

## Leaf Energy Budgets

### I. Introduction: the concept of an energy 'budget'

- A. Leaves interact with above-ground physical environment in two ways:
1. energy exchange = light absorption, heat transfer
  2. mass exchange = transpiration (water loss), photosynthesis (CO<sub>2</sub> uptake), trace gas emissions (e.g. isoprene)
- B. Temperatures of plants vary within single ecosystem because of differences in energy exchange characteristics or differences in height within the microclimatic profile:
1. may result in temperature differences between plants (refer back to microclimate II lecture figures)
  2. may result in differences in rates of metabolic processes
  3. may result in variations in transpiration rates
- C. When leaves are at thermal equilibrium, leaf temperature (T<sub>l</sub>) does not change so that the rate of energy absorption by the leaf equals the rate of energy loss. The mass of the leaf can influence this. Once known, the Energy absorbed must = the energy lost as Re-radiation + Convection + Transpiration – we will review the “**terms**” of the energy balance equation first and then end by summarizing them in the full equation (see section VI below).

### II. Leaf orientation

- A. Changes in the orientation of the leaf relative to the sun (cos(i)) can affect the fraction of the direct solar radiation beam that is received by the leaf
- a. steep leaf angles (*Arctostaphylos*, *Simmondsia*, *Lomatium*, *Eucalyptus*)
  - b. sun leaves of tree have steeper leaf angles than do the shade leaves
  - c. wilting to vertical position and resulting angle change (*Helianthus*, *Impatiens*)
  - d. leaf concavity (*Ceanothus*)
  - e. leaf curling (many grasses)
  - f. stem orientation - barrel cactus facing south in northern hemisphere and vice versa
- B. Many of the leaf orientation characters can change under water stress (= low transpiration)
- a. increased leaf angle with water stress (*Ceanothus*; figure)
  - b. paraheliotropic leaf movements (*Lupinus*, *Medicago*, *Trifolium*, *Macroptilium*; figures)

### III. Leaf absorptance characteristics

- A. Surface characteristics that can reduce the fraction of the incident solar radiation absorbed; reduction in absorptance is caused by an increase in reflectance
1. hairs (*Artemisia*, *Encelia*, *Salvia*) (figure)
  2. waxes (*Eucalyptus*, *Dudleya*)
  3. epidermal bladders (*Atriplex*) (figure)
- B. Leaf absorption of solar radiation is 400-700 nm waveband (PAR) accounts for 50% of the total solar radiation absorbed by most leaves
- a typical leaf absorptance (400-700 nm) is for green leaves is 0.85 (= 85%)
- hairs, waxes or epidermal bladders can reduce PAR absorptance to 0.30
- C. Absorptance of solar radiation by leaves in 400-3,000 nm waveband averages 0.50 across many different leaf types (figure). Much of this absorptance is linked to water and how it absorbs in the near

infrared wavebands where the leaf does not;

$$a_{400-3000} = 0.73 \cdot a_{400-700} - 0.119$$

**IV. Transpiration**

A. Leaf transpiration rate (E) can be described using an electrical resistance [Ohm's Law] analogy

$$E = (e_l - e_a) / (r_s + r_a) = (e_l - e_a) \cdot g$$

where: g = total leaf conductance to water vapor; r<sub>s</sub> = stomatal resistance; r<sub>a</sub> = air boundary layer resistance; (e<sub>l</sub> - e<sub>a</sub>) = the water vapor gradient between inside the leaf (l) and the outside air near the leaf surface (a).

B. The saturated air water vapor pressure (also = leaf vapor pressure) rises exponentially with increasing temperature (figure)

C. Leaf conductance depends on density and diameter of stomatal pores (figure)

**Stomatal distributions**

*Wild plant species in a British woodland (Salisbury, 1928, Weyers and Meidner, 1990)*

Average # of Stomates per mm<sup>2</sup> of leaf area

life form	# of species	upper surface	lower surface
trees	26	0	223
shrubs	29	0	196
shade herbs	40	7	86
sun herbs	110	20	145

<i>Crop species</i>	upper surface	lower surface
<i>Avena sativa</i>	51	45
<i>Hordeum vulgare</i>	72	85
<i>Triticum vulgare</i>	50	40
<i>Zea mays</i>	98	108-200
<i>Helianthus annuus</i>	120	175
<i>Medicago sativa</i>	169	188
<i>Nicotiana tabacum</i>	50	190-235

<i>Tree Species</i>	upper surface	lower surface
<i>Pinus strobus</i>	28	121
<i>Acer saccharum</i>	66	182
<i>Acer negundo (male)</i>	65	189
<i>Acer negundo (female)</i>	59	255
<i>Populus fremontii</i>	26	310
<i>Salix alba</i>	111	128
<i>Quercus rubra</i>	9	144
<i>Banksia pryoroides</i>	22	92
<i>Eucalyptus regnans</i>	76	134
<i>Eucalyptus marginata</i>	109	105

V. **Convection**

A. Convection coefficient ( $h_c$ ) is related to the resistance in the boundary layer around a leaf to the turbulent transfer of heat as,

$$h_c = c_p \rho / r_a$$

where:  $c_p$  is the volumetric heat capacity of air,  $\rho$  is the density of air and the boundary layer resistance ( $r_a$ ) is a function of wind velocity (m/s), leaf width (m), and leaf shape ( $k_1$  - a value near 4.0) as,

$$r_a = k_1 \sqrt{\text{leaf width} / \text{wind velocity}}$$

B. Boundary layer decreases with increasing wind speed (figures)

C. Boundary layer decreases also with (figures):

1. decreased leaf size
2. increased leaf serration
3. increased leaf lobing
4. compound leaves

D. Effective heat transfer across the boundary layer decreases with leaf size (figure)

E. Leaf size decreases with increasing water stress:

1. leaf tearing (*Musa*)
2. lobed leaves (sun x shade)
3. pinnate and compound leaves
4. filiform leaves
5. seasonal leaf dimorphism (*Brassica*)

VI. **Energy budget equation**

A. As noted above in section I. We draw the abovementioned terms together in the form of the Energy Balance Equation that states, at thermal equilibrium, leaf temperature does not change and the rate of energy absorption by the leaf equals the rate of energy loss (influenced by mass). Therefore, Energy absorbed = Re-radiation + Convection + Transpiration ( $W m^{-2}$ ):

$$\underbrace{a \cdot \cos(i) \cdot S_{\text{direct}} + [a \cdot S_{\text{diffuse}}] + \epsilon \cdot R}_{\text{Energy in}} = \underbrace{\epsilon \cdot \sigma \cdot (T_l + 273)^4 + h_c \cdot (T_l - T_a) + k \cdot L \cdot (e_l - e_a) \cdot g_{\text{tot}}}_{\text{Energy out (@ equilibrium)}}$$

external parameters:

