma ($\Psi_{s(p)} - \Psi_{s(a)}$). Also, the matric potential consists mostly of tension (negative pressure) in the pores of the apoplast. Therefore, the pressure difference across the plasmalemma also is large ($\Psi_{p(p)} - \Psi_{m(a)}$). At equilibrium, the difference in osmotic potential ($\Psi_{s(p)} - \Psi_{s(a)}$) equals the difference in pressure ($\Psi_{p(p)} - \Psi_{m(a)}$).

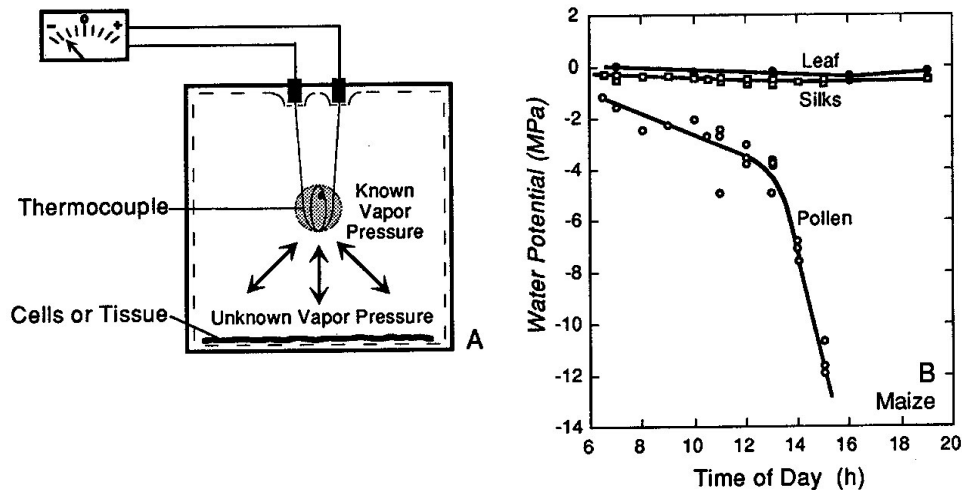


Figure 3.5 Thermocouple psychrometer (A) and measurements of water potentials in cells and tissues of maize made with a psychrometer (B). The droplet of known vapor pressure on the thermocouple can exchange water with the unknown sample on the bottom of the chamber and thus cool or warm the thermocouple. The solution neither cooling nor warming the thermocouple has a vapor pressure (water potential) equal to that of the sample. Since the solution water potential is known and is the same as that of the sample, the sample water potential is then known. The measurement is in the apoplast in equilibrium with the protoplasts. Typical measurements in maize (B) show that the water potential decreased only slightly during the day in the plant, but decreased markedly in pollen grains collected at various times from the same plant. The leaves and stigmas (silks) were connected through the xylem to the water supply in the soil but the mature pollen was not. Adapted from Westgate and Boyer (1986a).

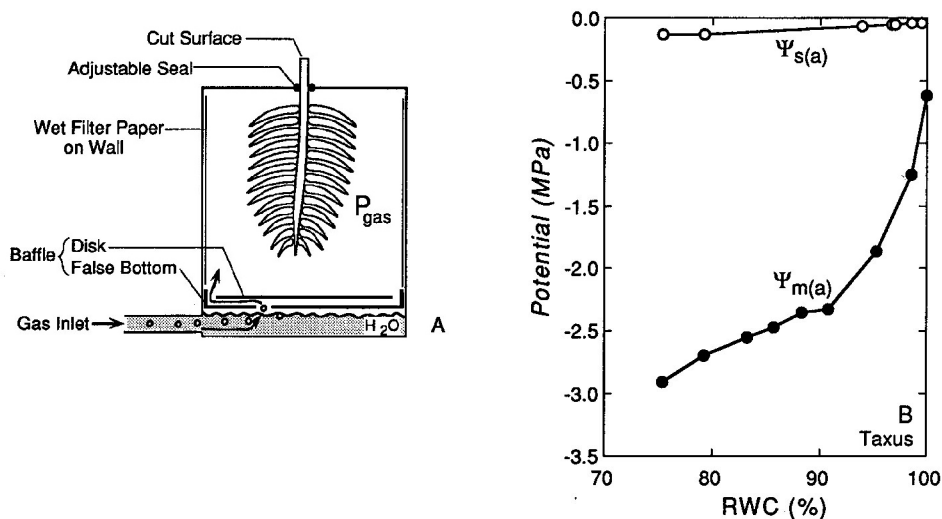


Figure 3.6 Pressure chamber (A) and measurements of the pressure in the apoplast of plant tissues using the pressure chamber (B). The incoming gas is humidified by bubbling through water, and the external pressure increases until it forces the xylem solution onto the cut surface. The pressure is adjusted to maintain the solution at the surface with no flow into or out of the tissue. This balancing pressure (P_{gas}) measures the internal pressure (tension $\Psi_{m(a)}$) on the apoplast solution according to $-P_{gas} = \Psi_{m(a)}$. In (B), the tension becomes more negative as the relative water content (RWC) decreases in the tissue (*Taxus* branch), indicating that a greater pull is being exerted by the leaves on the water in the xylem. Also shown is the osmotic potential of the apoplast solution ($\Psi_{s(a)}$) measured on xylem solution from the same *Taxus* branch. Note that $\Psi_{s(a)}$ is a small component at all RWC. The water potential of the apoplast solution is ($\Psi_{m(a)} + \Psi_{s(a)}$). Adapted from Boyer (1967b).

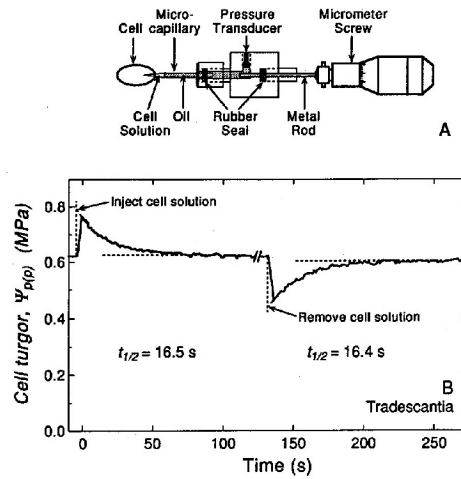


Figure 3.7 Pressure probe (A) for measuring and changing the turgor pressure inside plant cells (B). The probe is mostly filled with silicone oil (shaded), and a meniscus is visible between the cell solution and the oil in the tip of the microcapillary. When there is liquid continuity between the cell and the microcapillary, the pressure in the cell extends into the microcapillary and is sensed by the pressure transducer. The accurate measurement of cell turgor requires the meniscus to be returned to the position prior to entering the cell. Turning the micrometer screw forces the metal rod into the oil and moves the meniscus by changing the internal volume. The volume change causes the pressure to change as solution is injected into or removed from the cell (B) in a *Tradescantia* leaf. The volume of solution removed from or injected into the cell is determined from the distance the meniscus moves and the diameter of the microcapillary. Adapted from Tyerman and Steudle (1982).

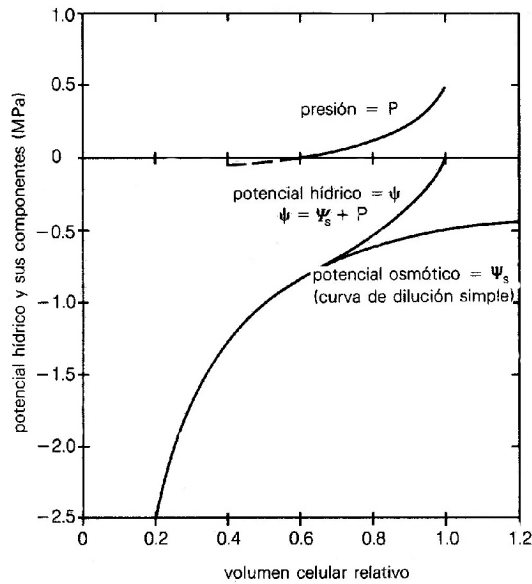


Figura 3-3 Diagrama de Höfler. Se muestra cómo varían los componentes del potencial hídrico con el volumen en un osmómetro (a veces el volumen celular). El potencial osmótico se representa como una curva de dilución que se calcula mediante la relación $\Psi_{s1} V_1 = \Psi_{s2} V_2$, como se describe en el texto. La curva de presión es arbitraria, pero expresa el hecho de que cuando una célula con presión de cero absorbe agua, dicha presión se incrementa, al principio de manera lenta y luego más rápido (exponencialmente). La curva del potencial hídrico es la suma algebraica de las curvas de presión y potencial osmótico, conforme a la ecuación 3.1.

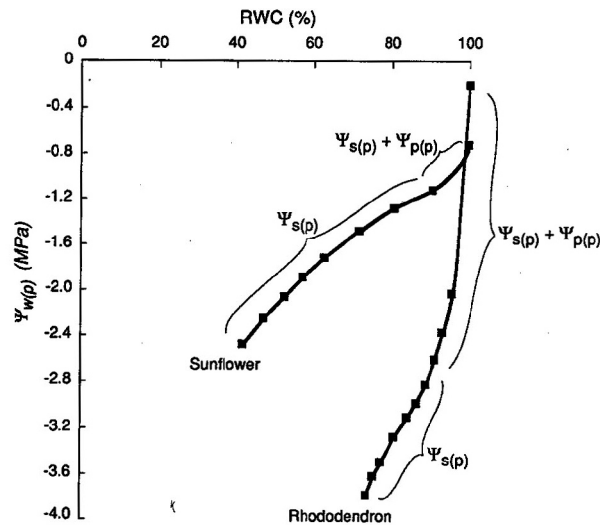
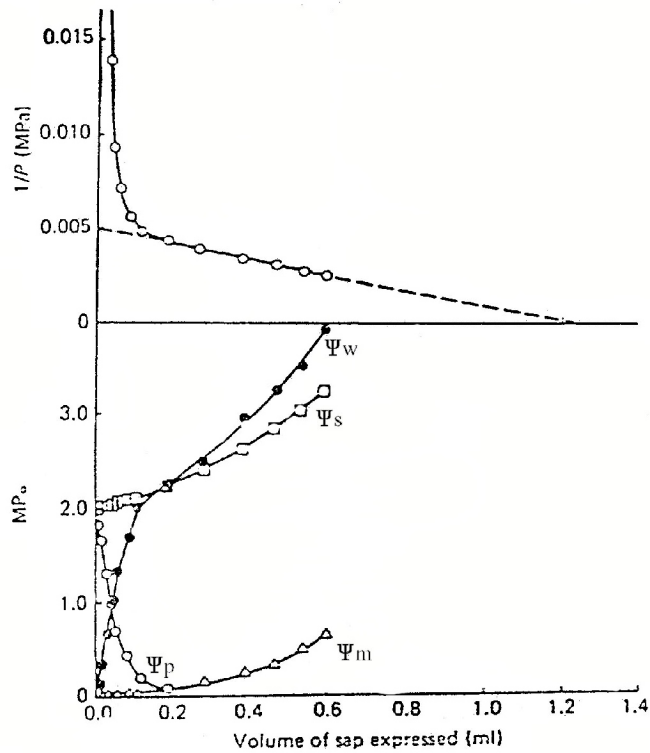


Figure 3.11 Water potential ($\Psi_{w(p)}$) at various relative water contents (RWC) in sunflower and rhododendron leaves measured with a pressure chamber. Both species show a greater decrease in $\Psi_{w(p)}$ when turgor is present ($\Psi_{s(p)} + \Psi_{p(p)}$) than when it is absent ($\Psi_{s(p)}$). However, rhododendron with thick relatively nonelastic cell walls ($\epsilon = 97$ MPa) shows a greater decrease than sunflower with thin elastic walls ($\epsilon = 6.4$ MPa). This results in very low $\Psi_{w(p)}$ in rhododendron with only moderate dehydration compared to sunflower. The Ψ_s was -2.6 and -1.1 MPa in hydrated rhododendron and sunflower respectively. Using ϵ , Ψ_s , and the change in RWC, the capacitance for water can be calculated for these tissues [Eq. (3.12)]. From the calculation, a decrease of 1 MPa in water potential from the fully hydrated state required a 1% decrease in RWC in rhododendron but a 13% decrease in sunflower. From J. S. Boyer (unpublished data).

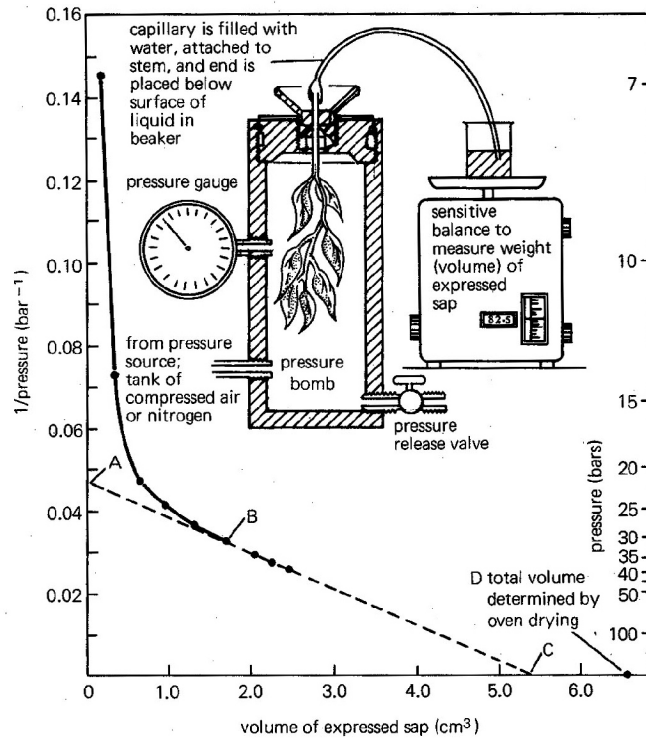


Figure 2-9 Illustrating the pressure bomb as a method for measuring several parameters concerning the water relations of plants. Point A: the water potential of hydrated tissue, about 21 bars. Point B: incipient plasmolysis, indicating an osmotic potential of about 31 bars. Point C: volume of free water in the tissue, about 5.35 cm³. Point D: total volume of tissue water, about 6.72 cm³. Bound water equals D minus C, or 1.37 cm³.

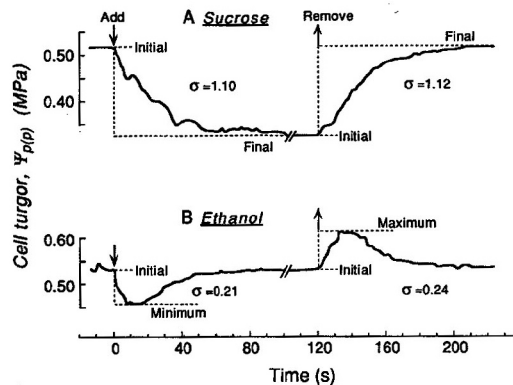


Figure 3.12 Plasmalemma reflection coefficients measured with a pressure probe in leaf epidermal cells of *Tradescantia*. The pressure probe measured the change in cell $\Psi_{p(p)}$. (A) Sucrose having Ψ_s of -0.18 MPa was added to the medium bathing the epidermis and caused water to move out. The turgor decreased by an amount that essentially equaled the Ψ_s of the sucrose, thus giving a reflection coefficient of about $-0.18/-0.18 = 1$ [see Eq. (3.15)]. At the upward arrow, the sucrose was removed and the pattern reversed as water moved in. When the reflection coefficient is 1 as for sucrose, the response is monophasic because only water moves. (B) Ethanol having Ψ_s of about -0.37 MPa caused turgor to decrease about 0.08 MPa to give a reflection coefficient of about $-0.08/-0.37 = 0.2$. Note that the ethanol caused a biphasic response. In the first phase, water moved outward and the cell shrank. In the second phase, ethanol entered and the cell swelled. At the upward arrow, the ethanol was removed and this pattern was reversed. Adapted from Tyerman and Steudle (1982).

Table 3.2 Reflection Coefficients (σ) of Plant Cell Membranes for Some Nonelectrolytes

Solute	Reflection coefficients			
	<i>Chara corallina</i> ^a	<i>C. corallina</i> ^b	<i>Nitella flexilis</i> ^c	<i>Tradescantia virginiana</i> ^d
Sucrose	0.95	—	0.97	1.04
Mannitol	1.02	—	—	1.06
Urea	—	1	0.91	1.06
Acetamide	—	—	0.91	1.02
Formamide	0.99	1	0.79	0.99
Dimethylformamide	0.76	—	—	—
Glycerol	—	—	0.80	0.93
Ethylene glycol	—	1	0.94	0.99
<i>n</i> -Butanol	0.14	—	—	—
Isobutanol	—	—	—	—
(2-methyl-1-propanol)	0.21	—	—	—
<i>n</i> -Propanol	0.24	0.22	0.17	−0.58
2-Propanol	0.45	—	0.35	0.26
Ethanol	0.40	0.27	0.34	0.25
Methanol	0.38	0.30	0.31	0.15
Acetone	0.17	—	—	—

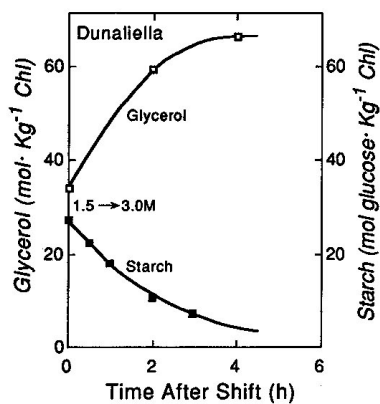


Figure 3.14 Osmotic adjustment in the marine alga *Dunaliella*. At zero time, the cells were shifted from a solution containing 1.5 M NaCl to a solution containing 3 M NaCl. The increase in cell glycerol came at the expense of cell starch (note that each glucose molecule released from starch produces two glycerol molecules). Adapted from Gimmler and Möller (1981).

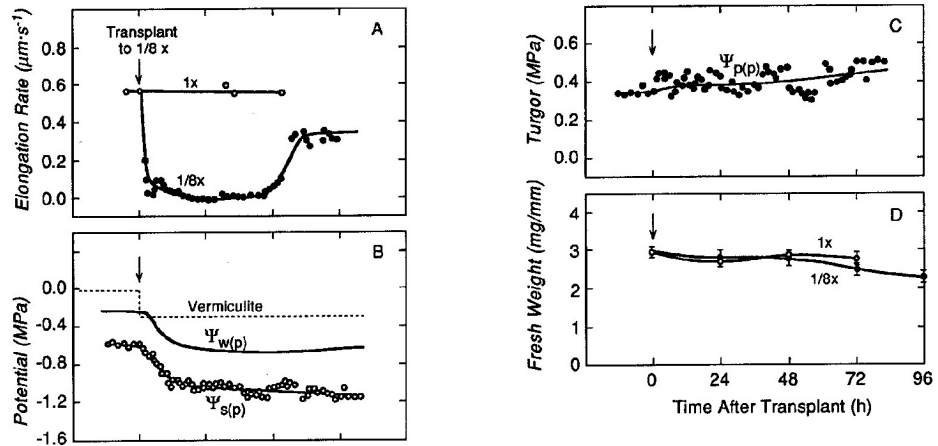


Figure 3.15 Osmotic adjustment in stems of soybean seedlings transplanted to vermiculite containing one-eighth of the water (1/8×) normally present in hydrated vermiculite (1×). (A) Stem elongation rates at 1/8× and 1×, (B) water potential of vermiculite (dashed line) and water potential ($\Psi_{w(p)}$) and osmotic potential ($\Psi_{s(p)}$) of the stem-elongating region in 1/8× plants, (C) turgor ($\Psi_{p(p)}$) of the stem-elongating region in 1/8× plants, (D) fresh weight of the stem-elongating region in 1× and 1/8× plants. Osmotic adjustment is seen in (B) as a decrease in $\Psi_{s(p)}$. The adjustment preserves turgor (C) and fresh weight (D) because the water content of the cells remains high. However, in mature cells of the stems of the same plants, osmotic adjustment was less and the turgor and water content decreased (after Bozarth *et al.*, 1987; Nonami and Boyer, 1989).

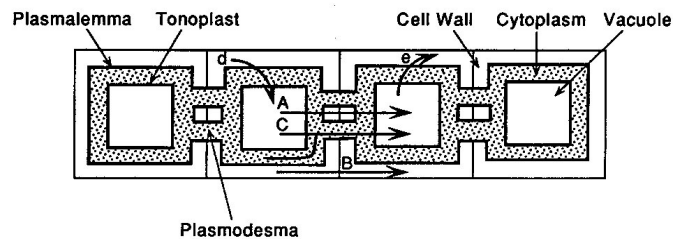


Figure 3.16 Diagrammatic representation of the water pathways in a tissue consisting of four cells. (A) Cell to cell path, (B) cell wall (apoplast) path, (C) cell to cell path through plasmodesmata (symplast), (d) water uptake by cells from apoplast, and (e) water loss by cells to apoplast. Plasma-lemma lines plasmodesmata to form continuous membrane between cells. The dimensions of the various compartments are not to scale (after Molz and Ferrier, 1982).

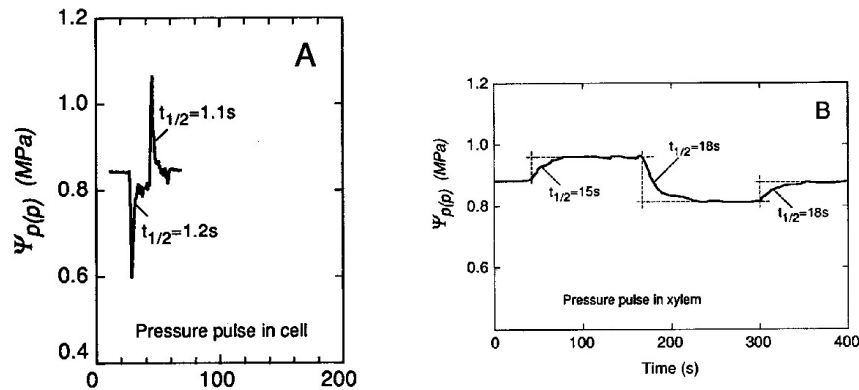


Figure 3.17 Turgor in maize cells situated in a leaf. (A) Turgor relaxation caused by a pressure pulse inside a cell using a pressure probe. (B) Turgor relaxation in the same cell when a pressure pulse was applied to water in the xylem. Relaxations are rapid in (A) where the path involves only the plasmalemma of the cell (d and e in Fig. 3.16) but slow in (B) where the path includes other cells. Note that if the apoplast was the main flow path between the cells, it would need to have a low resistance to flow. Water supplied by the xylem would be able to bypass intervening cells because of the low resistance and would reach each cell readily resulting in similar rates of relaxation in (A) and (B). However, because relaxations in (B) were much slower than in (A) for the same cell, the apoplast path was not the main contributor and water flowed mostly from cell to cell (paths A and C in Fig. 3.16). Adapted from Westgate and Steudle (1985).

Unidad I: EL AGUA

Capítulo 3: RETENCIÓN Y LIBERACIÓN DE EL AGUA EN EL SUELO

A) Características del suelo

- + Composición y textura
 - arena ($>2,0-0,02$ mm), limo ($0,02-0,002$ mm), arcilla ($<0,002$ mm)
 - efectos sobre el contenido de agua.
- + Estructura y porosidad
- + Perfiles del suelo

B) Terminología

- Potencial hídrico del suelo (Ψ_{suelo}) = $\Psi_p + \Psi_\pi + \Psi_m + \Psi_g$
- Capacidad de campo de un suelo (CC): contenido de agua del suelo inmediatamente luego que termina el drenaje. Varía entre el campo y laboratorio, y en las condiciones que se mide.
- Punto de marchitez permanente (PMP): contenido de agua del suelo en que una planta permanece marchita durante la noche o en una cámara húmeda, al menos que sea regada. Para muchos cultivos herbáceos PMP está entre -1,5 y -2,0 MPa.
- Agua disponible (AD): agua del suelo entre CC y PMP. Suelos con textura fina poseen mayor AD que aquellos con textura gruesa.
- Tasa de oferta y demanda de agua: $\Psi_{\text{suelo}} = -1,2$ MPa (maíz transpira 1.4 mm/día), $\Psi_{\text{suelo}} = -0,03$ MPa (6 mm/día).

C) Movimiento del agua en el suelo:

- Infiltración
- Escurrimiento superficial (runoff) y erosión
- Movimiento horizontal y hacia arriba.

D) Medición del agua en el suelo

-Balance hídrico en el suelo:

$\Delta W = P - (O + U + E_t)$, donde ΔW = cambio en el contenido hídrico del suelo entre muestreo, P = precipitación, O = escurrimiento superficial, U = drenaje profundo, E_t = evapotranspiración desde el suelo y plantas.

- Medición directa del contenido hídrico del suelo: lisímetro.

+ Mediciones indirectas del contenido hídrico del suelo:

- medidor de neutrones
 - atenuación de radiación gama
 - capacitancia eléctrica
 - conductancia eléctrica
 - conductancia de calor.
- ##### **+ Mediciones del potencial hídrico del suelo:**
- tensiómetros (Ψ_m)

- presión en placas (pressure plates, Ψ_m)
- medición del potencial osmótico (cámara psicrométrica)
- medición del potencial hídrico total del suelo (psicrómetro de suelo (en porcelana), útil en suelos desérticos).

E) Control del agua en el suelo

- + Riego: inundación, aspersores, goteros.
- + Programa de riego: Uso eficiente del agua tendente a prevenir el déficit hídrico en las plantas sin crear un excedente que drene por debajo de la zona de las raíces.
- Medición el agua en el suelo.
- Uso de datos de evaporación
- Uso del estado hídrico de la planta
- + Problemas del riego: suelo inundado, acumulación de sales
- + Control experimental del contenido hídrico del suelo

LEER:

Kramer P.J. y J.S. Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego. Capítulo 4.

Kramer P.J. 1983. Water Relations of Plants. Academic Press. Capítulo 3.

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 From Lyon and Buckman (1943, p. 43)

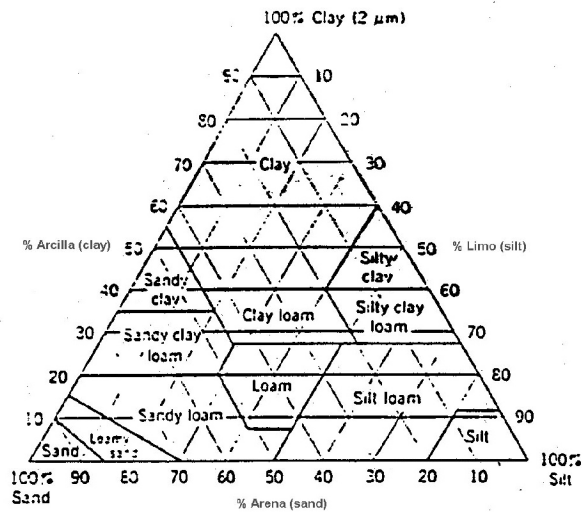


Fig. 3.3. Diagram showing the percentage of sand, silt, and clay in various soil classes. (From *Soil Sci. Soc. Am. Proc.* 29, 347, 1965.)

