

Plant Response to Water in the Environment

I. Terminology associated with water stress

1. **Water Stress** - an imposed change in the water relations of a plant induced by an unusual water status in the environment

DROUGHT

2. **Resistant** - the capacity of a plant to withstand periods of water deficit
avoidance - function when water is available
tolerance - can function when water is limiting, can endure water deficits

FLOODING

3. **Resistance/Tolerance** - the capacity of a plant to withstand long periods of excess water and the anaerobic conditions associated with it in its rooting environment

II. Water movement in the "soil-plant-atmospheric-continuum" (SPAC)

- A. Flux of water through any part of the plant and through the SPAC can be described using the Ohm's Law analogy (figure) and is best thought of in **conductances** and **resistances** terms:

$$\text{flux} = \text{driving force} \times \text{conductance}$$

$$\text{flux} = \text{driving force} / \text{resistance}$$

1. driving force for the liquid phase is the Ψ gradient
 2. driving force for the gaseous phase is vapor pressure and vapor density gradients
- B. water flow through the SPAC depends on a series of fixed and variable resistances and on the capacitance (water storage regions) in the system (figure)

III. Hydraulic conductivity, cavitation, embolism

1. xylem embolisms (air-filled tracheids or vessel members) can cause significant disruption in water transport through the xylem (figures)
2. embolisms are caused by cavitation (breaking of the water column in xylem conduits) induced by low ψ and freezing
3. once embolisms begin to form, they can increase in a cycle only to be refilled in some species in the spring by root pressure (i.e. air expulsion and dissolution caused by positive xylem pressures)
4. Zimmerman (1983) has hypothesized that xylem structure and branch structure are constructed in such a way to prevent the embolism process from "running away"
5. many woody plants function close to some threshold for xylem dysfunction - it has been proposed that a morphological and physiological balance between xylem structure and stomatal control over water loss allows plants to achieve optimal water use.

IV. Response to water stress - Osmotic and Elastic adjustment

1. in response to long- or short-term drought stress, internal relations characteristics change to maintain turgor - detected by pressure-volume analysis
2. change allows plant to maintain positive turgor over wider range of leaf (and thus soil) water potentials (figures) and to maintain higher stomatal conductance these benefits can be seen in P-V curves or in photosynthesis-stress curves (figure)
3. changes in osmotic potential are usually due to active synthesis of what are known as "stress metabolites"

such as simple sugars (mannitol, sorbitol) and amino acids (proline, glycine-betaine)

4. changes in tissue elasticity (ϵ ; bulk tissue elastic modulus) can provide at least two benefits for a plant. Bulk tissue elastic modulus is $\Delta P / \Delta$ tissue water volume (or content):

- **Higher ϵ** (lower elasticity) can result in lower P but steeper water potential gradients from the soil to the leaf, allowing a plant to obtain more "bound" water from the soil

- **Lower ϵ** (higher elasticity) can result in the maintenance of higher and more positive turgor at a particular tissue water content (figure)

V. Control over water loss

A. **Primitive plants** such as lichens and mosses have no means of preventing water loss and their activity is limited to those brief periods of moisture availability (diurnal or seasonal) (figure) respiration begins soon after wetting, photosynthesis is positive soon thereafter. These "resurrection plants" are capable of going from dehydrated state to active state in 1 hour or less

B. Plant resistances to water loss, including plant "capacitance"

- "leaf" conductance is the sum of stomatal, boundary layer, and cuticular components
- cuticular conductance is always much lower than stomatal conductance; how much lower depends on extent of epidermal suberization. cuticular conductance is also generally much lower than boundary layer conductance and this depends on leaf or canopy dimensions and the degree of "coupling" between the plants and the environment (see below)
- in water limited habitats where humidity can raise to 100%, several mechanisms exist to trap dew or fog
 - wettable surfaces for foliar uptake as in bromeliads
 - water repellent surfaces in coastal Peruvian trees and annuals
 - water may be taken up after 'dripping' from foliage (Redwoods)
- Moisture may be extracted from non-saturated atmospheres using epidermally excreted salts
 - Nolana mollis in the Atacama Desert of South America excretes calcium chloride which is hygroscopic down to RH = 32% (figure)
- Water can be channeled to roots
 - waxy and smooth bark to increase stem flow
 - non-wettable substances excreted into soil to allow water penetration into only certain parts
 - pitcher-forming epiphytes
- "Capacitance" or water storage
 - roots, stem, and sapwood are storage locations for water. In trees (figure) plants of the high elevations of Tropical mountains (S. America, Africa) and coniferous trees; water storage in herbs is minimal (figure)

Water Storage as hours of Transpiration

	<u>herb</u>	<u>conifer</u>	<u>giant rosette (tropical)</u>
foliage	0.3	1.1	0.6
cambium	1.3	1.0	0.75
"pithy" stem	0.1	0.9	28.0
sapwood	0.0	50.0	0.75
roots	2.8	14.0	1.0

7. plant resistances vary as a function of xylem structure, root systems, amount and vessel diameters and tradeoffs that exist between vessel diameter and susceptibility to cavitation under water stress - drought or freezing (last lecture!).

VI. *Stomatal closure*

one response to limited water in the environment is stomatal closure - costs can occur!

1. CAM plants can respond to severe water stress by "idling" rather than night-open, day-closed mode (figure) or facultative CAM can exist (switch from C₃ mode to CAM as water is limited).
2. Leaf energy balance is modified during the day if stomata close (T_l increases), so other changes may accompany stomatal closure like leaf movements or changes in leaf absorptance.

VII. *Stomatal regulation of water loss; the role of roots and/or leaves*

Stomata have been shown to respond to a wide variety of environmental conditions; light, Δw, plant water potential, CO₂ (figure). With respect to water, two responses are most important - water potential and Δw.

1. stomatal conductance to water vapor (g) responds both directly and indirectly to changes in soil water potentials and in the evaporative demand from leaf surfaces, the leaf-to-air vapor pressure gradient (Δw; in mmol H₂O per mol of air)
2. g declines with increasing Δw at constant leaf water potential (figure). The Δw or humidity response of stomata is related to leaf epidermal turgor and the inability of mesophyll tissues to supply enough water to replace that being lost from epidermal cells. As such, the rate of water loss from epidermal cells is highly dependent upon the Δw
3. g declines with decreasing leaf water potential at constant Δw (figure). The data collected to date suggest that for different species the signal for stomatal closure originates in the roots or the leaves (figures):
 - **root signal** caused by increased ABA and cytokinins and or hydraulic resistances
 - **leaf signal** caused by changes in ABA or the ABA/cytokinin ratio
4. if stomates were wide open and exert little influence or control over transpiration, then the diurnal transpiration pattern should be similar to the diurnal VPD (or Δw) pattern
5. midday stomatal closure (or partial closure) is a response to high midday Δw and low midday (figures)
6. leaves and especially canopies can be significantly "decoupled" from the environment (figure); raises the issue as to what "**controls**" Transpiration - the plant or the atmosphere - ?

6a. Jarvis and McNaughton (1986) described a way to look at the sensitivity of transpiration to the boundary layer between the canopy and the bulk air with a **stomatal decoupling coefficient** (Ω), a dimension-less number from 0 (strongly coupled) to 1 (strongly Decoupled) - see figures:

$$\Omega = 2 + \beta + g_r / g_b + 2 + \beta + (g_b + g_r) / g_s + g_r / g_b$$

where β is the ratio of increases in latent heat content to sensible heat content of saturated air (change in the Bowen Ratio), g_b is boundary layer conductance, g_r is long-wave radiative transfer 'conductance' [as; g_r = 4ΦσT_a/ρC_p, where Φ is canopy emissivity (0.97), σ is the Stefan-Boltzmann constant (5.67 × 10⁻⁸ W m⁻² K⁻⁴), T_a is the air temperature (°K), ρ is the vapor density of air, and C_p is the specific heat of air at a given pressure.

VII. *Plant Response to Salinity*

- Schimper (1898) was the first to propose that halophytic (salt-loving) species where physiological xerophytes
- high salinity causes lower soil osmotic potentials and thus much steeper water potential gradients from the soil to the leaf (figure)
- salts can be *excluded*, *excreted*, *accumulated* and sequestered in succulent tissues, or *removed*
 - exclusion - double endodermis of halophytic grasses, xylem "pumps"
 - excreted - salt glands are specialized locations where salt water is accumulated and allowed to pass out of the plant
 - accumulated - and sequestered in succulent tissues and thus effectively removed from exposure to metabolic processes (figure)
 - removed - either by leaching from frequent fogs or rain from the leaf epidermis OR via leaf abscission/shedding
- osmoregulation / osmotic adjustment appears to a common and very effective way for halophytic plants to tolerate salinity - steeper water potential gradients from saline soils to the leaf. Halophytes also commonly have very inelastic tissues (some exceptions can be found in marshes where salinity fluctuates dramatically)
- both C₄ and CAM photosynthesis exist in plants from saline habitats - higher WUE (below)

VIII. *Adaptation to Flooding/Anoxia*

In contrast to water stress induced by the lack of water is that which is induced by an excess of water

- flooding radically reduces O₂ supply to roots (lower solubility and diffusivity in water than in air) (figure)
- oxygen deficiency can cause stomatal closure and this closure, as with drought, is related to changes in ABA and cytokinin synthesis in roots and its transport to shoots
- low O₂ in the rooting environment is associated with higher anaerobic respiration in roots and soils. Byproducts (ETOH, aldehydes, lactic acid) accumulate resulting in injury (figure)
- adaptations to flooding:** TWO types -- morphological - stems or root modifications which allow more rapid diffusion of O₂ from the air or leaves to the roots (figure). Ethylene production caused by anaerobic respiration stimulates aerenchyma production OR the development of "knees" (pneumatophores) that enhance O₂ exchange - and -- physiological - increased tolerance to root anaerobic respiration (higher ADH levels than non-flooded plants)

IX. *Growth and water stress*

- different cell and whole plant functions show different sensitivities to water deficits (figure)
- though there is a large amount of variation among species, cell processes are generally most sensitive than leaf-level processes
- adaptations that allow for more favorable water balance and turgor maintenance will not only be advantageous from the survival and desiccation tolerance view, but can allow for more growth during periods of water stress.

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a series of resistances to water flux exist along the flow path from the soil to the plant to the atmosphere. Some of these are fixed and some are variable (stomata)

$$\text{conductance} = 1 / \text{resistance}$$

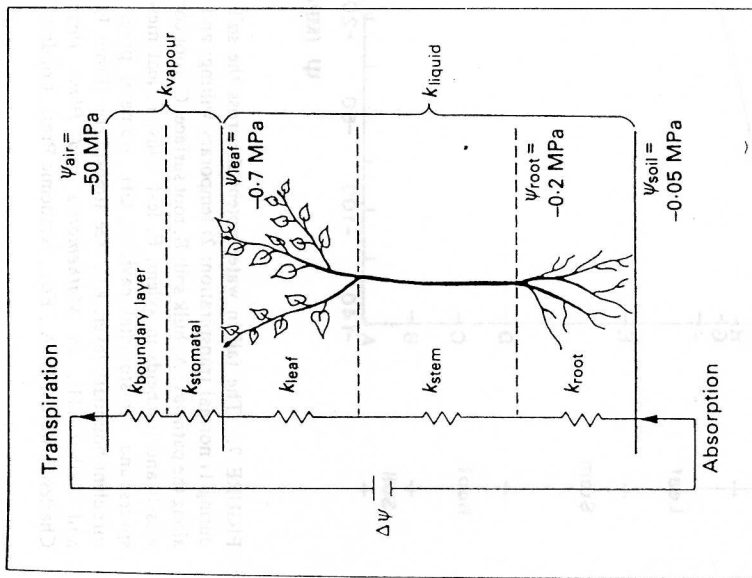
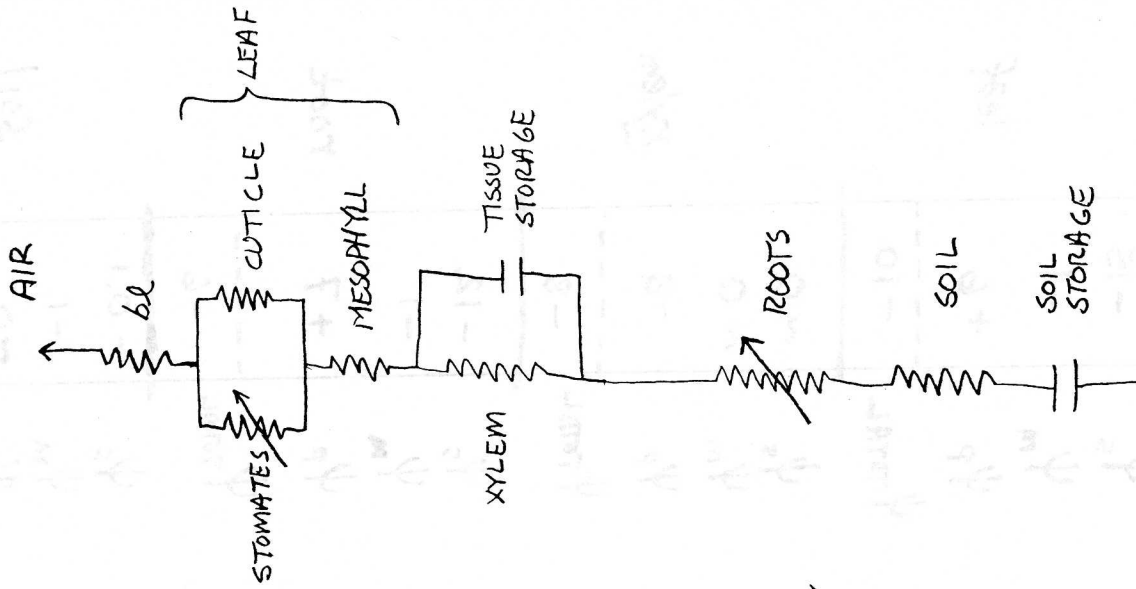


Figure 1. The simplest Ohm's law analogy. The total conductance is seen as resultant conductance (k) of the root, stem, leaf, stomates and boundary layer in series. The conductances in the vapour phase are much less than in the liquid phase. Water flow is driven by the differences in water potential between the soil (ψ_{soil}) and the atmosphere (ψ_{air}) (from Ewers & Cruiziat, 1990)



PART II
FIGURES
Lec Topic
12

components of water stress through the soil - plant. atmospheric continuum (SPAC).

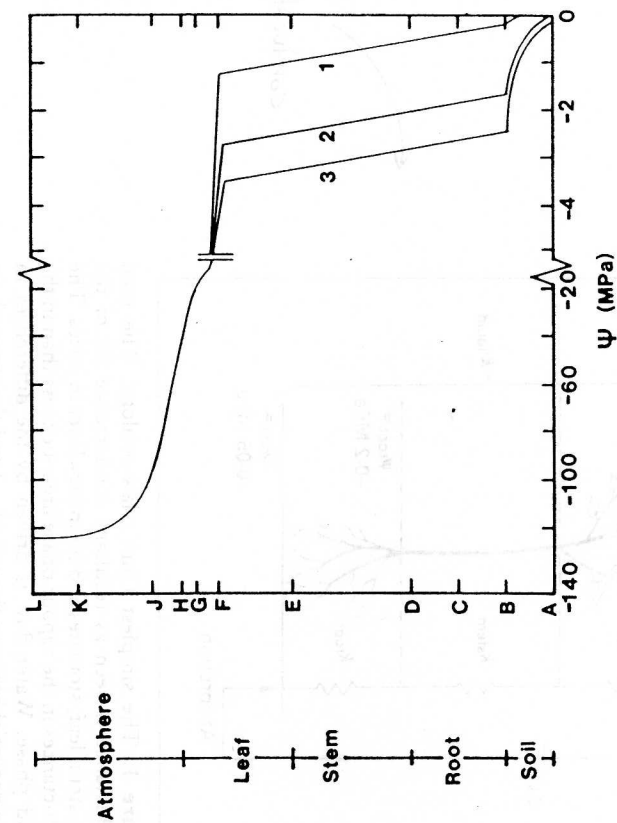
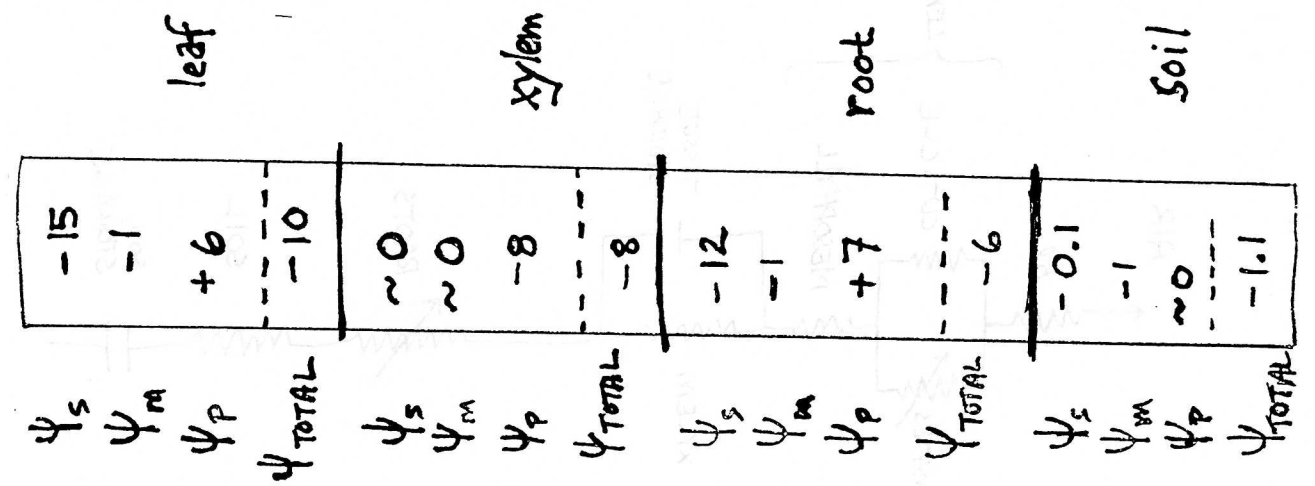


FIGURE 7. The fall in water potential across the soil-plant-atmosphere continuum during 1) normal transpiration; 2) temporary wilting; and 3) permanent wilting. Points along the pathway: A, bulk soil; B, root surface; C, root cortex; D, root endodermis; DE, vessels and tracheids in xylem; E, leaf veins; F, leaf mesophyll; FG, leaf intercellular spaces and sub-stomatal cavities; GH, stomatal pore; HJ, laminar sublayer; JK, turbulent boundary layer; KL, free atmosphere. (From Jarvis, P. G., Edwards, W. R., and Talbot, H., in *Mathematics and Plant Physiology*, Rose, D. A. and Charles-Edwards, D. A., Eds., Academic Press, London, 1981, 151. With permission.)