- $S_{\text{direct}}$  - incident direct solar radiation on leaf (300-4,000 nm)
- $S_{\text{diffuse}}$  - incident diffuse solar radiation on leaf (300-4,000 nm)
- R - terrestrial infrared radiation (includes both sky and ground components) (4,000-100,000 nm)
- T - temperature of leaf ( $T_l$ ) and air ( $T_a$ ) in °C
- e - water vapor pressure of leaf ( $e_l$ ) and air ( $e_a$ ) (mbar)

constants:

- $\sigma$  - Stephan Boltzman constant (blackbody radiation constant- see Appendix I)
- k - constant for vapor pressure to vapor density conversion (216.68)
- L - latent heat of vaporization (converts transpiration to energy units)

leaf parameters (coupling factors):

- cos(i) - cosine of leaf orientation to the sun's direct beam (last lecture)
- a - absorption coefficient to solar radiation (300-4,000 nm)
- $\epsilon$  - absorption coefficient to infrared radiation (4,000-100,000 nm) = emissivity (see Appendix I)
- $h_c$  - convection coefficient (a function of leaf characteristics and wind velocity)
- $g_{tot}$  - total leaf conductance (stomatal and boundary)

**Appendix I. Blackbody Radiation Laws**

1. Any object above 0° K will emit radiation
2. The amount of radiation emitted will be proportional to the fourth power of the object's temperature;

$$R_1 = \epsilon\sigma T^4$$

$R_1$  = energy emitted (W m<sup>-2</sup>)

$\epsilon$  = emissivity (0.99; dimensionless)

$\sigma$  = Stephan-Boltzman constant (5.67 x 10<sup>-8</sup> W m<sup>-2</sup> K<sup>-1</sup>)

T = temperature (°K)

3. Weins Displacement Law - **wavelength** ( $\lambda$ ) of maximum emission ( $\lambda_{MAX}$ ; in nm) is:

$$\lambda_{MAX} = 2,897,000/T$$

e.g.	sun	6000 K	480 nm
	earth	283 K	10,200 nm

4. **emissivity** ( $\epsilon$ ) is a measure of how close an object is to being a perfect blackbody. HINT: compare the  $\epsilon$  values for polished metals to the oxidized values; an oxidized metal will have high  $\epsilon$  because of the presence of oxygen (O<sub>2</sub>) and the O<sub>2</sub> allows the bonds to rotate more freely, thereby emitting more heat at a range of wavelengths and increasing the metals  $\epsilon$  (below):

<u>materials</u>	<u>emissivity</u>
polished aluminum	.04
polished copper	.05
silver	.02
brass	.22
copper oxide	.78
new cast iron	.65
old cast iron	.80
asbestos	.96
red brick	.93
glass	.94
water	.95
quartz	.93
<u>materials</u>	<u>emissivity</u>
<u>soils</u>	
sand	.93-.95
loam	.96-.98
<u>leaves</u>	
<i>Gossypium hirsutum</i> (cotton)	.96
<i>Phaseolus vulgaris</i> (common bean)	.94

<i>Zea mays</i> (corn)	.94
<i>Acer saccharum</i> (sugar maple)	.94
<i>Quercus robur</i> (English oak)	.97
<i>Helianthus annuus</i> (sunflower)	.97

5. Sky is **not** a perfect blackbody; its emittance is a function of gas composition within the air column;

- a. CO<sub>2</sub> and methane are "greenhouse gases" absorbing infrared radiation
- b. emittance of sky is a function of water vapor content ( $\xi$ , mbar of vapor) (Brunt, 1939):

$$\xi_{\text{air}} = 0.53 + 0.06e^{0.5}$$

c. over the range of conditions typically found, Swinbank (1963) showed that the amount of IR radiation emitted from the sky ( $IR_{\text{sky}}$ , W m<sup>-2</sup>) is:

$$IR_{\text{sky}} = 1.2\sigma T_{\text{air}}^4 - 171$$

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## Leaf Energy Balance References:

- Althawadi, A.M., and J. Grace. 1986. Water use by the desert cucurbit *Citrullus colocynthis* (L.) Schrad. *Oecologia* 70:475-480.
- Arp, G.K. and D.A. Phinney. 1980. Ecological variations in thermal infrared emissivity of vegetation. *Env. Ex. Bot.* 20:135-148.
- Balding, F.R. and G.L. Cunningham. 1976. A comparison of heat transfer characteristics of simple and pinnate leaf models. *Bot. Gaz.* 137:65-74.
- Bergen, J.Y. 1909. Concavity of leaves and illumination. *Bot. Gaz.* 48:459-461.
- Bews, J.W. 1927. Studies in the ecological evolution of the angiosperms. New Phytologist Reprint No. 16, Wheldon and Wesley, Ltd., London. 134 p.
- Billings, W.D. and R.J. Morris. 1951. Reflection of visible and infrared radiation from leaves of different ecological groups. *Amer. J. Bot.* 38:327-331.
- Birbebak, R. and R. Birkebak. 1964. Solar radiation characteristics of tree leaves. *Ecology* 45:646-649.
- Böcher, T.W. 1944. The leaf size of *Veronica officinalis* in relation to geographic and environmental factors. *Dansk. Bot. Ark.* 11:1-20.
- Böcher, T.W. and M.C. Lewis. 1962. Experimental cytological studies on plant species. *Biol. Skr.* 11(5):1-25.
- Bone, R.A., D.W. Lee, and J.M. Norman. 1985. Epidermal cells functioning as lenses in leaves of tropical rain-forest shadeplants. *Appl. Optics* 24:1408-1412.
- Bright, D.N. 1928. The effects of exposure upon the structure of certain health plants. *J. Ecol.* 16:323-365.
- Campbell, G.S. 1977. An Introduction to Environmental Biophysics. Springer Verlag, Heidelberg. 159 pp.
- Carlson, R.E., D.N. Yarger, and R.H. Shaw. 1971. Factors affecting spectral properties of leaves with special emphasis on leaf water status. *Agron. J.* 63:486-489.
- Comstock, J.P., and B.E. Mahall. 1985. Drought and changes in leaf orientation for two California chaparral shrubs: *Ceanothus megacarpus* and *Ceanothus crassifolius*. *Oecologia* 65:531-535.
- Dadykin, V.P., S.A. Stanko, G.S. Gorbunova, and Z.S. Igumnova. 1957. Light assimilation by plants in Yakutsk and Tiksi. *Dokl. Akad. Navk. SSSR (Bot. Sci. Sect.)* 115:129-131.
- Dadykin, V.P. and V.P. Bedenko. 1960. Concerning the geographical variability of optical properties in plant leaves. *Dokl. Akad. Navk. SSSR (Bot. Sci. Sec.)* 134:212-214.
- Dean, J.M. and A.P. Smith. 1978. Behavioral and morphological adaptations of a tropical plant to high rainfall. *Biotropica* 10:152-154.
- Dolph, G.E. and D.L. Dilcher. 1980. Variation in leaf size with respect to climate in the tropics of the Western Hemisphere. *Bull. Torrey Bot. Club* 107:154-162.
- Dolph, G.E. and D.L. Dilcher. 1980. Variation in leaf size with respect to climate in Costa Rica. *Biotropica* 12:91-99.
- Drake, B.G., K. Raschke, and F.B. Salisbury. 1970. Temperature and transpiration resistance of *Xanthium* leaves as affected by air temperature, humidity, and wind speed. *Plant Physiol.* 46:324-330.
- Ehleringer, J.R. 1981. Leaf absorptances of Mohave and Sonoran Desert plants. *Oecologia* 49:366-370.
- Ehleringer, J.R. 1982. The influence of water stress and temperature on leaf pubescence development in *Encelia farinosa*. *Amer. J. Bot.* 69:670-675.
- Ehleringer, J.R. 1988. Changes in leaf characteristics of species along elevational gradients in the Wasatch Front, Utah. *Amer. J. Bot.* 75:680-689.
- Ehleringer, J.R., and C.S. Cook. 1988. Comparative ecophysiology of *Encelia farinosa* and *Encelia frutescens*. I. Energy balance considerations. *Oecologia* 76:553-561.
- Ehleringer, J., O. Björkman, and H.A. Mooney. 1976. Leaf pubescence: effects on absorptance and photosynthesis in a desert shrub. *Science* 192:376-377.
- Ehleringer, J., and O. Björkman. 1978. Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa*. *Oecologia* 36:151-162.
- Eller, B.M., N. van Rooyen, G.K. Theron, and N. Grobbelaar. 1983. Spectral properties of some plant species of the Sourish Mixed Bushveld. *A. Afr. J. Bot.* 3:43-49.
- Gates, D.M. 1962. Energy Exchange in the Biosphere. Harper and Row, New York. 151 p.
- Gates, D.M. 1965. Energy, plants, and ecology. *Ecology* 46:1-13.
- Gates, D.M. 1968. Energy exchange in the biosphere, p. 33-43. In F.E. Eckardt (ed.), *Functioning of terrestrial ecosystems at the primary production level*, UNESCO, Paris.
- Gates, D.M. 1968. Transpiration and leaf temperature. *Ann. Rev. Plant Physiol.* 19:211-238.
- Gates, D.M., and W. Tantraporn. 1952. The reflectivity of deciduous trees and herbaceous plants in the infrared

- to 25 microns. *Science* 115:613-616.
- Gates, D.M., H.J. Keegan, J.C. Schleter, and V.R. Weidner. 1965. Spectral properties of plants. *Appl. Optics* 4:11-20.
- Gausman, H.W., R.M. Menges, D.E. Escobar, J.H. Everitt, and R.L. Bowen. 1977. Pubescence affects spectra and imagery of silverleaf sunflower (*Helianthus argophyllus*). *Weed Sci.* 5:437-440.
- Geller, G.N., and W.K. Smith. 1982. Influence of leaf size, orientation, and arrangement on temperature and transpiration in three high-elevation, large-leaved herbs. *Oecologia* 53:227-234.
- Ghorashy, S.R., J.W. Pendleton, R.L. Bernard, and M.E. Bauer. 1971. Effect of leaf pubescence on transpiration photosynthetic rate, and seed yield of three near-isogenic lines of soybeans. *Crop Sci.* 11:426-427.
- Gottschlich, D.E., and A.P. Smith. 1982. Convective heat transfer characteristics of toothed leaves. *Oecologia* 53:418-420.
- Grace, J. and J. Wilson. 1976. The boundary layer over a *Populus* leaf. *J. Exp. Bot.* 27:231-241.
- Grace, J., F.E. Fasehun, and M. Dixon. 1980. Boundary layer conductance of the leaves of some tropical timber trees. *Plant, Cell and Environ.* 3:443-450.
- Idso, S., and D. Baker. 1967. Relative importance of reradiation, convection, and transpiration in heat transfer from plants. *Plant Physiol.* 42:631-640.
- Jones, H.G. 1992. *Plants and Microclimate*. Cambridge University Press, Cambridge. 323 pp.
- Kreith, F. 1965. *Principles of Heat Transfer*. International Textbook Co., Scranton, Pa.
- Lancet, R.T. 1960. The effect of surface roughness on the convection heat transfer coefficient for fully developed turbulent flow in ducts with uniform heat flux. *Trans ASME Ser. C.* 81:168-174.
- Lee, D.W., and R. Graham. 1986. Leaf optical properties of rainforest sun and extreme shadeplants. *Amer. J. Bot.* 73:1100-1108.
- Lewis, M.C. 1972. The physiological significance of variation in leaf structure. *Sci. Prog.* 60:25-51.
- Linacre, E.T. 1964. Determination of the heat transfer coefficient of a leaf. *Plant Physiol.* 36:687-690.
- Linacre, E.T. 1964. A note on a feature of leaf and air temperatures. *Agric. meteorol.* 1L66-72.
- Linacre, E.T. 1967. Further notes on a feature of leaf and air temperatures. *Archiv. Meteorol. Geophys. Bioklim.* 15:422-436.
- McMillen, G.G., and J.H. McClendon. 1979. Leaf angle: an adaptive feature of sun and shade leaves. *Bot. Gaz.* 140:437-442.
- Medina, E., M. Sobrado, and R. Herrera. 1978. Significance of leaf orientation for leaf temperature in an Amazonian sclerophyll vegetation. *Rad. Env. Biol.* 15:131-140.
- Miller, P.C. 1967. Leaf orientation and energy exchange in quaking aspen (*Populus tremuloides*) and gambell's oak (*Quercus gambellii*) in central Colorado. *Oecol. Plant* 2:241-270.
- Monteith, J.L. 1973. *Principles of Environmental Physics*. Edward Arnold, London. 241 pp.
- Mooney, H.A., J. Ehleringer and O. Björkman. 1977. The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra*. *Oecologia* 29:301-310.
- Moss, R.A., and W.E. Loomis. 1952. Absorption spectra of leaves. I. The visible spectrum. *Plant Physiol.* 27:370-391.
- Mulroy, T.W. 1979. Spectral properties of heavily glaucous and non-glaucous leaves of a succulent rosette-plant. *Oecologia* 38:349-357.
- Orshansky, G. 1938. Seasonal leaf dimorphism in *Ononis natrix*. *Palast. J. Bot.* 1:233-234.
- Parkhurst, D.F., P.R. Duncan, D.M. Gates, and F. Kreith. 1968. Wind-tunnel modeling of convection of heat between air and broad leaves of plants. *Agric. Meteorol.* 5:33-47.
- Parkhurst, D.F., and O.L. Loucks. 1972. Optimum leaf size in relation to environment. *J. Ecol.* 60:505-537.
- Parlange, J.Y., P.E. Waggoner and G.H. Heichel. 1971. Boundary layer resistance and temperature distribution on still and flapping leaves. *Plant Physiol.* 48:437-442.
- Pearman, G.I. 1965. Preliminary studies of the loss of heat from leaves under conditions of free and forced convection. *Austr. J. Bot.* 13:153-160.
- Pearman, G.I. 1966. The reflectance of visible radiation from leaves of some western Australian species. *Austr. J. Biol. Sci.* 19:97-103.
- Raschke, K. 1960. Heat transfer between the plant and the environment. *Ann. Rev. Pl. Physiol.* 11:111-126.
- Rosenberg, N.J. 1974. *Microclimate: The Biological Environment*. John Wiley and Sons, New York.
- Schwintzer, C.R. 1971. Energy budgets and temperatures of nyctinastic leaves on freezing nights. *Plant Physiol.* 48:203-207.
- Shaver, G.S. 1978. Leaf angle and light absorptance of *Arctostaphylos* species (Ericaceae) along elevational gradients. *Madrono* 25:133-138.
- Shul'gin, I.A. 1961. The optical characteristics of xeromorphy and succulence of plant leaves. *Dokl. Akad. Navk. SSSR (Bot. Sci. Sect.)* 134:218-226.