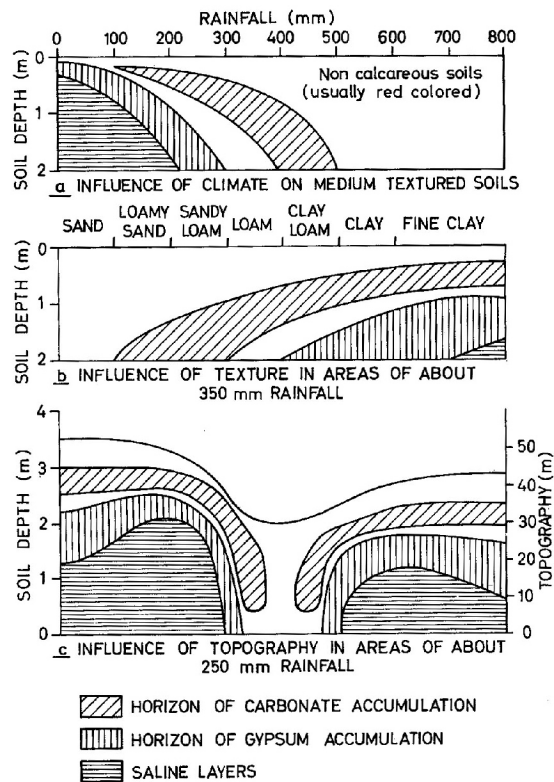


Fig. 2. The effect of rainfall, soil texture, and topography on soil leaching in arid regions. a) In their leaching stage, well-drained, medium-textured upland soils reflect the influence of climate. In humid areas chloride and salt are leached throughout. When aridity increases, leaching is restricted, so that lime, gypsum, and finally even soluble salts are redeposited in the deeper soil layers. b) Although 350 mm is sufficient to leach all the salt and carbonates from sandy soils, it is not sufficient to leach medium- and fine-textured soils. This lime is redeposited in the deeper layers of medium-textured soils; in fine-textured soils gypsum and salts also are redeposited at depth. c) In arid areas, 250 mm or less rainfall is insufficient to leach lime, gypsum, and soluble salts that are reprecipitated in the deeper soil layers. In well-drained depressions, however, the runoff water accumulates and leaches the soluble compounds

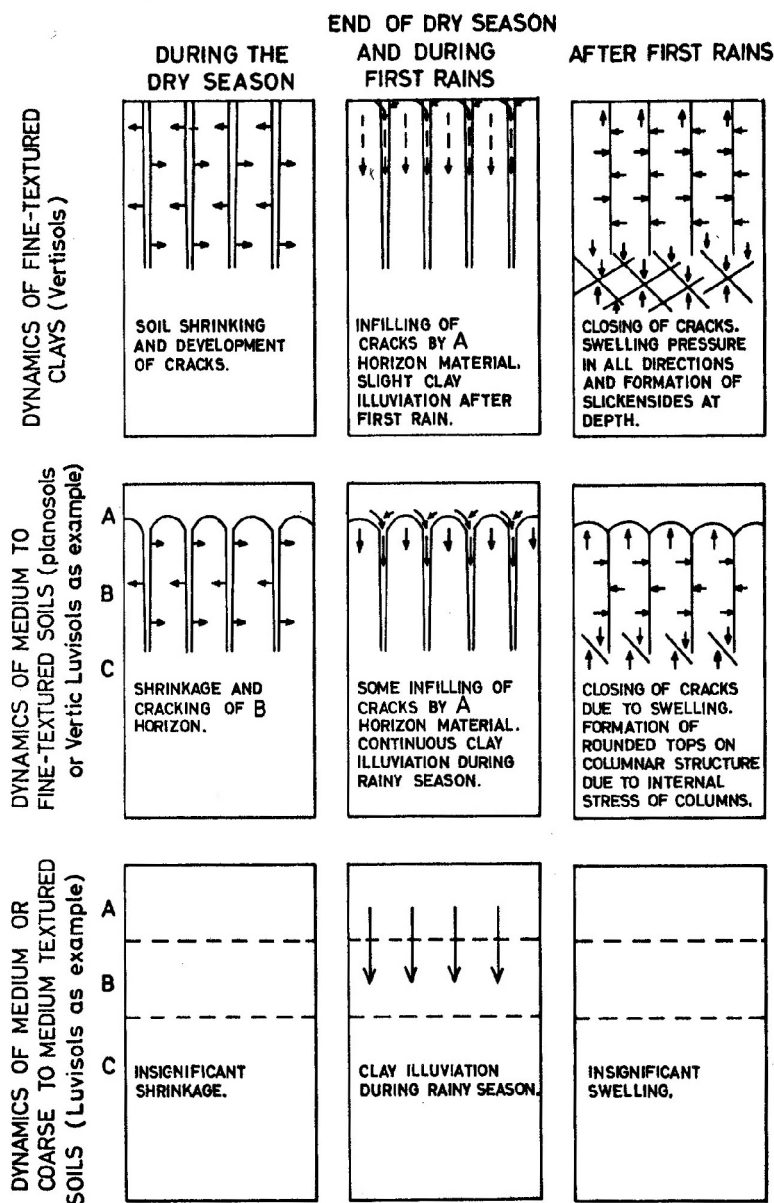


Fig. 3. The dynamics of illuviations and churning processes in soils of various textures in arid regions that are characterized by expanding clay lattice.

Fine-textured montmorillonitic clays crack during the summer. Afterward, materials from the top layer fall into the cracks. This soils swells again after the first rains. The same process also occurs in the B-horizon of medium- to fine-textured soils but with less intensity. Clay illuviation may be quite significant and an illuvial A-horizon is formed. In medium-textured soils no pressure cracks occur and only the illuviation process is well marked

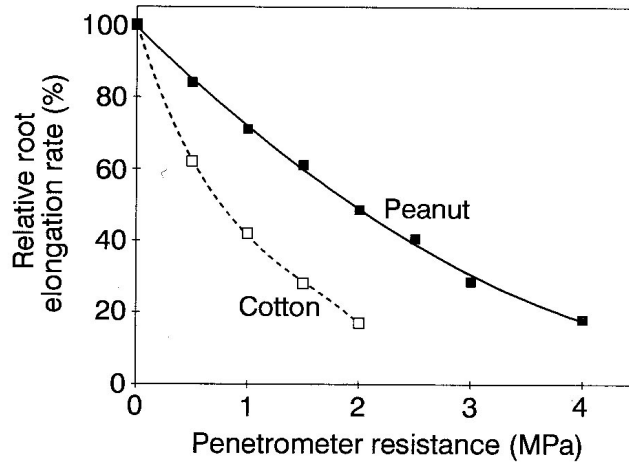


Fig. 14.12 Root elongation rates of peanut and cotton as a function of soil strength (resistance to root penetration). (Based on Taylor and Ratliff, 1969.)



Fig. 14.13 Root system of young barley plants grown in the field in soils with different bulk densities. (*Left*) 1.35 g cm^{-3} ; (*right*) 1.50 g cm^{-3} . (From Scott-Russell and Goss, 1974.)

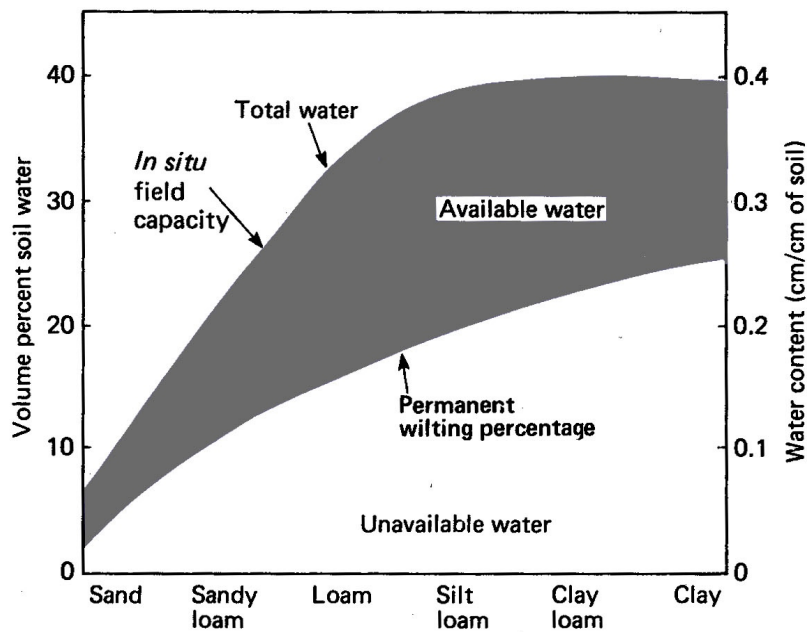


Figure 4.1 Diagram showing the relative amounts of available and unavailable water in soils ranging in texture from sands to clay. Amounts are expressed as percentages of soil volume and centimeters of water per centimeter of soil. After Cassel (1983), from Kramer (1983).

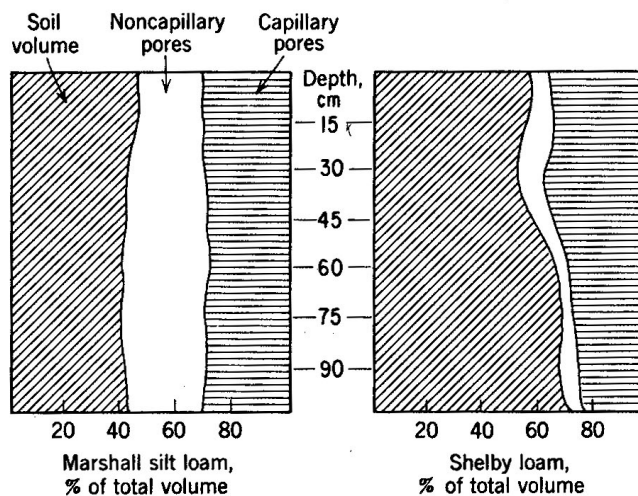


Figure 4.2 Examples of the differences in amount of capillary and noncapillary pore space in two dissimilar soils. A large proportion of noncapillary pore space promotes drainage and improves aeration. After Baver (1948), from Kramer (1983).

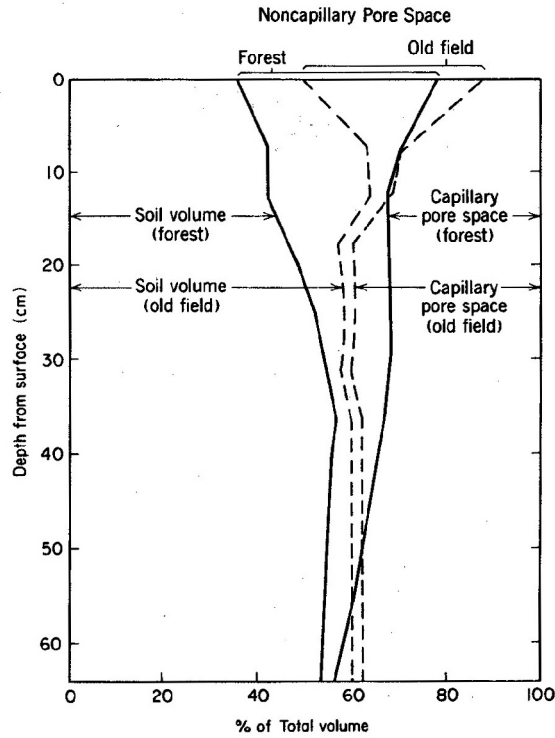


Figure 4.3 Difference between amount of capillary and noncapillary pore space in an old field soil and an adjacent forest soil on the same type of soil. The large volume of noncapillary pore space in the forest soil provides better root aeration and more rapid infiltration of water (Fig. 4.6), reducing surface runoff and erosion during heavy rains. After Hoover (1949), from Kramer (1983).

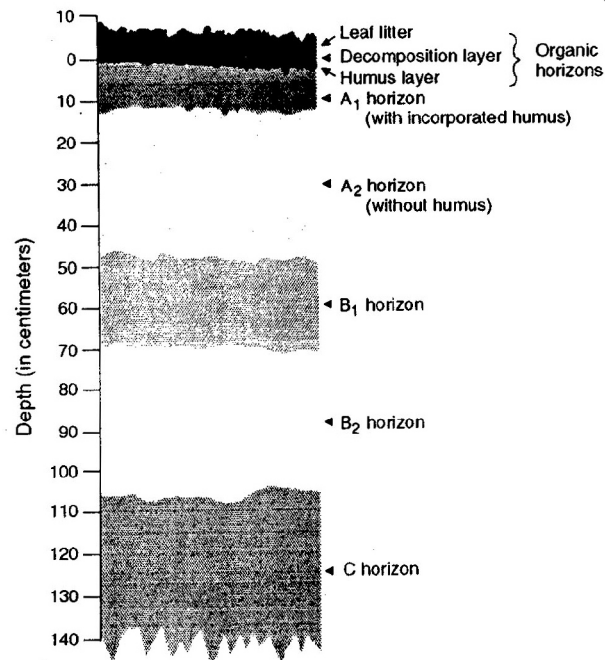


Figure 4.4 A soil profile under an old shortleaf pine stand in North Carolina. Modified from Billings (1978), from Kozłowski *et al.* (1991).

Table 4.1 Water Content of Soils of Various Textures at Matric Potentials of -0.03 and -1.5 MPa and at First Permanent Wilting

Name of soil	Water content as percentage of dry weight	
	-0.03 MPa	-1.5 MPa
Hanford sand	4.5	2.2
Indio loam	4.6	1.6
Yolo loam	12.6	7.1
Yolo fine sandy loam	12.6	5.5
Chino loam	19.7	8.0
Chino silty clay	40.8	21.9
Chino silty clay loam	48.9	15.0
Yolo clay	45.1	26.2

Note. From Kramer (1983), based on data of Furr and Reeve (1945) and Richards and Weaver (1944).

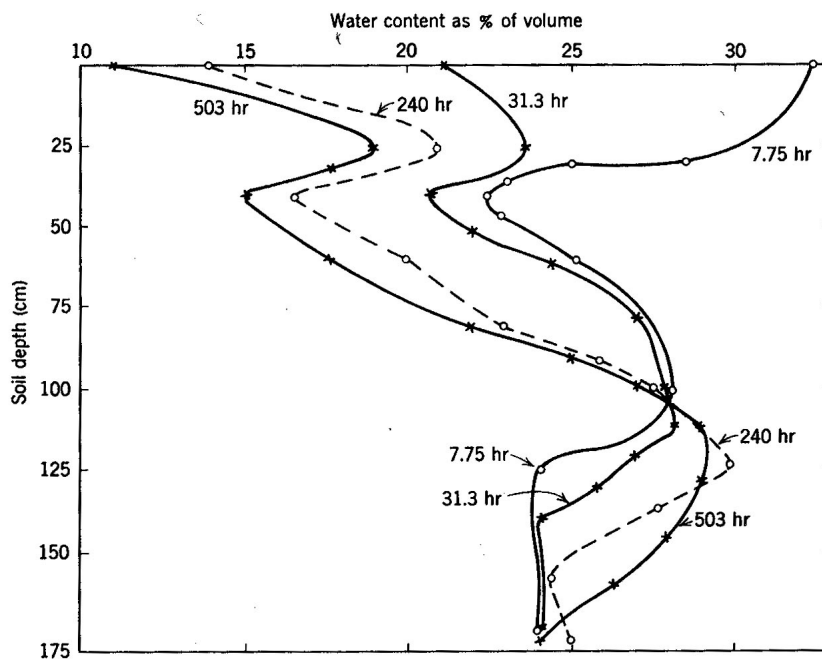


Figure 4.5 Profiles of water content of a nonuniform soil at various times after irrigation. The surface horizon is a sandy loam, changing to a fine sandy loam at about 25 cm, and at 75–100 cm to a clay which holds much more water. The original water content at 125 to 175 cm was about 24%. Over a period of 21 days (503 hr) there was a decrease in water content near the surface and an increase at 100 to 150 cm below the surface. From Kramer (1983) after Rose *et al.* (1965).

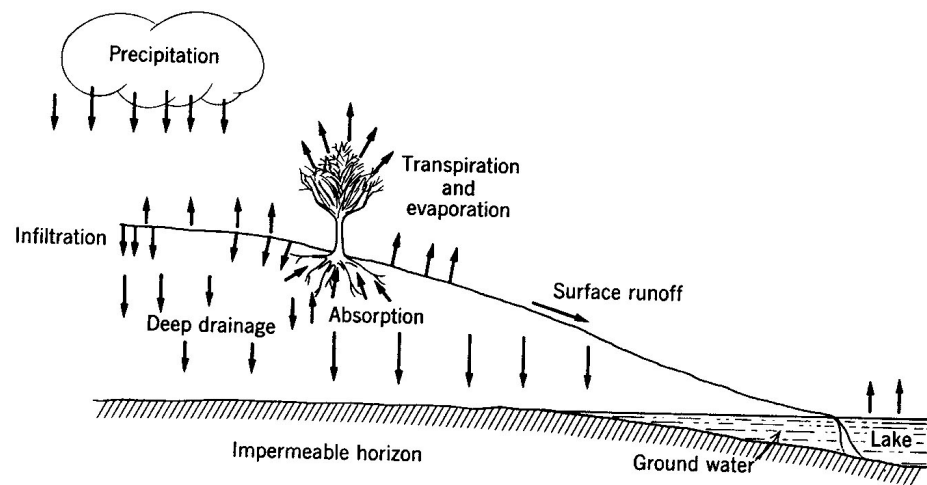


Figure 4.8 The hydrologic cycle, showing disposal of precipitation by surface runoff, infiltration, and deep drainage, and its removal from the soil by evaporation and transpiration. From Kramer (1983).

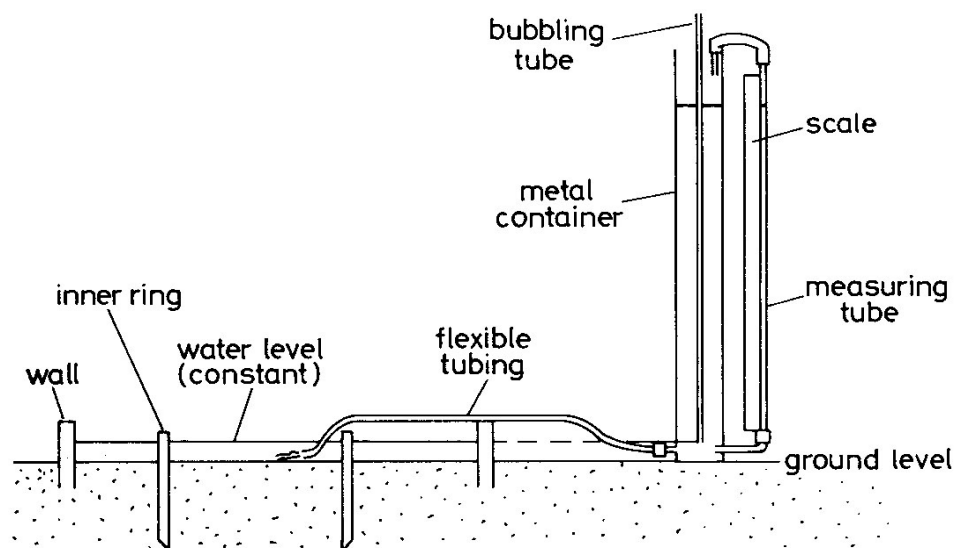


Fig. 7. Double ring infiltrometer setup for measurement in the field

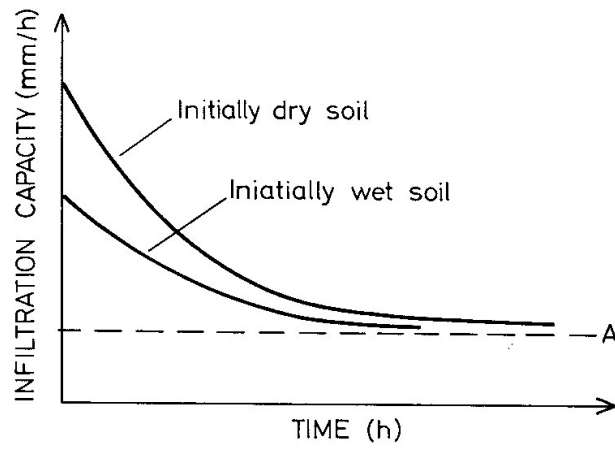


Fig. 6. Infiltrability curves for dry and wet soils

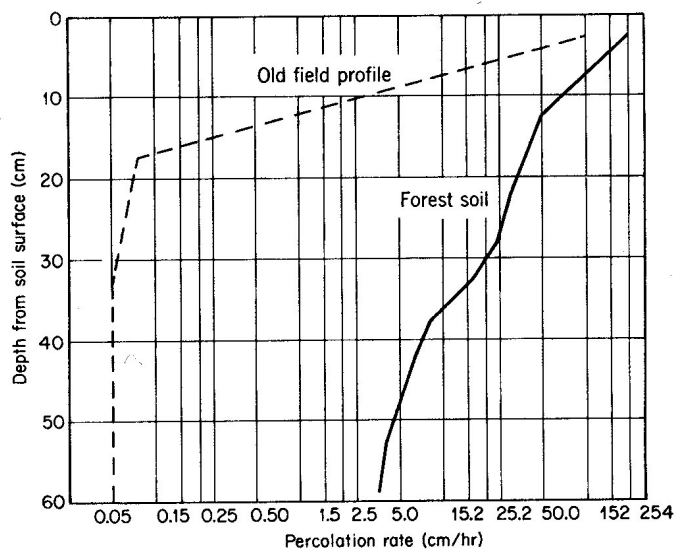


Figure 4.6 Comparison of rates of infiltration into a forest soil and an adjacent old field on the same soil type. Figure 4.3 shows the differences in capillary pore space in the two soils. From Kramer (1983), after Hoover (1949).

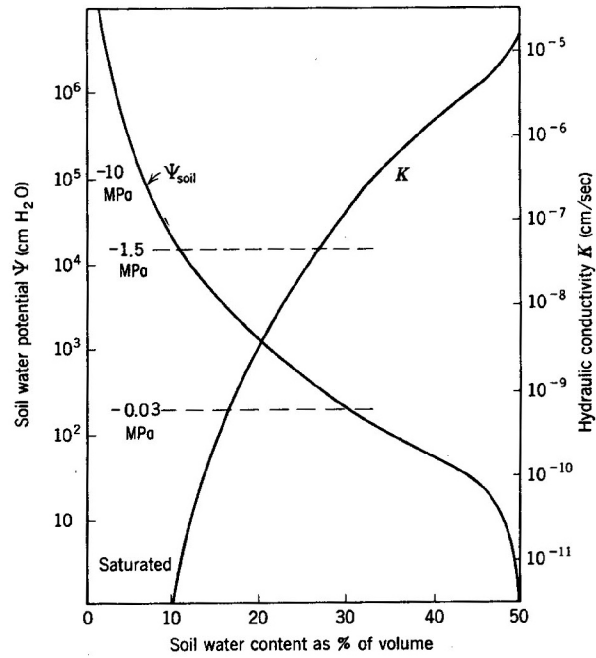
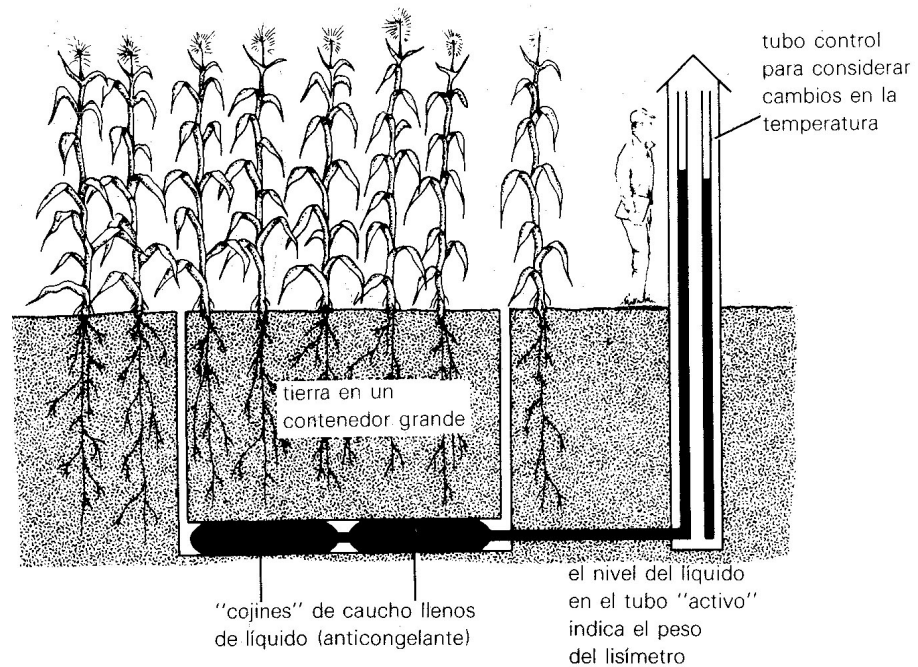


Figure 4.7 Diagram showing approximate decrease in hydraulic conductivity (K) and soil water potential (ψ_w soil) with decreasing soil water content. From Kramer (1983), after Philip (1957).



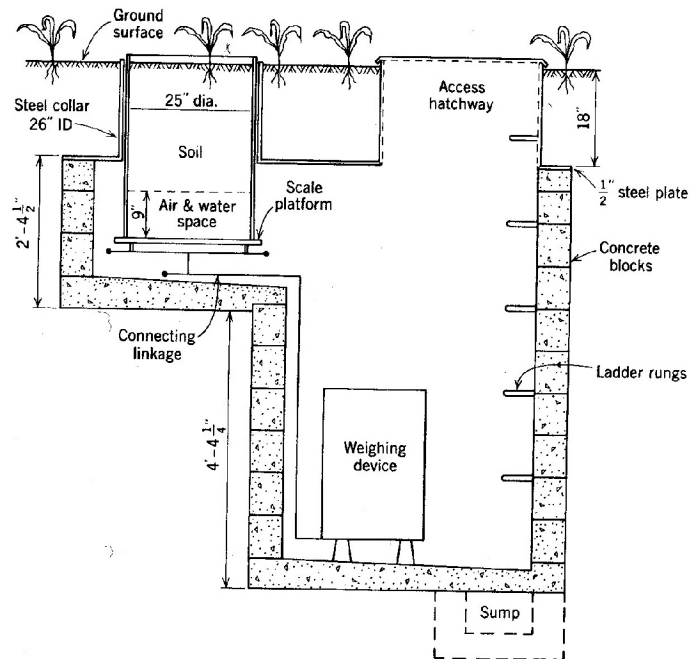


Figure 4.9 The principal components of a weighing lysimeter, modified from England and Lesesne (1962). It consists of a large container filled with soil, mounted on a weighing device. Electronic weighing mechanisms are often used. The lysimeter must be surrounded by a border of similar vegetation if 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) and in Stewart and Nielsen (1990). From Kramer (1983).

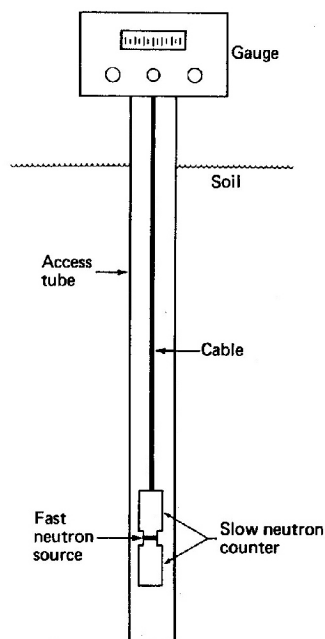


Figure 4.10 The essential features of a neutron meter. A source of fast neutrons and a counter for slow neutrons are lowered to any desired depth in an access tube installed in the soil. The water content of a spherical mass about 20 cm in radius is measured, the size of the mass increasing with decreasing water content. From Kramer (1983).

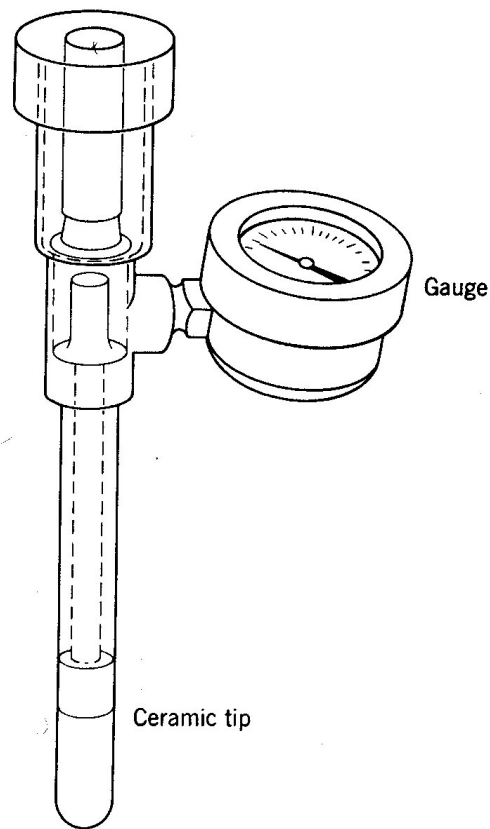


Figure 4.12 Essential features of a tensiometer, consisting of a plastic tube with a porous porcelain cup attached to the lower end, a screw cap at the upper end for refilling, and a vacuum gauge attached at the side. From Kramer (1983).

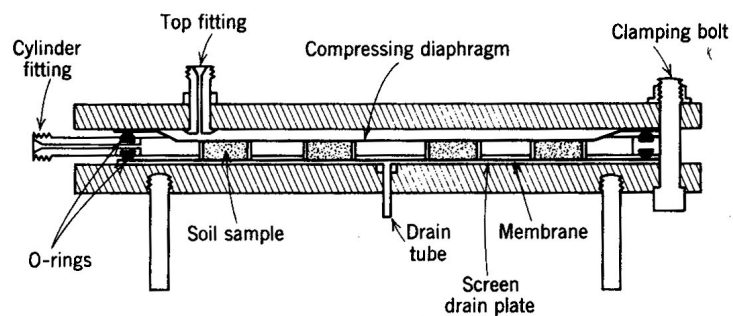


Figure 4.13 A pressure plate apparatus for measuring the matric potential of soil at various water contents. The soil samples are contained in metal rings 5.0 cm in diameter and 1.2 cm deep placed on a cellulose acetate membrane. Compressed air is supplied through the cylinder fitting and air at a slightly higher pressure is supplied through the top fitting to keep the soil samples pressed firmly against the membrane. Sometimes the cellulose acetate membrane is replaced by a porous ceramic plate. The displaced water leaving through the drain tube is collected and measured. Data obtained with this type of equipment are shown in Fig. 4.14. From Kramer (1983).

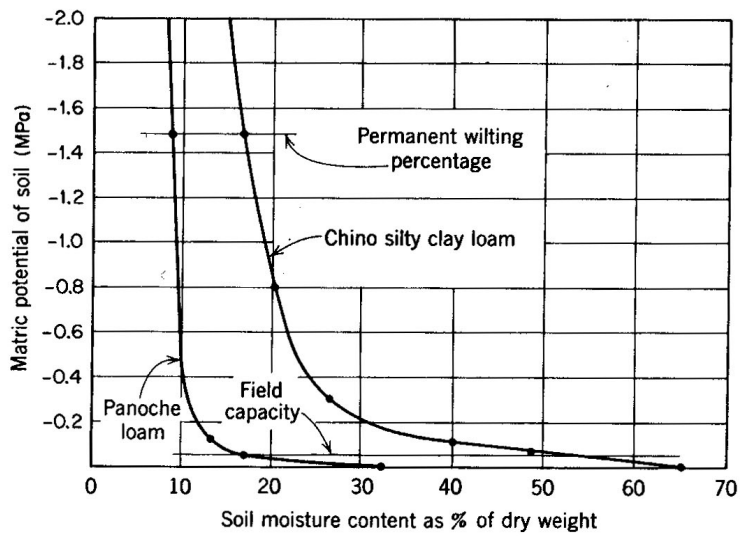


Figure 4.14 Matric potentials of sandy loam and clay loam soils plotted over water content. The curve for the Panoche sandy loam is from Wadleigh *et al.* (1946) and the chino clay loam is from data of Richards and Weaver (1944). From Kramer (1983).