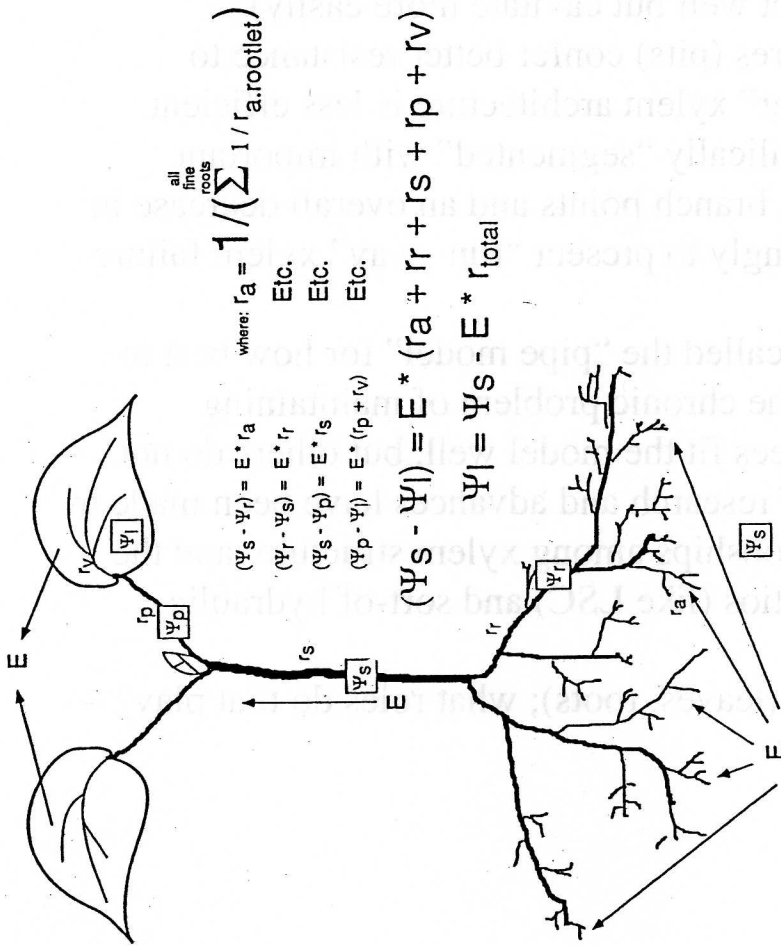
FLUX

Hydraulic conductivity, cavitation, embolism

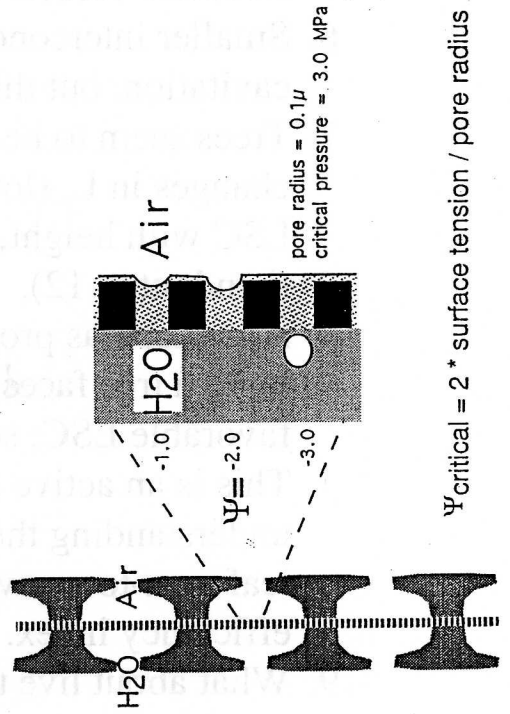
Points to remember:

1. Hydraulic conductance is largely determined by vessel diameter (r^4) and to some extent by vessel length, the water potential gradient in the xylem and the side-wall pit characteristics (handout pp. 9 and 11).
2. Cavitation caused by freeze-thaw cycles and to a much lower degree by drought-induced air seeded embolism will be influenced by xylem structure we call “hydraulic architecture” (handout p. 10).
3. The xylem vulnerability to cavitation largely determines the degree of desiccation tolerance in woody plants and this is influenced by hydraulic architecture (handout, p. 11).
4. Some xylem conduits can be “re-filled” with root or stem pressure, but to a very limited extent. Other mechanisms are under investigation.
5. There is a tradeoff between conductance and safety (e.g., larger diameter vessels conduct well but cavitate more easily).
6. Smaller interconduit pores (pits) confer better resistance to cavitation, but this “safer” xylem architecture is less efficient.
7. Trees seem to be hydraulically “segmented” with important changes in L_p (lower) at branch points and an overall decrease in LSC with height, seemingly to prevent “run away” xylem failure (handout p. 12).
8. A model was proposed called the “pipe model” for how best to build a tree faced with the chronic problem of maintaining favorable LSC; some trees fit the model well, but others do not. This is an active area of research and advances have been made in understanding the relationships among xylem structure, and the leaf area-to-sapwood ratios (like LSC) and sort-of hydraulic efficiency index.
9. What about live tissues (leaves, roots); what roles do they play? – next!

Whole-Plant Hydraulic Architecture



Air-seeding mechanism of cavitation



$$\Psi_{\text{critical}} = 2 \cdot \text{surface tension} / \text{pore radius}$$

1) Ohm's Law Analogy

Flux = Conductance * Driving Force

$$E = \text{Hydraulic conductance} \cdot \Delta \Psi = \frac{\Delta \Psi}{\text{hydraulic resistance}}$$

** Resistances are additive in series, Conductances are additive in parallel

2) Hagen-Poiseuille

$$L_p = \frac{r^4 \pi}{8 \eta}$$

L_p = hydraulic conductance

r = radius of capillary

η = viscosity of water

3) Maximum tension tolerance of xylem water

$$\Psi_{\text{critical}} = 2 \cdot T / r$$

r = pore size

T = surface tension of water

Ψ_{critical} = water potential at which air-water interface can be pushed through pore

I. Hydraulic Architecture

A. Definitions

1. Hydraulic conductance (h_c): the capacity to transport liquid water,

$$\frac{\text{kg} \cdot \text{m}}{\text{s} \cdot \text{MPa}}$$

2. Leaf-Specific hydraulic conductance (LSC)

$$\frac{\text{kg} \cdot \text{m}}{\text{s} \cdot \text{MPa} \cdot \text{m}^2}$$

3. Capacitance: the change in water content per change in water potential

4. Hydraulic Architecture: the specific pattern of resistances (reciprocal of hydraulic conductance) and capacitances, scattered throughout the plant in roots, stems, and leaves.

a. paths in parallel and in series

b. capacitance

(1) avoided by steady-state measurement

(2) sometimes important

c. during water transport from soil to leaf, water potential drops are proportional to the resistances at each stage of the pathway

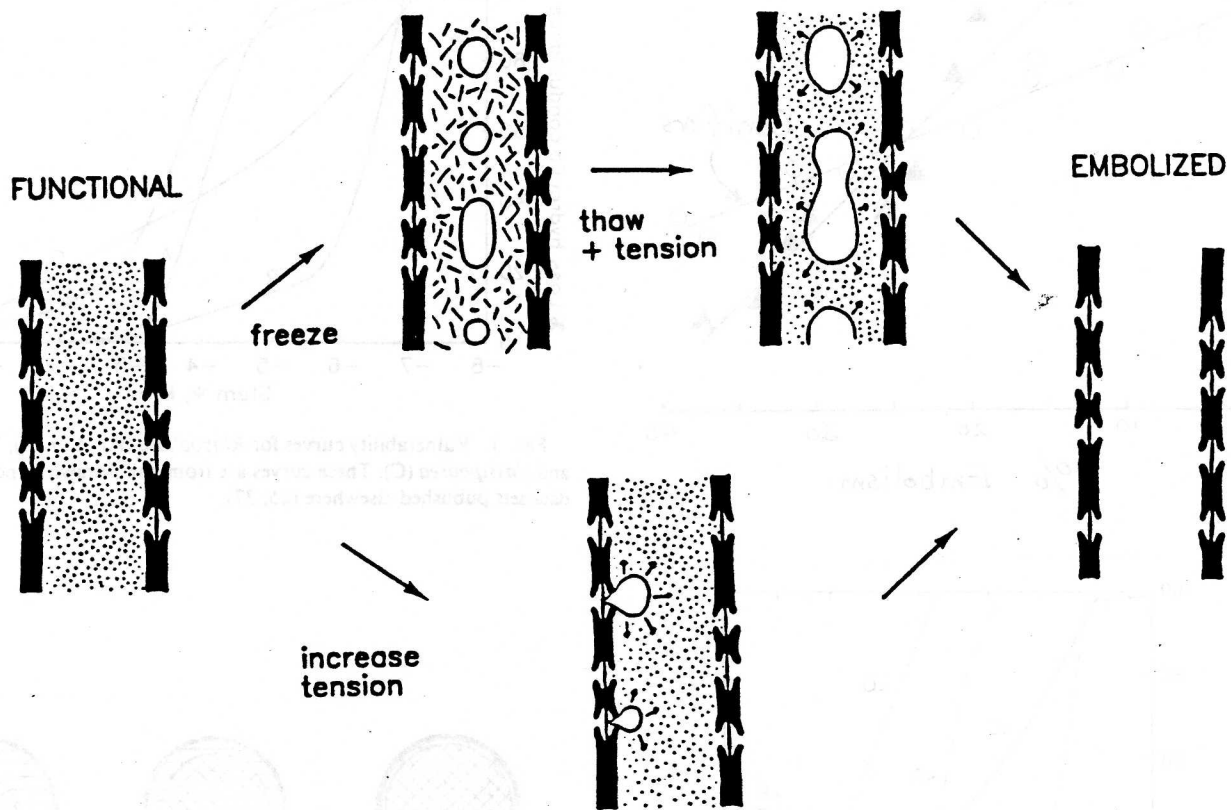


Figure 5. Diagrammatic representation of the mechanisms causing cavitation and then embolism in xylem conduits (after Sperry, 1991). Cavitation is the process, embolism is the result.

The upper route shows the response to freezing. Gases are forced out of solution when the xylem sap freezes. When the xylem sap thaws, bubbles expand to cause embolism if they are large enough and the xylem is under enough tension. The larger the conduit volume, the more vulnerable they are to cavitation and embolism during freeze-thaw cycles.

The lower route shows the response to increasing xylem tensions that can occur during soil water stress. Air is "pulled" into functional water-filled xylem conduits from embolized and air-filled neighboring conduits through pores in the inter-conduit pit membranes. Embolism can be caused by leaf abscission, broken branches, or physical breakage of the water column when put under extreme water stress. The greater the permeability of pit membranes to air, the more vulnerable xylem conduits are to embolism.

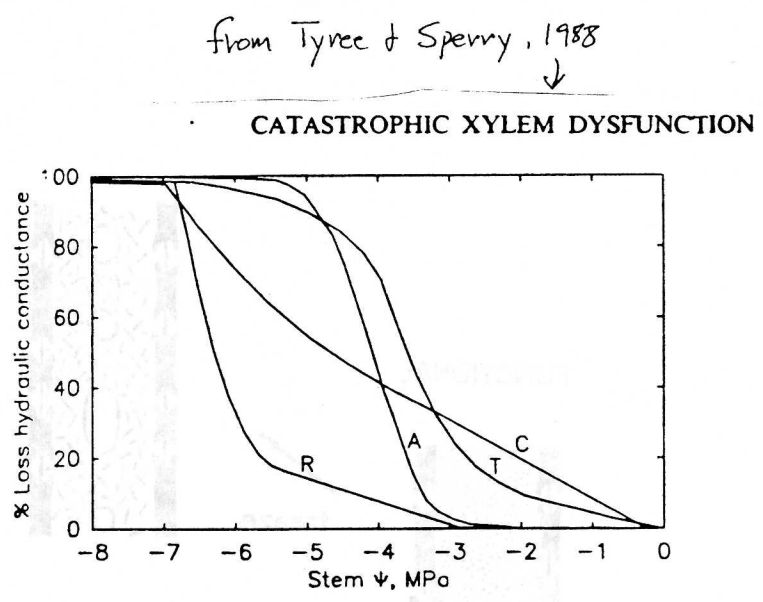
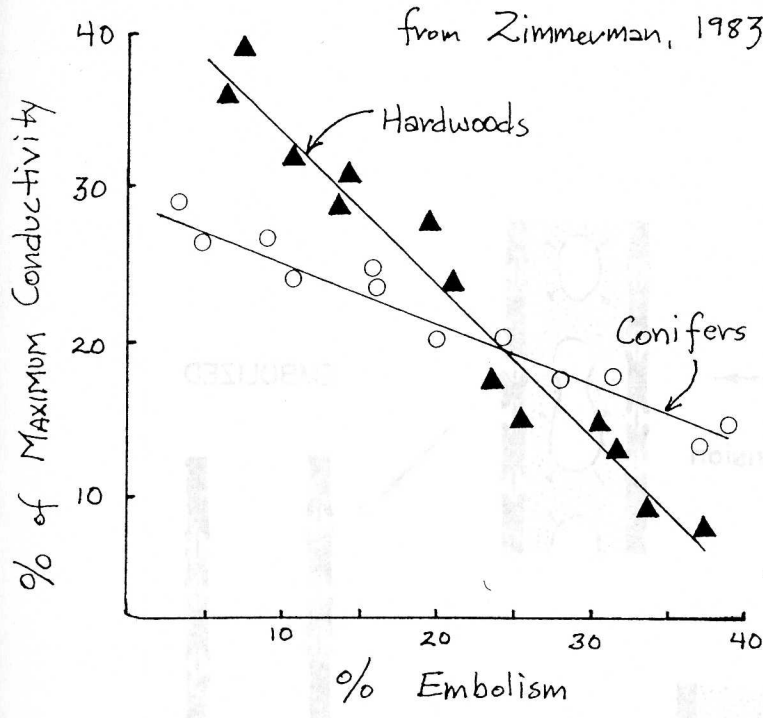


FIG. 1. Vulnerability curves for *Rhizophora* (R), *Acer* (A), *Thuja* (T), and *Cassipourea* (C). These curves are from hand-drawn trends through data sets published elsewhere (25, 27).

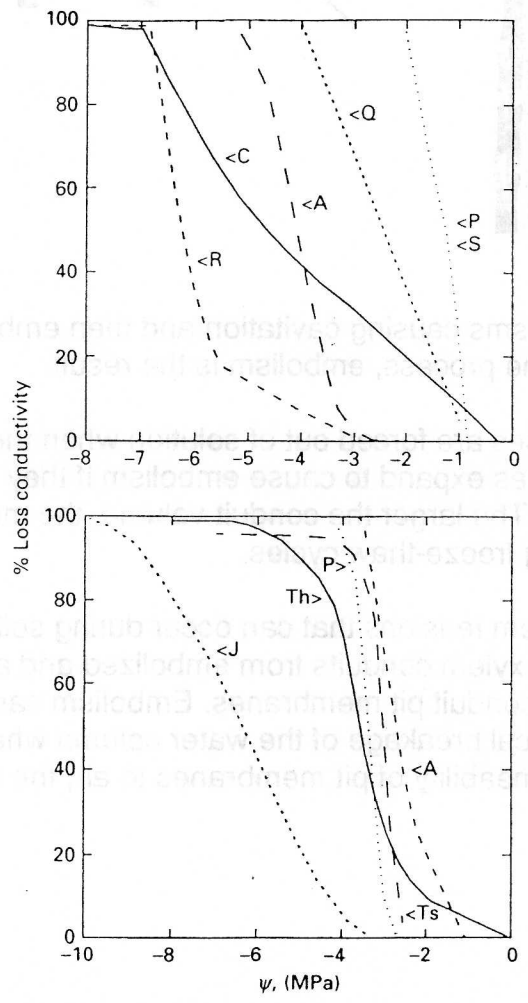


Figure 6. Vulnerability of various species to embolism measured as the percentage loss hydraulic conductivity versus water potential. Upper panel are angiosperms: R, *Rhizophora mangle*; A, *Acer saccharum*; C, *Cassipourea elliptica* (Sw.) Poir.; Q, *Quercus rubra* L.; P, *Populus deltoides*; S, *Schefflera morotoni*. Lower panel are gymnosperms: J, *Juniperus virginiana*; Th, *Thuja occidentalis*; Ts, *Tsuga canadensis*; A, *Abies balsamea*; P, *Picea rubens* Sarg.