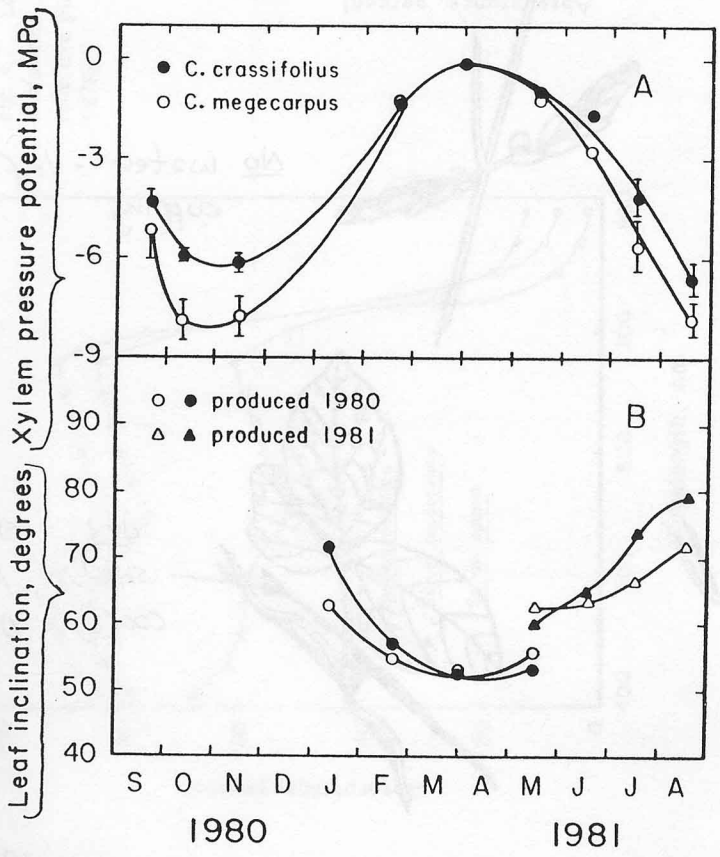
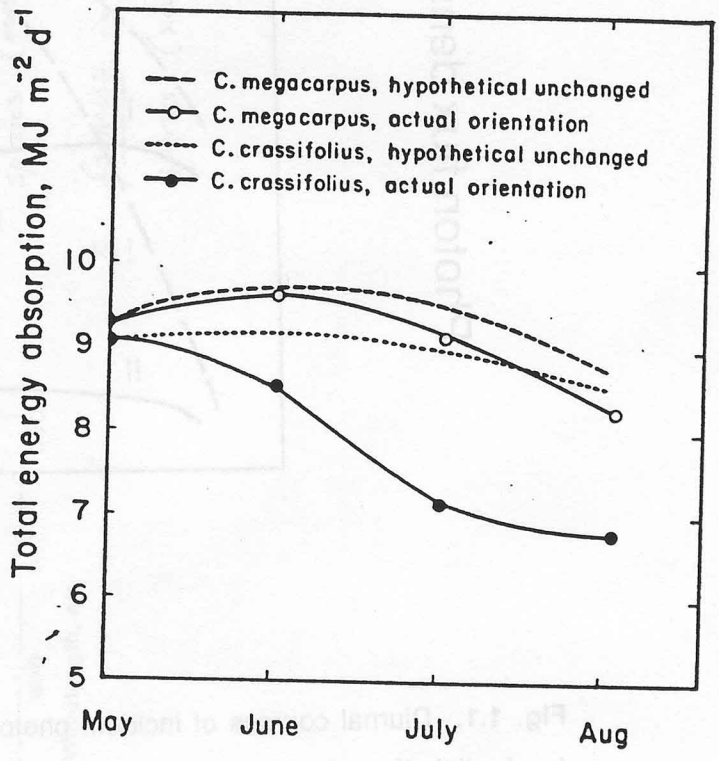
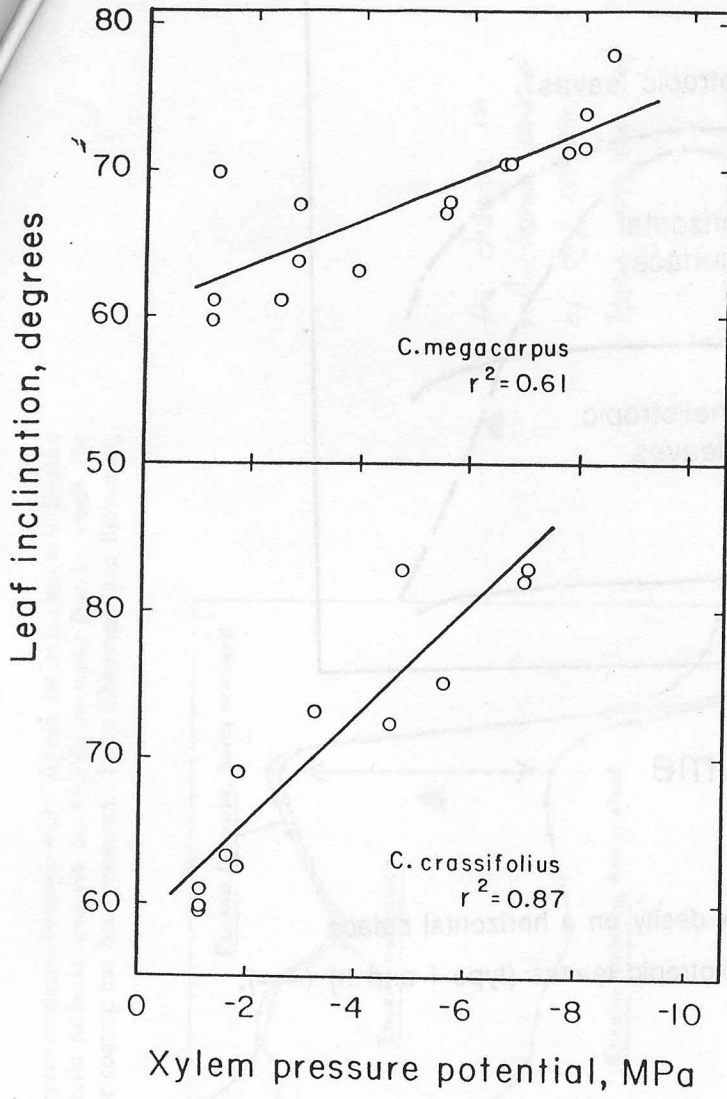