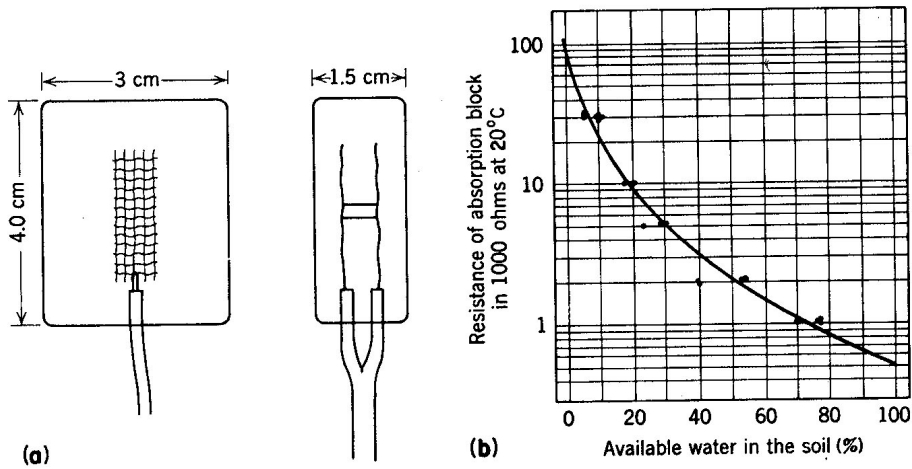


Figure 4.11 Resistance or conductance blocks. (a) Surface and edge diagrams showing location of electrodes in a plaster of paris block. The electrodes are two pieces of stainless-steel screen, separated by a piece of plastic. (b) Resistance in ohms of a plaster of paris resistance block plotted over percentage by weight of available soil water in a silt loam soil in which it was buried. From Kramer, 1983, after Bouyoucos (1954).

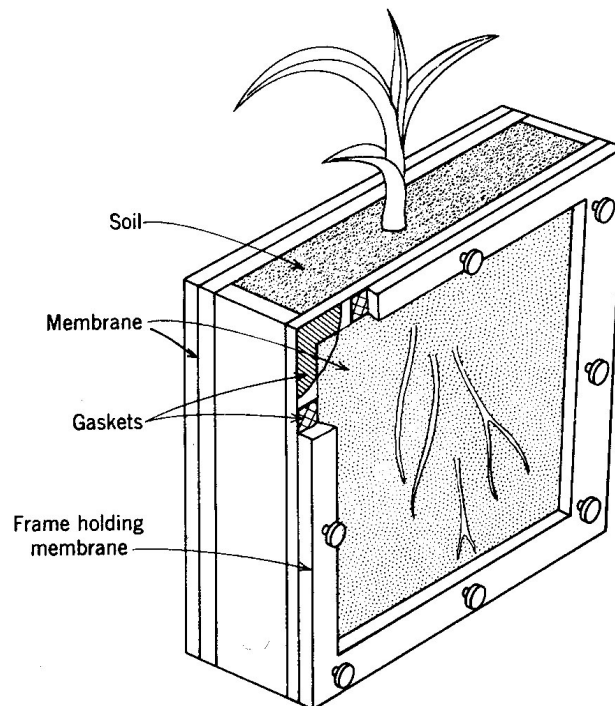


Figure 4.15 A plastic chamber in which plants can be grown in soil maintained at a fixed water potential by immersion in a solution of polyethylene glycol kept at the desired Ψ_w . The soil may be only a few centimeters thick because of slow water conduction at low soil water potential. Designed by Dr. David Lawlor. From Kramer (1983).

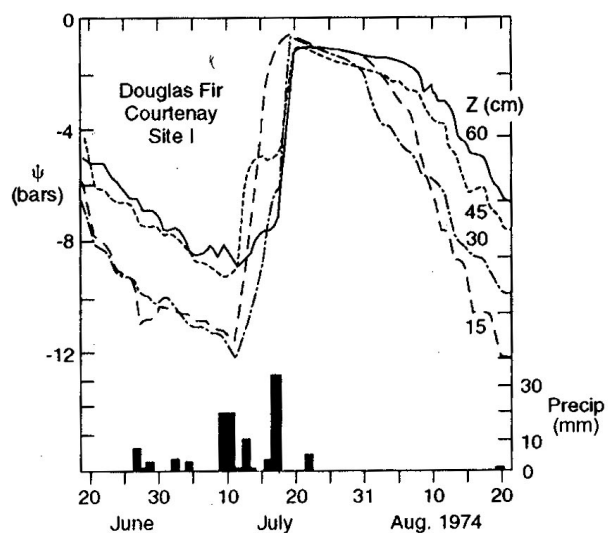


Figure 4.16 Soil water potentials at four depths beneath a Douglas fir forest on Vancouver Island in British Columbia during two drying cycles, before and after midsummer rains. Notice that water was removed most rapidly from the upper soil horizons. From Nnyamah and Black (1977).

Unidad II: EL AGUA EN LA PLANTA

Capítulo 4: CRECIMIENTO Y DESARROLLO DEL SISTEMA RADICULAR

A) El crecimiento de las raíces y sus funciones

- Funciones: órgano de sostén y anclaje, órgano absorbente, síntesis de reguladores del crecimiento (citoquininas, giberelinas, ABA) y de compuestos orgánicos (p.e., a-a, nicotina), sensores del estrés hídrico.
- Crecimiento primario de la raíz: epidermis y pelos radiculares, corteza, endodermis (banda de Caspari), periciclo, xilema y floema.
- Crecimiento secundario: destrucción de epidermis y pelos radiculares, suberización y desarrollo del cambium del corcho.
- Raíces contráctiles.
- Tasa de crecimiento radicular y periodicidad
- Crecimiento en profundidad y lateral de las raíces
- Longevidad de las raíces
 - + Zonas absorbentes de la raíz: raíces jóvenes vs raíces suberizadas (reducción de la permeabilidad).
- Capacidad de absorción (L_R , en $\text{cm}^3 \text{s}^{-1} \text{MPa}^{-1}$) = $L_p A_R$, donde L_p es la permeabilidad o conductancia hidráulica (en $\text{cm}^3 \text{cm}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) y A_R es la superficie de la raíz en cm^2 .
- Micorrizas (incremento de absorción de P): micorrizas endotróficas (Micorriza Vesículo arbuscular, VA), micorrizas ectotróficas.

B) Desarrollo del sistema radicular.

- Inter-relaciones entre raíz y tallo (parte aérea)
 - efectos del tallo sobre las raíces (fotosintatos, competencia con otros sumideros, fuente de AIA).
 - Efectos de la raíz sobre el tallo (control de absorción, resistencia a salinidad, ABA).
 - proporción raíz/tallo
- Injerto de raíces.
- Costo metabólico del sistema radicular: 50% de la producción primaria neta anual de materia seca en un bosque deciduo se destina a la producción de nuevas raíces. El 75% en el caso de comunidades con gramíneas y arbustos.

C) Factores ambientales que afectan el crecimiento de las raíces.

- Textura y estructura del suelo (compactación)
- Humedad del suelo
- ¿Hidrotropismo?
- Aireación del suelo
 - O_2/CO_2 (aumento de CO_2 reduce permeabilidad de raíces)
 - Daño por inundación.
 - Diferencias en la tolerancia a la inundación.
 - Formación de espacios intercelulares y aerénquima.

- Canales formados por raíces muertas y lombrices.
- Relación entre aireación y enfermedades
- Toxicidad del oxígeno: superóxido ($O_2^{\cdot-}$), H_2O_2 y OH^- pueden dañar enzimas y reaccionar con ácidos grasos insaturados, causando daño a las membranas celulares y de organelos.
- Minerales, concentración de sales y pH (efecto sobre raíz/tallo).
- Temperatura del suelo
- Competencia entre raíces.
- Alelopatía
- Problemas con las rotaciones (re-plantación): productos provenientes de las raíces muertas, nemátodos, hongos, drenaje pobre, aireación no adecuada. Nemátodos y hongos más importantes que compuestos alelopáticos.
- Bioquímica de la competición e infección: competición entre raíces, alelopatía y autotoxicidad, relaciones simbióticas (hongos micorrizicos, bacterias fijadoras de nitrógeno), y organismos parásitos.

D) Métodos para el estudio de los sistemas radiculares

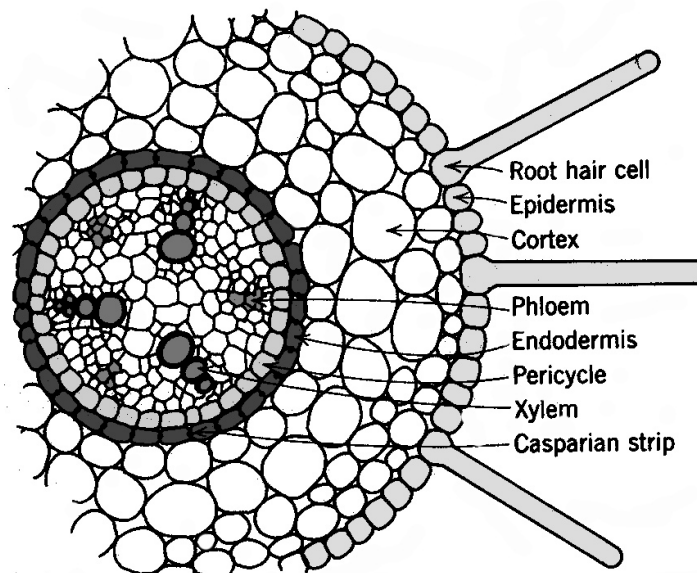
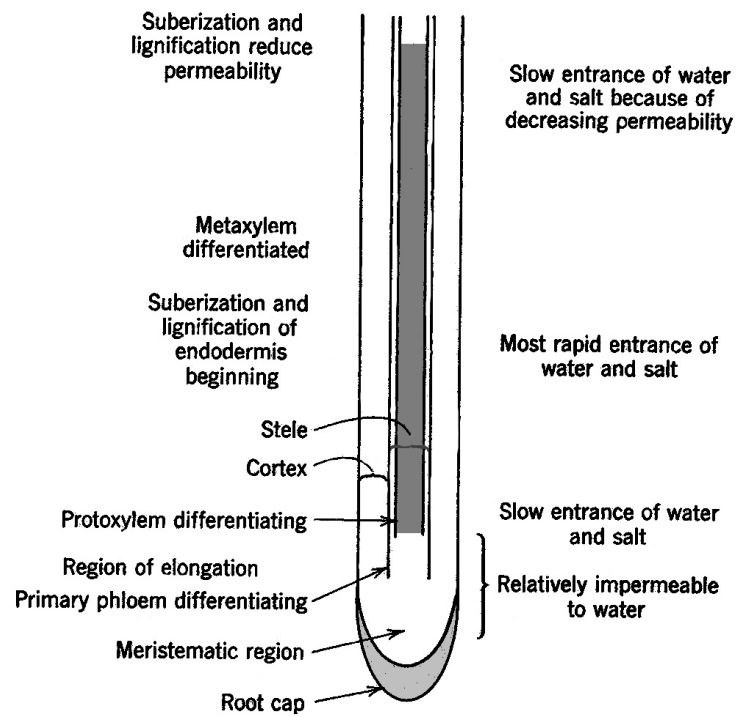
- Excavaciones: requiere mucho tiempo, energía y paciencia para terminar empolvado (Kramer y Boyer, 1995).
- Ventanas en el suelo hasta túneles de observación: rizotrones y micro-rizotrones.
- Radiografía de neutrones e imágenes de resonancia magnética nuclear.
- Uso de isótopos radioactivos de fósforo, azufre o rubidio.
- Uso de isótopos estables del agua en el xilema (2H , ^{18}O).

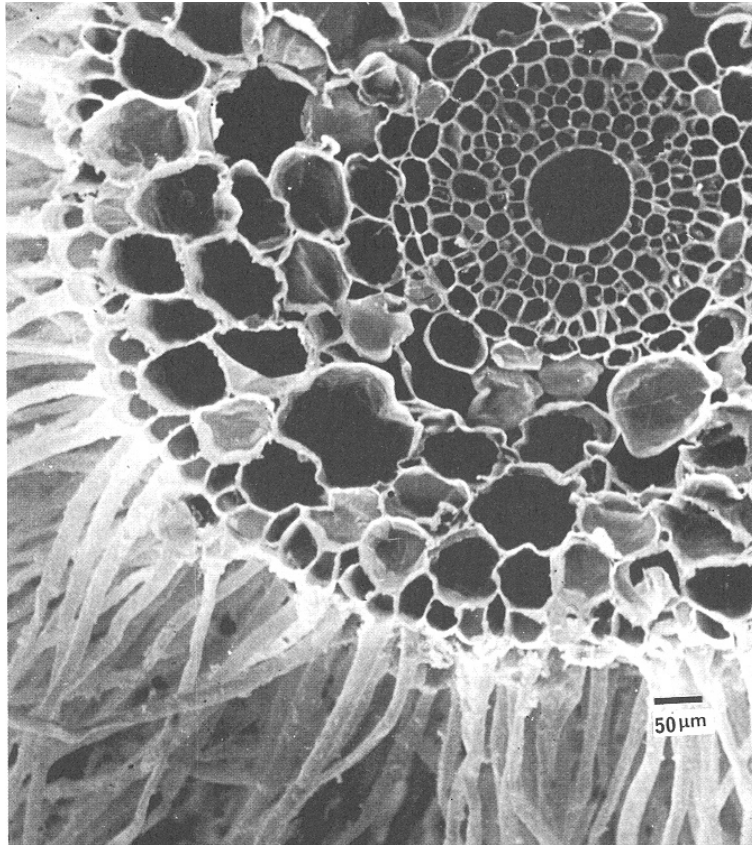
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Kramer P.J. y J.S. Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego. Capítulo 5.

Kramer P.J. 1983. Water Relations of Plants. Academic Press. Capítulo 5 y 6.

Pearcey R.W., J. Ehleringer, H.A. Mooney y P.W. Rundel (1990) Plant Physiological Ecology: Field Methods and Instrumentation. Chapman and Hall. Capítulo 16.





Raíz de cebada joven

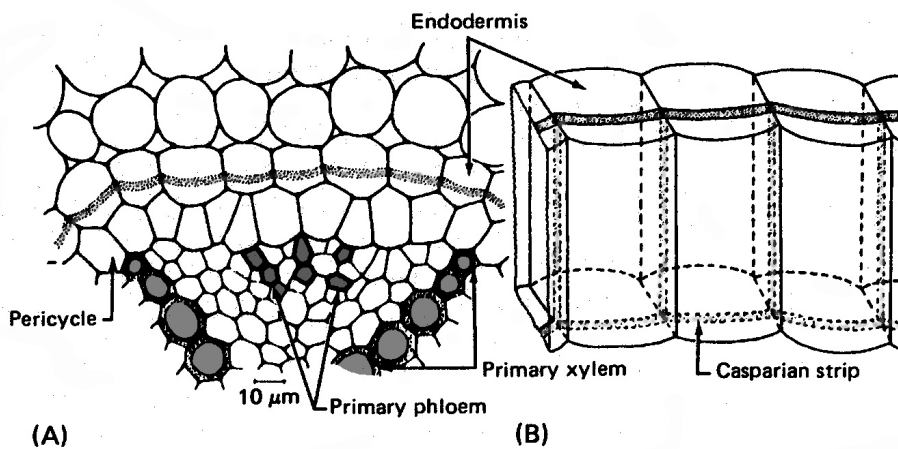


Figure 5.4 Structure of endodermis. (A) Cross section of part of a morning glory root (*Convolvulus arvensis*) showing location of endodermis. (B) Diagram of endodermal cells, showing Casparian strips on radial walls of endodermal cells. From Kramer (1983). Adapted from Esau (1965) by permission of John Wiley and Sons, New York.

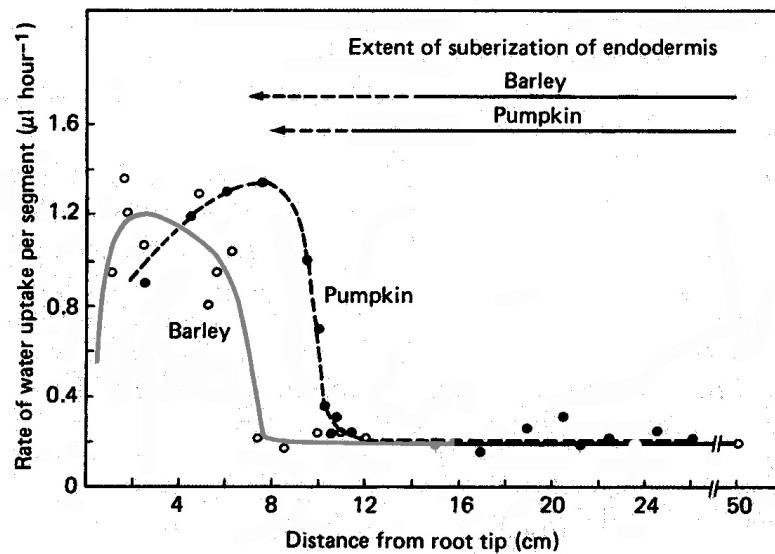


Figure 5.5 Rate of water uptake at various distances behind the apex of barley and pumpkin (*Cucurbita pepo*) roots with varying degrees of suberization of the endodermis. Note that there is measurable uptake even where suberization is complete. From Kramer (1983), after Agricultural Research Council Letcombe Laboratory Annual Report (1973, p. 10).

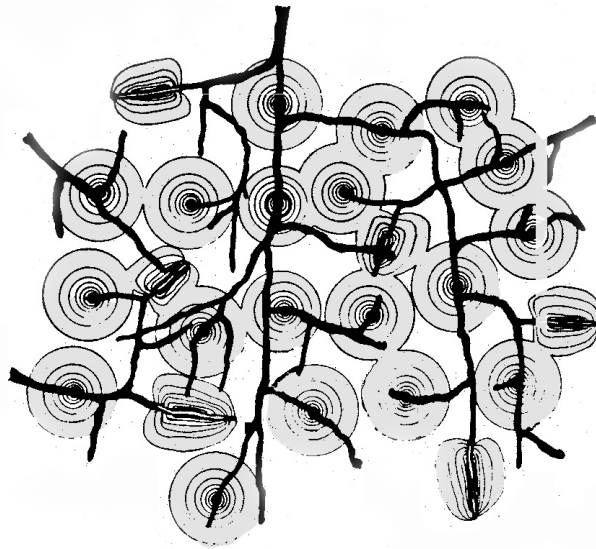


Figure 8.8. Patterns of water uptake indicated by contours of decreasing water potential approaching regions of uptake at individual roots for a perennial plant root system. Most of the root system is suberized. Uptake is considered to occur at widely spaced points where the suberization is disrupted, such as cracks, or at unsuberized root tips, which are shown as white roots. Water flow around cracks is in a spherical configuration. For the unsuberized root tips, the water-uptake pattern is ovoid, with increasing radius toward the basal region of the roots, because the roots are actively growing (from Caldwell 1976).

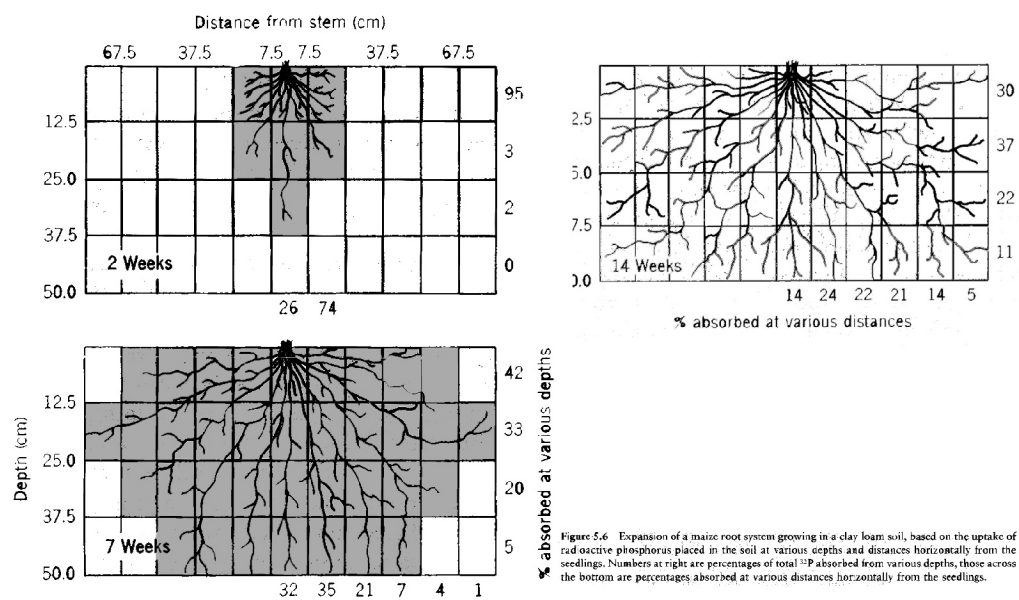
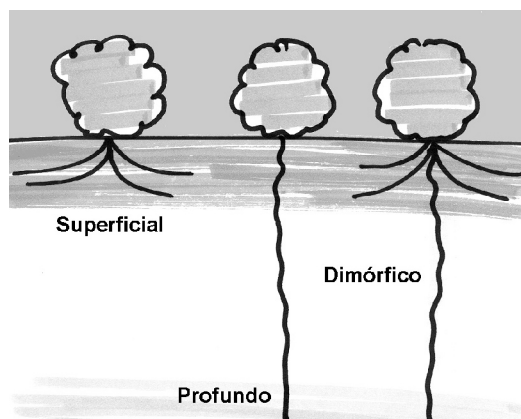


Figure 5.6 Expansion of a maize root system growing in a clay loam soil, based on the uptake of radioactive phosphorus placed in the soil at various depths and distances horizontally from the seedlings. Numbers at right are percentages of total ^{32}P absorbed from various depths, those across the bottom are percentages absorbed at various distances horizontally from the seedlings.



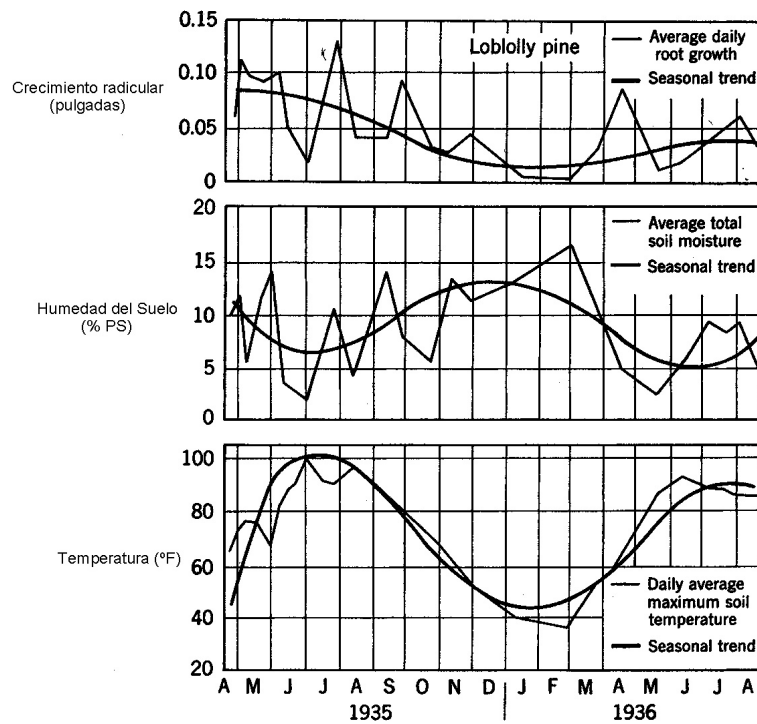


Figure 5.7 Effects of soil temperature and water content on growth of roots of shortleaf pine (*Pinus echinata*) in a forest at Durham, North Carolina. From Kramer (1983), after Reed (1939).

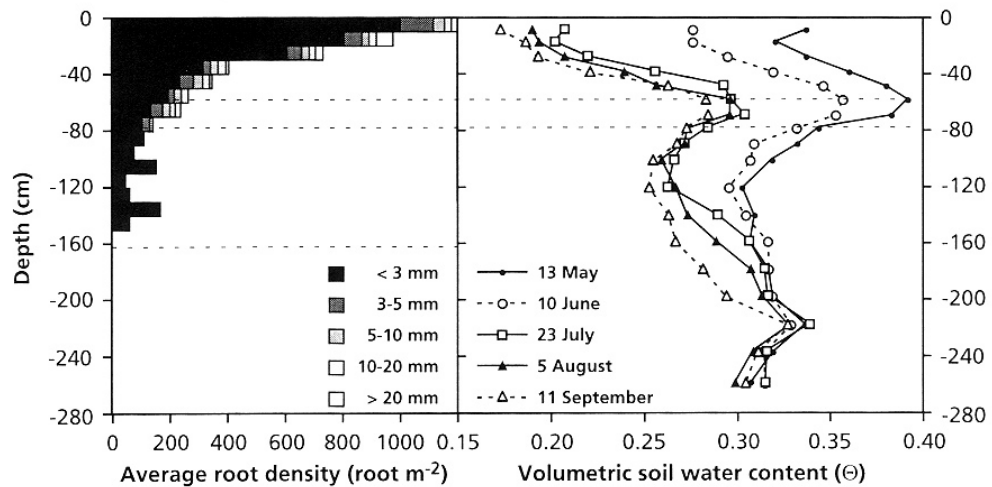


FIGURE 4. (Left) Rooting profile of *Quercus petraea* (sessile oak) as dependent on soil depth. Roots were divided in different diameter classes, indicated in the box. (Right) Volumetric water content of the soil in which the oak tree was growing, as dependent on depth and time of the year

(indicated in the box). A clay-enriched horizon at around 50 cm depth is indicated by the two broken lines. The third broken line at 160 cm depth indicates the depth of the trench that was dug to make the measurements (Bréda et al. 1995). Copyright Blackwell Science Ltd.

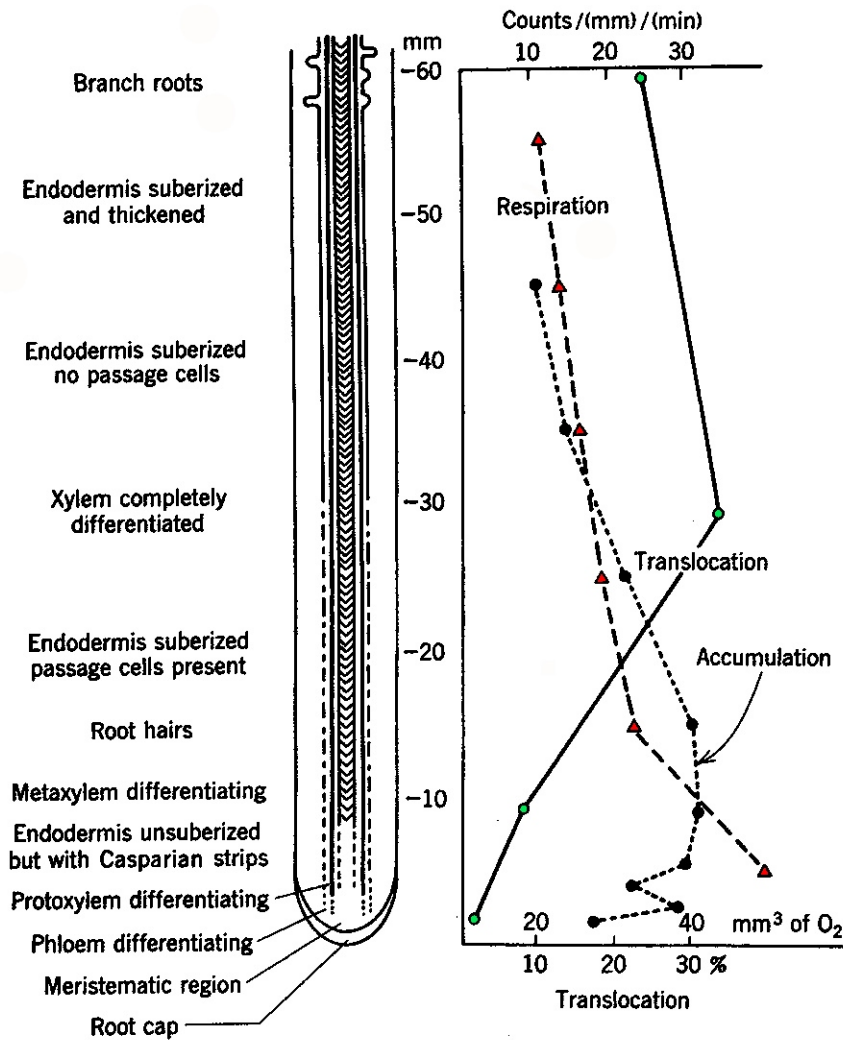


Figure 5.8 Diagram of the apical region of a barley root showing the relationship between the regions where salt is accumulated and where it is absorbed and translocated to the shoot. The curve for respiration is based on data of Machlis (1944), that for translocation on data of Wiebe and Kramer (1954), and that for accumulation on data of Steward and Sutcliffe (1959). The relative positions of those regions probably are similar in most or all growing roots, but the actual distances behind the root tip will vary with the species and the rate of growth. From Kramer (1983).