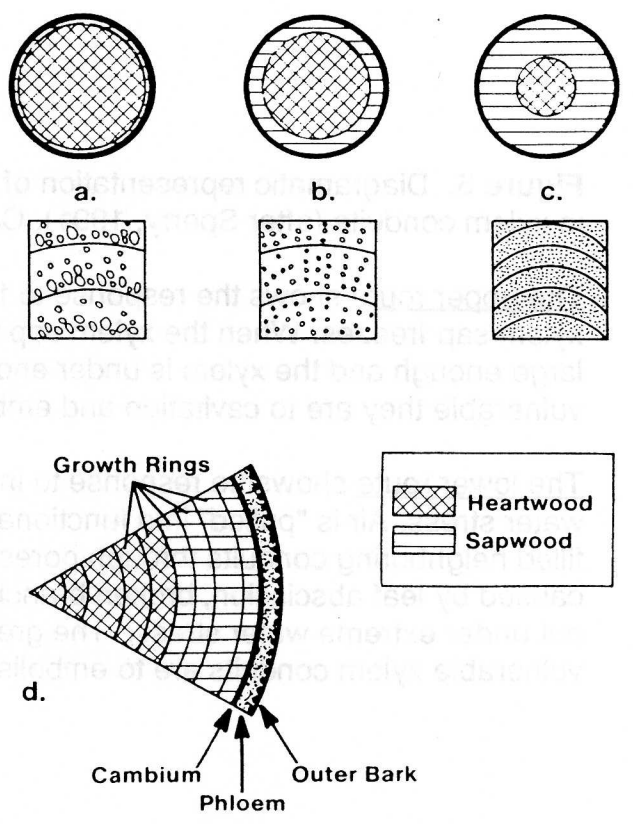


FIGURE 4. Arrangement of heartwood, sapwood, vascular cambium, phloem, and outer bark in stems of temperate trees: (a) Number of layers of sapwood fewest in ring-porous species, (b) intermediate in diffuse-porous species, and (c) greatest in nonporous wood (c). Details shown in (d).

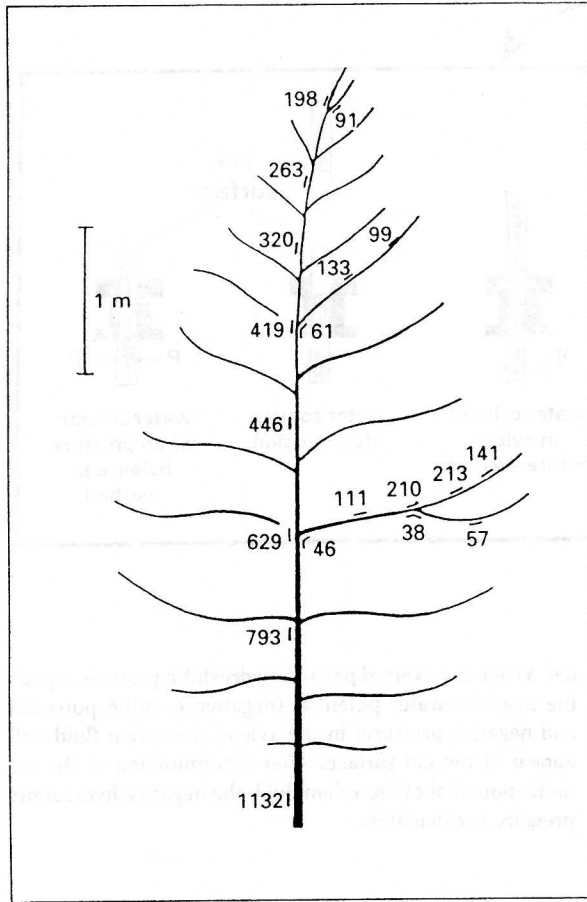


Figure 4. Pattern of LSC (leaf specific conductivity) in the crown of a *Tsuga canadensis*. LSC values are reported in $10^{-6} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$. Note that LSCs are higher in the trunk than in branches, and higher in first-order than in second-order branches. Branch junctions have hydraulic constrictions (modified from Ewers & Zimmermann, 1984a).

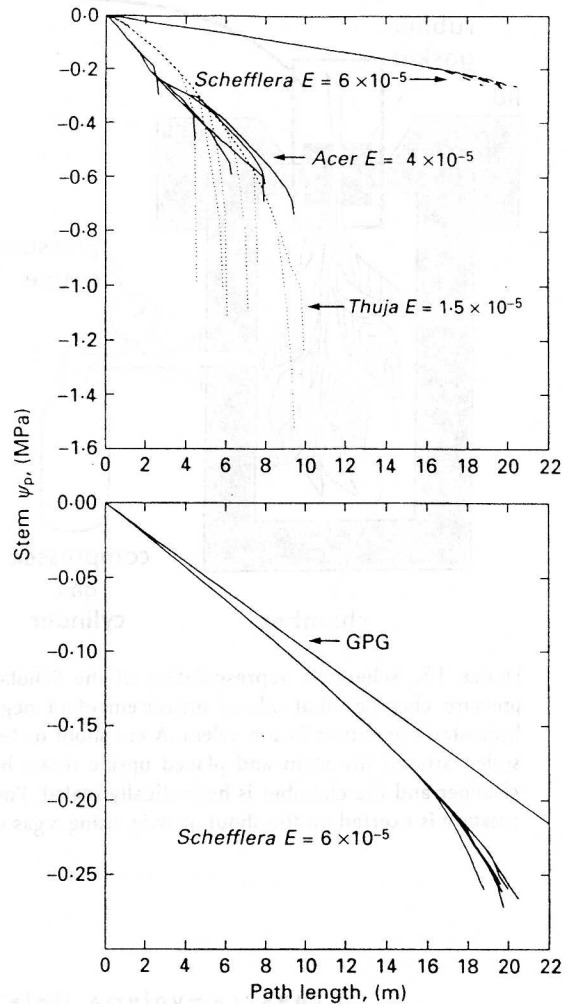


Figure 5. Profiles of pressure potential of stems versus the distance (path length) water must travel from the base of the tree to a stem apex. The lower diagram shows *Schefflera* on an expanded scale of ψ_p . All values include the gravitational potential gradient (GPG) required to lift water up the tree. These curves are calculated from the hydraulic maps and representative evaporative flux density ($E \text{ kg s}^{-1} \text{ m}^{-2}$) for each species in the graph (modified from Tyree *et al.*, 1991).

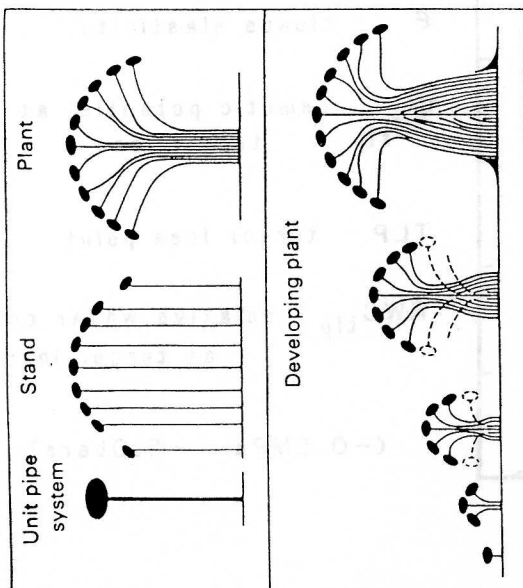


Figure 2. The unit pipe model of plant form; the tree is viewed as an assemblage of 'unit pipes' (from Ewers & Cruiziat, 1990).

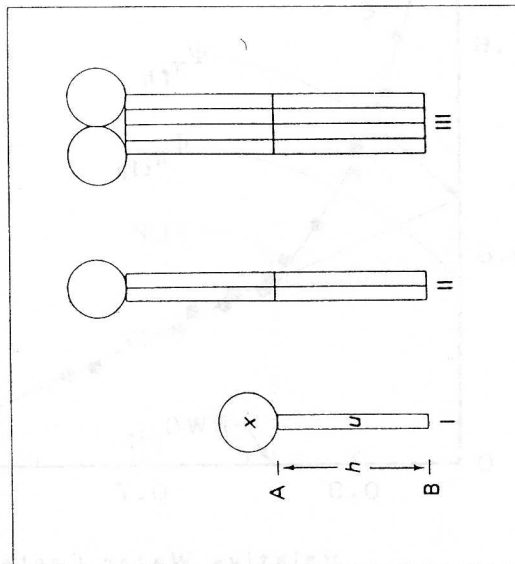


Figure 3. Three conditions showing the problem of maintaining constant conductivity in the unit pipe model as the pipe length and leaf area change. u , a unit pipe; x , leaf area; h , height. See text for details.

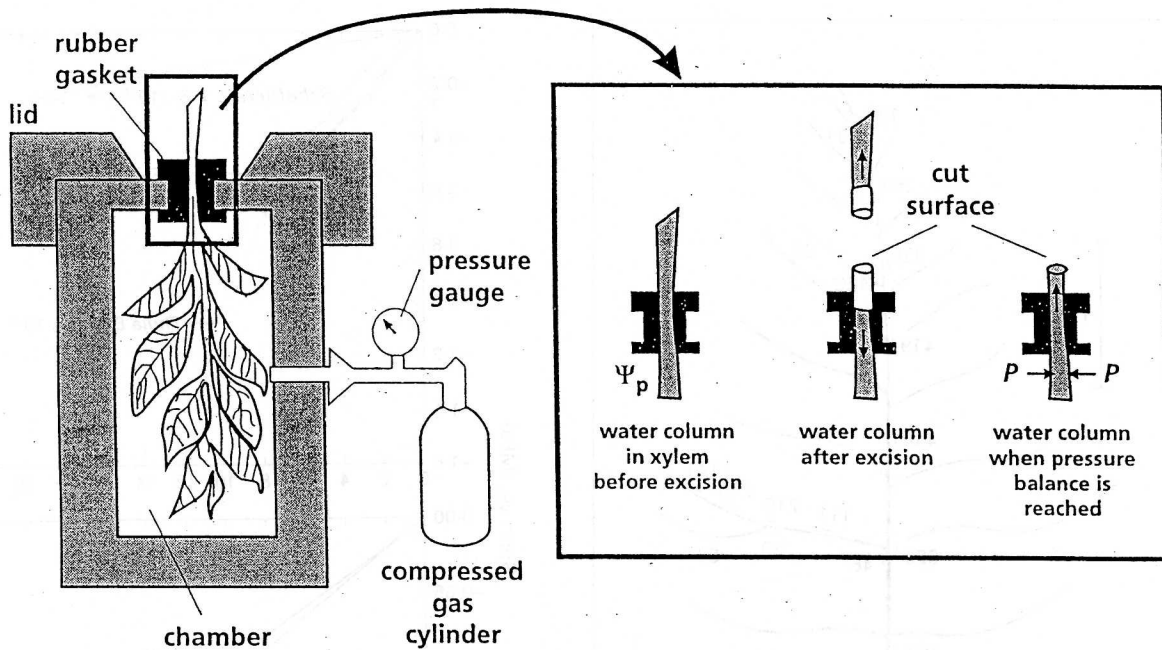
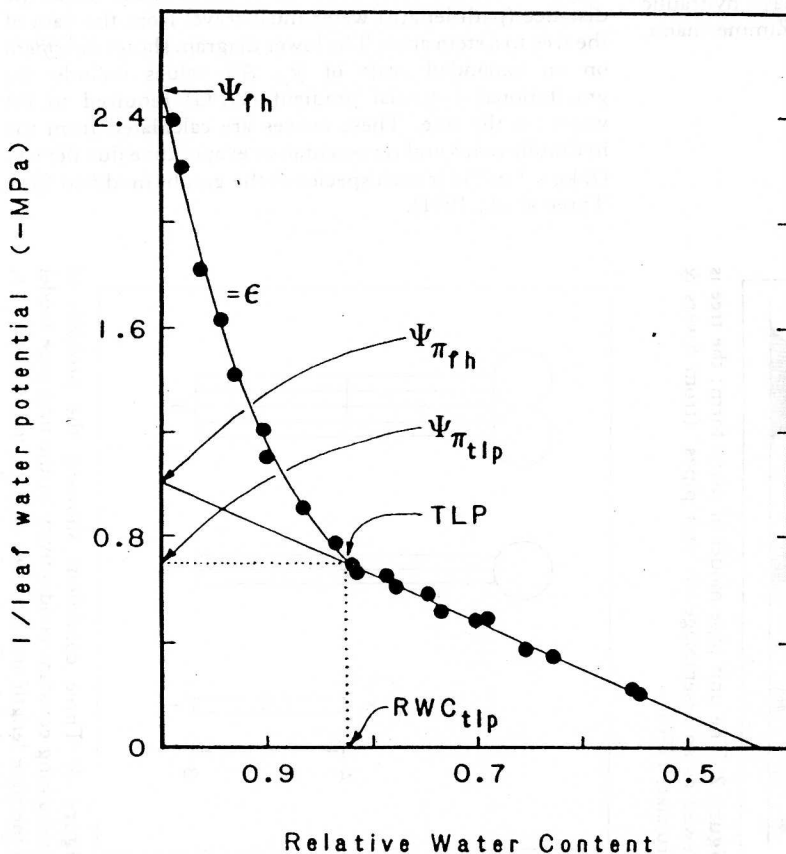


FIGURE 13. Schematic representation of the Scholander pressure chamber that allows measurement of negative hydrostatic pressures in the xylem. A cut shoot or twig is sealed around the stem and placed upside down in the chamber and the chamber is hermetically sealed. Positive pressure is exerted on the shoot or twig, using a gas cylinder.

When the exerted positive hydrostatic pressure equals the negative water potential (negative osmotic potential and negative pressure) in the xylem, the xylem fluid will appear at the cut surface. After determination of the osmotic potential of the xylem fluid, the negative hydrostatic pressure is calculated.