- Shull, C.A. 1929. A spectrophotometric study of reflection of light from leaf surfaces. *Bot. Gaz.* 87:583-607.
- Sinclair, R. 1970. Convective heat transfer from narrow leaves. *Austr. J. Biol. Sci.* 23:309-321.
- Sinclair, R., and D.A. Thomas. 1970. Optical properties of leaves of some species in arid south Australia. *Austr. J. Bot.* 18:261-273.
- Smith, W.K. 1978. Temperatures of desert plants: another perspective on the adaptability of leaf size. *Science* 201:614-616.
- Smith, W.K., and G.N. Geller. 1980. Leaf and environmental parameters influencing transpiration: theory and field measurements. *Oecologia* 46:308-313.
- Tageeva, S.V., and A.B. Brandt. 1961. Study of optical properties of leaves depending on the angle of light incidence, p. 163-169. In B. C. Christensen (ed.), *Progress in Photobiology*, Elsevier Publ. Co., Amsterdam.
- Tageeva, S.V., A.B. Brandt, and V.G. Derevyanko. 1961. Changes in the optical properties of leaves in the course of the growing season. *Dokl. Akad. Navk. SSSR (Bot. Sci. Sect.)* 135:266-268.
- Talbert, C.M., and A.E. Holch. 1957. A study of the lobing of sun and shade leaves. *Ecology* 38:655-658.
- Taylor, S.E., and O.J. Sexton. 1972. Some implications of leaf tearing in Musaceae. *Ecology* 53:143-149.
- Thomas, J.R., and H.W. Gausman. 1977. Leaf reflectance vs. leaf chlorophyll and carotenoid concentrations for eight crops. *Agron. J.* 69:799-802.
- Thorpe, M.R., and D.R. Butler. 1977. Heat transfer coefficients for leaves on orchard apple trees. *Boundary Layer Meteor.* 12:61-73.
- Vogel, S. 1968. 'Sun leaves' and 'shade leaves': differences in convective heat dissipation. *Ecology* 49:1203-1204.
- Vogel, S. 1970. Convective cooling at low air speeds and the shapes of broad leaves. *J. Exp. Bot.* 21:91-101.
- Werger, M.J.A., and G.A. Ellenbroek. 1978. Leaf size and leaf consistence of a riverine forest formation along a climatic gradient. *Oecologia* 34:297-308.
- Werk, K.S., and J.R. Ehleringer. 1984. Non-random leaf orientation in *Lactuca serriola* L. *Plant Cell Environ.* 7:81-87.
- Westman, W.E. 1981. Seasonal dimorphism of foliage in Californian coastal sage scrub. *Oecologia* 51:385-388.
- Whiteman, P.C., and D. Koller. 1967. Species characteristics in whole plant resistances to water vapor and CO<sub>2</sub> diffusion. *J. Appl. Ecol.* 4:363-377.
- Wiegand, K.M. 1910. The relation of hairy and cutinized coverings to transpiration. *Bot. Gaz.* 49:430-444.
- Wiegand, C.L., and W.A. Swanson. 1973. Time constants for thermal equilibrium of leaf, canopy, and soil surfaces with change in isolation. *Agron. J.* 65:722-724.
- Wolpert, A. 1962. Heat transfer analysis of factors affecting plant leaf temperature. Significance of hairs. *Plant Physiol.* 37:113-120.
- Wong, C.L., and W.R. Blevin. 1967. Infrared reflectance of plant leaves. *Austr. J. Biol. Sci.* 20:501-508.
- Wuenschel, J.E. 1970. The effect of leaf hairs of *Verbascum thapsis* on leaf energy exchange. *New Phytol.* 69:65-73.
- Zangerl, A.R. 1978. Energy exchange phenomena, physiological rates and leaf size variation. *Oecologia* 34:107-112.