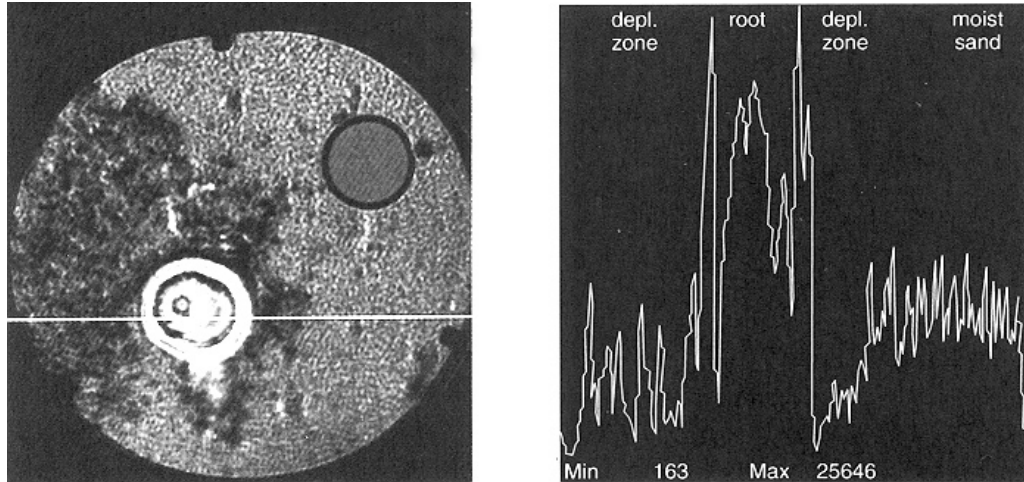


Figure 5.9 (A) A magnetic resonance image showing water depletion (the dark region) around the taproot of a *Pinus taeda* seedling in sand initially at field capacity, after 4.5 hr of transpiration. The circular object at the upper right is a reference tube containing a solution of CuSO_4 and H_2O which has a density similar to sand containing 25% water. On the right (B) is a plot of the relative water content along the white line shown in (A). The diameter of the taproot was about 5 mm. From MacFall *et al.* (1991a).

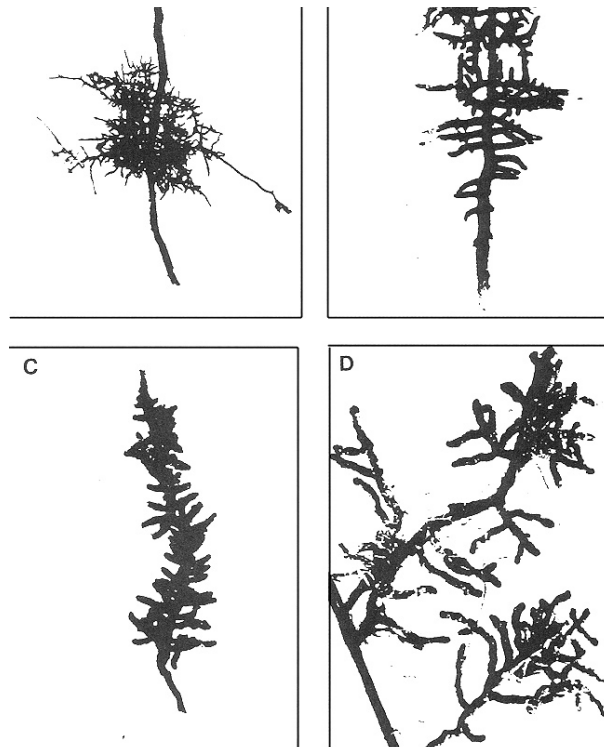


Figure 5.10 Mycorrhizal root development on Douglas fir. (A) Typical cluster, (B) pinnately branched cluster, (C) orange mycorrhiza, and (D) yellow mycorrhiza with rhizomorphs extending into the soil. From Kozłowski *et al.* (1991).

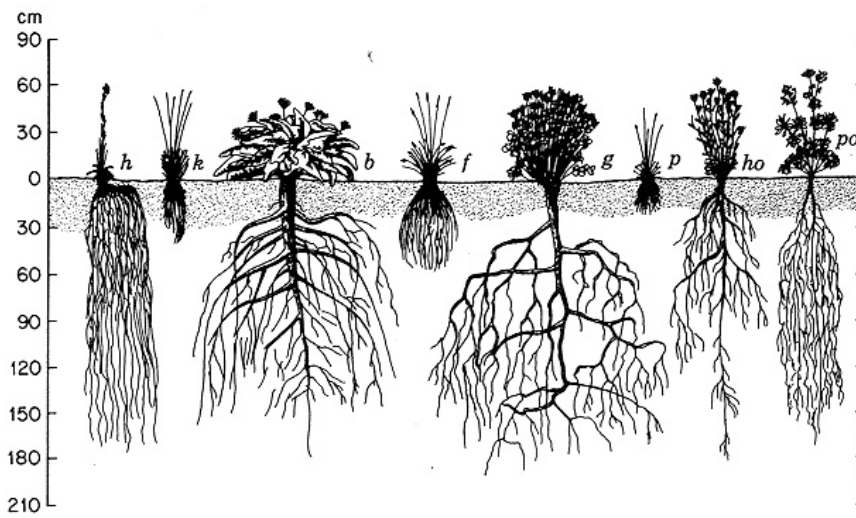


Figure 5.11 Differences in depth and spread of root systems of several species of prairie plants growing in a dry, well-aerated prairie soil: *h*, *Hieracium scouleri*; *k*, *Koeleria cristata*; *b*, *Balsamina sagittata*; *f*, *Festuca ovina ingrata*; *g*, *Geranium viscosissimum*; *p*, *Poa sandbergii*; *ho*, *Hoorebekia racemosa*; *po*, *Potentilla blaschkeana*. (From Kramer (1983), after Weaver (1919).

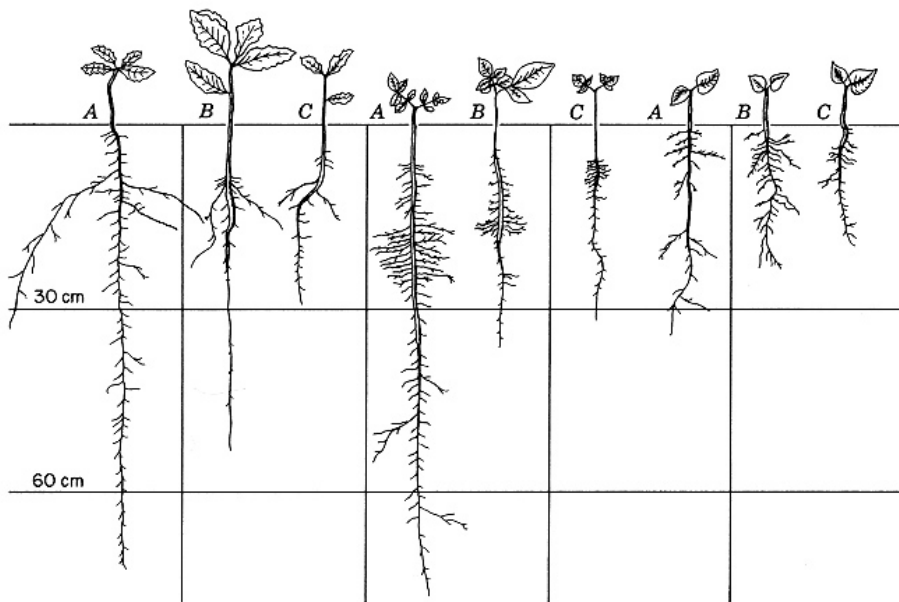


Figure 5.12 Interaction of heredity and environment on amount of root growth produced by three tree species growing in three environments. Left, *Quercus rubra*; center, *Hicoria ovata*; right, *Tilia americana*. Seedlings A were growing in open prairie, B in an oak forest, and C in the deep shade of a moist linden forest. It was necessary to water the linden seedlings in the prairie to prevent death from desiccation. Oak developed the deepest and linden the shallowest root systems in all three habitats. From Kramer (1983), after Holch (1931).

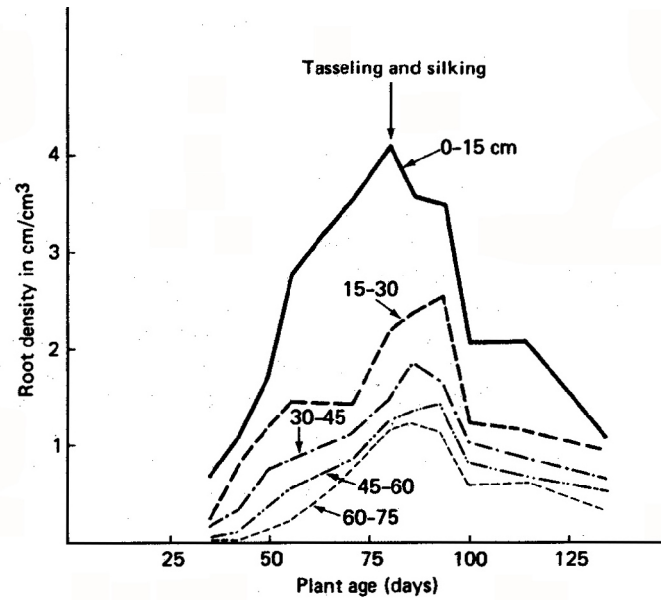


Figure 5.13 Effects of seed development and filling on root growth of maize. Note that root density began to decrease at all depths in the soil after tasseling and silking because old roots died more rapidly than new roots were formed. From Kramer (1983), after Mengel and Barber (1974).

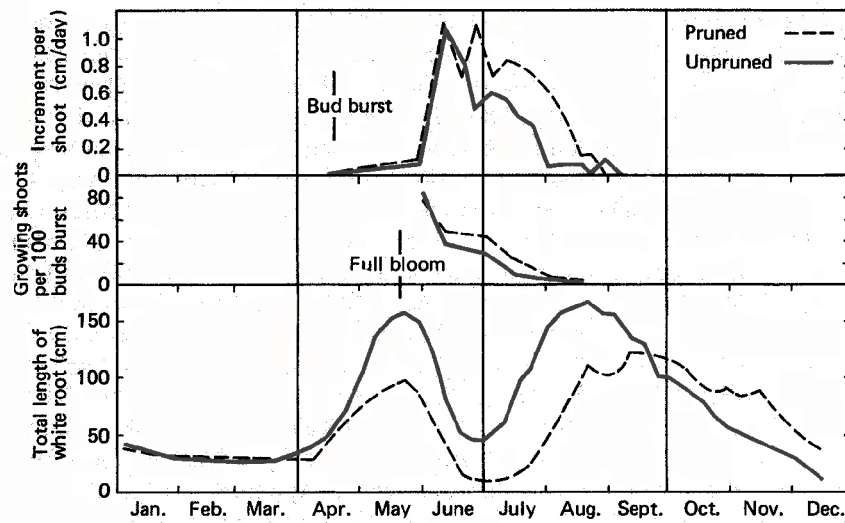


Figure 5.14 Relationship between root and shoot growth of apple. As shoot growth (upper curves) increased, root production (lower curve) decreased. Pruning stimulated shoot growth and reduced midsummer root growth. From Kramer (1983), after Head (1967).

Table 5.1 Amount of Dry Matter in Metric Tons per Hectare Incorporated Annually into Roots and Shoots of Various Plant Species

Species	Roots	Shoots	Root-shoot ratio
<i>Zizania aquatica</i> (wild rice)	0.6	4.0	0.15
<i>Hordeum</i>	3.0	12.0	0.25
<i>Andropogon scoparium</i> (first year)	3.5	14.2	0.25
<i>Triticum</i> (average)	2.0	6.8	0.29
<i>Medicago sativa</i> (average)	3.2	7.4	0.43
<i>Zea mays</i> (average)	4.5	8.7	0.52
<i>Solanum tuberosum</i> (average)	4.0	2.6	1.54
<i>Beta</i> (average)	9.5	3.1	3.06
<i>Pinus sylvestris</i> (average)	1.6	8.9	0.17
<i>Picea abies</i> (average)	2.1	11.9	0.18
<i>Fagus sylvatica</i> (average)	1.6	8.2	0.19
Ghana rain forest	2.6	21.7	0.12

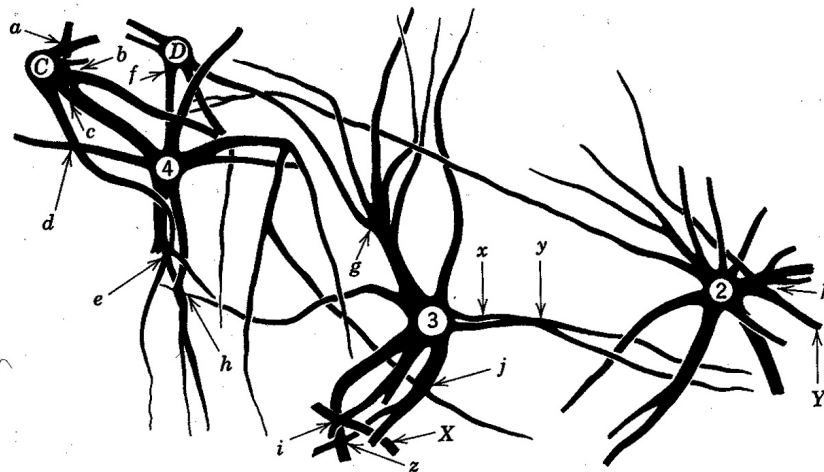


Figure 5.15 Root grafting among roots of three 18-year-old trees of *Pinus radiata* and roots from living stumps of two trees removed 9 years previously. Grafts *a* through *g* were between trees 3 and 4 and roots of stumps C and D. Grafts *h* through *k* were between roots of trees 3 and 4 or between trees 3 and 4 and roots X and Y of trees removed during root excavation. Grafts *x*, *y*, and *z* are between two roots of the same tree. From Kramer (1983), after Will (1966).



Figure 5.16 Effect of a compacted layer of soil on root penetration by 11-week-old oat plants. (Left) Undisturbed soil with dense mass of roots above the compacted layer, but few below it. (Right) Uniform penetration of roots into soil loosened by tillage to a depth of 50 cm. The restriction of root penetration was caused by mechanical resistance, as aeration was not limiting below the compacted layer. From Kramer (1983). Courtesy of H. D. DeRoo, Connecticut Agricultural Experiment Station.

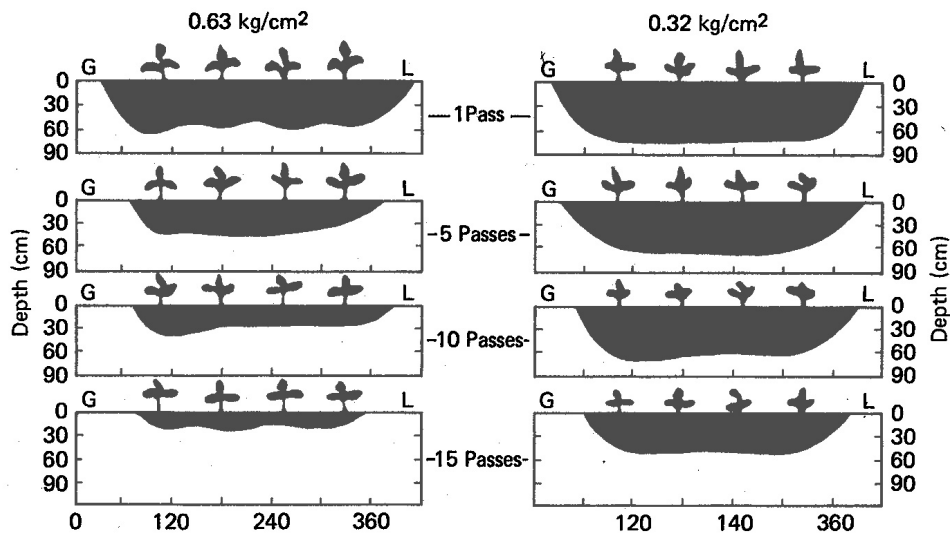
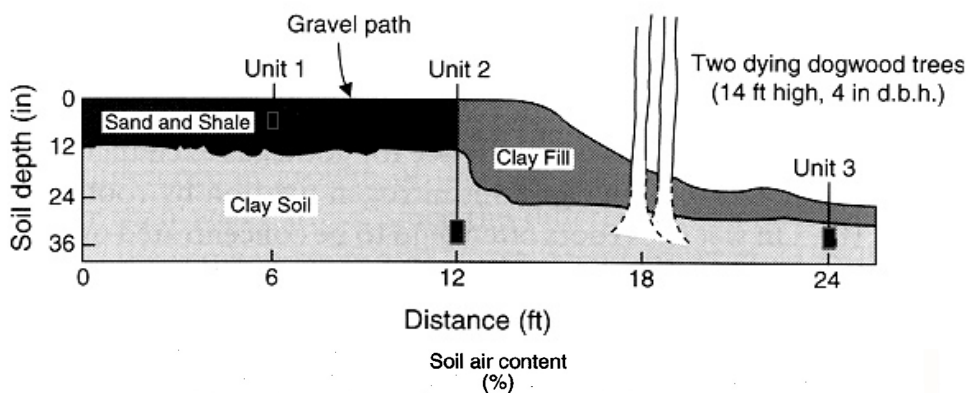


Figure 5.17 Effect on root penetration of soil compaction at 0.63 and 0.32 kg cm⁻² for 1, 5, 10, and 15 passes over a clay soil prior to seeding. From Kramer (1983), after Cassel in Raper and Kramer (1983).

Table 5.2 Oxygen Consumption and Carbon Dioxide Production from a Bare Soil and under Kale in Summer and Winter at Rothamsted, England (Rates are in g · m⁻² · day⁻¹)

Soil temperature at 10 cm	July (17°C)		January (3°C)	
	Cropped	Bare	Cropped	Bare
Oxygen used	24	12	2.0	0.7
Carbon dioxide produced	35	16	3.0	1.2

^aFrom Wild (1988, p. 300).



Date	6 ft		12 ft		24 ft	
	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂
8/10/62	Installed		Installed		Installed	
8/17/62	18.0	2.5	4.0	>20.0	8.0	12.5
10/13/62	19.0	1.5	4.0	>20.0	4.5	15.5
11/16/62	19.0	1.0	4.0	>20.0	6.0	15.0
3/31/63	-	-	1.0	>20.0	-	-

Figure 5.18 Changes in oxygen and carbon dioxide concentration of soil beneath sand and clay fills. From Kozłowski *et al.* (1991), after Yelenosky (1964).

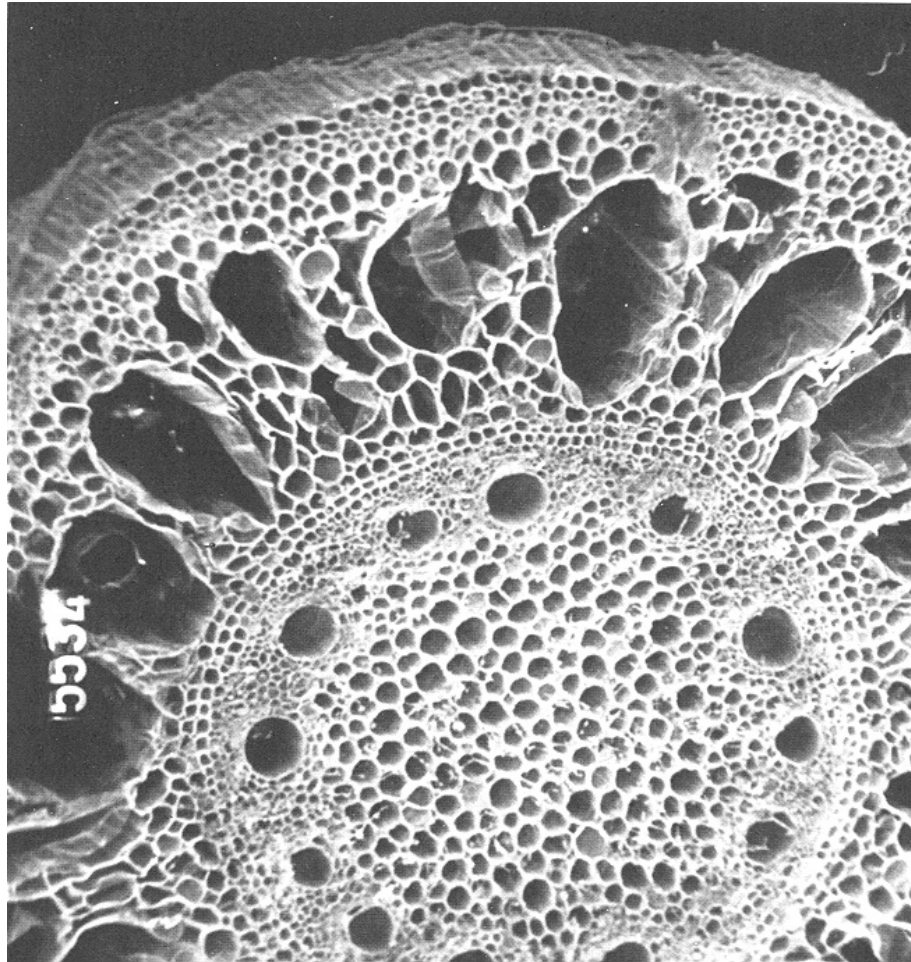


Figure 5.19 Scanning electron micrograph of an adventitious root of corn grown in an unaerated nutrient solution. The section was made 8 to 10 cm behind the root tip. The air spaces in the cortex are formed lysigenously by the breakdown of cells. From Kramer (1983), from Agricultural Research Council Letcombe Laboratory Annual Report (1978, p. 42); courtesy of M. C. Drew.

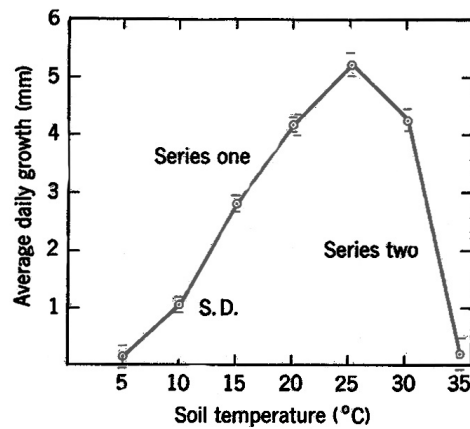


Figure 5.20 Relationship between soil temperature and root elongation of *Pinus taeda* seedlings under controlled conditions. From Kramer (1983), after Barney (1951).

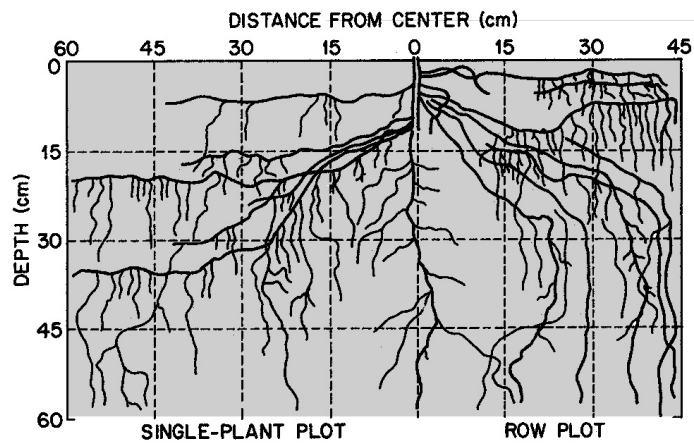


Figure 5.21 Difference in lateral root extension of an isolated soybean root system (left side) and that of a plant growing in a row. From Kramer (1983), after Raper and Barber (1970a).

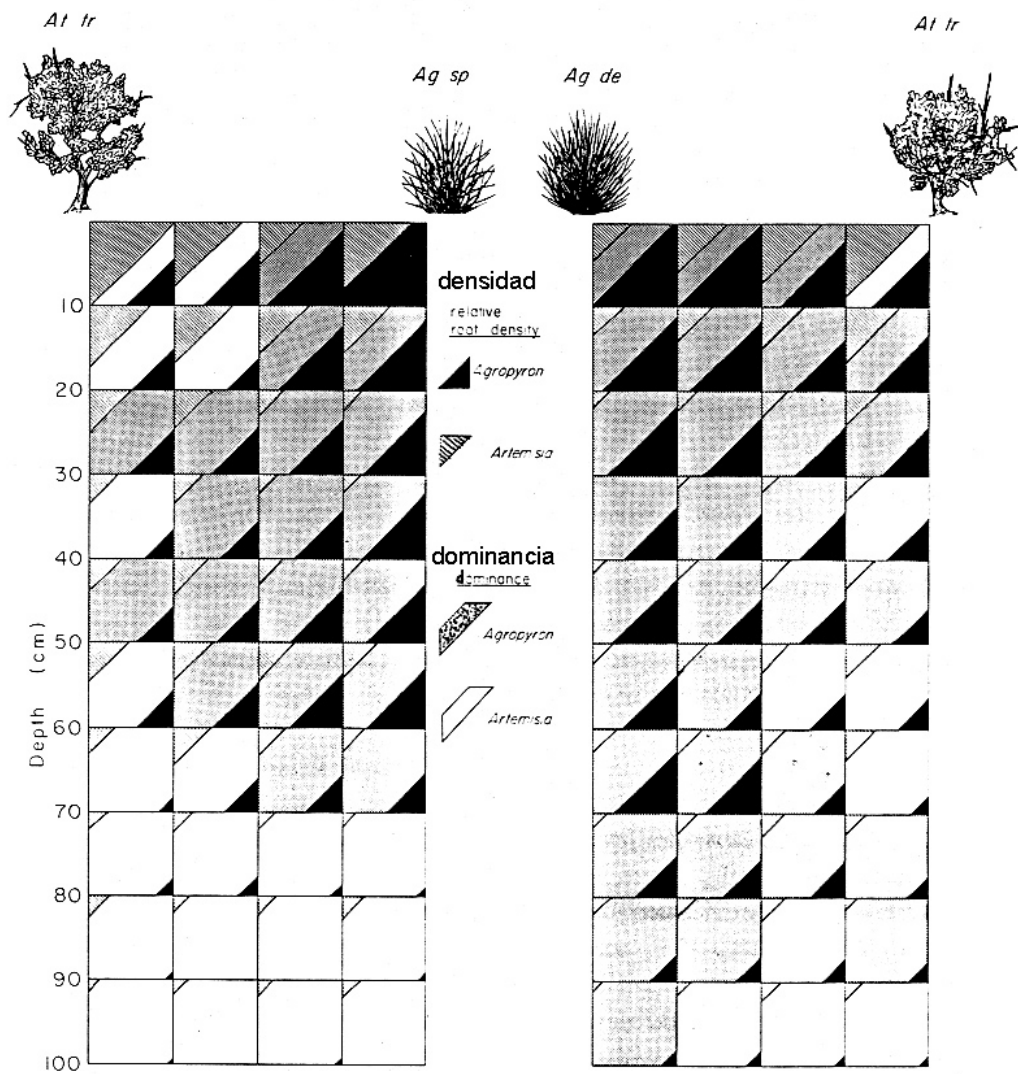


Figure 8.10. Root-system distribution of neighboring *Agropyron* bunchgrasses and *A. tridentata* shrubs. The relative rooting densities of higher-order roots of each species and the dominance in each soil cell are indicated.

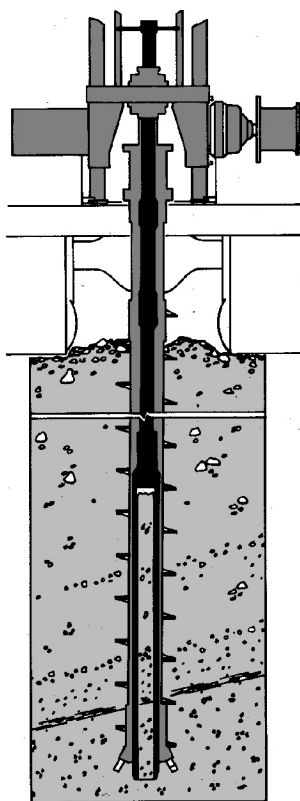


Fig. 16.1 Schematic diagram of a continuous flight split-tube augering system capable of obtaining intact soil cores to depths of 30 m. The outer rotating auger cuts and removes soil such that the inner split tube may be pushed into the soil in advance of the rotating auger. This system provides an intact core with minimal disturbance to soil structure and roots.

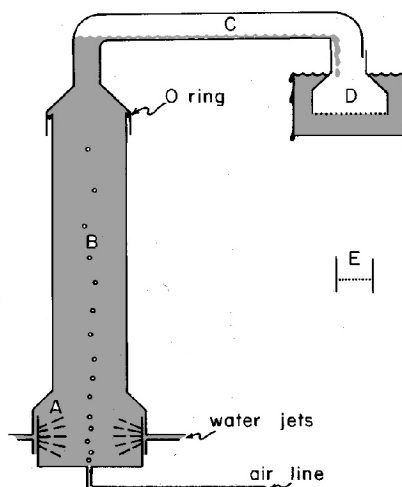


Fig. 16.2 Schematic representation of a hydro-pneumatic elutriation system for separating roots from soil. (A) A high kinetic-energy washing chamber, (B) elutriation chamber, (C) transfer tube, (D) low kinetic-energy primary sieve and (E) secondary sieve. The transfer tube (C) can be removed from the elutriation chamber (B) in order to remove soil and fragments from the previous sample and to insert a new soil-root sample. After the primary sieving (D), the roots can be placed on the secondary sieve (E) by inverting and washing on to the fine secondary sieve. (Adapted from Smucker *et al.*, 1982.)