Pressure-volume Relationship



- Ψ_{fh} water potential at full hydration
 - $\Psi_{\pi_{fh}}$ osmotic potential at full hydration
 - ϵ tissue elasticity
 - $\Psi_{\pi_{tlp}}$ osmotic potential at turgor loss
 - TLP turgor loss point
 - RWC_{tlp} relative water content at turgor loss
- (-0.5MPa = -5.0bars)

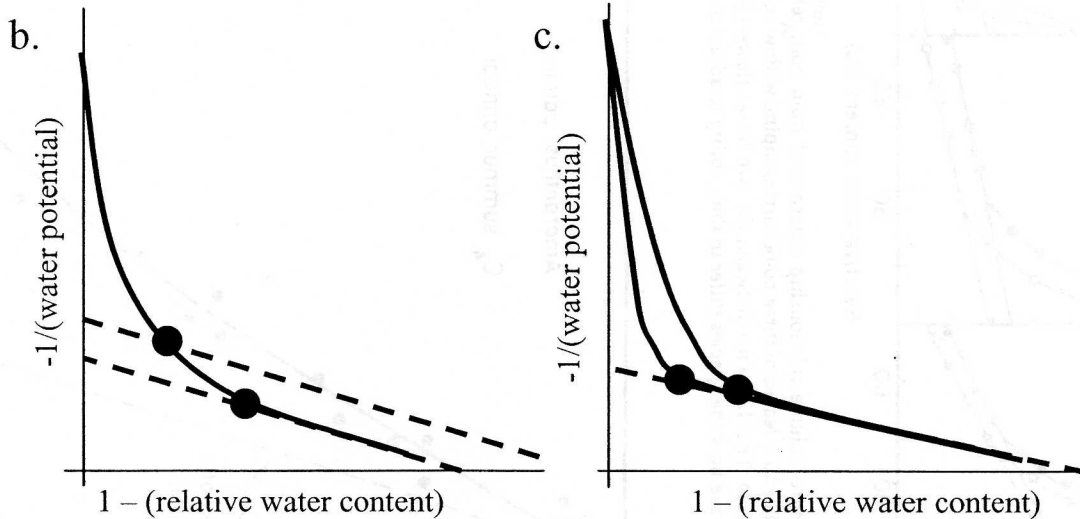
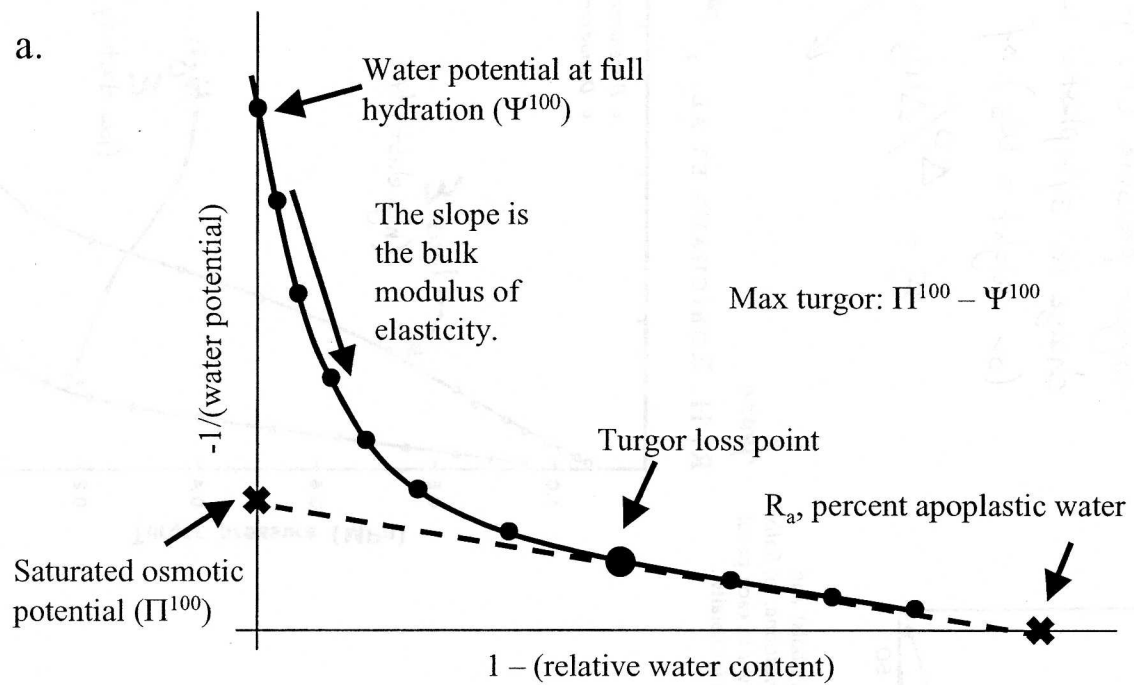


Figure 1. a) The parameters calculated from a pressure-volume curve. A higher bulk modulus of elasticity equates with less elastic tissue. b) The effect of changing the saturated osmotic potential on the water potential and relative water content at turgor loss. c) The effect of changing tissue elasticity on the water potential and relative water content at turgor loss.

ϵ (bulk tissue elastic modulus) is defined as a change (Δ) in tissue turgor pressure (P) for a fractional change in symplectic water volume (or weight = W_s) of tissue

$$\epsilon = \frac{\Delta P}{\Delta W_s}$$

from
R. H. ROBICHAUX ET AL., 1986

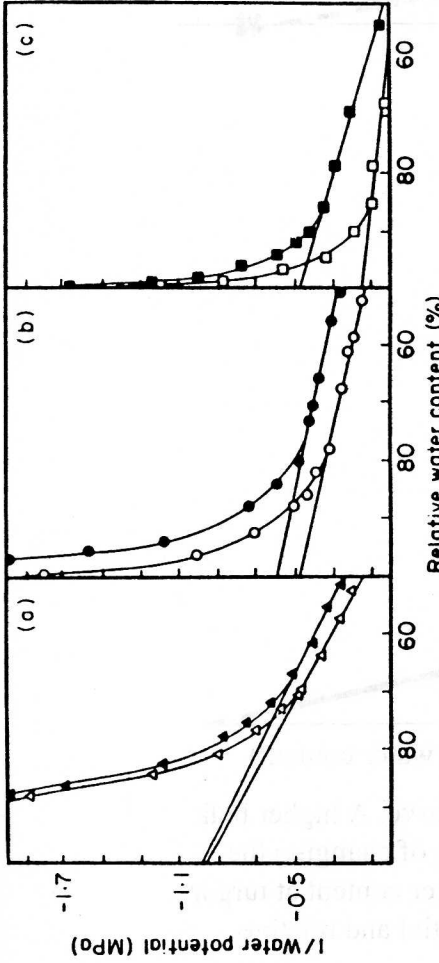


Fig. 4. Representative pressure-volume relationship determined from both rehydrated (open symbols) and rehydrated (closed symbols) mature leaves of three co-occurring alpine willow species: (a) *Salix reticulata*; (b) *Salix arctica*; and (c) *Salix reticulata*. The difference between the two linear (lower) portions of the curves in each panel provides a graphical way to see how the species differ in their ability to adjust osmotically (see text for details).

Dawson 1990

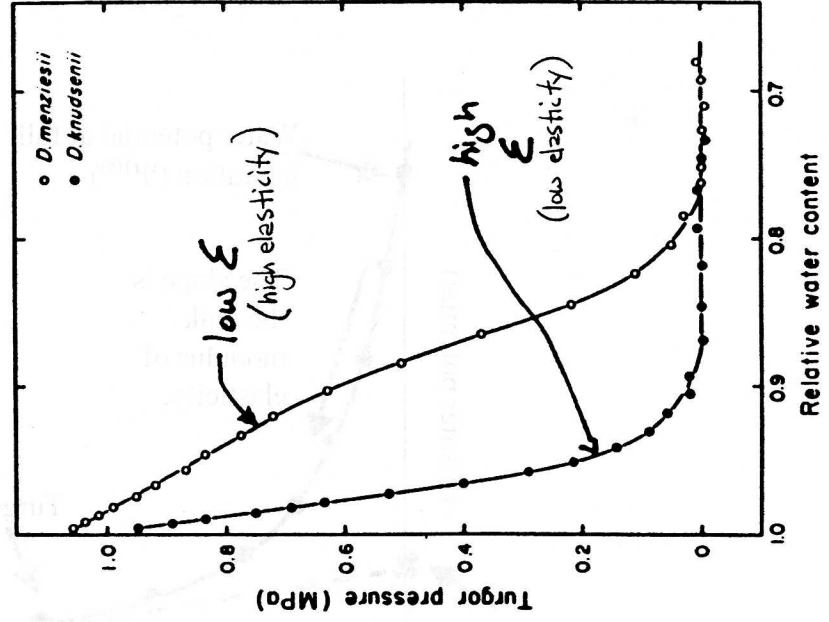
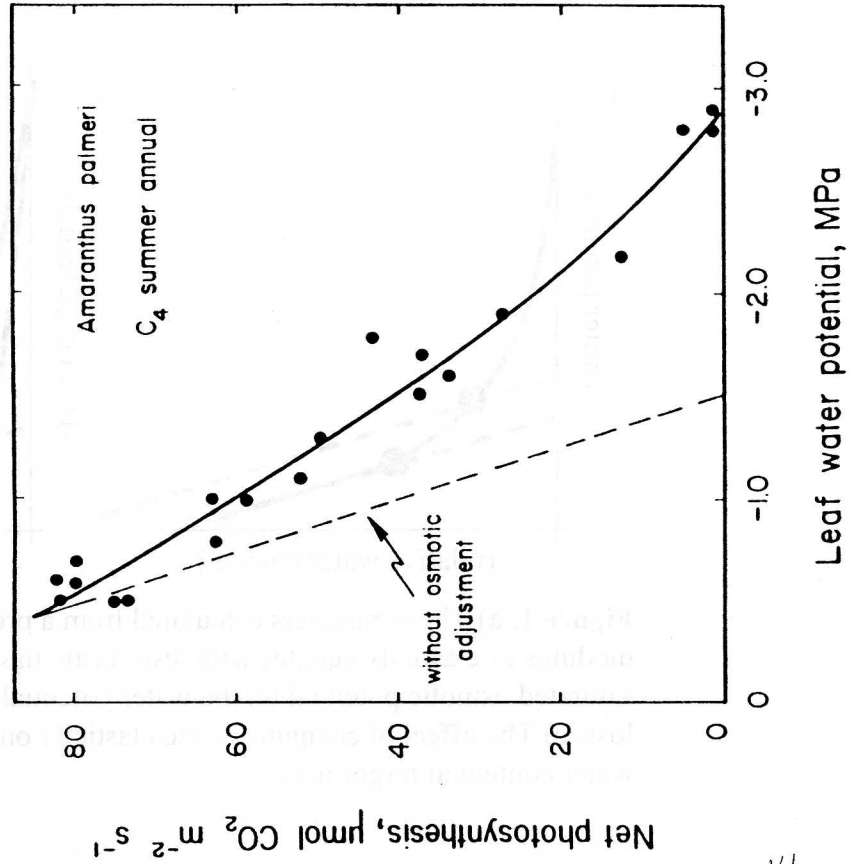


Figure 12.11. Relationships between tissue turgor pressure and tissue water content for *Dubautia menziesii* and *D. knudsenii* (Robichaux and Canfield 1985).



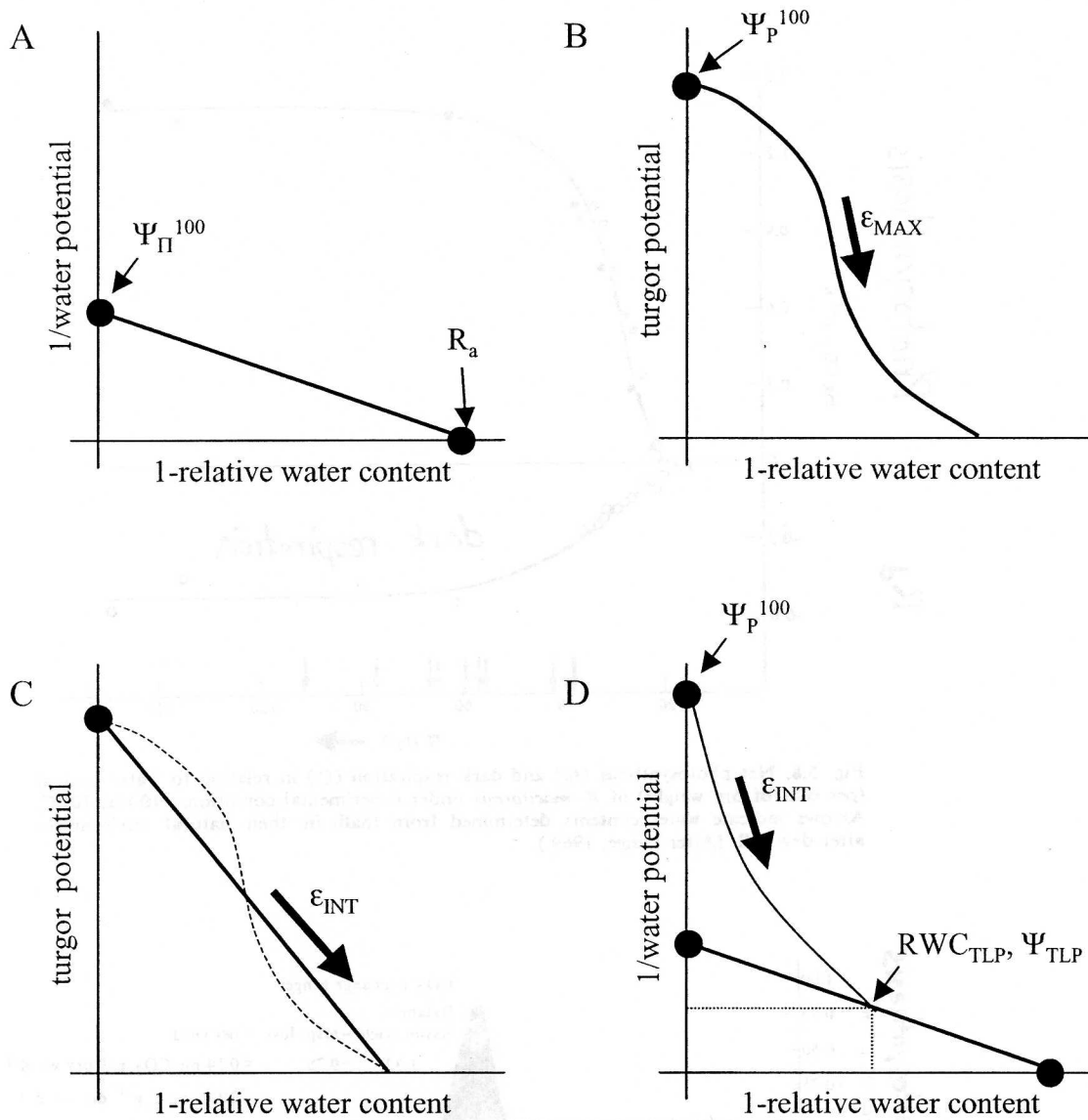


Figure 1. Lines and parameters derived from a pressure volume curve. A) the straight line through the post-turgor loss coordinates, used to derive the saturated osmotic potential (Ψ_{Π}^{100}) and the proportion apoplastic water (R_a). B) the plot of turgor potential versus relative water content used to determine the instantaneous bulk modulus of elasticity (e.g. ϵ_{MAX}). C) a line integrating bulk modulus of elasticity (ϵ_{INT}) between full turgor (Ψ_P^{100}) and turgor loss. D) the intersection of the lines shown in figures A and C yields the relative water content and water potential at turgor loss.

Photosynthesis in lichen (Ramalina maciformis)

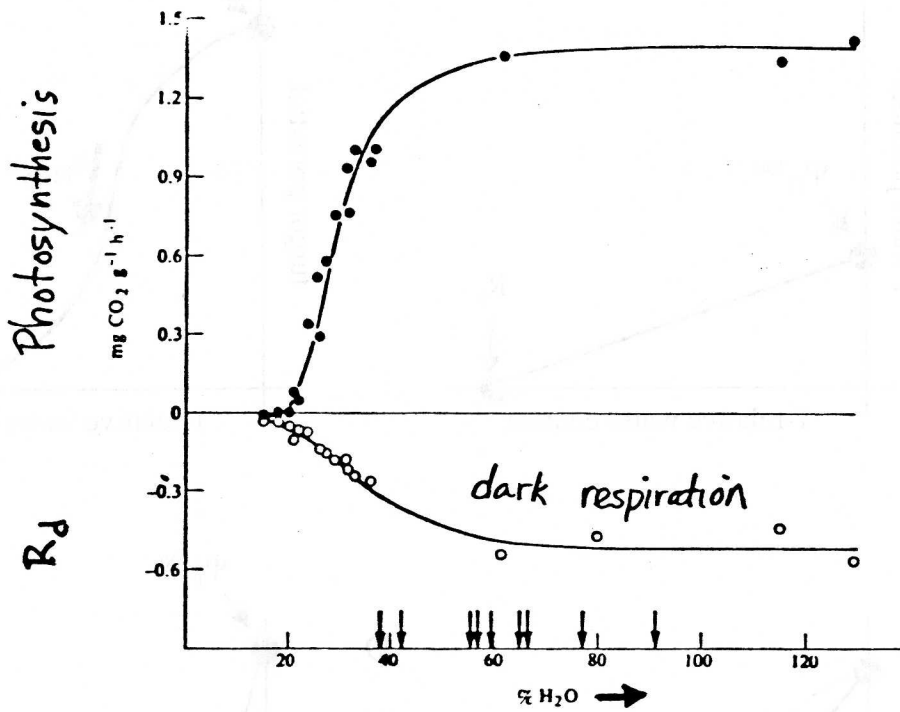


Fig. 5.8. Net photosynthesis (●) and dark respiration (○) in relation to water content (per cent of dry weight) of *R. maciformis* under experimental conditions: 10 klx, 10 °C. Arrows indicate water contents determined from thalli in their natural environment after dew fall. (After Lange, 1969.)