#### Leaf Structure References:

- Bailey, I.W. and E.W. Sinnott. 1916. The climatic distribution of certain types of angiosperm leaves. *Amer. J. Bot.* 3:24-39.
- Chrysler, M.A. 1904. Anatomical notes on certain strand plants. *Bot. Gaz.* 37:461-464.
- Clements, E.S. 1904. The relation of leaf structure to physical factors. *Trans. Amer. Micr. Soc.* 26:19-102.
- Copeland, E.B. 1904. The variation of some California plants. *Bot. Gaz.* 38:401-426.
- Coulter, J.M., C.R. Barnes, and H.C. Cowles. A textbook of botany. Amer. Book Co., New York. 964 p.
- Dahlgren, R. 1971. Multiple similarity of leaf between two genera of Cape plants, *Cliffortia* L. (Rosaceae) and *Aspalathus* L. (Fabaceae) *Bot. Notiser* 124:292-304.
- Hanson, H.C., 1971. Leaf structure as related to environment. *Amer. J. Bot.* 4:533-560.
- Jackson, L.W.R. 1967. Effect of shade on leaf structure of deciduous tree species. *Ecology* 48:498-499.
- Jardeni, D. 1938. The dimorphism of *Ononis leiosperma* var. *tamarae*. *Palast. J. Bot.* 1:235-237.
- Lewis, M.C. 1969. Genecological differentiation of leaf morphology in *Geranium sanguinem* L. *New Phytol.* 68:481-503.
- McDougall, W.B. and W.T. Penfound. 1928. Ecological anatomy of deciduous forest plants. *Ecology* 9:349-353.
- Mooney, H.A., and A.T. Harrison. 1972. The vegetational gradient on the lower slopes of the Sierra San Pedro Martir in northwest Baja California. *Madrono* 21:439-445.
- Pease, V.A. 1917. Duration of evergreen leaves. *Amer. J. Bot.* 4:145-160.

- Raunkiaer, C. 1934. The Life Forms of Plants and Plant Geography. Clarendon Press, Oxford. 632 p.
- Schimper, A.F.W. 1903. Plant Geography upon a Physiological Basis. Clarendon Press, Oxford. 824 p.
- Shields, L.M. 1950. leaf xeromorphy as related to physiological and structural influences. bot. Rev. 16:399-447.
- Turesson, G. 1922. The genotypical response of the plant species to the habitat. Hereditas 3:211-350.
- Turesson, G. 1925. The plant species in relation to habitat and climate. Hereditas 6:147-236.
- Warming, E. 1909. Oecology of Plants. Oxford Univ. Press, Oxford.
- Webb, L.J. 1959. A physiognomic classification of Australian rain forests. J. Ecol. 47:551-570.
- Weyers, J.D.B. and H. Meidner. 1990. Methods in Stomatal Research. Longman Scientific & Technical
- Wylie, R.B. 1951. Principles of foliar organization shown by sun-shade leaves from ten species of deciduous dicotyledonous trees. Amer. J. Bot. 38:355-361.
- Yapp, R.H. 1912. *Spiraea ulmaria* L. and its bearing on the problem of xeromorphy in marsh plants. Ann. Bot. 26:815-870.



Ceanothus is a shrub  
widespread throughout  
California

from Comstock and Mehall  
(1985)

Photon flux density

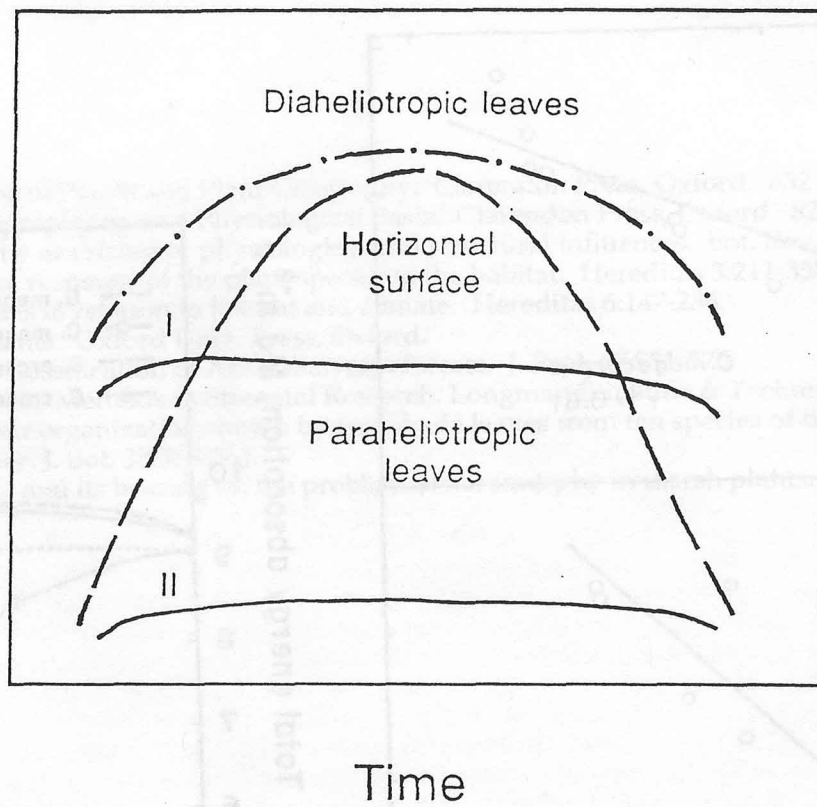
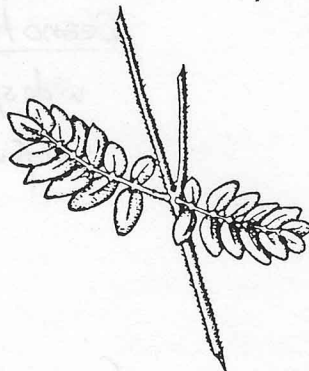


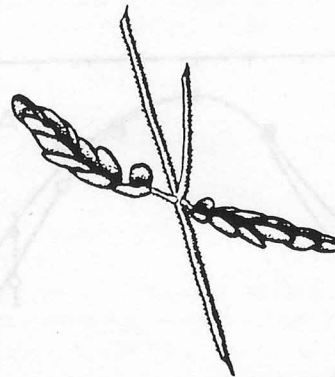
Fig. 1.1. Diurnal courses of incident photon flux density on a horizontal surface (---), diaheliotropic leaves (- • -), and paraheliotropic leaves (type I and II) (—).