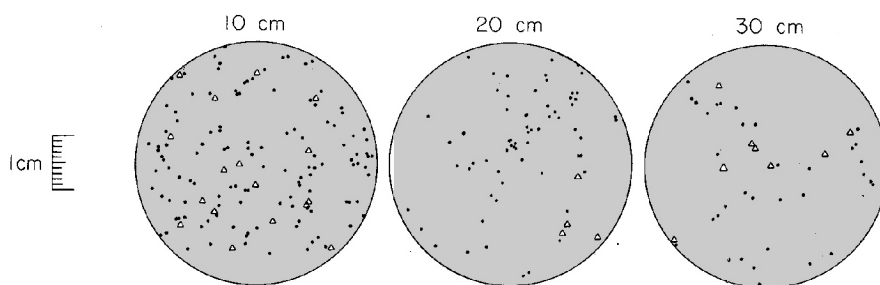


Fig. 16.3 The distribution of individual roots in cross-sections of soil between *Artemisia tridentata* (Δ) and *Agropyron desertorum* ($\bullet$) at three depths. Parcels of soil previously frozen with liquid nitrogen were excavated and then sectioned at -70°C with a lapidary saw. The position where individual roots intersected the cut plane was mapped from the cut soil sections and from enlarged photographs of them. To determine whether the individual roots belong to *Artemisia* or the grass, a fluorescence technique has been developed and tested on roots of *Artemisia* and *Agropyron* of different ages and phenological status. On partial thawing of the soil, individual root segments (~ 1 cm) were removed from the soil and dried. A basic extract of the roots (2 M NaOH) was dried on chromatography paper and the spots observed under a UV-A lamp. The *Artemisia* and *Agropyron* roots are clearly distinguished by color and intensity of fluorescence (from Caldwell *et al.*, 1987).



“Las excavaciones requieren mucho tiempo, energía y paciencia para terminar empolvado (Kramer y Boyer, 1995)”

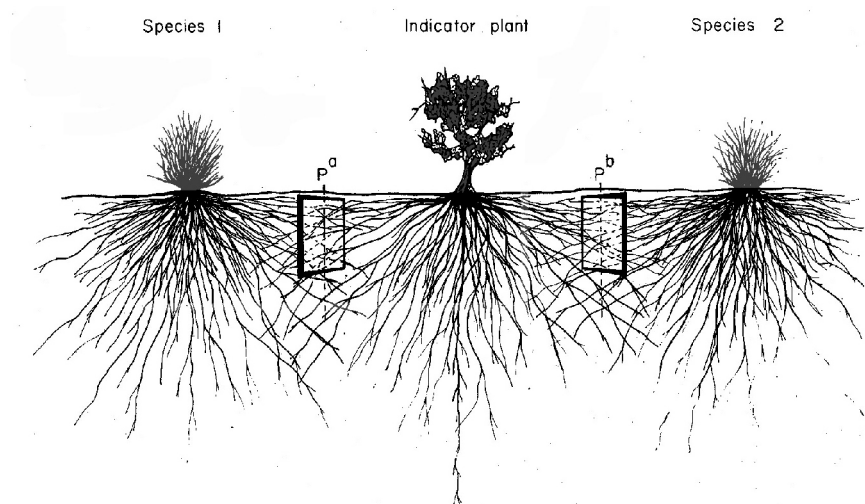
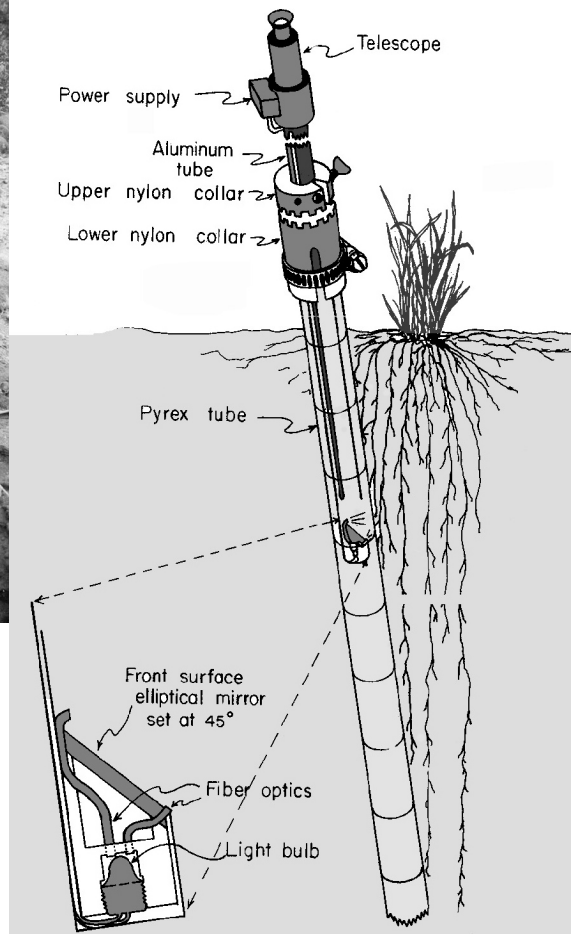


Fig. 16.8 Experimental design for assessing the ability of an indicator plant to acquire phosphorus radioisotopes from two test species. The two isotopes, ^{32}P and ^{33}P , are placed as orthophosphoric acid in a row of small vertical holes previously punched into the soil. The isotope solutions injected into the row of holes form a plane of isotope in the soil interspace between each test species and the indicator plant. Small tissue samples of the indicator plant are then assessed for ratios of the isotopes. Adapted from Caldwell and Eissenstat (1987). See also Caldwell *et al.* (1985).

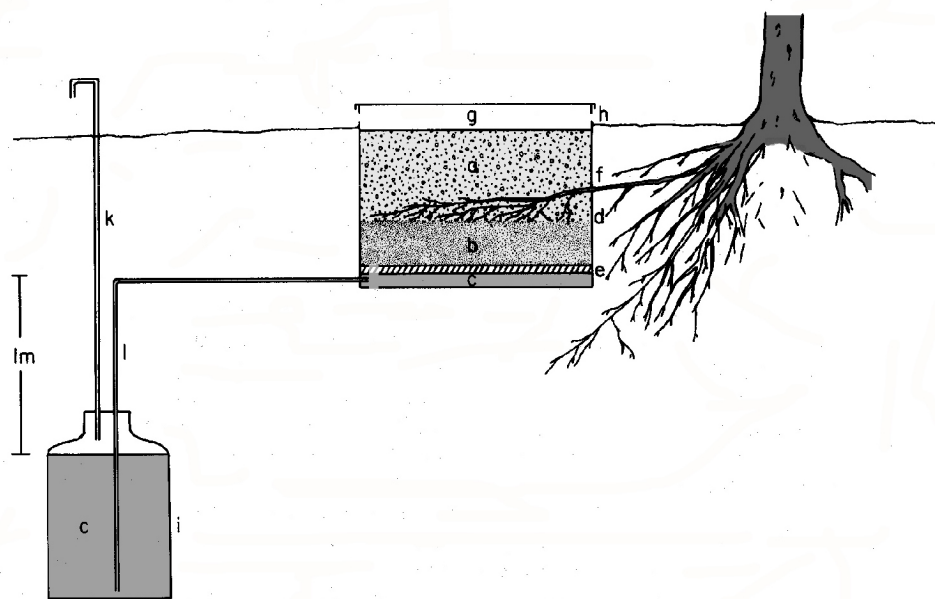


Fig. 16.9 A root chamber used to assess the reaction of roots to different growing media and soil chemicals in the field. (a) Soil with intact tree root, (b) a nonbuffered small-grain sand, (c) nutrient solution, (d) fine PVC mesh netting (1 mm² pore diameter), (e) ceramic plate, (f) side opening, (g) air ventilation space, (h) opening for ventilation, (i) flask as nutrient solution reservoir, (k) pressure equilibration tube and (l) interconnecting tubing. Adapted from Glavac and Ebben (1986).

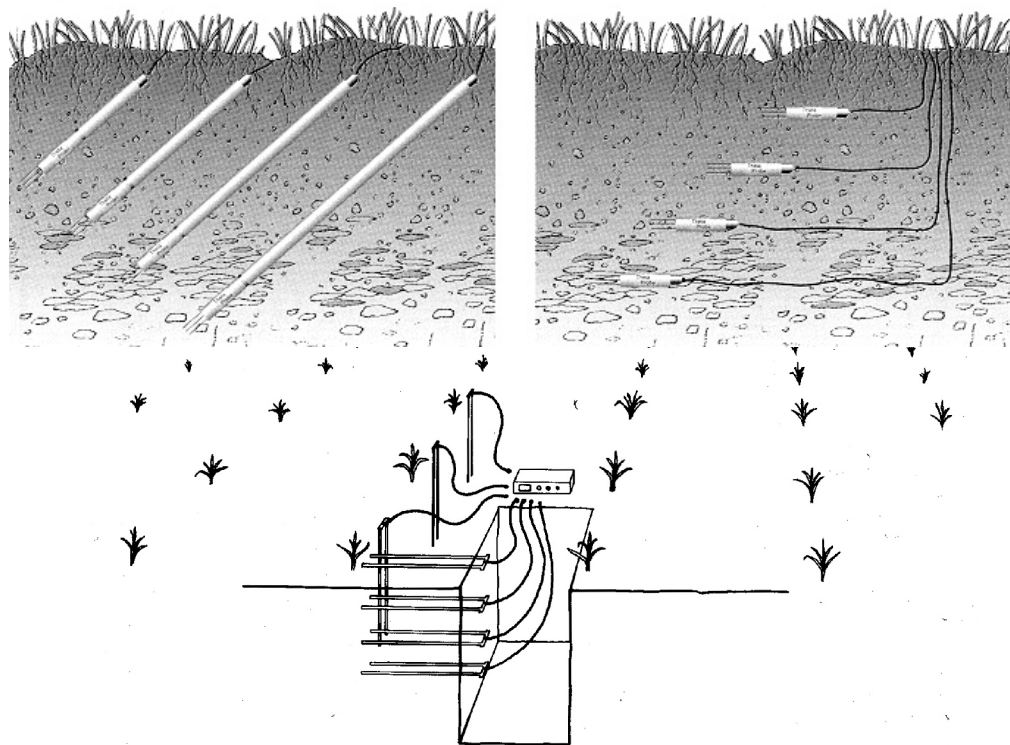


Fig. 16.6 Diagram of vertical and horizontal installation of time-domain reflectometry probes in an agricultural field. The small case represents the electronic package for determination of dielectric constants. Adapted from Topp and Davis (1985).

Unidad II: EL AGUA EN LA PLANTA

Capítulo 5: LA ABSORCIÓN DEL AGUA Y LOS POTENCIALES HÍDRICOS DE LA RAÍZ Y EL TALLO

A) La absorción del agua y las presiones de la raíz y el tallo.

* Mecanismos de Absorción

- Absorción pasiva en plantas que están transpirando (potencial de presión, alta tasa de transpiración + lejos de la CC). (flujo de masa - transpiración)

$$\text{Absorción} = ((\Psi_m + \Psi_s)_{\text{suelo}} - (\Psi_p + \Psi_s)_{\text{raíz}}) / (r_{\text{suelo}} + r_{\text{raíz}})$$

- Absorción osmótica y presión radical (presión radical, glutación, baja tasa de transpiración + suelo cerca de CC)

- teorías de secreción o no-osmóticas
- teorías electro-osmóticas
- teorías osmóticas

- transición entre absorción activa (osmótica) a pasiva (tensión)

$J_v = L_p (\Delta \Psi_p + \sigma \Delta \Psi_s)$, donde J_v es el flujo volumétrico, L_p es la conductancia al flujo hidráulico, σ = coeficiente de reflexión.

* características de la presión radical..

- Diferencias entre especies (magnitud de la presión, volumen y composición del exudado, periodicidad)

- presión radicular (hierbas 0.05 - 0.19 MPa; tomate 0,6 MPa).

- Composición savia: agua + sales minerales + (azúcar y a-a) + reguladores del crecimiento (citoquininas y giberelinas))

- Potencial osmótico (algodón -0.15 a -0.24 MPa).

- Periodicidad (ciclo circadiano - asociado a cambio en permeabilidad de raíces).

- Glutación

* Presión del tallo (exudado de savia no explicable por presión radicular).

- Flujo de savia en *Acer saccharum* y *A. nigrum* (Maple trees).

- Otros ejemplos: palma chilena.

* Absorción de neblina a través de las hojas.

B) Transporte.

- Flujo = - K * fuerza conductora, donde K es el factor de proporcionalidad referido a las propiedades del sistema. El signo menos indica que el flujo es colina abajo.

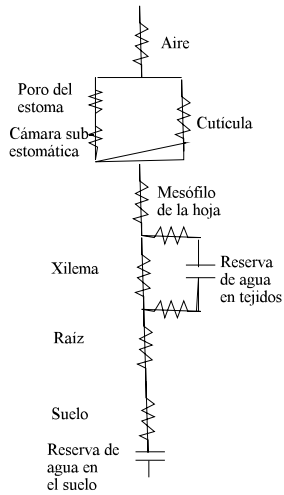
- Ecuaciones de transporte de agua.

- Ley de Darcy (flujo de agua en medio poroso): $J_v = - L_{\text{suelo}} d\Psi_{\text{suelo}}/dx$, donde L_{suelo}/dx = es el coeficiente de conductancia hidráulica

- Ley de Poiseuille: Flujo volumétrico (J_v) = $-(r^4/8\eta)(d\Psi_p/dx)$, donde r = radio del cilindro, η = viscosidad de la solución, $-(d\Psi_p/dx)$ = gradiente negativo de presión hidrostática.

- J_v aumenta si r ó $(d\Psi_p/dx)$ aumentan, ó η disminuye.

- membrana como barrera al flujo de agua.



* Analogía con la Ley de Ohm

- Flujo de agua = $\Delta \Psi$ / resistencia

- Corriente eléctrica = voltaje / resistencia

- Ley de Van den Honest (1949)

$$\text{Flujo en equilibrio} = (\Psi_{\text{suelo}} - \Psi_{\text{sup. Raíz}}) / r_{\text{suelo}} = (\Psi_{\text{sup.raíz}} - \Psi_{\text{xilema raíz}}) / r_{\text{raíz}} = (\Psi_{\text{xilema .raíz}} - \Psi_{\text{hoja}}) / (r_{\text{xilema}} + r_{\text{hoja}}) = (\Psi_{\text{hoja}} - \Psi_{\text{aire}}) / (r_{\text{hoja}} - r_{\text{aire}}).$$

Problemas del modelo:

- 1.- Supone equilibrio (más apropiado secuencia de cuasi equilibrios).
- 2.- Supone resistencias constantes
- 3.- El agua se mueve en forma líquida en el suelo y en la planta ($J_v \propto \Delta \Psi$), pero el flujo de vapor es $\propto \Delta e$, donde Δe es la diferencia de presión de vapor, DPV)

- Diagrama simplificado del movimiento de agua a través del CSPA. Muestra resistencias y condensadores.

* factores que afectan la absorción de agua por las raíces.

- eficiencia del sistema radicular en la absorción.

- movimiento radial del agua en las raíces.

+ resistencias al movimiento de agua en el sistema Suelo-Planta.

- resistencias del suelo versus resistencia radicular.

- resistencia dentro de la planta.

- cambio de resistencia con cambio en la tasa de flujo de agua.

- enfermedades de las raíces.

- factores ambientales

- disponibilidad de agua en el suelo.

- concentración y composición de la solución del suelo.

- aireación de las raíces.

- temperatura.

- Capacitancia (parénquima, anuales pueden perder 25-30% de PF por transpiración y se recuperan de noche).

* Salida de agua desde las raíces y levantamiento hidráulico (hidraulic lift).

LEER:

Kramer P.J. y J.S. Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego. Capítulo 6.

León M y F.A. Squeo (2003) Levantamiento hidráulico: la raíz del asunto. En (F Bozinovic y HM Cabrera, eds): Fisiología Ecológica y Evolutiva en Animales y Plantas.

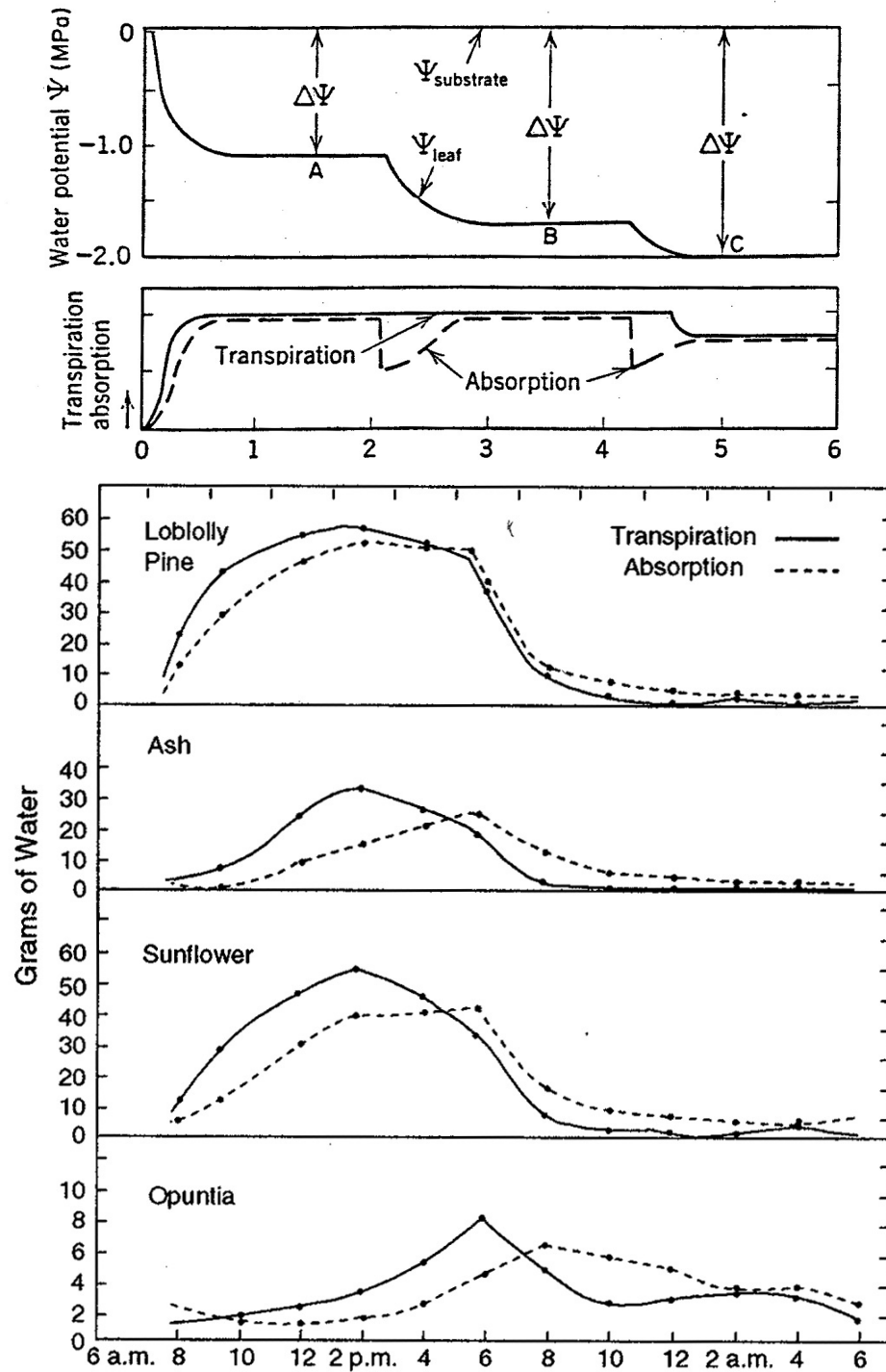


Figure 6.1 The lag of absorption behind transpiration on a hot summer day for four different kinds of plants growing in soil supplied with water by an autoirrigator system that permitted measurement of both water loss and water uptake. Note the evening maximum in transpiration of *Opuntia*, which is a CAM plant, and the midday decrease in sunflower, probably caused by a temporary water deficit and partial closure of stomata. From Kramer (1983), after Kramer (1937).

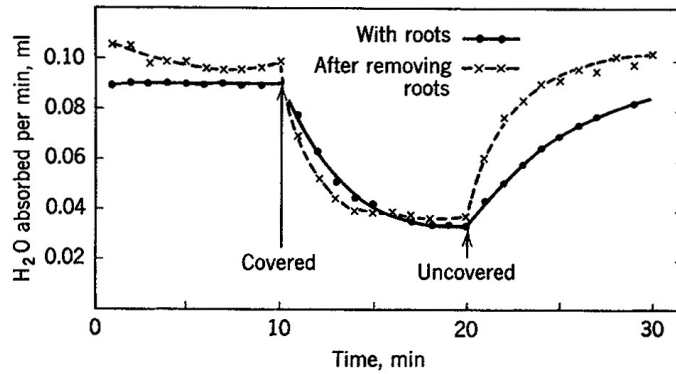


Figure 6.2 Removal of roots decreases the lag of absorption behind transpiration for sunflower plants in a dilute nutrient solution. Absorption of intact plants was measured for 10 min. The shoots were then covered for 10 min to reduce transpiration and uncovered for another 10 min. The root systems were then removed and the experiment was repeated. From Kramer (1983), after Kramer (1938).

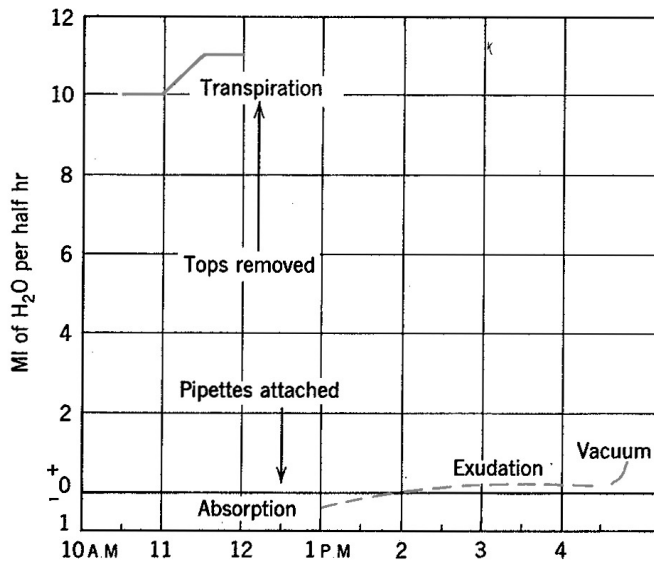


Figure 6.3 The gradual change from absorption to exudation of root systems following the removal of shoots of tomato plants growing in soil at field capacity. Because of a water deficit in the transpiring plants and possibly in the soil immediately surrounding the roots, the roots absorbed water through the stumps for over an hour after the removal of shoots. The maximum rate of exudation was much lower than the rate of transpiration and was increased by application of a vacuum of 64 cm Hg. From Kramer (1983), after Kramer (1939).

Tabla. Potenciales hídricos relativos en suelo, corteza de la raíz, y savia del xilema de plantas transpirando rápido y lento. Suelo cerca de la capacidad de campo.

Componente del Ψ	Suelo	Transpiración Lenta		Transpiración Rápida	
		células (raíz)	xilema	células (raíz)	xilema
Ψ_{π}	-0.01	-0.5	-0.2	-0.5	-0.05
Ψ_m	-0.02	-	-	-	-
Ψ_p	0.0	+0.4	+0.05	+0.1	-0.5
Ψ_{total}	-0.03	-0.1	-0.15	-0.4	-0.55

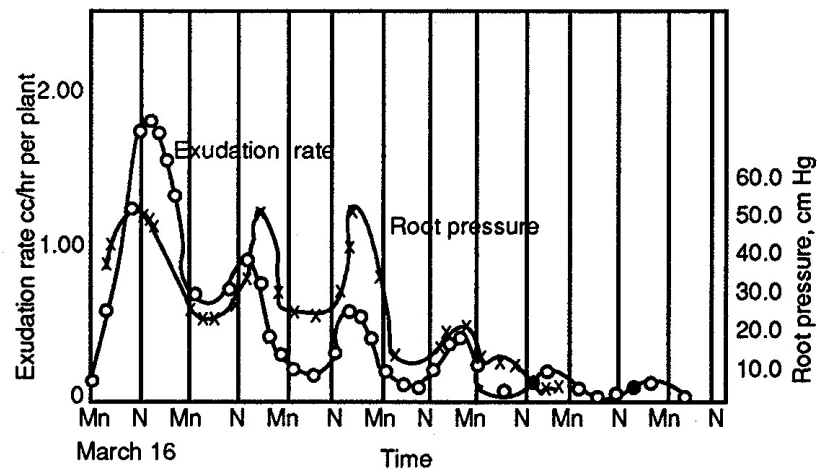


Figure 6.4 Diurnal variation in volume of exudation and root pressure of sunflower plants kept at a constant temperature in half-strength Hoagland solution. From Kramer (1969), after Vaadia (1960).



Glutación. Gotas de agua grutada en la mañana temprana en las hojas producto de la presión radical. Notese las gotas de agua en el borde de las hojas

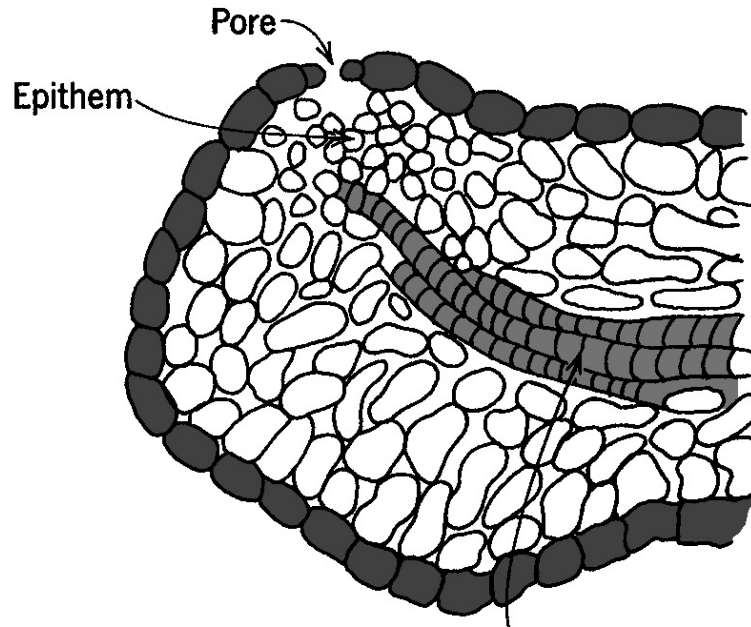


Figure 6.6 Diagram of a hydathode showing a pore, the loose mass of parenchyma cells termed the epithem, and the termination of the xylem. Hydathodes resemble stomata with nonfunctional guard cells and usually occur along margins and at tips of leaves. From Kramer (1983).

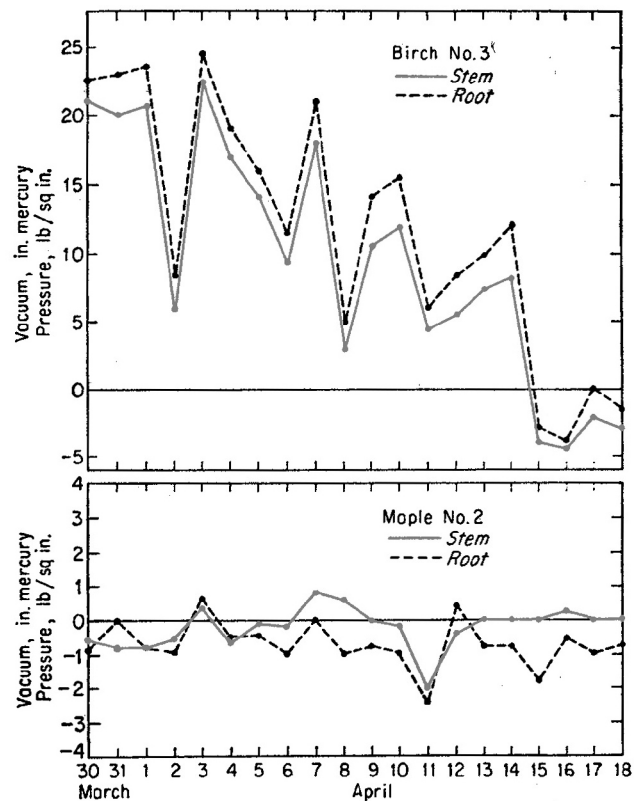


Figure 6.7 Simultaneous measurements of root and stem pressure in river birch and red maple. In birch, root pressure always exceeded stem pressure and the two change simultaneously. In maple, root pressure was usually negative even when positive pressure existed in the stems. Measurements were made on trees in a bottomland forest. From Kramer and Kozlowski (1979).