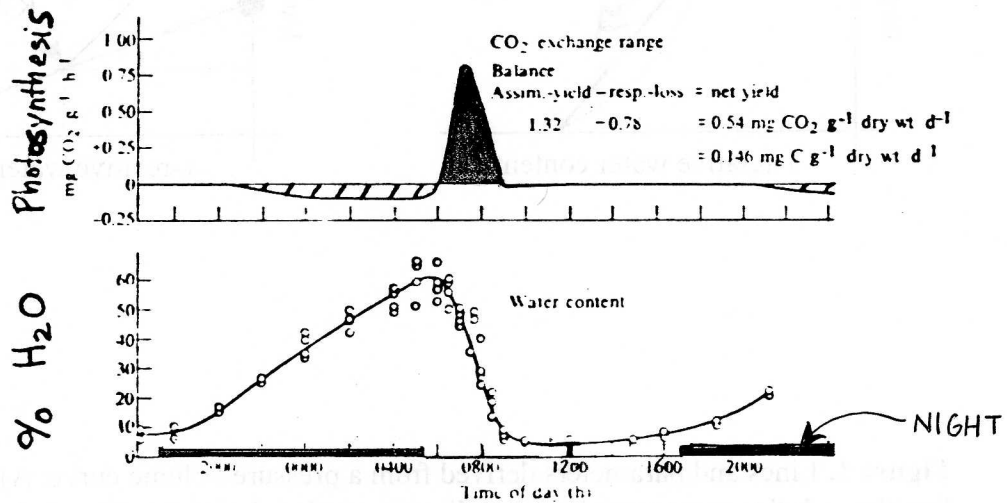


Fig. 5.13. Apparent CO₂-exchange rate during 24 h in September 1967 and calculation of the daily balance and carbon gain of *R. maciformis*. The curve of CO₂-exchange rate is a result of several fragmentary curves (cf. Fig. 5.11). Water content of the thalli in per cent of dry weight is shown below. (After Lange, Schulze & Koch, 1970.)

respiration commences as thallus rehydrates
 photosynthesis occurs only when H₂O and light available

resistances to water flow

	stomates	cuticle
<u>mesophytes</u>		
Alcocasia	2.4	60
Gossypium	1.8	60
Lycopersicon	4.8	19
Phaseolus	4.8	19
<u>xerophytes</u>		
Atriplex	24	160
Haloxyton	26	400
Koekia	8	44
Pinus	17	140
Rehumuria	14	48
Zygophyllum	8	96

$$c_s = 9$$

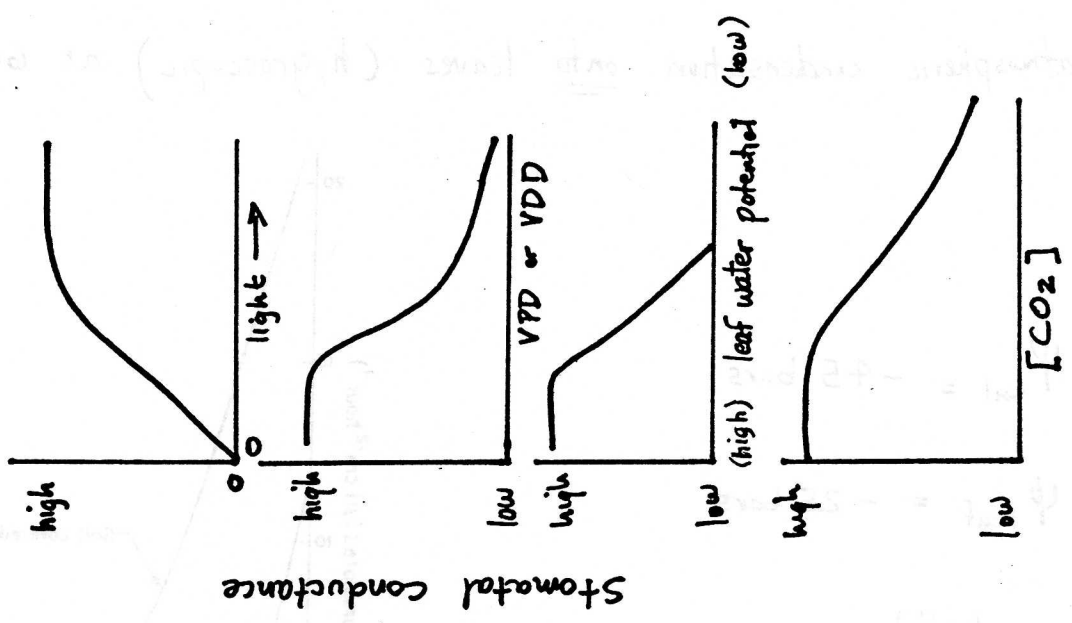
$$2.4 \approx 0.42$$

$$60 \approx 0.017$$

$\frac{v_s}{\text{Sec cm}^{-1}}$ $\frac{\text{cm}^{-1}}{\text{Sec}}$

conductance = $\frac{1}{\text{resistance}}$

Stomatal responses to the environment



Nolana mollis (Atacama Desert)

atmospheric condensation onto leaves (hygroscopic) at 60-90% r.h.

$$\Psi_{\text{soil}} = -45 \text{ bars}$$

$$\Psi_{\text{leaf}} = -25 \text{ bars}$$

Water potential gradient from plant to soil?

incorrect direction but energy provided from Respiration can allow water uptake

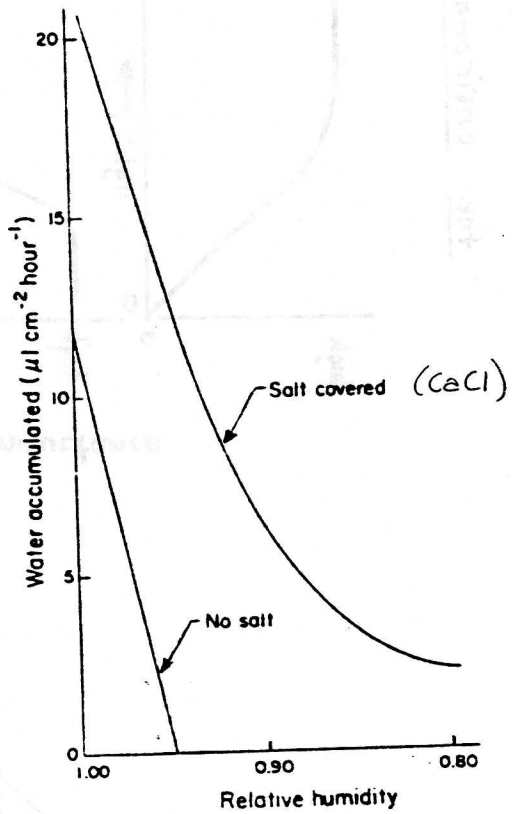


Fig. 3 (right). Simulations of hourly water uptake by leaves of *Nolana* at different relative humidities. The environmental conditions used for the energy budget simulations were typical of nighttime conditions. Leaf resistance, 99 sec cm^{-2} ; wind speed, 50 cm sec^{-1} ; downward infrared radiation, 279 W m^{-2} ; and air and soil temperatures, 15°C . The water uptake under natural or "no salt" conditions is the result of dew formation. The salt concentration of the leaf was set as saturated sodium chloride (osmotic potential about -40 MPa). Simulations were done on a minute-by-minute basis and totaled for an hour.

CaCl will remove water from air down to $\approx 35\% \text{ RH}$
 NaCl " " " " " " " " $80\% \text{ RH}$

Table 1. Atmospheric leaf water accumulation at various relative humidities and energy requirements for water transport to mesophyll.

Relative humidity	Water accumulated* ($\mu\text{l cm}^{-2} \text{ hour}^{-1}$)	Energy	
		Required† ($\text{MJ cm}^{-2} \text{ hour}^{-1}$)	Available from respiration‡ ($\text{MJ cm}^{-2} \text{ hour}^{-1}$)
0.99	20	1.5	35
0.95	13	2.7	35
0.90	6	7.0	35
0.85	3	14.1	35
0.80	2	20.2	35

*Based on computer simulations; see legend to Fig. 3. †Calculated from work/mole = $RT \ln (r_{\text{leaf surface}}/r_{\text{leaf interior}})$. The leaf surface vapor pressure was calculated from a surface salt concentration of $20.45 \mu\text{mole of NaCl per square centimeter}$ and the water volumes were obtained from approximations of Raoult's law. The tissue water potential was set at -1.5 MPa or relative vapor pressure of 0.99. This is the leaf water potential measured at dawn with thermocouple psychrometers. ‡Calculated on the basis of a measured (as CO_2) respiration rate at 20°C of $0.149 \mu\text{mole cm}^{-2} \text{ hour}^{-1}$, and if 50 percent of the energy released is available for work. Respiration rates were measured on plants grown at a coastal habitat in northern California (Hodega Head) with a thermal regime similar to that at Pan de Azucar. Measurements were made with an infrared gas analysis system (13).

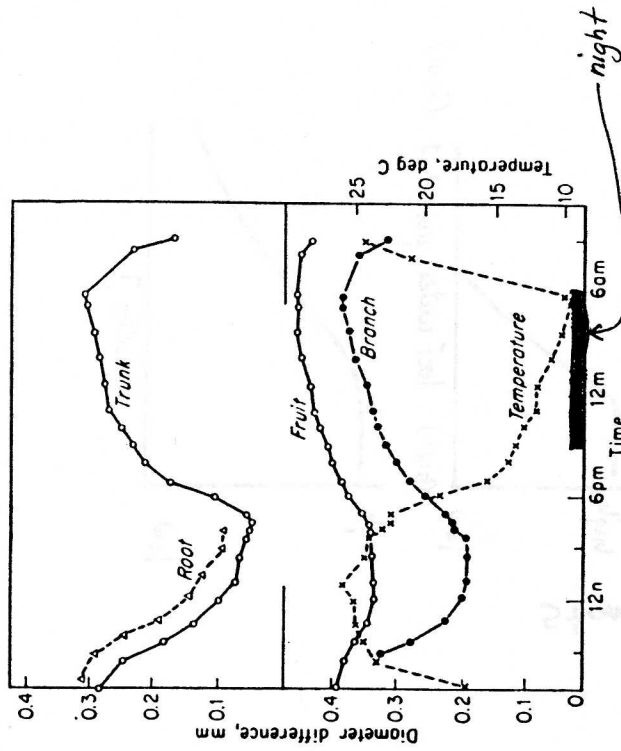
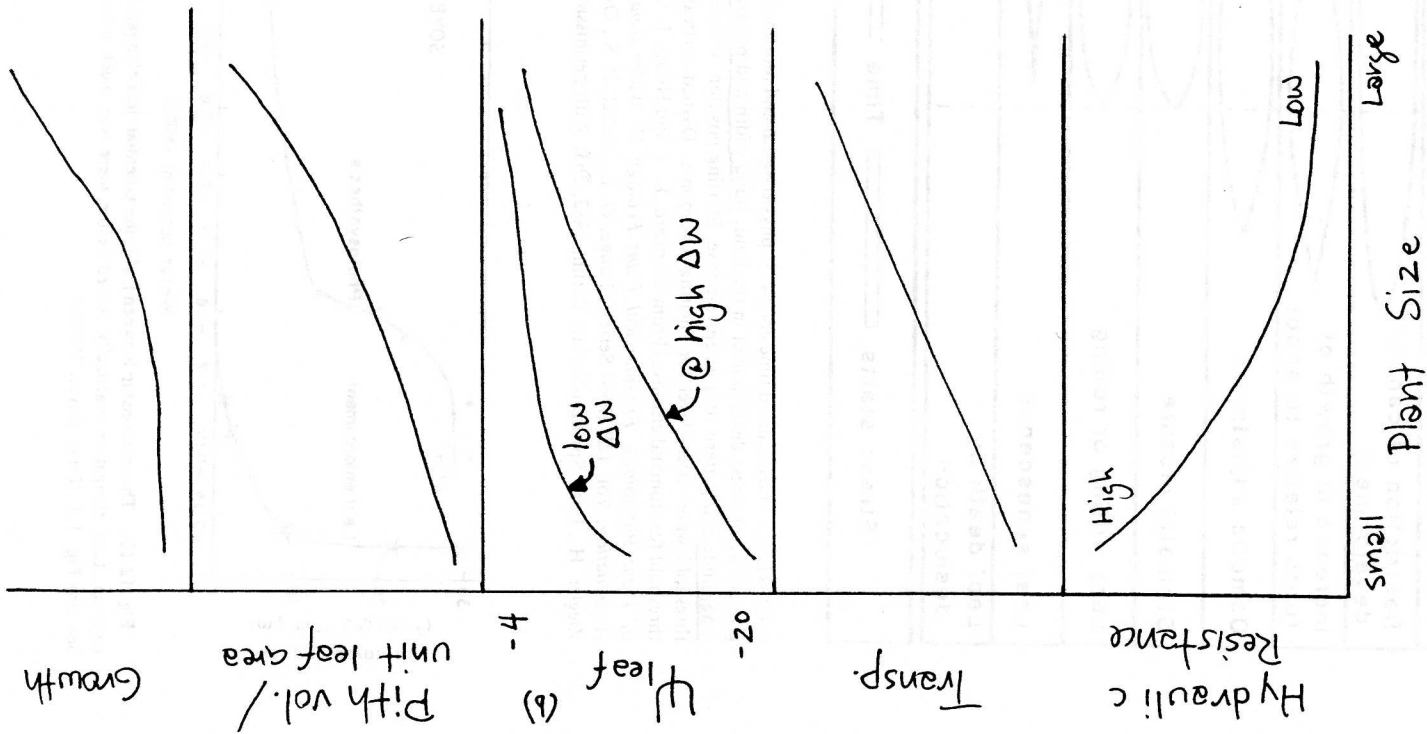


Fig. 12.4. Midday shrinkage of various parts of an avocado tree caused by rapid transpiration. (From Schroeder and Wieland, 1956.)

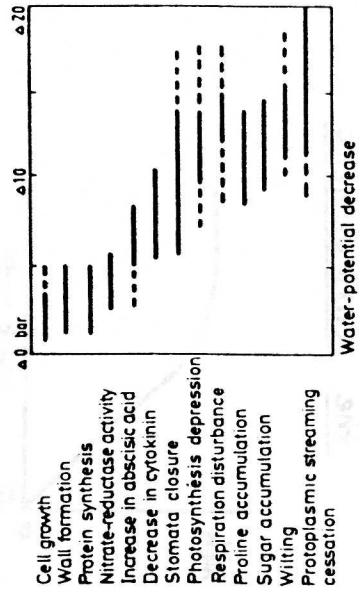


Fig. 5.34. Sensitivity of cell functions to water deficiency, and changes in the plant as it dries out. The lines indicate the range in which a clear effect begins to appear in most plant species. The measure of desiccation stress used here is the change in water potential as compared with that when there is a good supply of water. After Hsiao (1973), supplemented by data of Arvidsson (1951) and Kamiya (1959)

from:
Kramer, 1983

Stomatal responses to the environment

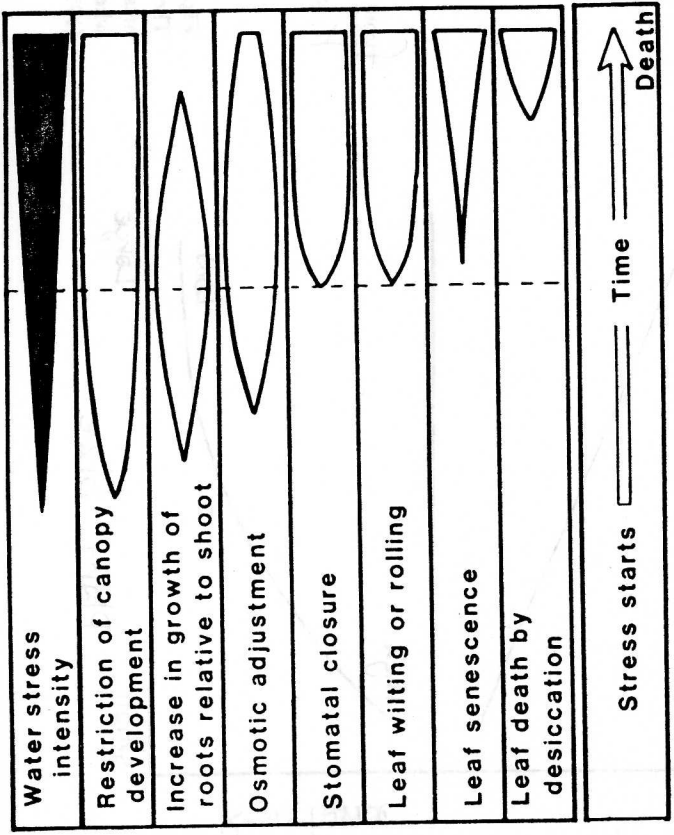
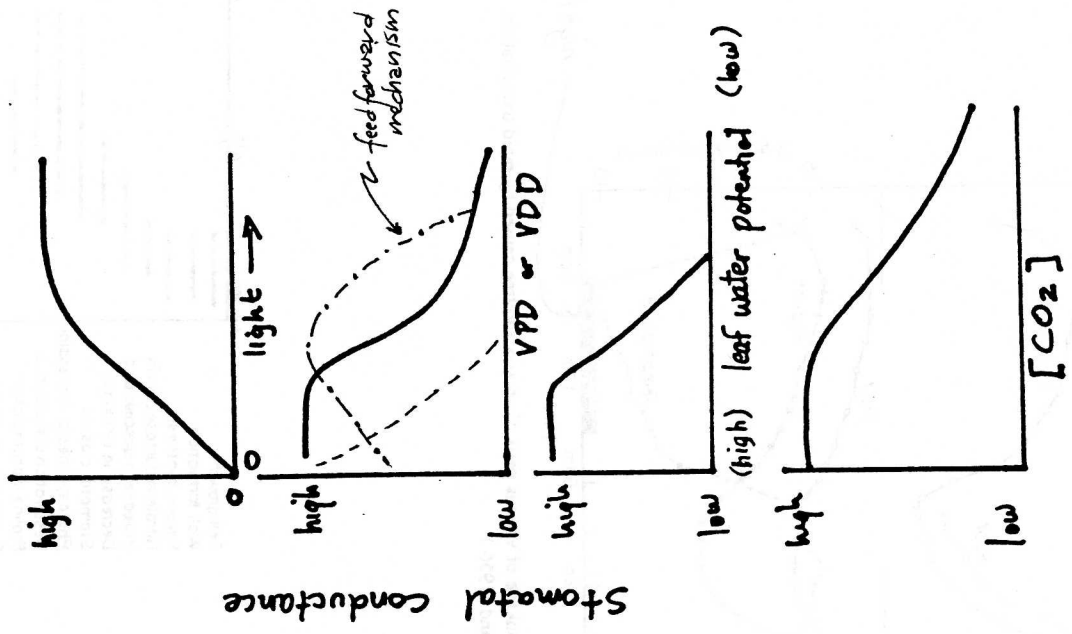


FIGURE 10. Generalized time course of physiological and morphological responses to gradual water stress development in the field. Band width and pattern indicates relative magnitude and pattern of a given response. Starting position of band indicates relative threshold water stress level for eliciting a response. Dashed vertical line indicates the threshold for stomatal closure. (From Bradford, K. J. and Hsiao, T. C., in *Encyclopedia of Plant Physiology, Physiological Plant Ecology II: Water Relations and Carbon Assimilation*, Vol. 12B (New Series), Lange, O. L., Nobel, P. S., Osmond, C. B., and Ziegler, H., Eds., Springer-Verlag, Berlin, 1982, 263. With permission.)