Kalistromia (summer annual plant)

Well-watered

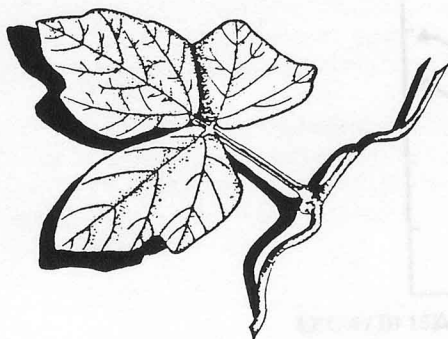


No water - leaf cupping

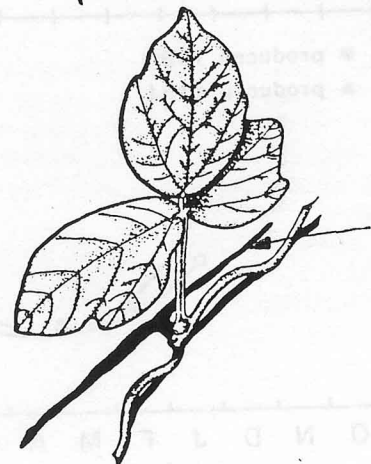


Macroptilion

Wet - large shadow, leaf flat on ground  
 $\cos(i) = 0.8$



dry - small shadow, leaf  
 $\cos(i) = 0.11$



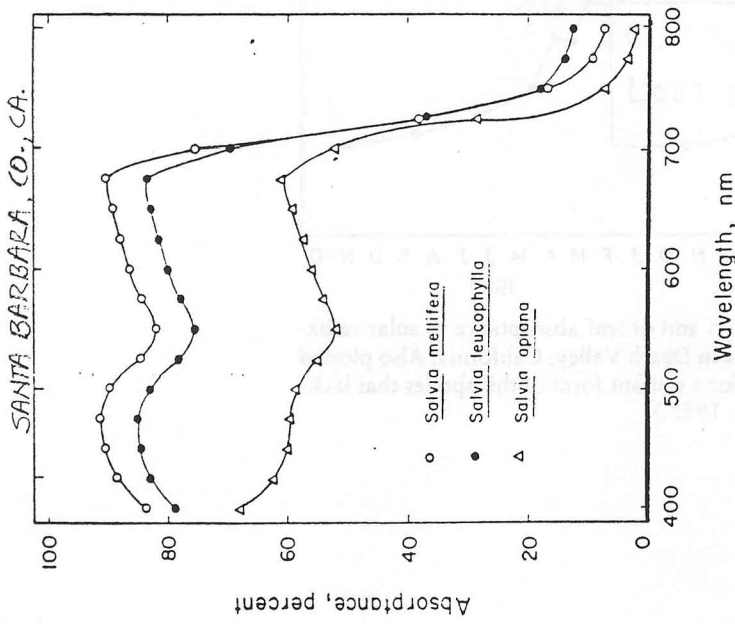
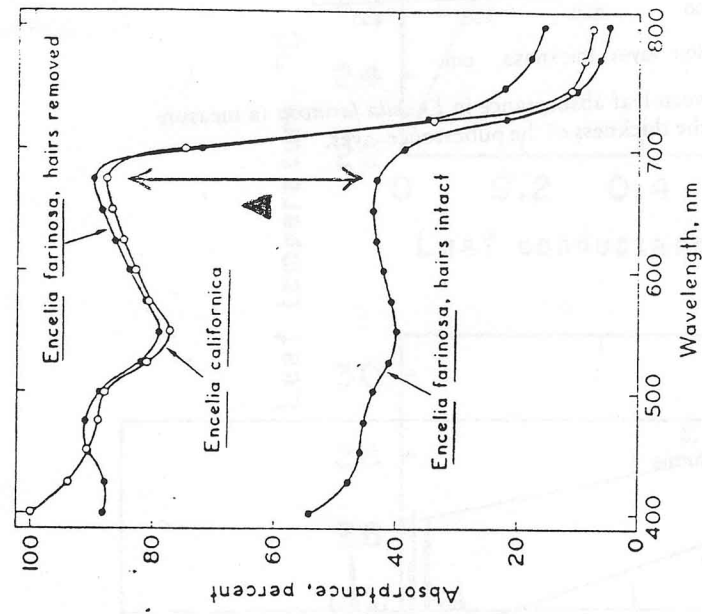


Fig. 9.7 Leaf absorbance spectra between 400–700 nm for intact leaves of *Encelia californica* and *Encelia farinosa* and for an *Encelia farinosa* leaf in which the reflective pubescence coating has been removed. (From Ehleringer and Björkman, 1978a.)



▲ = the change in reflectance caused by dry cellulose hairs on the leaf

*E. californica* is a coastal species (mesic)

*E. farinosa* is a desert species (xeric)

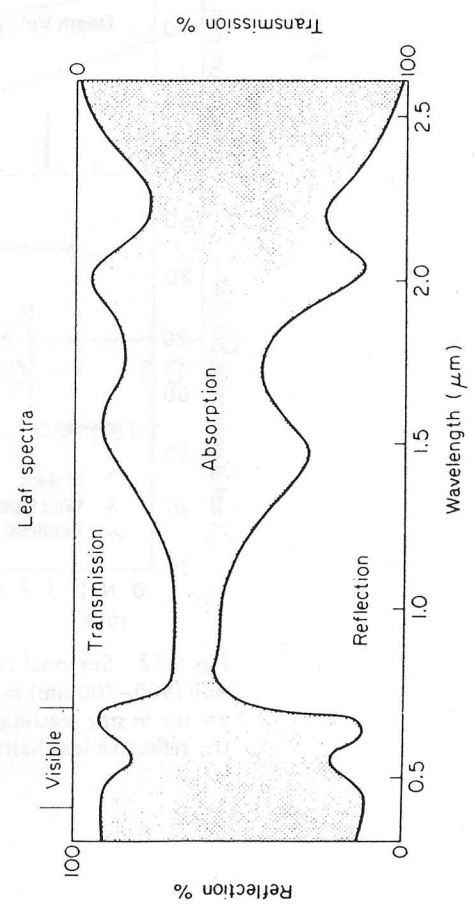


Fig. 6.5 Idealized relation between the reflectivity, transmissivity and absorptivity of a green leaf.

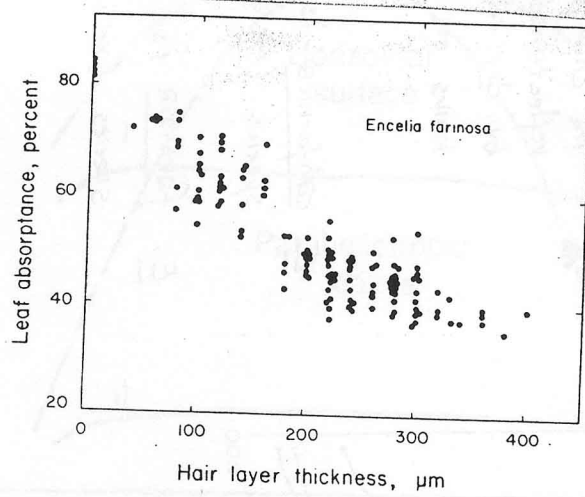


Fig. 9.9 The relationship between leaf absorptance in *Encelia farinosa* (a measure of pubescence abundance) and the thickness of the pubescence layer.