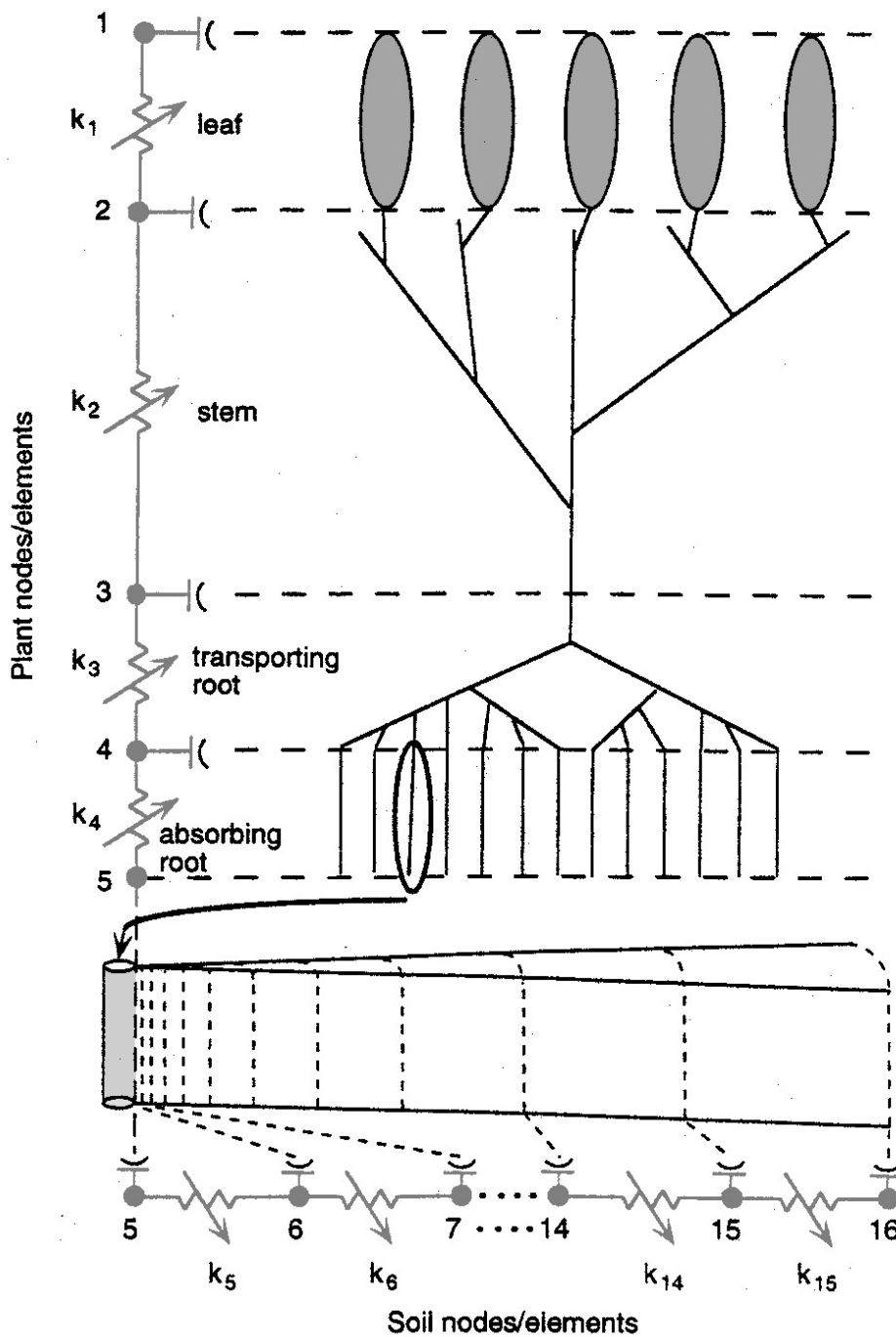


Figure 2. Model organization showing division of the soil-plant hydraulic continuum into 16 nodes and 15 elements. Element conductance is symbolized as variable electrical resistance. Nodes exchange water with a volume of plant or soil. Shoot and root branching was represented by the series conductance of hydraulically equivalent units (k_1 : leaves, k_2 : shoots, k_3 :

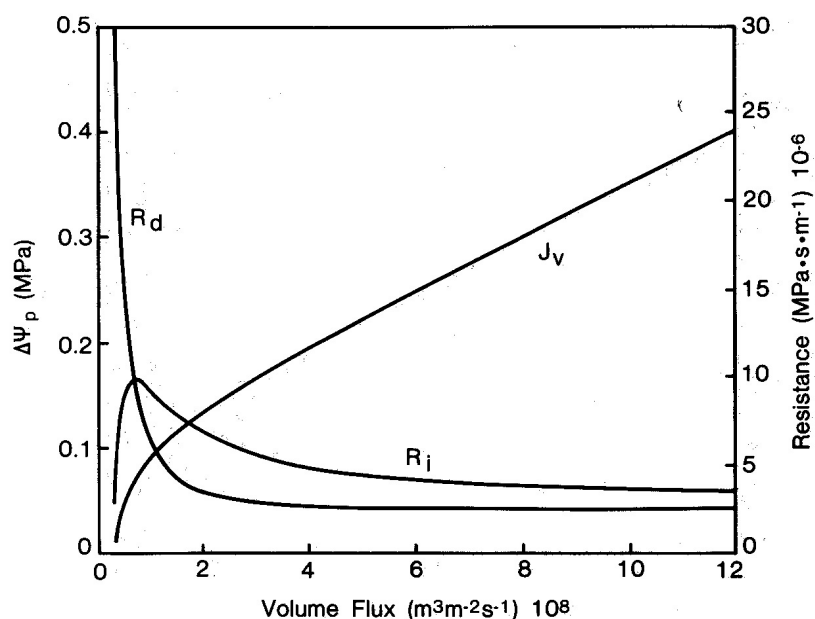


Figure 9.1. Total volume flux and instantaneous and differential resistance functions for a typical *Phaseolus* root system. $L_p = 4 \times 10^{-7} \text{ m s}^{-1} \text{ MPa}^{-1}$; $J_s^* = 1.5 \times 10^{-6} \text{ mol m}^{-2} \text{ s}^{-1}$; $\omega = 1 \times 10^{-6} \text{ mol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$; $\sigma = 0.97$; $\Pi^o = 0.11 \text{ MPa}$.

Table 6.1 Relative Permeabilities of Grape Roots of Various Ages to Water and ^{32}P

Zone and condition of roots	Relative permeabilities	
	Water	^{32}P
Roots of current season (growing)		
A. Terminal 8 cm, elongating, unbranched, unsuberized	1	1
B. Unsuberized, bearing elongating branches (dormant)	155	75
C. Main axis and branches dormant and partially suberized before elongation is completed	545	320
D. Main axis and branches dormant and partially suberized	65	35
Roots of preceding seasons (segments bearing branches)		
E. Heavily suberized main axis with many short suberized branches	0.2	0.4
F. Heavily suberized, thick bark, and relatively small xylem cylinder		
Intact	0.2	0.02
Decorticated	290.0	140.00

Note. Measurements were taken under a pressure gradient of about 66 KPa.

^aFrom Queen (1967).

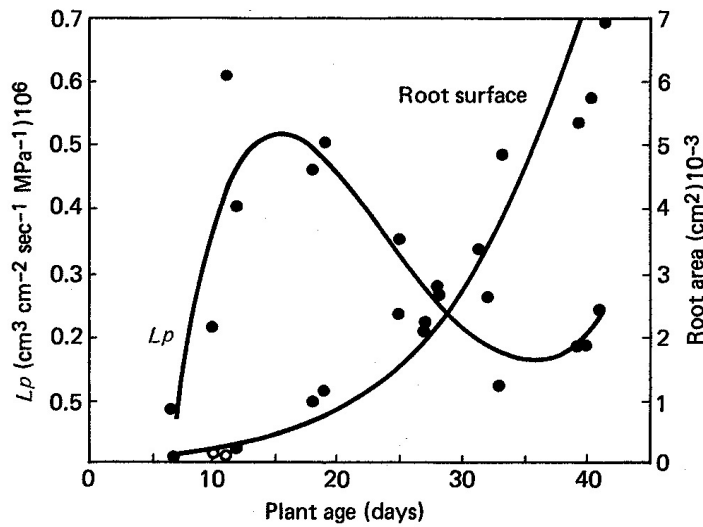


Figure 6.8 Changes in surface area and average hydraulic conductance (L_p) of the root system of growing seedlings of bean (*Phaseolus vulgaris*). While root surface increased steadily with time, the average hydraulic conductance first increased, then decreased over time, probably because of changes in the proportion of the root system in various stages of maturation. From Kramer (1983), after Fiscus and Markhart (1979).

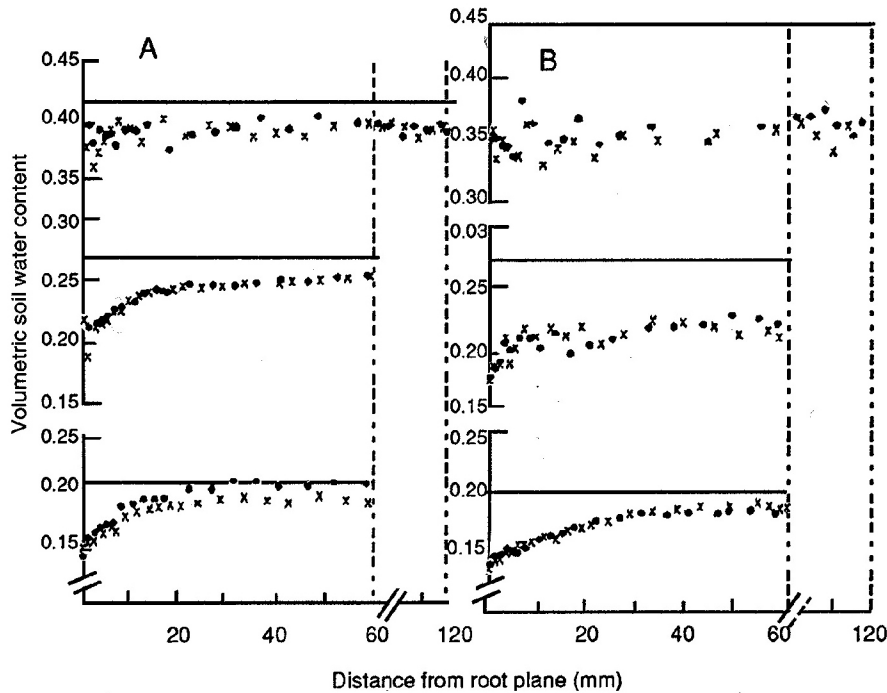
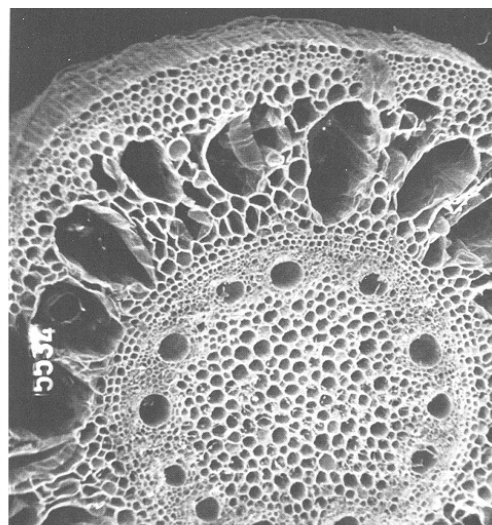
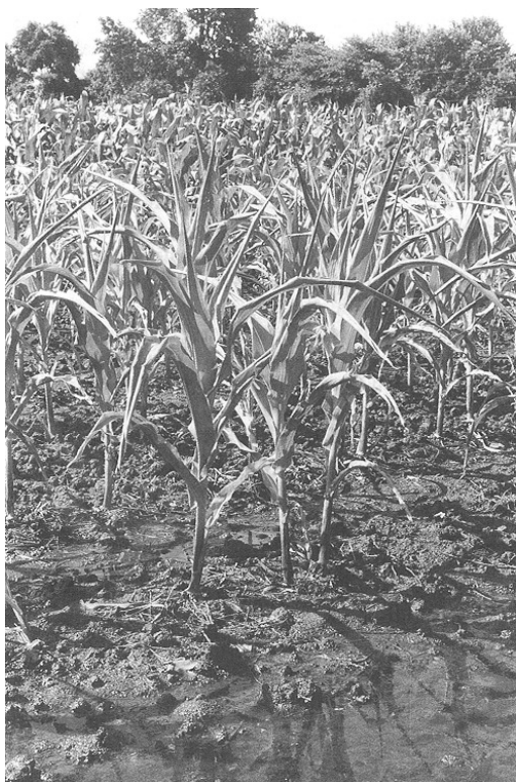


Figure 6.9 A decrease in soil water content near a mat of onion roots attached to transpiring shoots after 2.5 days (A) and 6 days (B). The roots were in sandy soil which initially contained 42–45% (upper curves), 27% (middle curves), or 20% (lower curves) water. The two curves in each part of the figure give the moisture content on opposite sides of the root mat. Readers are referred to the original paper for details. After Dunham and Nye (1973).



Efecto Inundación

Figure 6.10 Wilted maize in a flooded field. Water is standing between the rows which were flooded for 3 weeks. Photograph by J. S. Boyer.

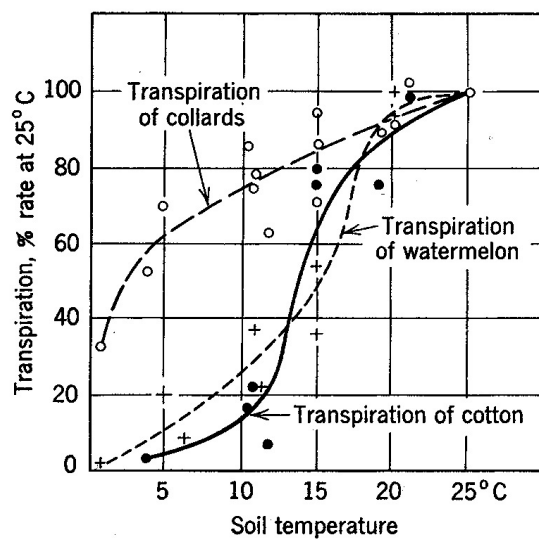


Figure 6.11 Difference in effects of low soil temperature on absorption of water by cool season (collards) and warm season plants (cotton and watermelon), as measured by rate of transpiration. From Kramer (1983), after Kramer (1942).

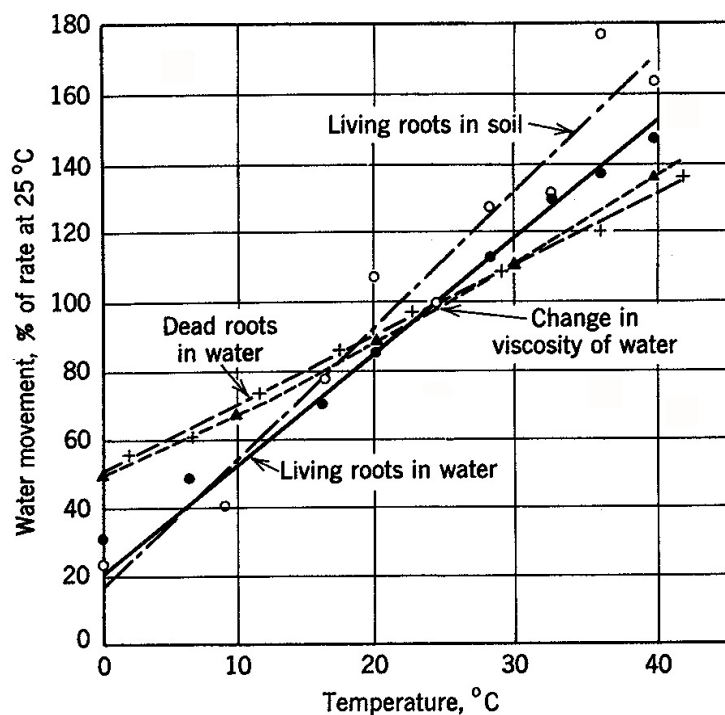


Figure 6.12 Water movement through living and dead root systems in water subjected to a vacuum of about 0.08 MPa for 1 hr. A different set of plants of identical past treatment was used for each temperature and the rates are plotted as a percentage of the rates at 25°C. The curve for the viscosity of water is the reciprocal of the viscosity plotted as a percentage of the value at 25°C. Temperature affects water movement through dead roots less than movement through living roots.

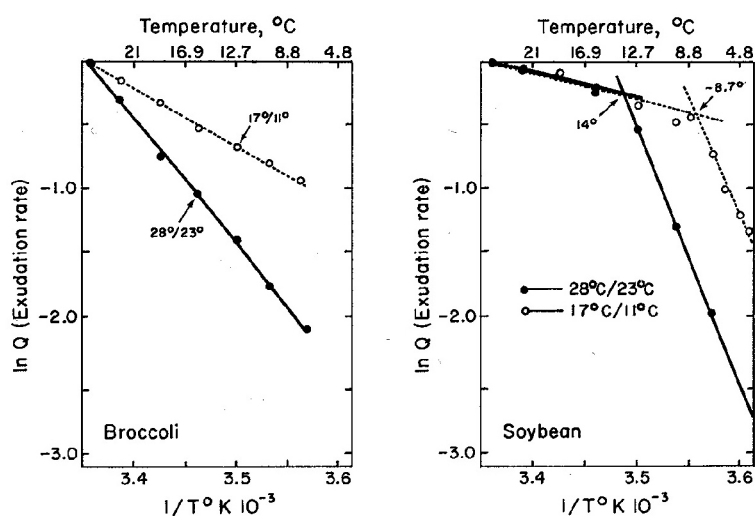


Figure 6.13 Effect of previous growth temperature on the rate of water movement through root systems of broccoli and soybean under a pressure of about 0.05 MPa. Plants were grown at day night temperatures of 28/23°C and 17/11°C, and absorption was reduced much more by cooling in roots grown at the higher temperature. The rates for individual root systems were normalized to the rate at 25°C to permit comparison. The rates are graphed as Arrhenius plots with the natural log of water flow (Q) on the ordinate and the reciprocal of the Kelvin temperature ($1/T$) on the abscissa. Celsius temperatures are given at the top for convenience. Plants of both species grown at low temperatures were less affected by cooling than those grown at higher temperatures. Also, there are sharp changes in slope for soybean. From Kramer (1983), after Markhart *et al.* (1979).

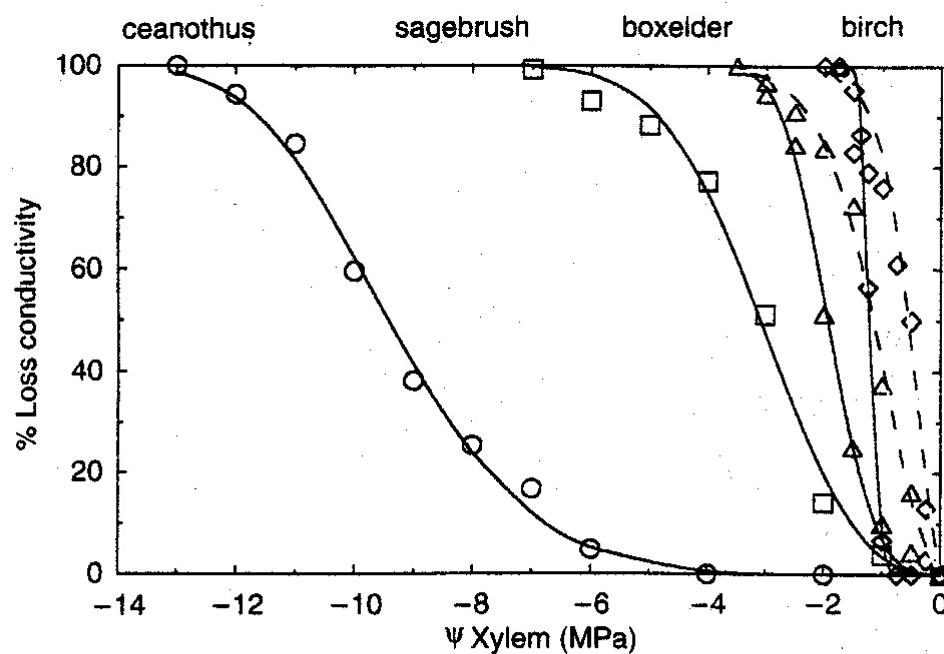


Figure 3. The $K(\Psi)$ functions for plant elements (k_1 to k_4 in Fig. 2) in terms of percentage loss in hydraulic conductivity.

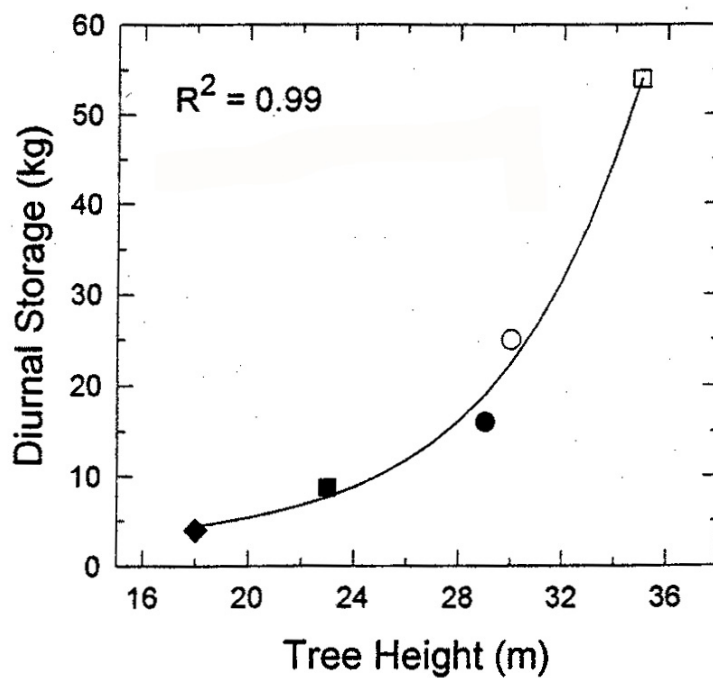


Figure 4. Diurnal water storage in relation to tree height for the five study trees.

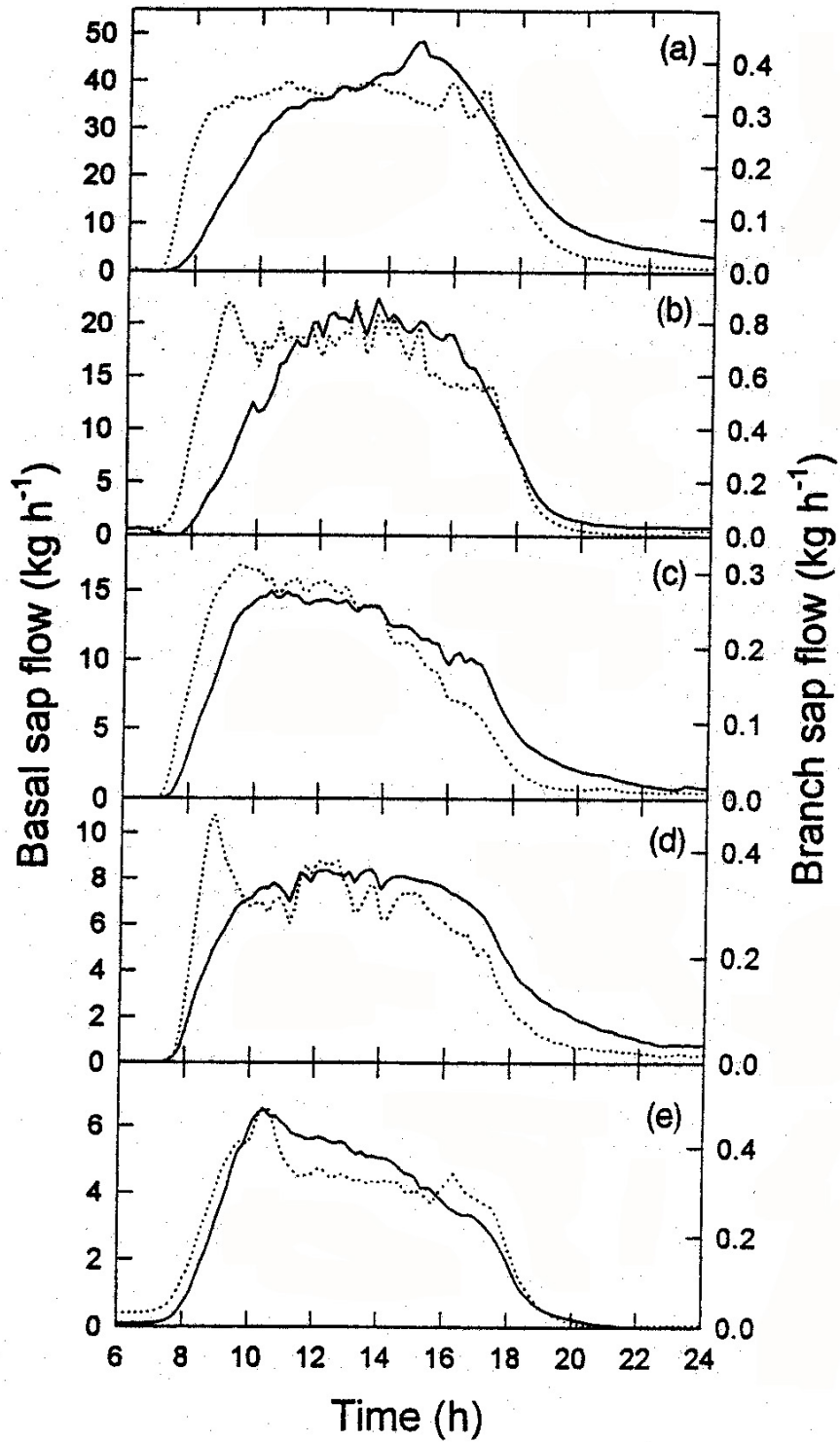


Figure 1. Daily courses of branch sap flow (dotted line) and basal sap flow (solid line) in (a) *Anacardium excelsum*, (b) *Ficus insipida*, (c) *Luehea seemannii*, (d) *Spondias mombin*, and (e)

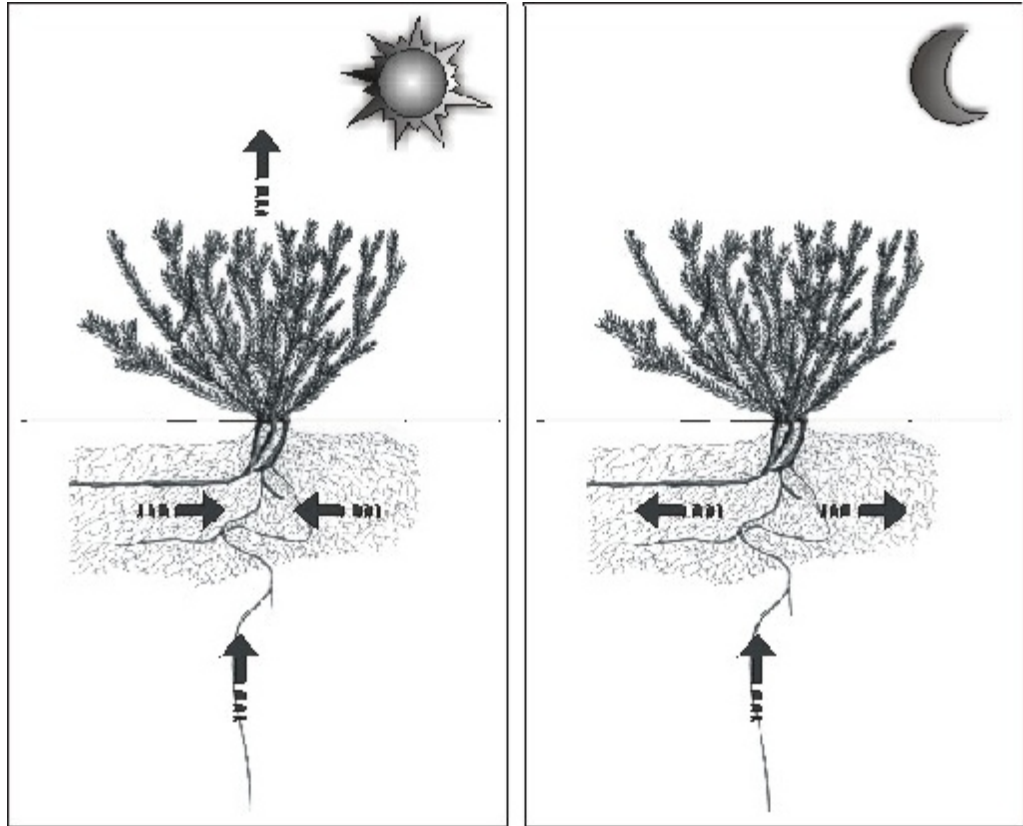


Fig. 1. Patrones del movimiento de agua a través del sistema radicular de un arbusto (*Pleocarpus revolutus*) de acuerdo a la hipótesis del levantamiento hidráulico. Durante el día, las raíces absorben agua desde las profundidades del suelo la cual es transpirada por las hojas. Durante la noche, la transpiración es mínima y los potenciales hídricos de la planta pueden aumentar por sobre los potenciales hídricos del suelo de modo que el principal transporte de agua ocurre desde las capas más profundas del suelo a través de las raíces de la planta a las capas superficiales y secas del suelo. Este proceso nocturno es pasivo, conducido por una diferencia de potencial hídrico a favor del suelo (León & Squeo 2003)

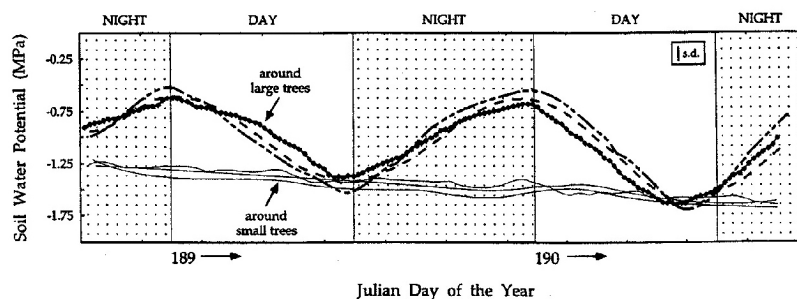


Figure 2. Diel pattern of average soil water potential (MPa) around the root systems of three large (bold lines) and three small (thin lines) *Acer saccharum* trees during the early July drought period (see Figure 1). The day-night change seen around the large trees was due to nighttime soil water recharge caused by hydraulic lift. The standard deviation (s.d.) of the grand mean for all data is shown.