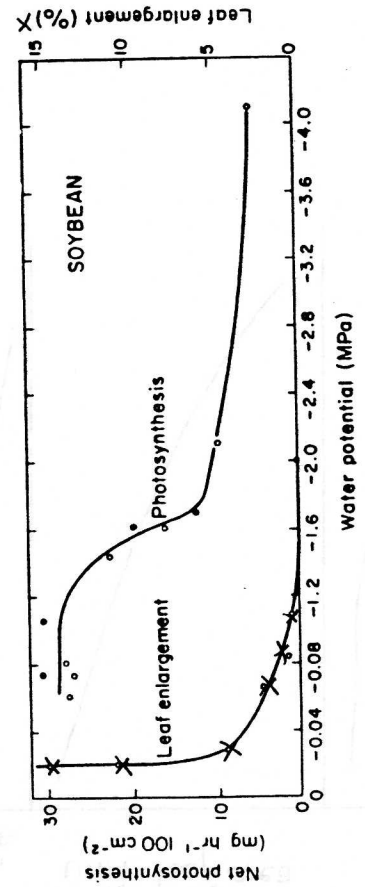


Fig. 12.10. The relationship between leaf water potential, leaf elongation, and photosynthesis in soybean. Leaf elongation practically ceased before there was much reduction in photosynthesis. See also Fig. 1.4. (From Boyer, 1970a.)

Fig. 5.19. Daily fluctuations in the transpiration of spruce shoots on a sunny August day which had been preceded by dry weather. With an inadequate supply of water, the shoots in the shade at the base of the crown first reduce their water loss, then the twigs in the sun at the lower margin of the crown, and finally the shoots in the sunny top of the crown. After Pisek and Tranquillini (1951)

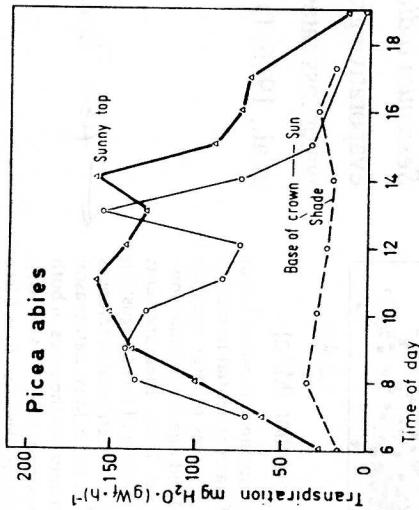


Fig. 5.20. Diurnal fluctuations in transpiration of savanna trees during the dry season. Both species have roots extending far enough into the ground to reach the ground water, but they are of different types with respect to water economy. After Vareschi (1960). Classical examples of changes in transpiration of woody plants in tropical and arid climates during the day are given in the following publications: trees of tropical rainforest, Stocker (1935b); savanna trees, Stocker (1970); oil palms, Ringoet (1952); cocoa trees, Lemée (1956); sclerophyllous shrubs in periodically dry regions, Killian (1931, 1932), Rouschal (1938), Ferri and Labouriau (1952), Grievé (1956), Hellmuth (1971), and Lange and Lange (1963)

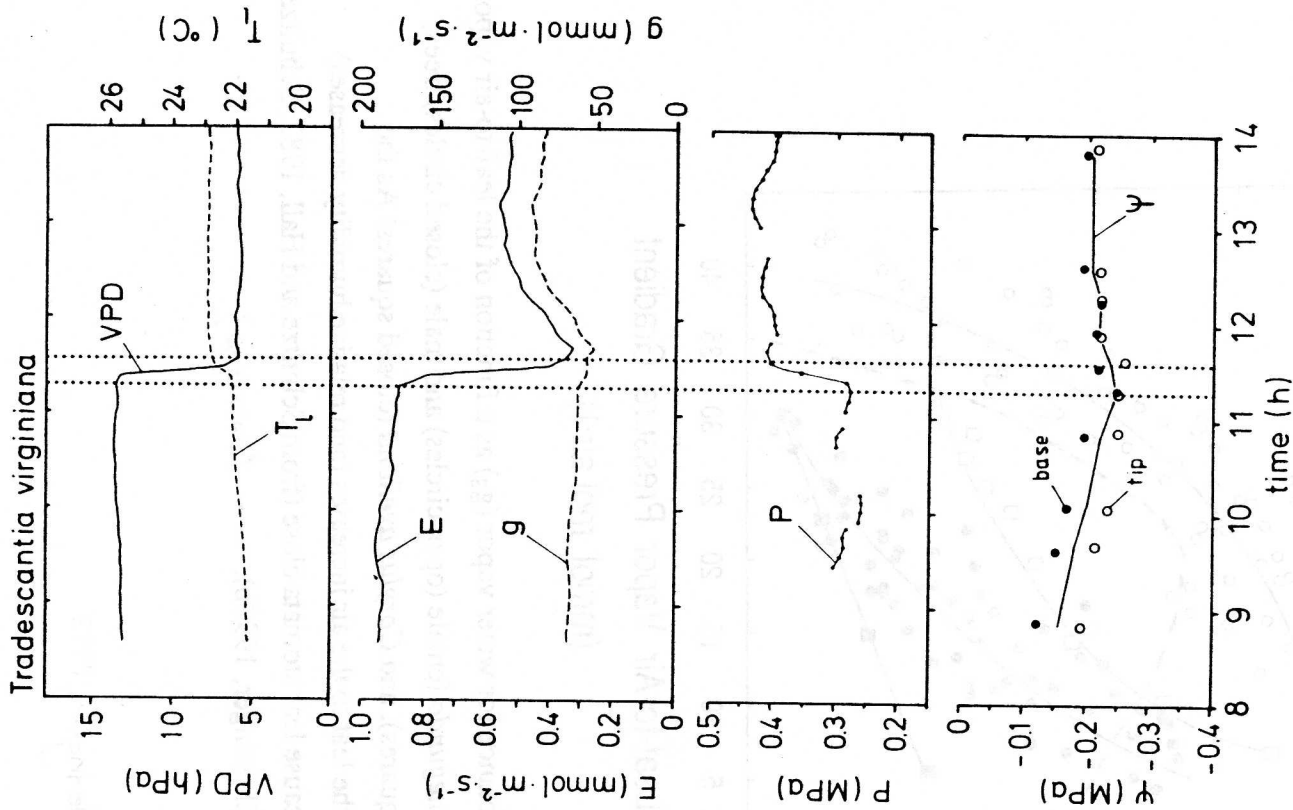
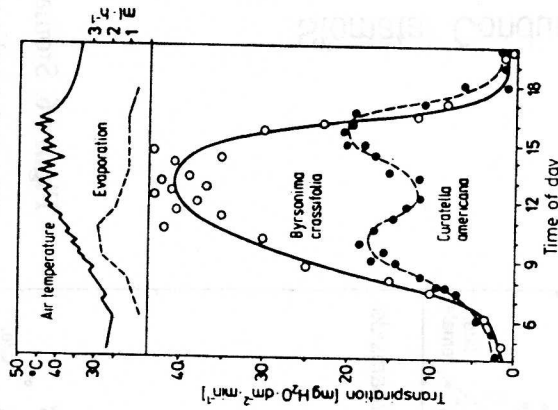


Figure 3 The effect of a step decrease in vapor pressure deficit VPD, on leaf transpiration E , leaf conductance g , turgor of epidermal cells P , and xylem water potential ψ , below (base) and above (tip) the point of turgor measurement. T_l : leaf temperature. The two dotted lines indicate the start (left) and the end (right) of the VPD change. Adapted from Shackel & Brinckmann (1116).

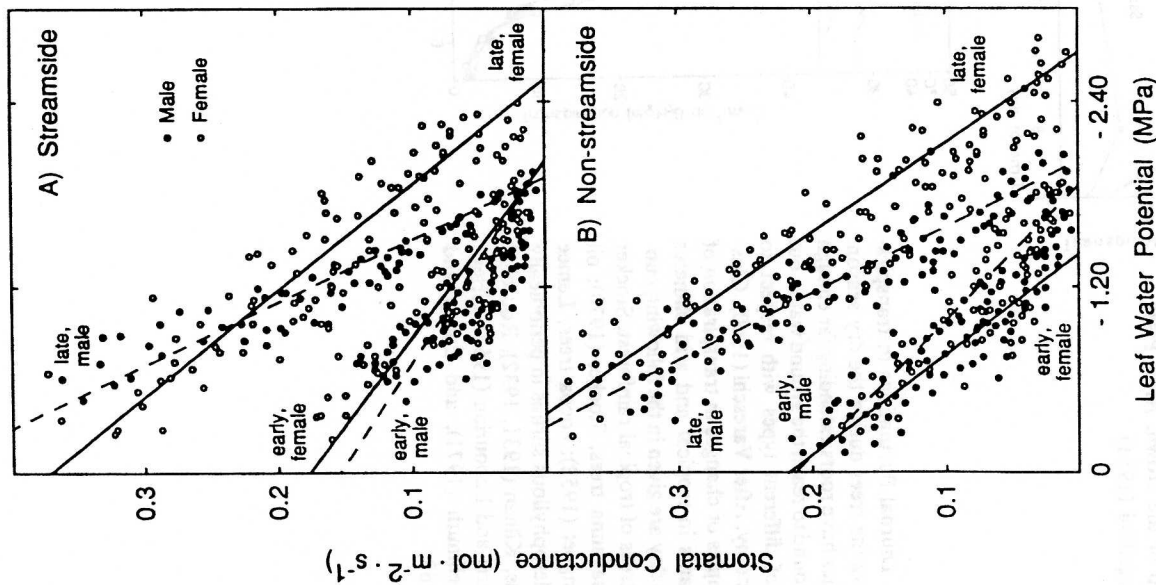


FIG. 3. The rate of stomatal conductance to water vapor as a function of the minimum leaf water potential in mature male (●, ---) and female (○, —) trees of *Acer negundo* inhabiting streamside (upper panel) and non-streamside (lower panel) sites in Red Butte Canyon, Utah. Measurements were made in the field, both early (May) and late (August) in the 1989 and 1990 growing seasons. No statistical differences were found between the sexes in either site in May. Late season responses were found to be different between the sexes in both sites (streamside, $P = .0489$; non-streamside, $P = .0501$). Significant differences between the sexes were also found (see Table 4).

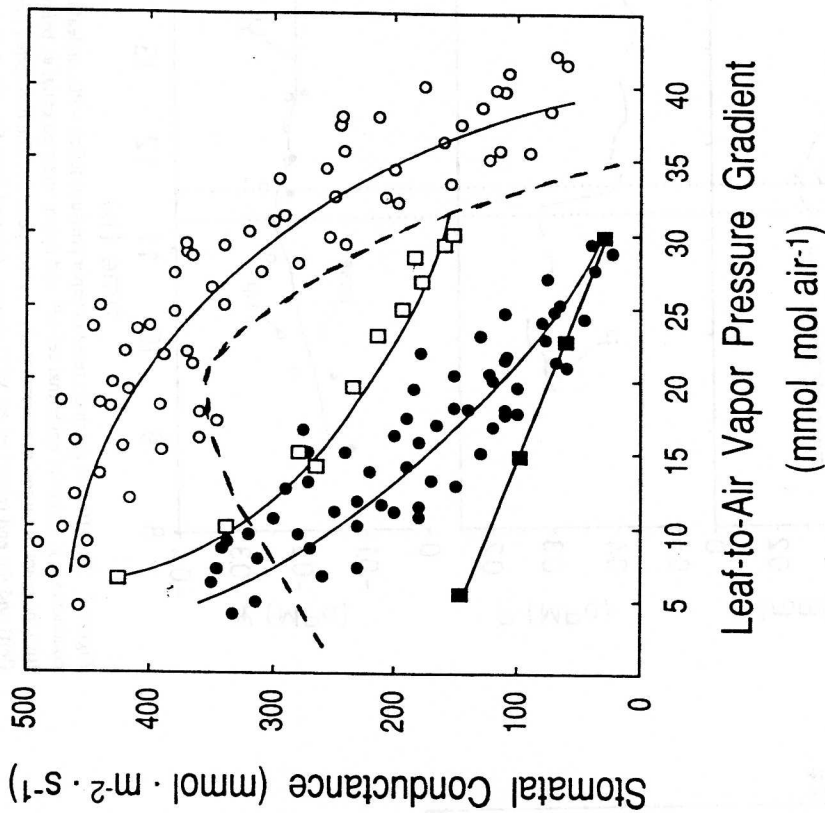


Figure 6. Stomatal conductance for water vapor (g_s) as a function of the leaf-to-air vapor pressure gradient for *Acer negundo* female (open circles) and male (closed circles) trees, *Sesamum indicum* (open squares), and *Corylus avellana* (closed squares). As the evaporative gradient from the leaf to the air increases (and relative humidity decreases) water loss rates decline because leaf stomata close (from Schultze and Hall, 1982; Schultze et al., 1986; Dawson and Ehleringer, 1993b). --- (*Salix spp.*)

← from Dawson & Ehleringer, 1993

from: Dawson & Ehleringer, 1993

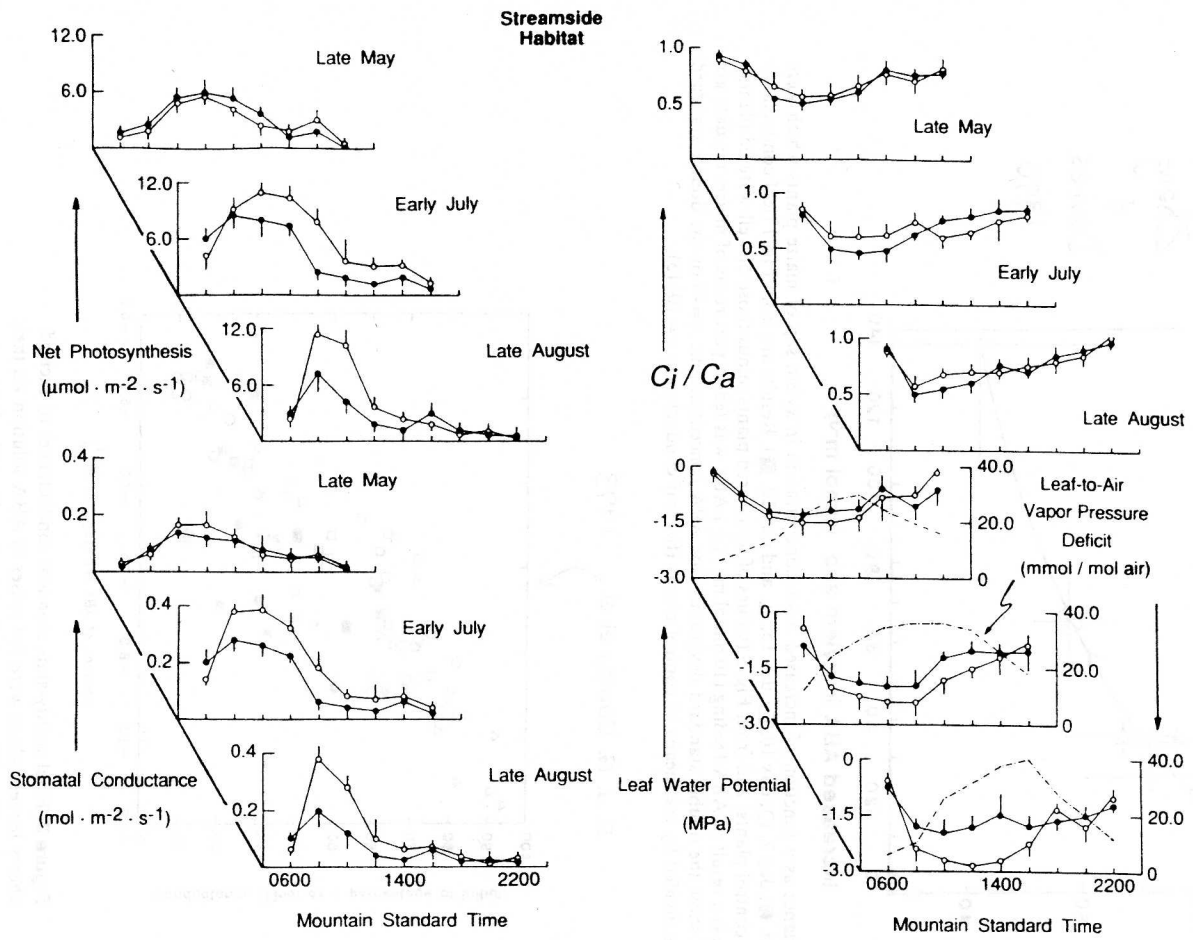


FIG. 2. Diurnal course of net photosynthesis (upper left), stomatal conductance (lower left), the ratio of the leaf internal (c_i) to ambient (c_a) CO_2 concentration (c_i/c_a ; upper right), and leaf water potential (lower right) for three periods during the 1989 growing season in mature male (●) and female (○) trees of *Acer negundo* inhabiting a streamside (wet) site in Red Butte Canyon, Utah. Other symbols as in Fig. 1.