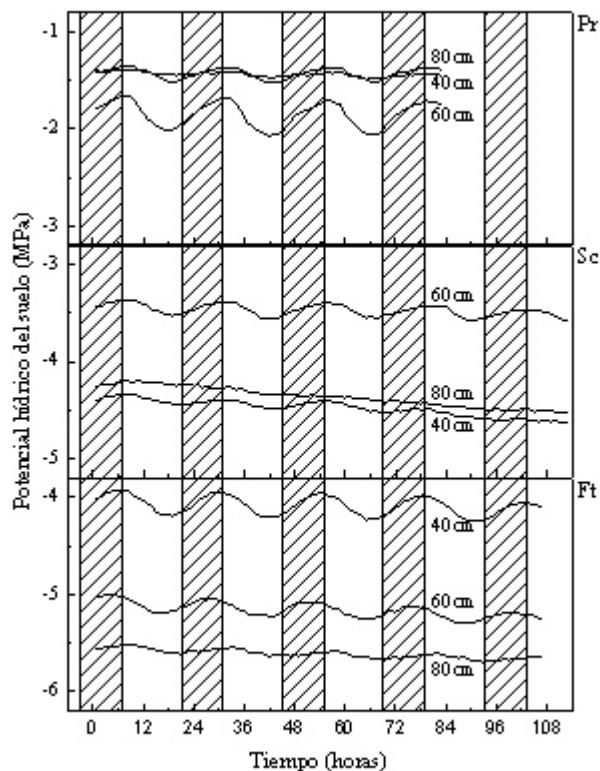


Fig. 2. Fluctuaciones diarias de los potenciales hídricos del suelo en la rizosfera de *Pleocarpus revolutus* (Pr), *Senna cumingii* (Sc) y *Flourensia thurifera* (Ft) durante varios días consecutivos durante enero 2001 en Quebrada El Romeral, IV Región, Chile. La zona achurada representa un ciclo de 24 horas (León & Squeo 2003).

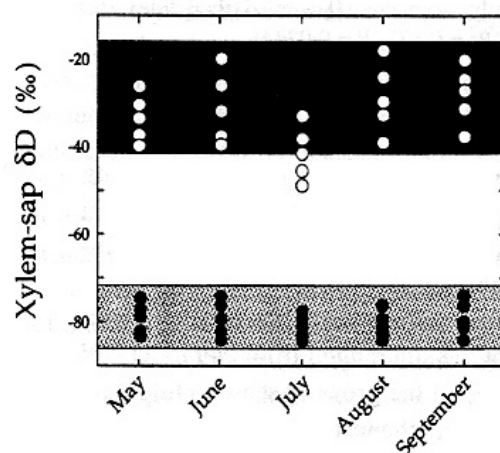


Figure 3. The stable hydrogen isotopic composition (δD , ‰) of water extracted from the xylem sap of small (○) and large (●) trees of *Acer saccharum* at the midpoint of each month during the 1993 growing season. The solid band across the top of the figure represents the range of soil water δD values observed at this site during the period. The stippled band across the bottom of the figure is the range of groundwater δD values observed at this site during the period. As shown, two small trees used some groundwater during the July drought period (see Figure 1).

Unidad II: EL AGUA EN LA PLANTA

Capítulo 6: LA TRANSPIRACIÓN Y LA SUBIDA DE LA SAVIA.

A) La transpiración y la subida de la savia.

- la importancia de la transpiración
- + El proceso de la transpiración
- Evaporación desde superficies
- Fuerzas conductoras y resistencias

Evaporación (E , en $\text{g m}^{-2} \text{s}^{-1}$) = $(C_{\text{agua}} - C_{\text{aire}}) / r_{\text{aire}}$, donde C_{agua} y C_{aire} son las concentraciones de vapor de agua en la superficie que evapora y en el aire, respectivamente (Δe , en g m^{-3}), y r_{aire} es la resistencia a la difusión de vapor de agua de la capa límite (s m^{-1}).

$\Delta C = \Delta e$ es válido sólo a nivel del mar. Δe es independiente de la altura.

$$\text{Transpiración } (T, \text{ en } \text{g m}^{-2} \text{s}^{-1}) = (C_{\text{hoja}} - C_{\text{aire}}) / (r_{\text{hoja}} + r_{\text{aire}})$$

- Relaciones energéticas

Presupuesto energético: $R_n + H \pm E_l + A = 0$, donde R_n es la radiación neta absorbida por las hojas, y consiste en la radiación solar total más la recibida del ambiente, menos la radiación reflejada y menos la radiación re-irradiada; H es el flujo de calor sensible entre la hoja y el ambiente (convección + conducción); E_l es la pérdida de calor latente por evaporación de agua o ganancia por condensación; A es la energía consumida por la fotosíntesis.

- Gradientes de presión de vapor: Humedad Relativa y Absoluta

- Resistencia a la difusión

- conductancia (g , cm/s) = $1 / \text{resistencia } (r, \text{s/cm})$.

- Resistencia foliar: $1/r_{\text{hoja}} = 1/r_c + 1/r_s$ y $r_s = r_i + r_p$, donde r_c , r_s , r_i , r_p , son las resistencias cuticulares (c), estomáticas (s), de los espacios intercelulares (i) y de los poros estomáticos (p), respectivamente.

- Resistencias de la capa límite (externa)

* Otros factores que afectan la transpiración

- hojas: temperatura foliar y presupuesto energético, área foliar, proporción raíz/tallo, tamaño y forma de las hojas, orientación de las hojas, características de la superficie foliar, estructura de la hoja, estomas, residuos sobre las hojas.
- enfermedades, ruptura de la cutícula, daño a raíces.
- filotaxia.

* Efecto de la raíz sobre la transpiración.

- Control estomático sobre la transpiración y control de la raíz sobre la absorción (e indirectamente sobre la apertura estomática)
- Control químico (ABA) e hidráulico de la raíz sobre la transpiración (se recomienda leer Tardieu y Davies (1993)).

* Resistencias durante el movimiento de agua dentro de la planta

- resistencia radial al mov. del agua (corteza, mesófilo) es $\gg$ por unidad de distancia que la resistencia al mov. longitudinal por xilema.
- tasa de absorción = transpiración = $0,01 \text{ cm/hr}$, flujo xilemático = 1000 cm/hr .

- tasa de conducción en algunas especies (coníferas 2,5-12 cm/h, Betula (30 cm/hr, Algodón 80-110 cm/h, Quercus 275-600 cm/hr, casos extremos 2500 cm/hr).

* Importancia relativa de varias resistencias

Especies	Resistencias (%)			Fuente
	r raíz	r tallo	r hojas	
Girasol	52	13.5	34.5	Jensen et al. 1961
Tomate	54.3	13	32.6	Jensen et al. 1961
Maíz	50-70	15-25	15-30	Neumann et al. 1974
Girasol	70	8	20	Neumann et al. 1974

- r suelo y r suelo-raíz (deshidratación causa reducción de zona de contacto)
 - difusión por vapor es muy lenta comparada con una película líquida.
 - r flujo longitudinal.

* Variación en r raíz.

- edad y desarrollo; tasa de flujo (aumento del flujo disminuye la r raíz); deshidratación (crecimiento de la raíz + alteración de la permeabilidad); cambios diurnos; interacción raíz-tallo

* Cavitación

- Daño en el sistema conductor
 - Curvas de vulnerabilidad a la cavitación

* Medidas de la transpiración

- método gravimétrico
 - método rama-cortada (gravimétrico)
 - métodos volumétricos (potómetro)
 - pérdida de vapor de agua - resistencia estomática (porómetro)
 - velocidad de flujo de savia (pulso de calor)
 - tasas de transpiración
 - evapotranspiración a nivel comunitario.

LEER:

Kramer P.J. y J.S. Boyer (1995) Water Relations of Plants and Soils. Academic Press, San Diego. Capítulo 7.

Salisbury F.B. y C.W. Ross (1994) Fisiología Vegetal. Grupo Editorial Iberoamérica, S.A., México. Capítulo 4.

Table 7.1 Relative Water Losses by Transpiration and Evaporation from an Illinois Cornfield during the Period from Mid-June to Early September

Year	Total evapo- transpiration from uncovered plot (cm)	Transpiration from covered plot (cm)	Transpiration as percentage of evapotran- spiration	Total precipitation (cm)	Excess of evapotranspiration over rainfall (cm)
1954	32.25	16.5	51%	18.5	13.75
1955	34.50	17.5	51%	23.0	11.50
1957	33.75	15.1	45%	24.0	9.75

^aFrom Peters and Russell (1959).

Table 7.2 Amounts of Water Lost in Various Ways by a North Carolina Watershed Covered with a Deciduous Forest (1940–1941) and the Increase in Runoff Which Followed Cutting of All Woody Vegetation and Elimination of Transpiration (1941–1942)^a

Process	1940–1941	1941–1942
Precipitation	158.0	158.4
Interception	16.6	9.5
Runoff	53.4	93.0
Soil storage	–0.4	9.7
Evaporation	39.7	46.0
Transpiration	48.7	00.0

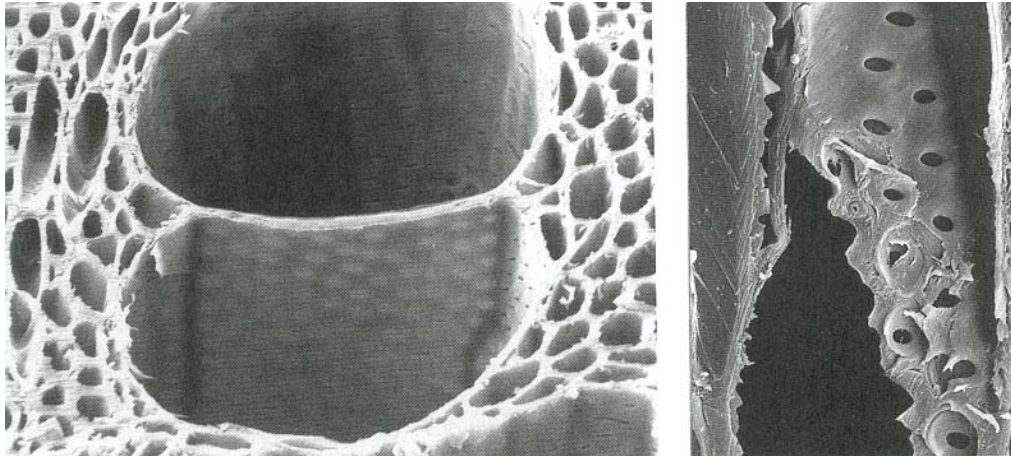
Note. Data in centimeters.

^aFrom Hoover (1944).

Table 7.3 Water Requirement or Transpiration Ratio in Grams of Water per Gram Dry Matter for the Years 1911–1917 at Akron, Colorado, and the Evaporation from a Free Water Surface from April to September 1^a

Plant	1911	1912	1913	1914	1915	1916	1917
Alfalfa	1068	657	834	890	695	1047	822
Oats, Burt	639	449	617	615	445	809	636
Barley, Hannchen	527	443	513	501	404	664	522
Wheat, Kubanka	468	394	496	518	405	639	471
Corn, N.W. Dent	368	280	399	368	253	495	346
Millet, Kursk	287	187	286	295	202	367	284
Sorghum, Red Amber	298	239	298	284	303	296	272
Evaporation: April 1 to September 1 (mm)	1239	957	1092	1061	848	1196	1084

^aFrom Miller (1938).

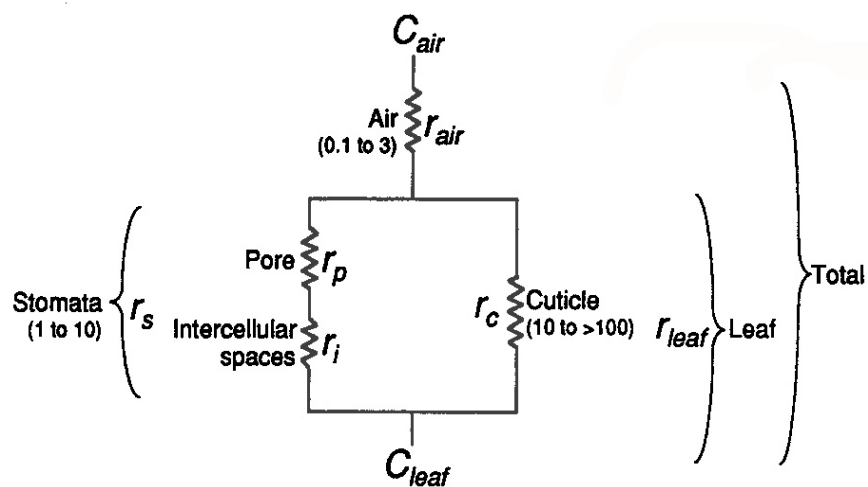


(Izquierda) Vasos xilemáticos de *Eucalyptus marginata* (ver punteaduras)
(Derecha) Punteaduras revordeadas en *Populus nigra*

TABLE 6. Hydraulic conductance of xylem conduits, maximum velocity of water transport through the conduits and xylem diameter for stems of different types of plants.

	Hydraulic conductivity of xylem lumina ($\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$)	Maximum velocity (mm s^{-1})	Vessel diameter μm
Evergreen conifers	5–10	0.3–0.6	<30
Mediterranean sclerophylls	2–10	0.1–0.4	5–70
Deciduous diffuse porous	5–50	0.2–1.7	5–60
Deciduous ring porous	50–300	1.1–12.1	5–150
Herbs	30–60	3–17	
Lianas	300–500	42	200–300

Source: Milburn 1979; Zimmerman & Milburn 1982.



Resistencias a la difusión al vapor de agua en la hoja

Table 7.4 Resistance to Movement of Water Vapor through the Boundary layer (r_a), Stomata (r_s), and Cuticle (r_c) in Leaves of Several Species^a

Species	Resistance to water vapor (sec · cm ⁻¹)		
	r_a	r_s	r_c
<i>Betula verrucosa</i>	0.80	0.92	83
<i>Quercus robur</i>	0.69	6.7	380
<i>Acer platanoides</i>	0.69	4.7	85
<i>Circaea lutetiana</i>	0.61	16.1	90
<i>Lamium galeobdolon</i>	0.73	10.6	37
<i>Helianthus annuus</i>	0.55	0.38	—

^aFrom Holmgren *et al.* (1965).

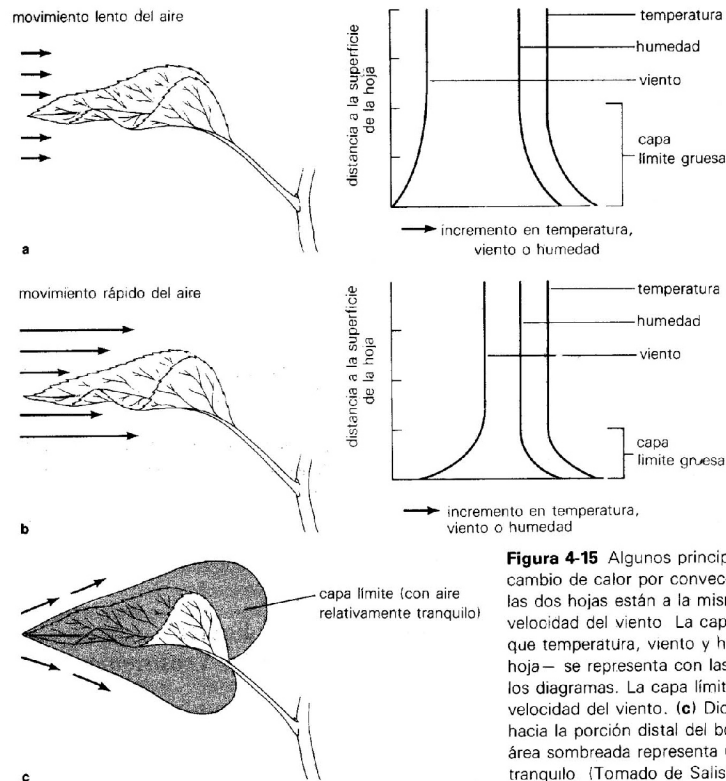


Figura 4-15 Algunos principios de la capa límite y el intercambio de calor por convección. (a) y (b) Se supone que las dos hojas están a la misma temperatura; sólo varía la velocidad del viento. La capa límite —la capa de aire en la que temperatura, viento y humedad son influenciadas por la hoja— se representa con las partes curvas de las líneas en los diagramas. La capa límite se adelgaza al aumentar la velocidad del viento. (c) Dicha capa se hace más gruesa hacia la porción distal del borde de ataque de la hoja. El área sombreada representa una capa de aire relativamente tranquilo. (Tomado de Salisbury, 1979.)

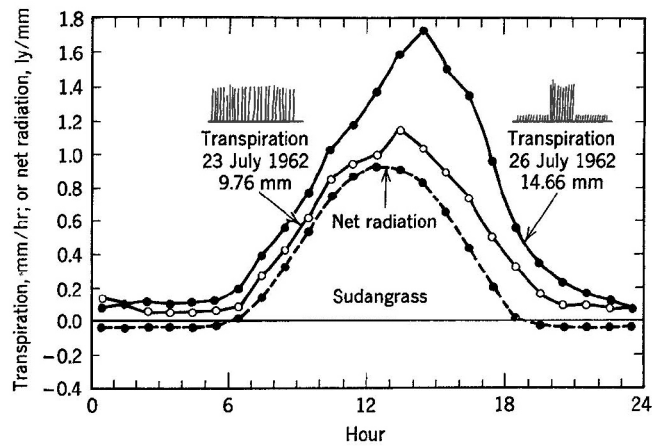
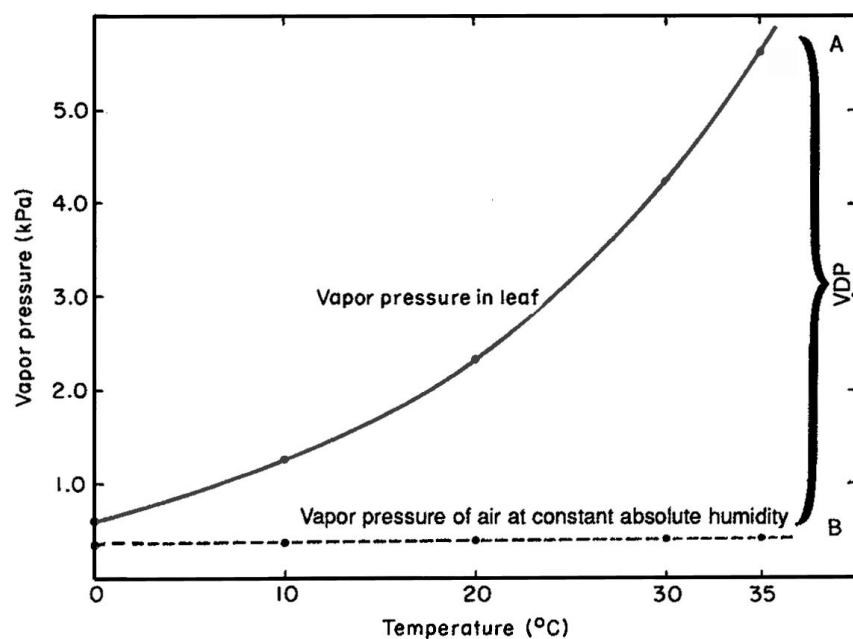


Figure 7.2 The “oasis effect” as shown by the increase in transpiration from a lysimeter in a closed stand of Sudan grass after removal of the surrounding crop, exposing the plants in the lysimeter. Although radiation was similar on the 2 days, additional energy supplied by increased exposure to air movement and advection resulted in a much higher transpiration after the plot was exposed. From Kramer (1983), after Van Bavel *et al.* (1963).

Table 7.5 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% at 30°C^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

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



Effect of Increasing Temperature of Leaf and Air on Vapor Pressure Gradient from Leaf to Air, with Relative Humidity of 80% at 10°C and No Change in Absolute Humidity from that at 10°C

	Leaf and air temperature (°C)		
	10	20	30
Relative humidity of air in %	80	43	30
Vapor pressure at evaporating surface of leaf (kPa)	1.228	2.339	4.246
Vapor pressure in air (kPa)	0.981	1.015	1.051
Vapor pressure gradient from leaf to air (kPa)	0.247	1.324	3.196

Table 7.7 Transpiration Rates per Unit of Leaf Surface and per Seedling of Loblolly Pine and Hardwood Seedlings for the Period August 22–September 2.^a

	Loblolly pine	Yellow poplar	Northern red oak
Transpiration ($\text{g} \cdot \text{day}^{-1} \cdot \text{dm}^{-2}$)	5.08	9.76	12.45
Transpiration ($\text{g} \cdot \text{day}^{-1} \cdot \text{tree}^{-1}$)	106.70	59.10	77.00
Average leaf area per tree (dm^2)	21.00	6.06	6.18
Average height of trees (cm)	34.00	34.00	20.00

^aAverage of six seedlings of each species.

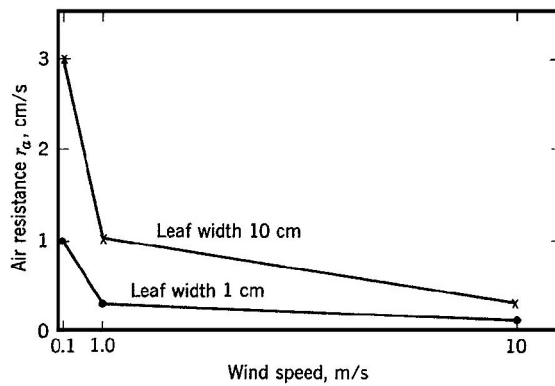
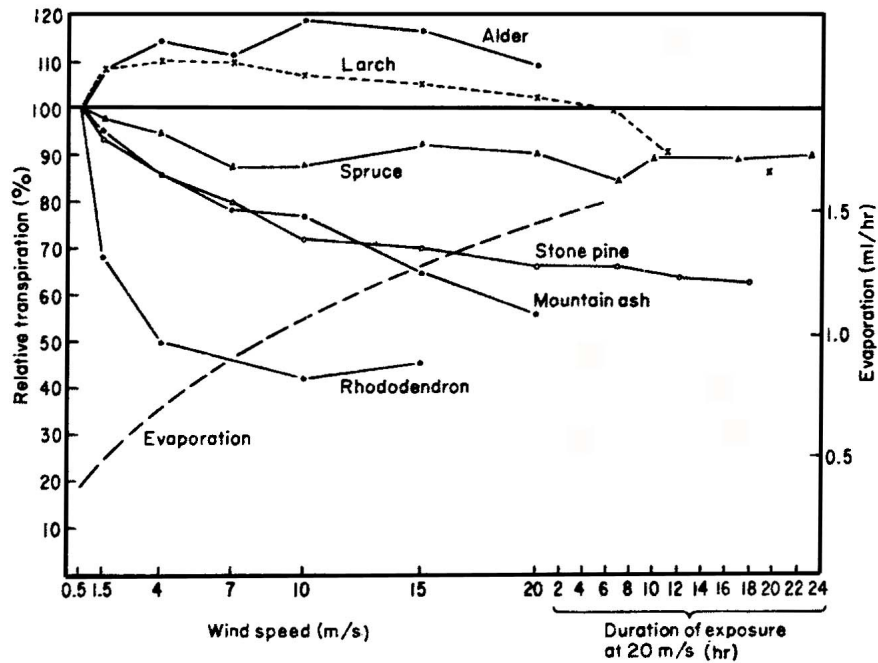


Figure 7.6 Approximate boundary layer resistance at three wind speeds for a cotton leaf 10 cm wide and a grass leaf 1 cm wide. From Kramer (1983), after data of Slatyer (1967).

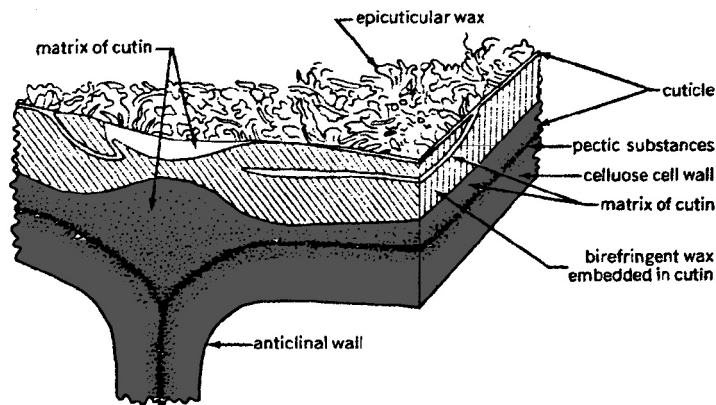


Figure 7.7 Diagram of an upper surface of an epidermal cell of pear leaf, showing cuticle, composed of cutin and wax. The cutin is anchored to the cellulose wall by a layer of pectin. From Kramer (1983), after Norris and Bukovac (1968).

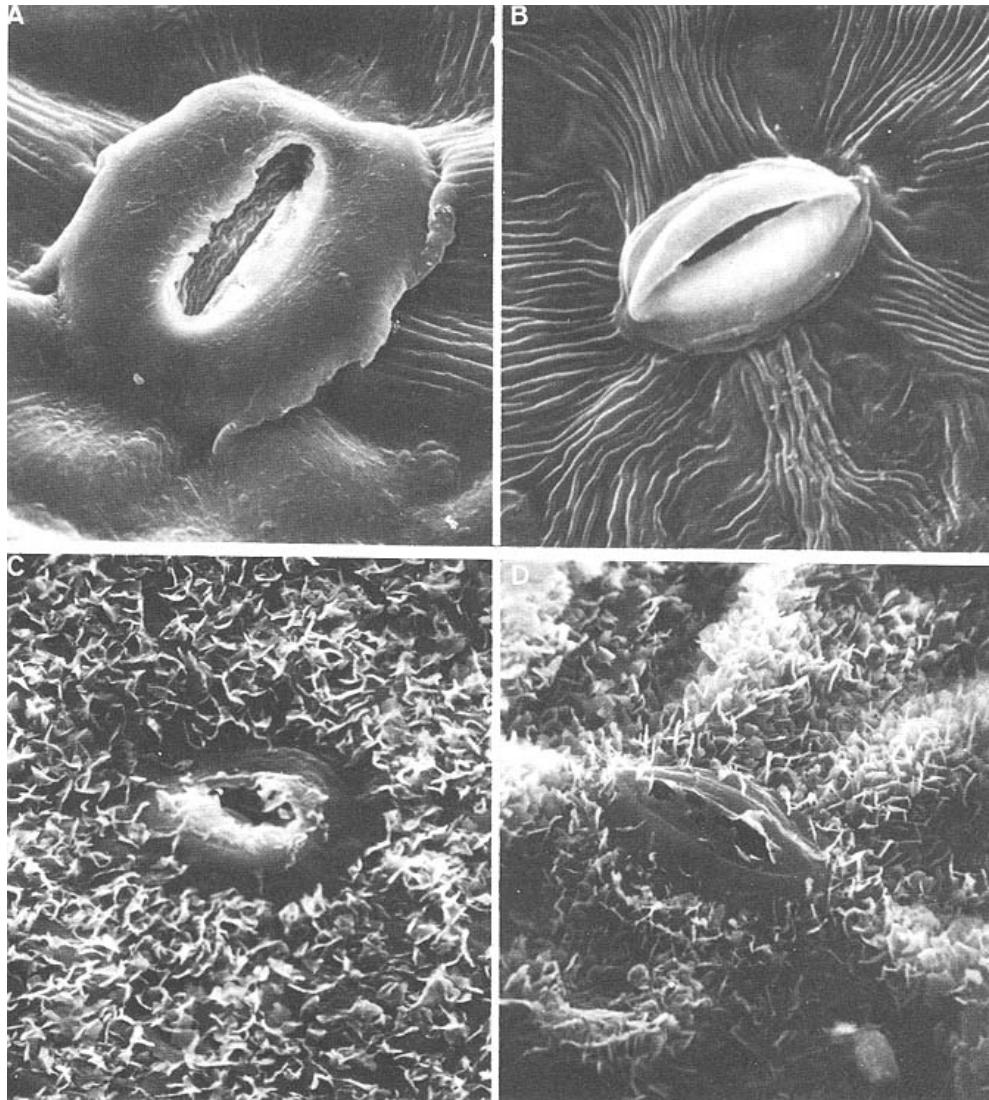


Figure 7.8 Variations in patterns of wax deposited on leaves of four tree species: (A) American elm, (B) white ash, (C) sugar maple, and (D) redbud. Also note differences in appearance of stomata. Photographs by W. J. Davies, from Kramer (1983).

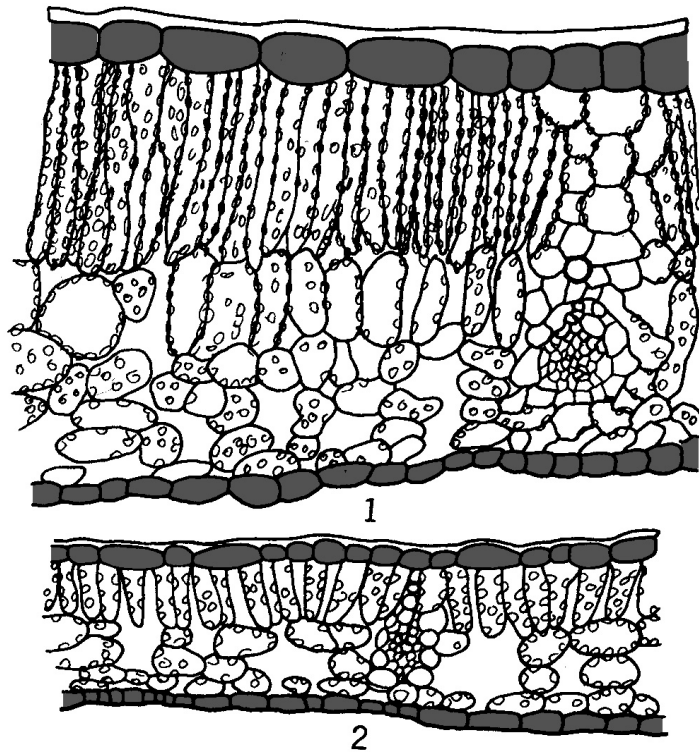


Figure 7.9 Difference in structure of sun leaves from the southern edge (1) and shade leaves from the center of the crown (2) of an isolated sugar maple (*Acer saccharum*). From Kramer (1983), after Weaver and Clements (1938).