from: Larcher, 1982

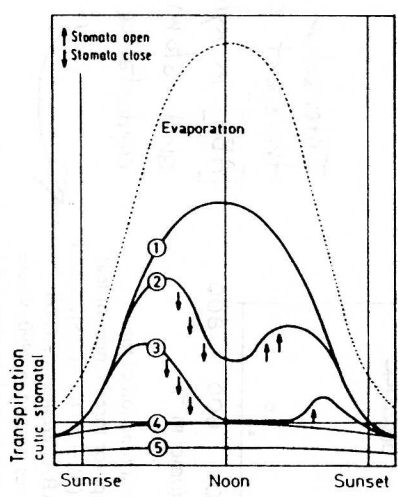


Fig. 5.27

Fig. 5.27. Diagram of daily changes in transpiration as it becomes progressively more difficult (curves 1–5) to maintain the water supply. The arrows indicate the stomatal movements elicited by changes in the water balance. The stippled area shows the range in which transpiration is exclusively cuticular. 1, unrestricted transpiration; 2, limitation of transpiration at noon as the stomata begin to close; 3, full closure of the stomata at midday; 4, complete cessation of stomatal transpiration by permanent closure of the stomata (only cuticular transpiration continues); 5, considerably reduced cuticular transpiration as a result of membrane shrinkage. After Stocker (1956). Recent review on response and adaption of plants to water stress (Turner and Begg, 1981)

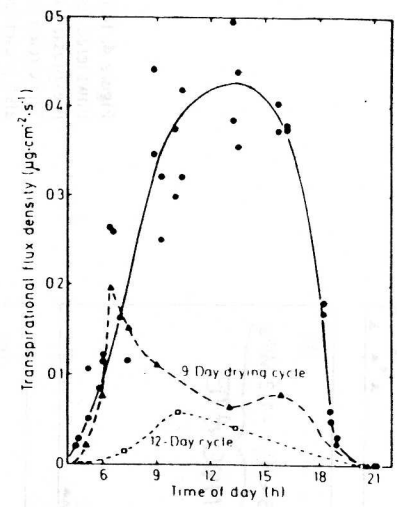


Fig. 5.28

Fig. 5.28. Diurnal changes in transpiration of two-year-old seedlings of *Pinus radiata* during progressive drying of the soil. From Kaufmann (1977). For restriction of transpiration due to drying in eucalyptus trees see Gindl (1973); in avocado trees, Sterne et al. (1977)

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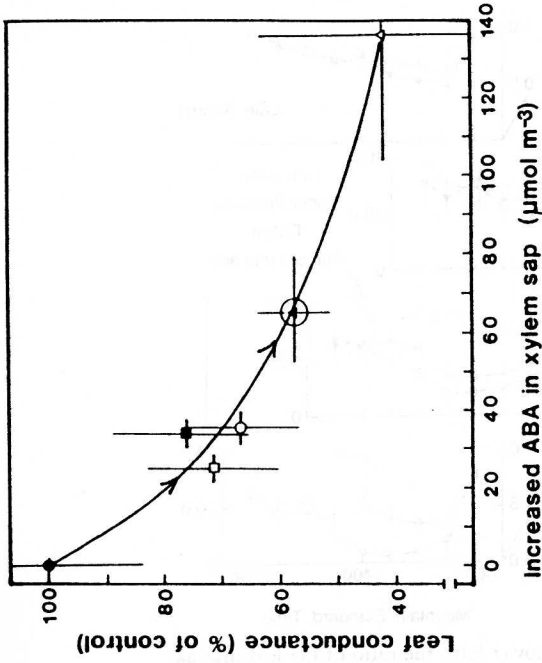


Figure 4. Relative leaf conductance as a function of increased ABA concentration in xylem sap of maize plants which were unwatered for up to 20 d (day 0, ●; day 7, ○; day 15, △; and day 20, ■). Results are from Fig. 1 (leaf conductance is expressed as a percentage of control plants) and from Fig. 3 (values of unwatered plants minus those of well-watered plants). The circled point in the middle is a result of ABA feeding (10 mmol m^{-3} (\pm)-ABA was fed to part roots of maize, the data are also presented in Fig. 7). Bars show the double standard deviations (for ABA concentrations, $n=4$) or the double standard deviations of unwatered plants divided by the means of control plants (for leaf conductance, $n=10-15$).

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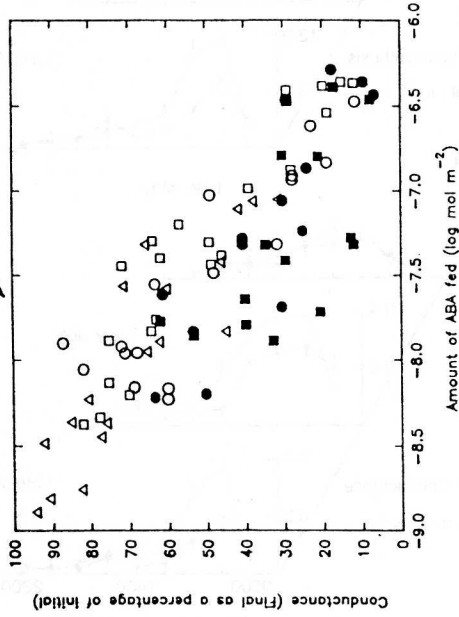


Figure 3. Final steady-state stomatal conductances of excised cherry leaves, which were fed pulses of ABA solution via their petioles. The different symbols show the effect of ABA concentration in the feeding solution on the relationship between final conductance and the amount of ABA entering the leaf: (■) 300; (●) 100; (□) 10; (○) 3; and (△) 3 mmol m^{-3} . Each point represents an individual leaf.

Interaction between
transport capacity,
[ABA] in xylem
and stomata
conductance (gs)

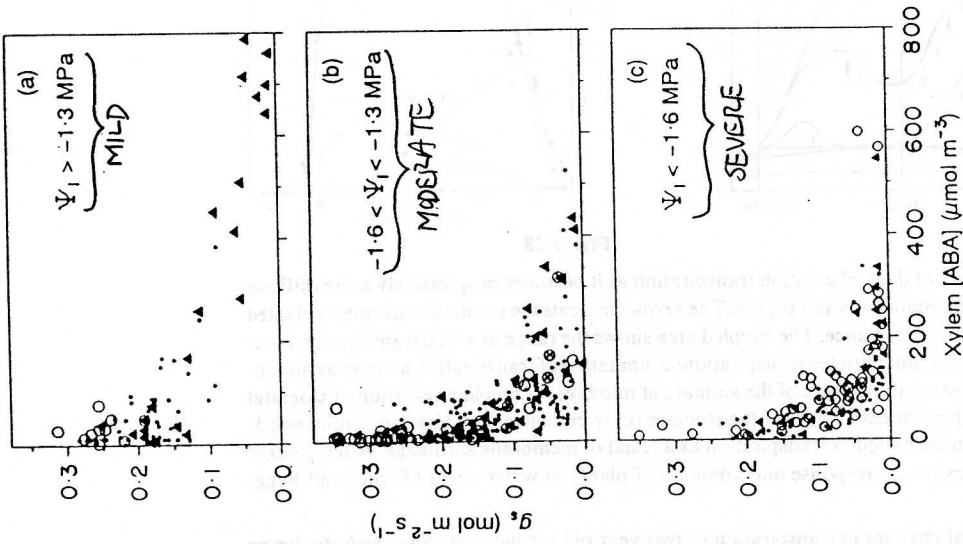


Figure 5. Stomatal conductance (g_s) as a function of the concentration of ABA in the xylem sap, for three ranges of leaf water potential (Ψ_1): (a) $> -1.3 \text{ MPa}$; (b) -1.6 to -1.3 MPa ; and (c) $< -1.6 \text{ MPa}$. Leaves with xylem [ABA] greater than $800 \text{ } \mu\text{mol m}^{-3}$ are not presented. (●) Leaves studied in 1990, where variations in Ψ_1 correspond to change with time of the day; (▲) fed plants; (●) rainfed plants; (○, ⊗) plants protected from the rain by a mobile shelter, sampled in the afternoon (air VPD $> 2 \text{ kPa}$) or in the early morning (air VPD approximately 1 kPa , PPF $> 800 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$), respectively. Each point represents coupled values corresponding to one leaf.

from: Tardieu et al. 1993

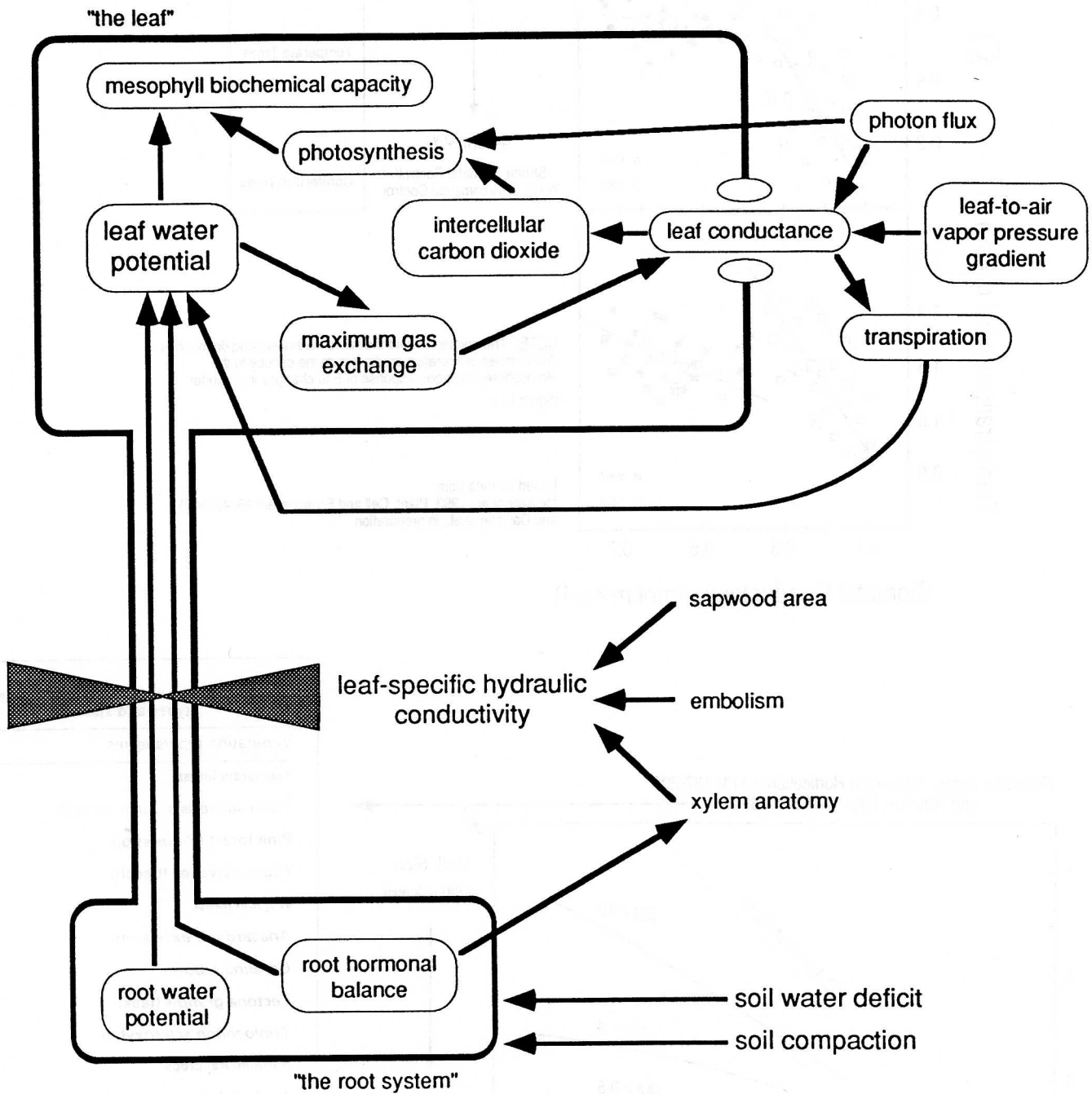


Figure 4. A conceptual model of the influences that hydraulic architecture and root hormonal balance on the regulation of plant water use and carbon fixation. Plants exposed to soil water deficits (or compaction) may use a combination of both hydraulic and hormonal responses to mediate leaf gas exchange.

(after Dawson, unpublished)

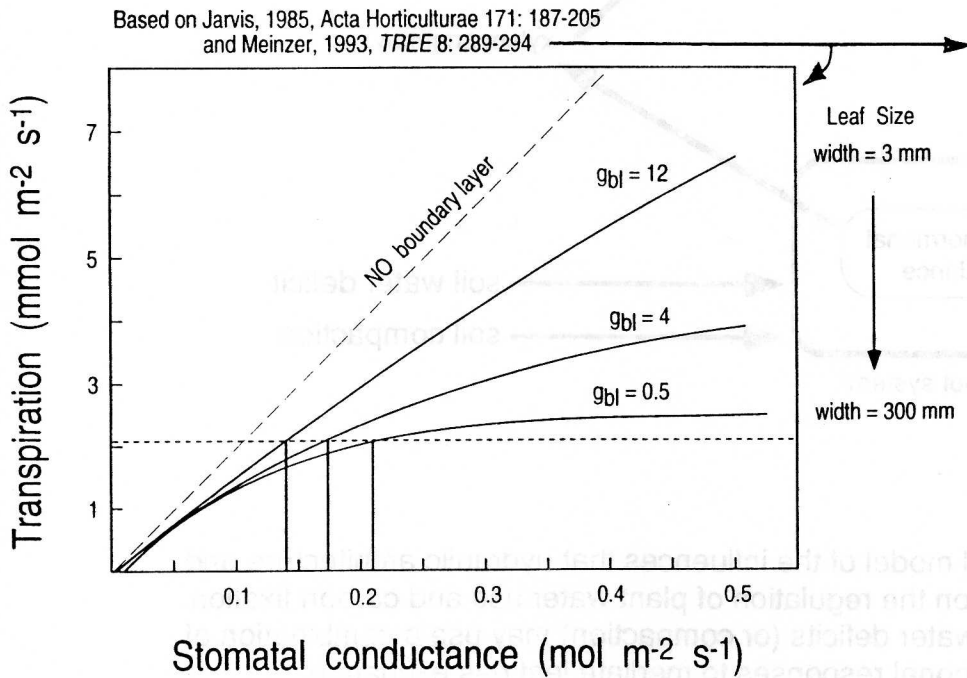
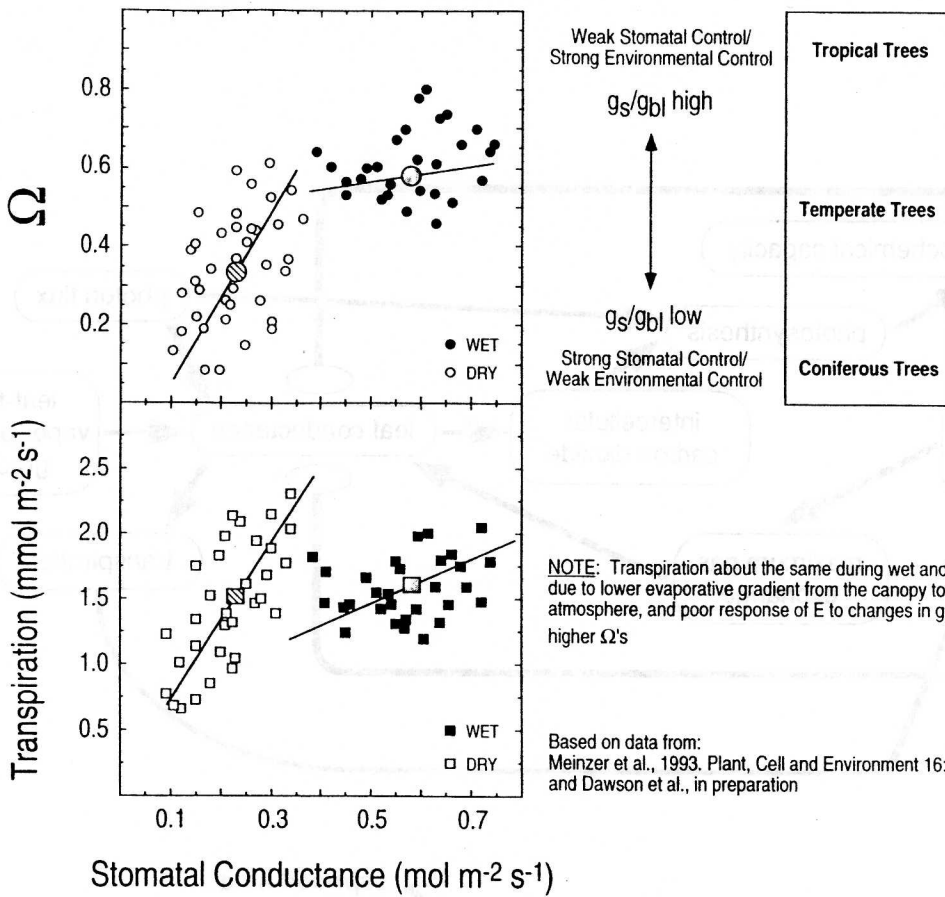