Table 7.8 Midsummer Transpiration Rates of Various Species of Trees^{a,b}

Species	Location	Season	Duration (days)	Number of Plants	Average transpiration (g · dm ⁻² · day ⁻¹)
<i>Liriodendron tulipifera</i> ^c	Columbus, OH	August	1	7	10.11
<i>Liriodendron tulipifera</i> ^d	Durham, NC	August	3	4	11.78
<i>Quercus alba</i> ^d	Durham, NC	August	3	4	14.21
<i>Quercus rubra</i> ^d	Durham, NC	August	3	4	12.02
<i>Quercus rubra</i> ^e	Fayette, MO	July	14	6	8.1
<i>Acer saccharum</i> ^e	Fayette, MO	July	14	6	12.2
<i>Acer negundo</i> ^e	Fayette, MO	July	14	6	6.4
<i>Platanus occidentalis</i> ^e	Fayette, MO	July	14	6	8.8
<i>Pinus taeda</i> ^d	Durham, NC	August	3	4	4.65
<i>Clethra alnifolia</i> ^d	Durham, NC	August	3	4	9.73
<i>Ilex glabra</i> ^d	Durham, NC	August	3	4	16.10
<i>Myrica cerifera</i> ^d	Durham, NC	August	3	4	10.80
<i>Gordonia lasianthus</i> ^d	Durham, NC	July	23	4	17.77
<i>Liriodendron tulipifera</i> ^f	Durham, NC	August 26	12	6	9.76
<i>Quercus rubra</i> ^f	Durham, NC	September 2	12	6	12.45
<i>Pinus taeda</i> ^f	Durham, NC	August 26	12	6	5.08
		September 2	12	6	

^aExpressed as grams of water lost per square decimeter of leaf surface per day.

^bAll seedlings were grown in soil near field capacity.

^cFrom Meyer (1932).

^dFrom Caughey (1945).

^eFrom Biswell (1935).

^fFrom Kramer (unpublished).

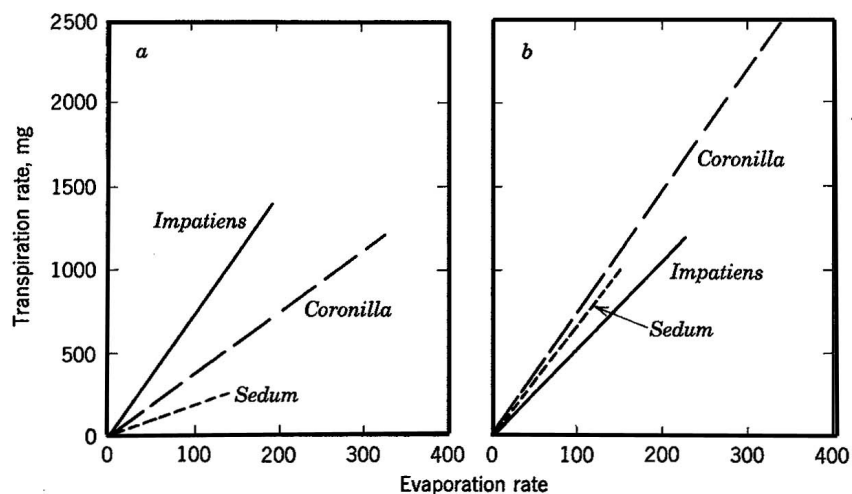


Figure 7.10 Transpiration of three species (*Impatiens noli-tangere*, *Coronilla varia*, and *Sedum maximum*) expressed in (a) milligrams per gram of leaf fresh weight and (b) milligrams per square decimeter of leaf surface. The rate of transpiration is plotted over the rate of evaporation from a filter paper atmometer. The transpiration of *Sedum* varied most with the method used to express it because of its low ratio of surface to mass. Adapted from Pisek and Cartellieri (1932), from Kramer (1983).

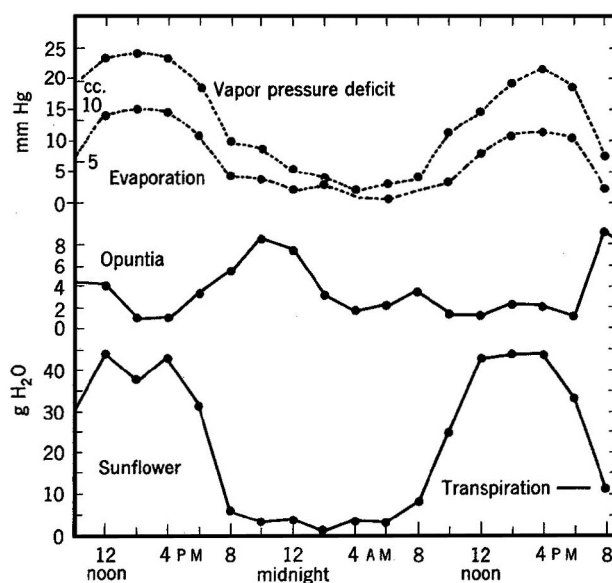


Figure 7.11 Transpiration of sunflower and *Opuntia* plants in soil at field capacity on a hot summer day. The maximum rate of transpiration of *Opuntia* occurred at night, a characteristic of plants with CAM. The early afternoon decrease in the transpiration of sunflower the first day probably resulted from a decrease in turgor and partial closure of stomata. From Kramer (1983), after Kramer (1937).

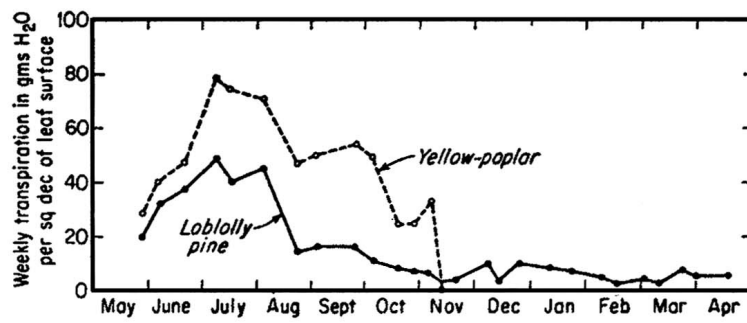


Figure 7.12 Seasonal course of transpiration of potted seedlings of an evergreen and a deciduous species growing outdoors at Durham, North Carolina. From Kramer and Kozlowski (1979).

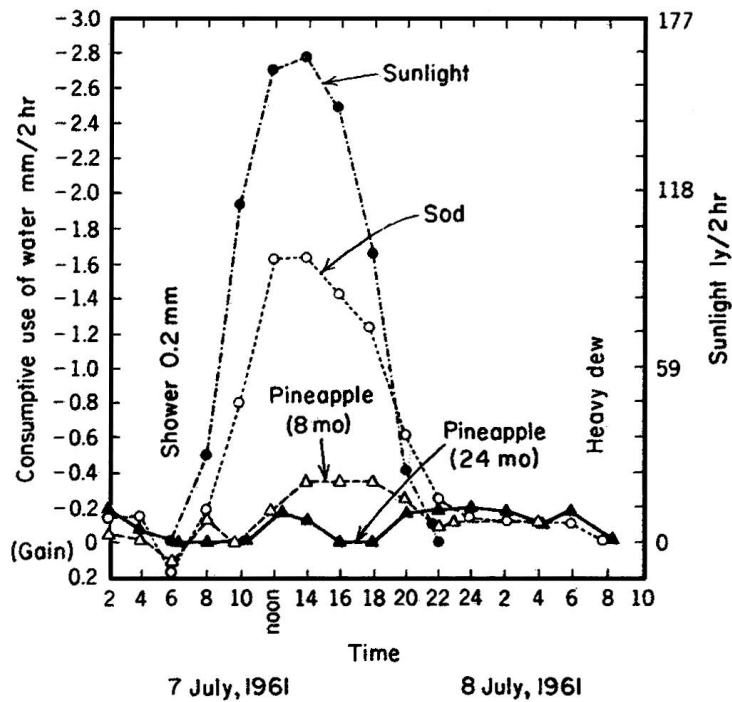


Figure 7.13 Evapotranspiration from a Bermuda grass sod and from stands of pineapple 8 and 24 months after planting. All plants were grown in soil in lysimeters in Hawaii. From Kramer (1983), after Ekern (1965).

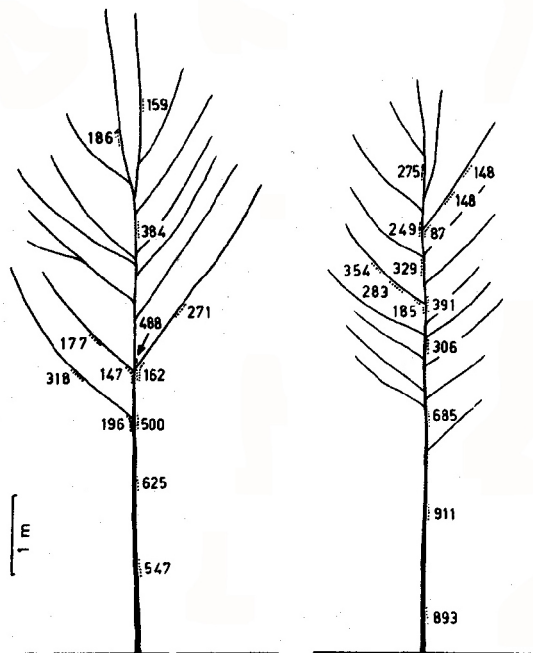


Figure 7.14 Leaf specific conductivity in microliters per hour, per gram fresh weight of leaves supplied, for two paper birch trees (*Betula papyrifera*). Conductivity decreases from lower to upper trunk and in the branches. It also is low when branches are attached to the trunk, as further indicated by the high velocity of sap flow at the point of branch attachment shown in Fig. 7.18. From Kramer (1983), after Zimmermann (1978).

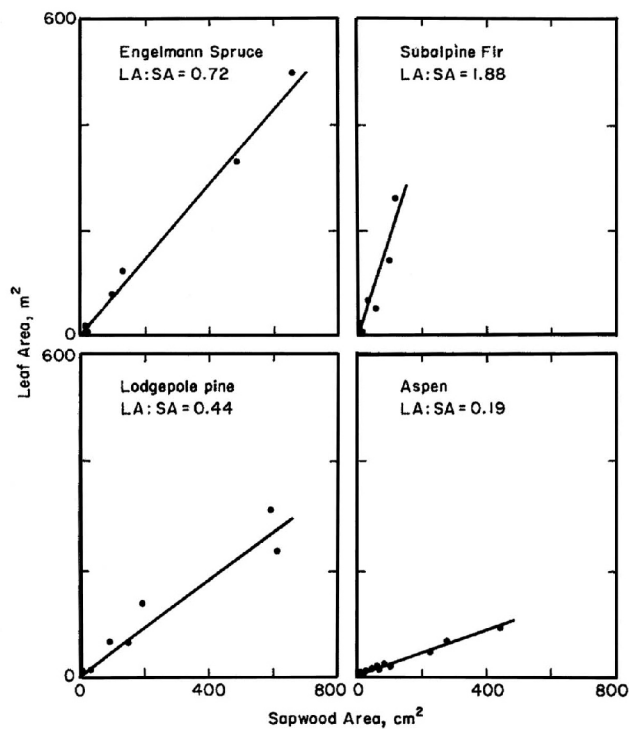


Figure 7.15 Relationship between leaf areas (LA) in square meters and cross-sectional area of sapwood (SA) at 1.37 m above ground for four subalpine forest tree species in Colorado. From Kramer (1983), after Kaufmann and Troendle (1981).

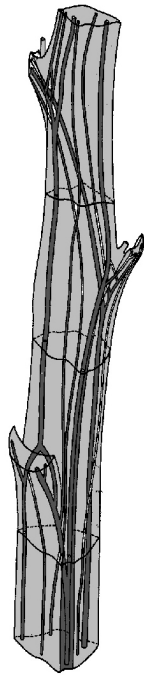


Figure 7.16 Vascular system of a potato stem (*Solanum tuberosum*) showing the complex branching at the nodes. Readers are referred to Dimond (1966) for a study of water flow in tomato stem which have a similar structure. From Kramer (1983), after Eames and MacDaniels (1947).

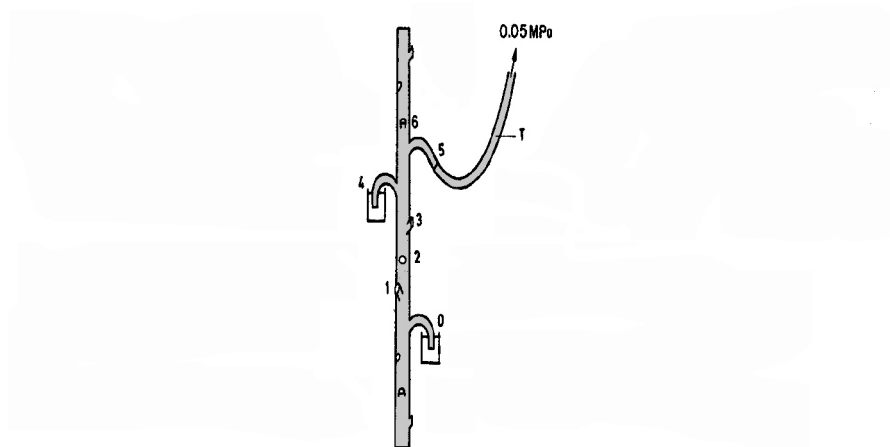


Figure 7.17 Diagram showing leaf attachment on a tobacco plant with 2/5 phyllotaxy. Leaves at positions 0 and 5 are supplied by the same vascular strand whereas leaves at positions 4 and 6 are on different vascular strands. By supplying different dyes to petioles 0 and 4 and removing sap by suction from petiole 5, it was demonstrated that resistance to lateral movement of water from petiole 4 to 5 is much greater than the resistance to longitudinal movement from 0 to 5. From Kramer (1983), after Fiscus *et al.* (1973).

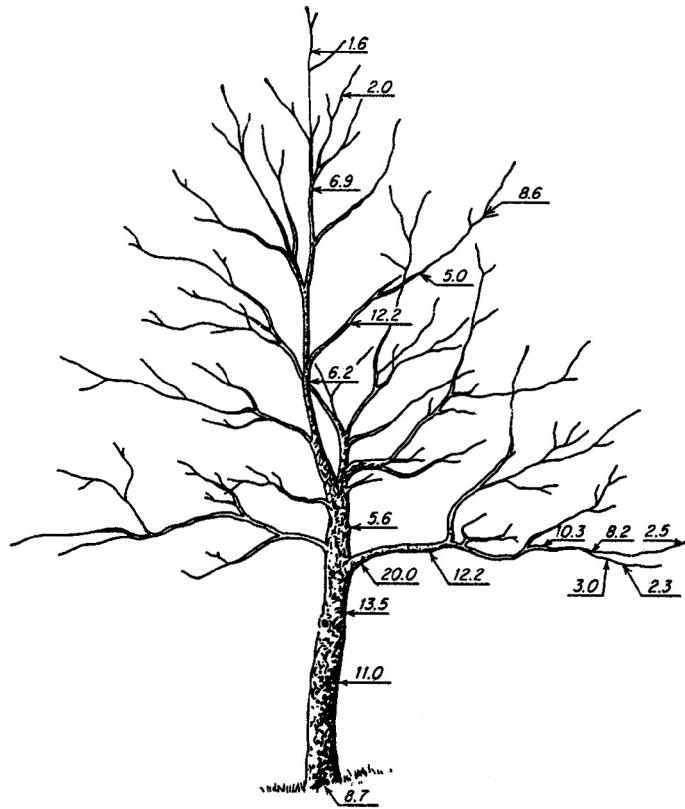


Figure 7.18 Velocity of sap flow in meters per hour in various parts of an oak tree at midday, measured by the thermoelectric method. The rate of flow decreases toward the top because the relative conducting surface (ratio of xylem cross section to leaf area supplied with water) increases toward the top in oak. In birch (see Fig. 7.14) the relative conducting surface decreases toward the top and the velocity of flow increases. From Kramer (1983), after Huber and Schmidt (1937).

Table 7.9 Rates of Water Movement in Xylem Measured by Various Methods^a

Investigator	Method	Material	Velocity (m · hr ⁻¹)
Bloodworth <i>et al.</i> (1956)	Heat pulse	Cotton	0.8–1.1
Greenidge (1958)	Acid fuchsin	<i>Acer saccharum</i>	1.5–4.5
	Acid fuchsin	<i>Ulmus americana</i>	4.3–15.5
Huber and Schmidt (1937)	Heat pulse	Conifers	0.5
	Heat pulse	<i>Liriodendron tulipifera</i>	2.6
	Heat pulse	<i>Quercus pedunculata</i>	43.6
	Heat pulse	<i>Fraxinus excelsior</i>	25.7
Klemm and Klemm (1964)	³² P	<i>Betula verrucosa</i>	± 3.0
Kuntz and Riker (1955)	⁸⁶ Rb	<i>Quercus macrocarpa</i>	27.5–60.0
Moreland (1950)	³² P	<i>Pinus taeda</i>	1.2
Owston <i>et al.</i> (1972)	³² P	<i>Pinus contorta</i>	0.1–0.8
Decker and Skau (1964)	Heat pulse	<i>Juniperus osteosperma</i>	0.25

^aKramer and Kozlowski (1979).

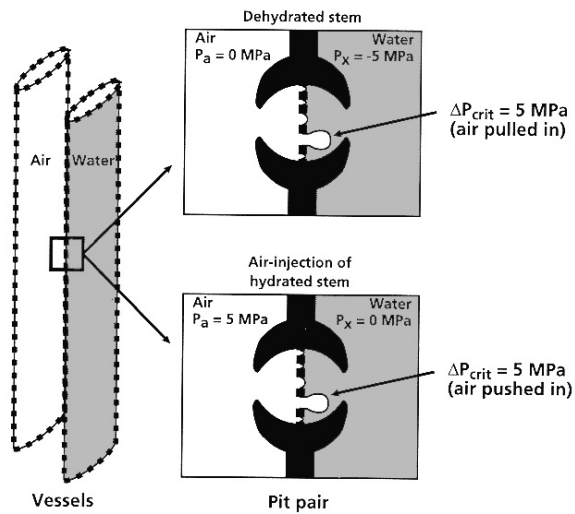


TABLE 7. Typical ratios of foliage area (A_f) to sapwood area (A_s) of conifers.

Species	Common name	$A_f:A_s$ ($m^2 m^{-2}$)
Mesic environments		
<i>Abies balsamea</i>	Balsam fir	6700–7100
<i>A. amabilis</i>	Pacific silver fir	6300
<i>A. grandis</i>	Grand fir	5100
<i>A. lasiocarpa</i>	Subalpine fir	7500
<i>Larix occidentalis</i>	Western larch	5000
<i>Picea abies</i>	Norway spruce	4600
<i>P. engelmanni</i>	Engelmann spruce	2900–3400
<i>P. sitchensis</i>	Sitka spruce	4500
<i>Pseudotsuga menziesii</i>	Douglas fir	3800–7000
<i>Tsuga heterophylla</i>	Western hemlock	4600
<i>T. mertensiana</i>	Mountain hemlock	1600
Average		5000 $\pm$ 500
Xeric environments		
<i>Juniperus monosperma</i>	One-seeded juniper	800
<i>J. occidentalis</i>	Western juniper	1800
<i>Pinus contorta</i>	Lodgepole pine	1100–3000
<i>P. edulis</i>	Pinyon pine	2500
<i>P. nigra</i>	Austrian pine	1500
<i>P. ponderosa</i>	Ponderosa pine	1900
<i>P. sylvestris</i>	Scotch pine	1400
<i>P. taeda</i>	Loblolly pine	1300–3000
Average		1800 $\pm$ 200

Source: Margolis et al. 1995.

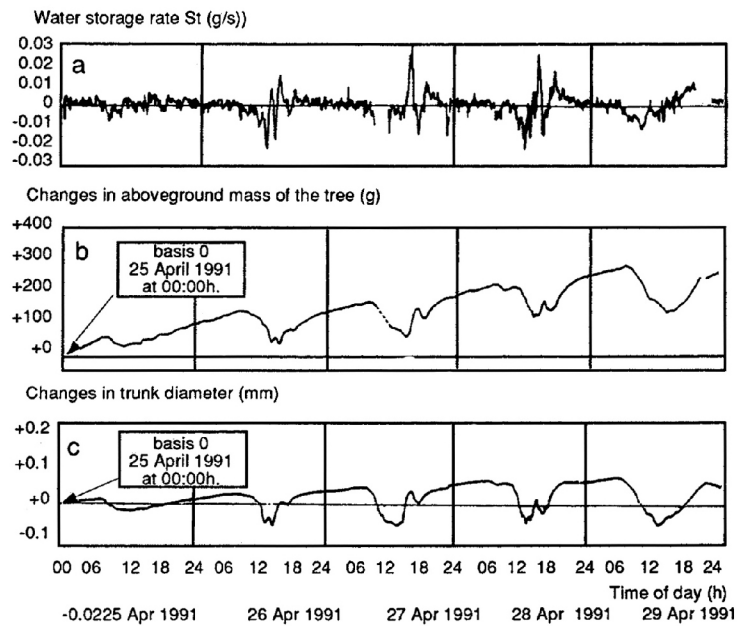


Figure 7.20 Diurnal changes in water content, stem mass, and stem diameter of a 5-year-old peach tree. (a) Gain or loss in stem water in $\text{g} \cdot \text{sec}^{-1}$. Changes in shoot mass (b) and in trunk diameter (c). The first day was cloudy, the others were sunny. Note the good correlation among loss of water, afternoon loss of shoot mass, and stem diameter. From Simonneau *et al.* (1993).

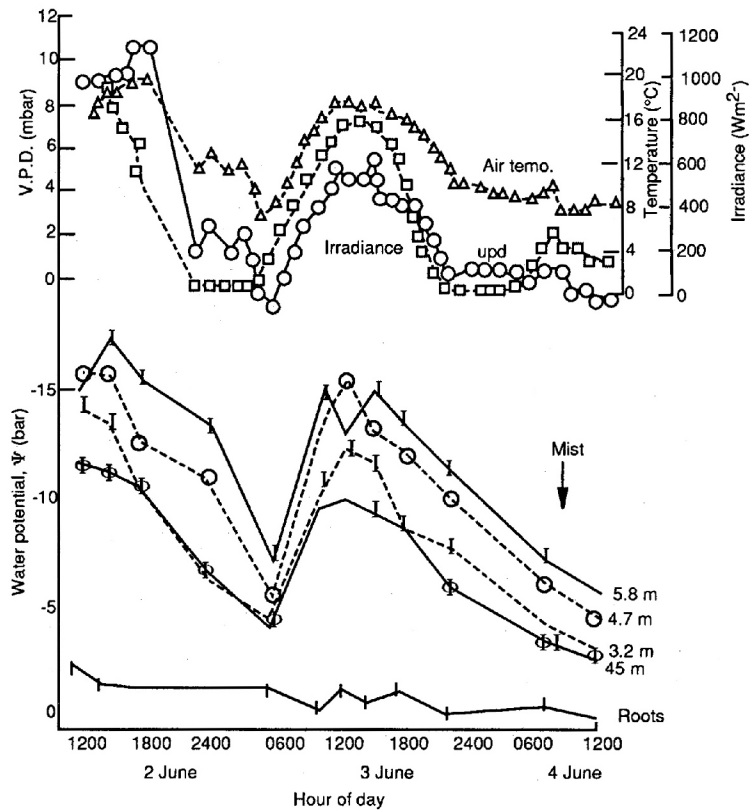


Figure 7.19 Diurnal variation in water potential at four heights on a Sitka spruce tree on a sunny day. The heights are at the point of attachment of the branches on which water potentials were measured with a pressure chamber. From Hellkvist *et al.* (1974), by permission of the authors.

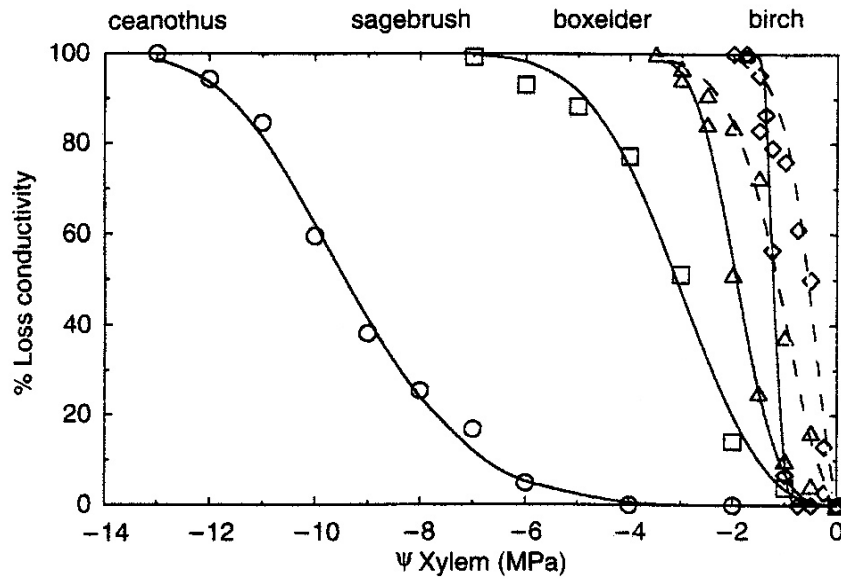


Figure 3. The $K(\Psi)$ functions for plant elements (k_1 to k_4 in Fig. 2) in terms of percentage loss in hydraulic conductivity.

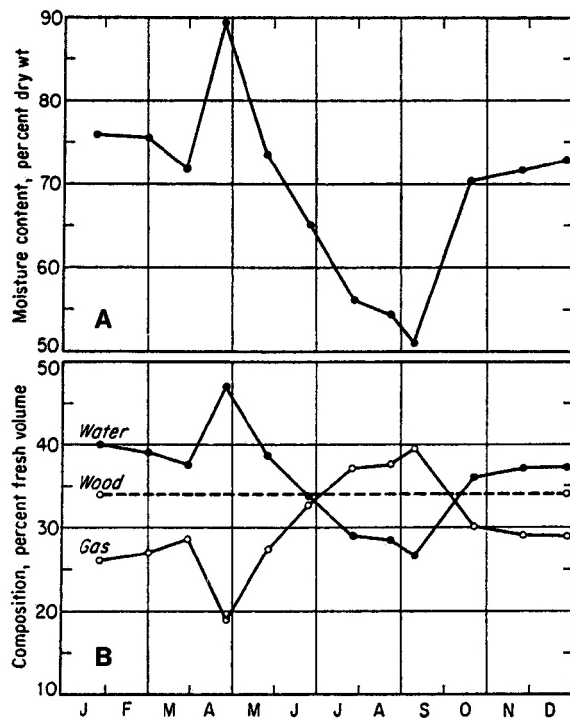


Figure 7.21 (a) Seasonal change in water content of yellow birch tree trunks calculated from disks cut from the base, middle, and top of the trunks. (b) Changes in gas and water content of yellow birch tree trunks calculated as a percentage of total volume. From Kramer (1983), after Clark and Gibbs (1957).

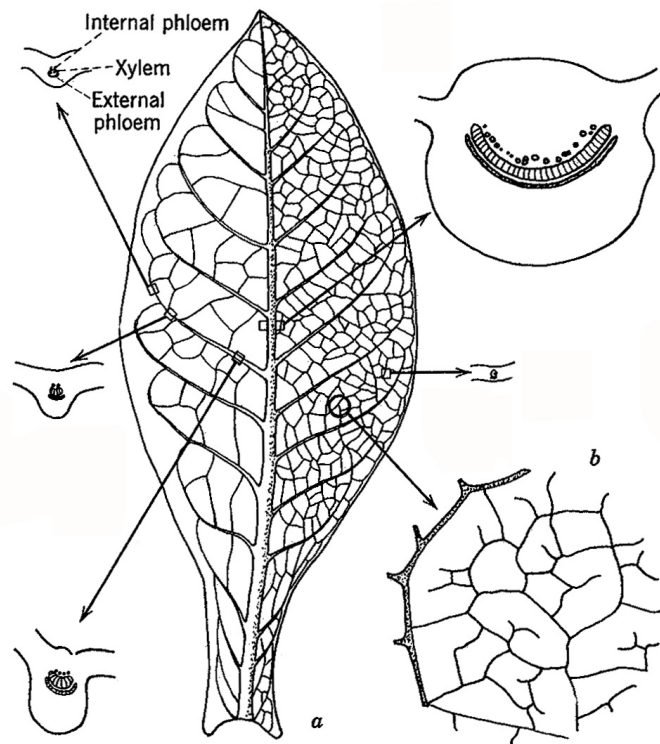


Figure 7.22 (a) Diagrams of venation of a mature tobacco leaf, showing midrib and principal lateral veins, also cross sections of midvein and lateral veins of various sizes. (b) Enlargement of a small section of a leaf blade to show the network of small veins. There were 543 mm of veins per square centimeter on this leaf. From Kramer (1983), after Avery (1933).