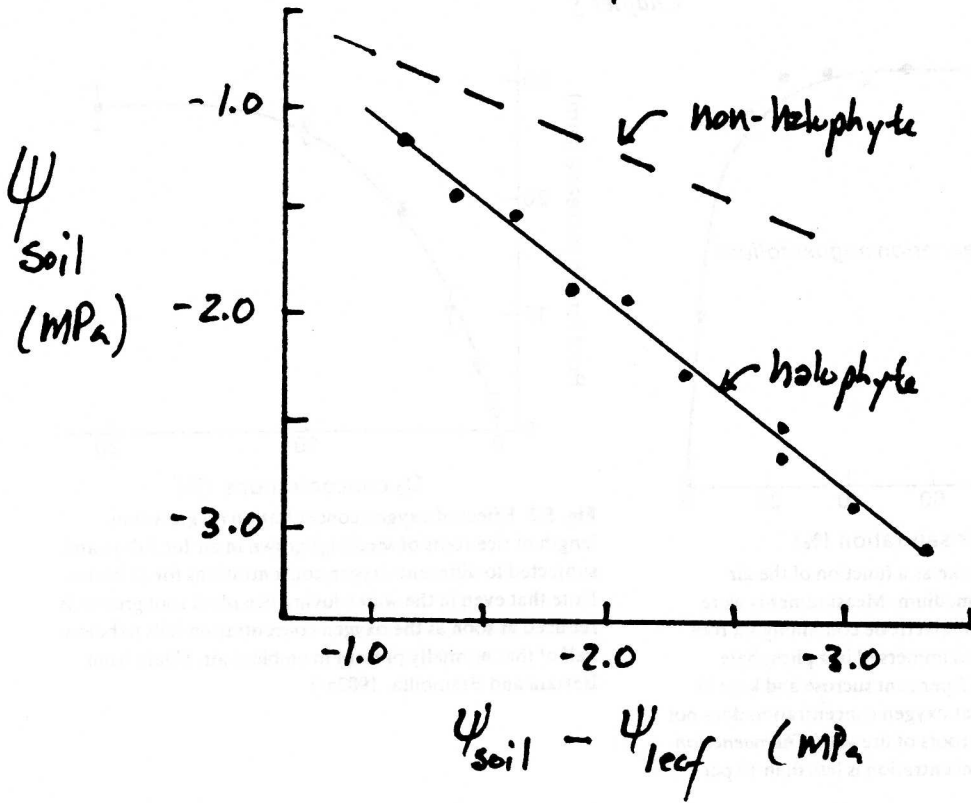
Table 1. Values of Ω for different vegetation types and species^a

Vegetation type/species	Ω^b
Temperate forest	
<i>Picea sitchensis</i> (Sitka spruce)	0.1
Pine forest (<i>Pinus</i> spp.)	0.1
<i>Fagus sylvatica</i> (beech)	0.2
Tropical forest	
<i>Anacardium excelsum</i>	0.6
<i>Gmelina arborea</i>	0.9
<i>Tectona grandis</i> (teak)	0.9
<i>Triplochiton scleroxylon</i>	0.6
Horticultural crops	
Apple (<i>Malus sylvestris</i>)	0.3
Cherry (<i>Prunus serotina</i>)	0.1
Citrus (<i>Citrus</i> spp.)	0.3
Field crops	
Alfalfa (<i>Medicago sativa</i>)	0.9
Cotton (<i>Gossypium</i> spp.)	0.4
Sugarcane (<i>Saccharum</i> spp.)	0.9
Wheat (<i>Triticum aestivum</i>)	0.6

^aData from Refs 1,9-11.

^bValues are estimated averages over various ranges of stomatal conductance and wind speed.

adapted from Kramer, 1983



From: Crawford, 1989

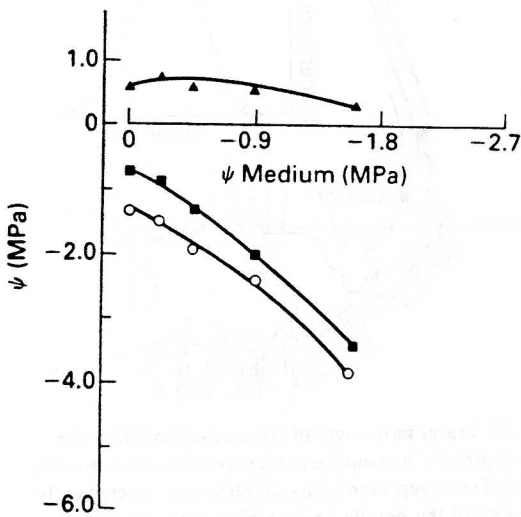


Fig. 6.21 Leaf water potential and component potentials in sea scurvy grass (*Cochlearia officinalis*) grown at different salinities: Leaf $\psi = \blacksquare$; $\psi_s = \circ$; $\psi_p = \blacktriangle$. (Reproduced by courtesy of Professor G.R. Stewart.)

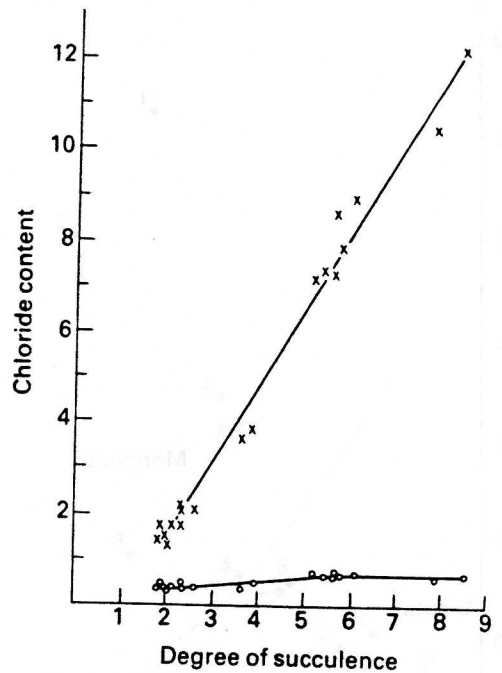


Fig. 6.20 The effect of succulence in reducing tissue chloride in leaves of the mangrove *Laguncularia racemosa* is illustrated in the manner in which the leaf content of salt is expressed: x = mmol δm^{-2} of leaf surface and shows as chloride content rises succulence increases; o in mmol g^{-1} of sap which remains constant due to the increased volume of the leaf with increasing succulence. (Redrawn with permission from Kinzel, 1982.)

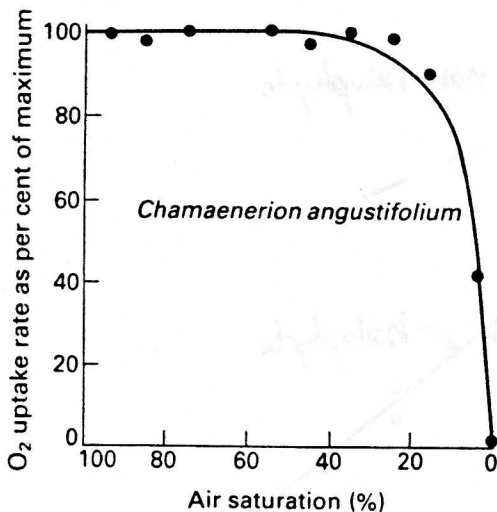


Fig. 5.2 Root oxygen uptake as a function of the air saturation of the bathing medium. Measurements were made using a Clark oxygen-electrode containing six root tips 1 cm each in length and immersed in a phosphate buffer pH 6.0 (0.1M) with 2 per cent sucrose and kept at 20°C. The figure shows that oxygen concentration does not limit the rate of uptake in roots of fireweed *Chamaenerion angustifolium* until the concentration is less than 10 per cent of air saturation.

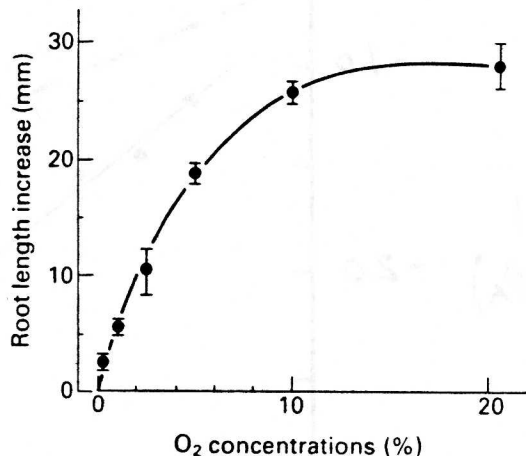


Fig. 5.3 Effect of oxygen concentration on growth in length of rice roots of seedlings grown in air for 3 days and subjected to different oxygen concentrations for 24 hours. Note that even in the water-loving rice plant root growth is reduced as soon as the oxygen concentration falls to below half of that normally present in ambient air. (Data from Bertani and Brambilla, 1982a.)

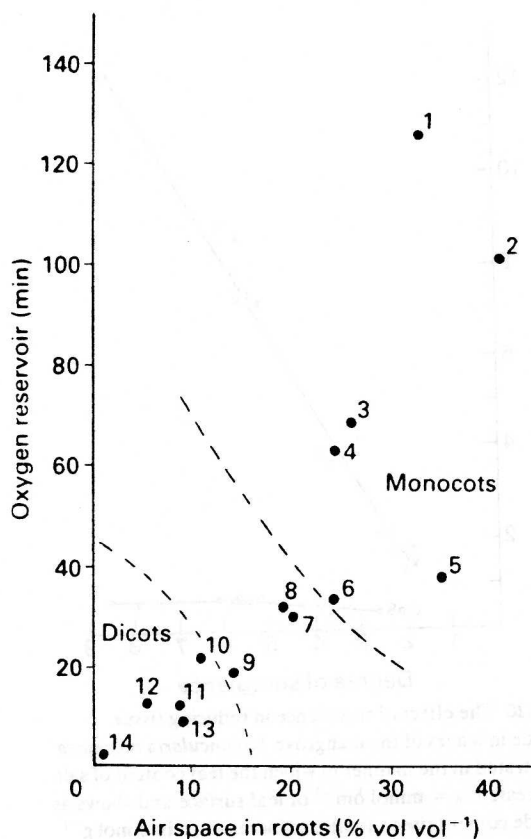


Fig. 5.25 Relationship between the capacity of the oxygen reservoir in roots to maintain aerobic respiration at the normal rate in air and the percentage air space in the roots of a number of wetland species.

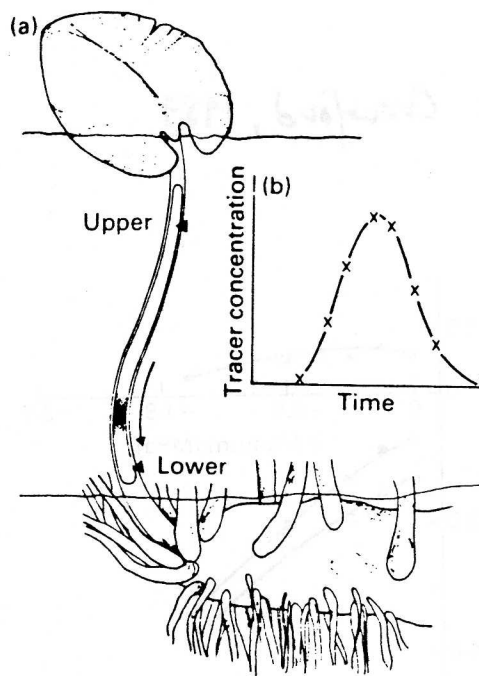


Fig. 5.26 Tracer movement of ethane used to follow the influx of air into the young emergent petioles of a water lily leaf. (a) Tracer represented by stippling was injected at the upper end of the petiole and sampled at the lower end. (b) The plot of tracer concentration as a function of time at the sampling point took the form of a typical elution curve seen in gas chromatography. The volume rate of gas flow was calculated and the elution curve integrated to show that virtually all the injected tracer passed the sampling point. The direction of gas flow was reversed in the older emergent (efflux) petioles. (Reproduced with permission from Dacey, 1980.)

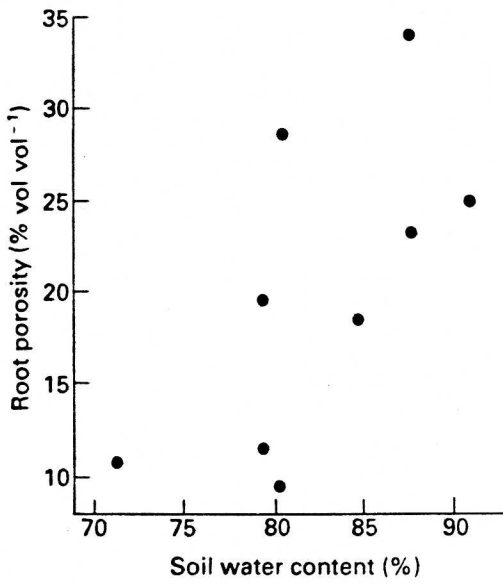
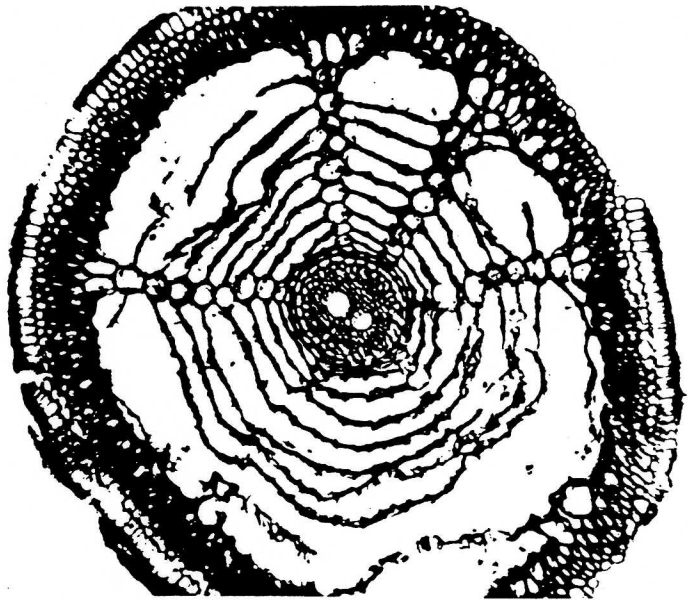
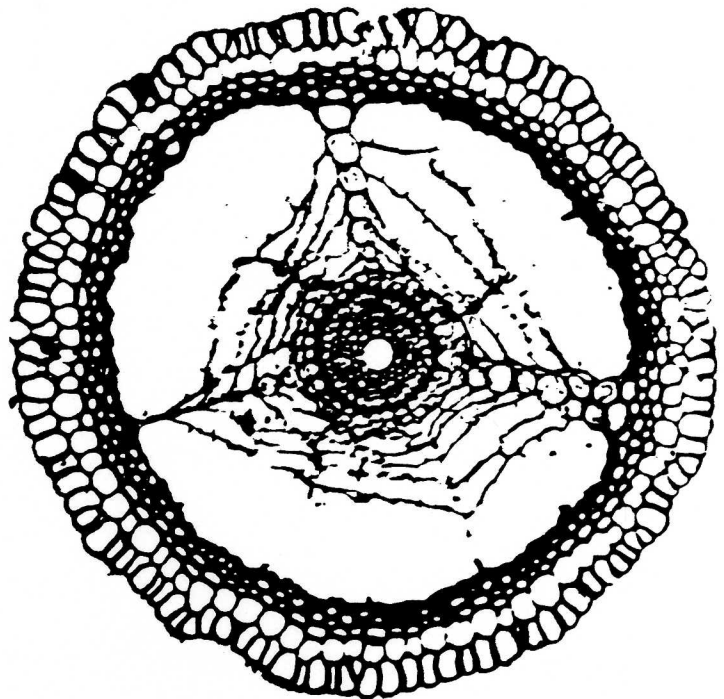


Fig. 5.7 The relationship between soil water content and the air space of root systems of *Senecio aquaticus* plants growing in an Orkney valley mire. (Reproduced from Smirnov and Crawford, 1983.)

Crawford
1989



(a)



(b)

Fig. 5.8 Transverse sections of roots, taken from at least 2 cm behind the tip showing the structure of cortical aerenchyma in (a) *Eriophorum vaginatum* and (b) *Carex curta*. (Reproduced from Smirnov and Crawford, 1983.)