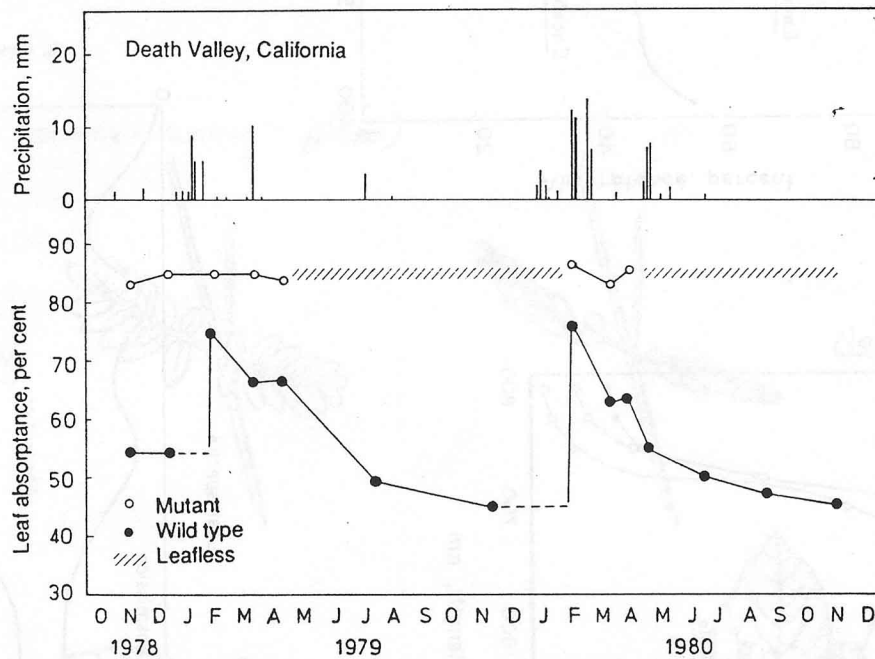
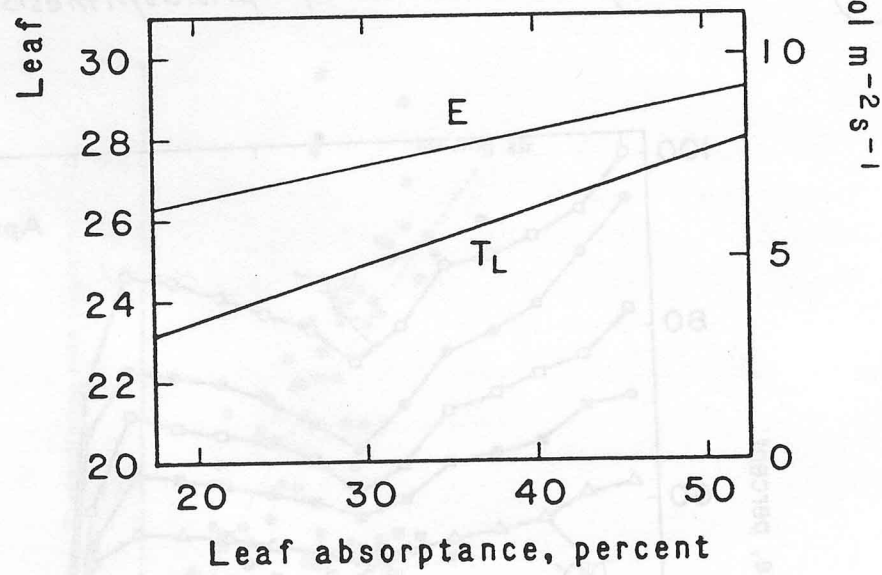
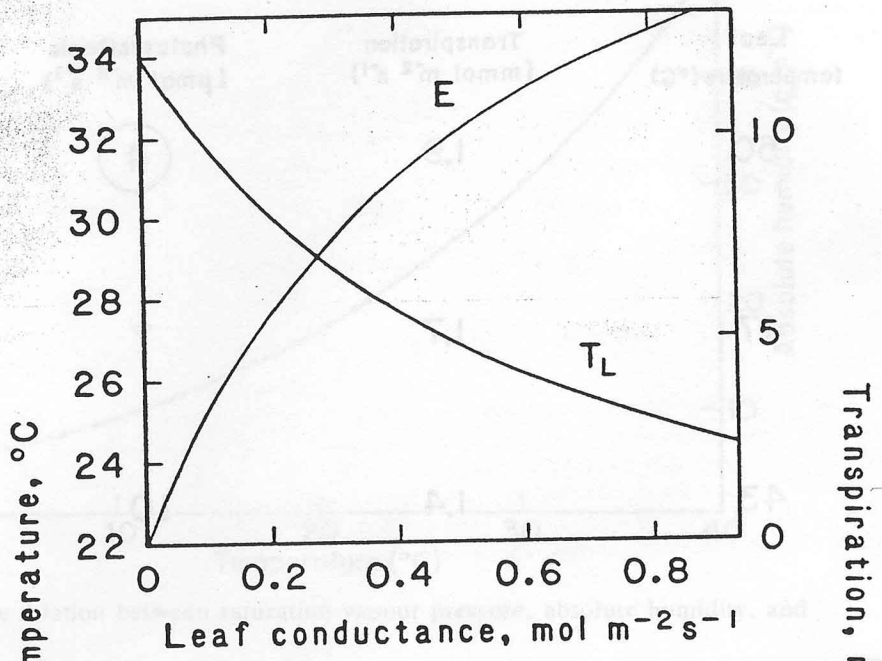





Fig. 9.12 Seasonal courses of precipitation and of leaf absorptance to solar radiation (400–700 nm) in leaves of *E. farinosa* in Death Valley, California. Also plotted are the *in situ* seasonal leaf absorptances for a mutant form of this species that lacks the reflective leaf hairs. (From Ehleringer, 1983.)



Atriplex hymenelytra summer day  
 (a species with salt bladders on leaves)

leaf conductance,  $0.02 \text{ mol m}^{-2} \text{ s}^{-1}$

	Leaf temperature ( $^{\circ}\text{C}$ )	Transpiration ( $\text{mmol m}^{-2} \text{ s}^{-1}$ )	Photosynthesis ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	WUE ( $\mu\text{mol / mmol}$ )
	50	1.9	4	2.1
	47	1.7	7	4.1
	43	1.4	10	7.1

○ = some photoinhibition of photosynthesis had occurred

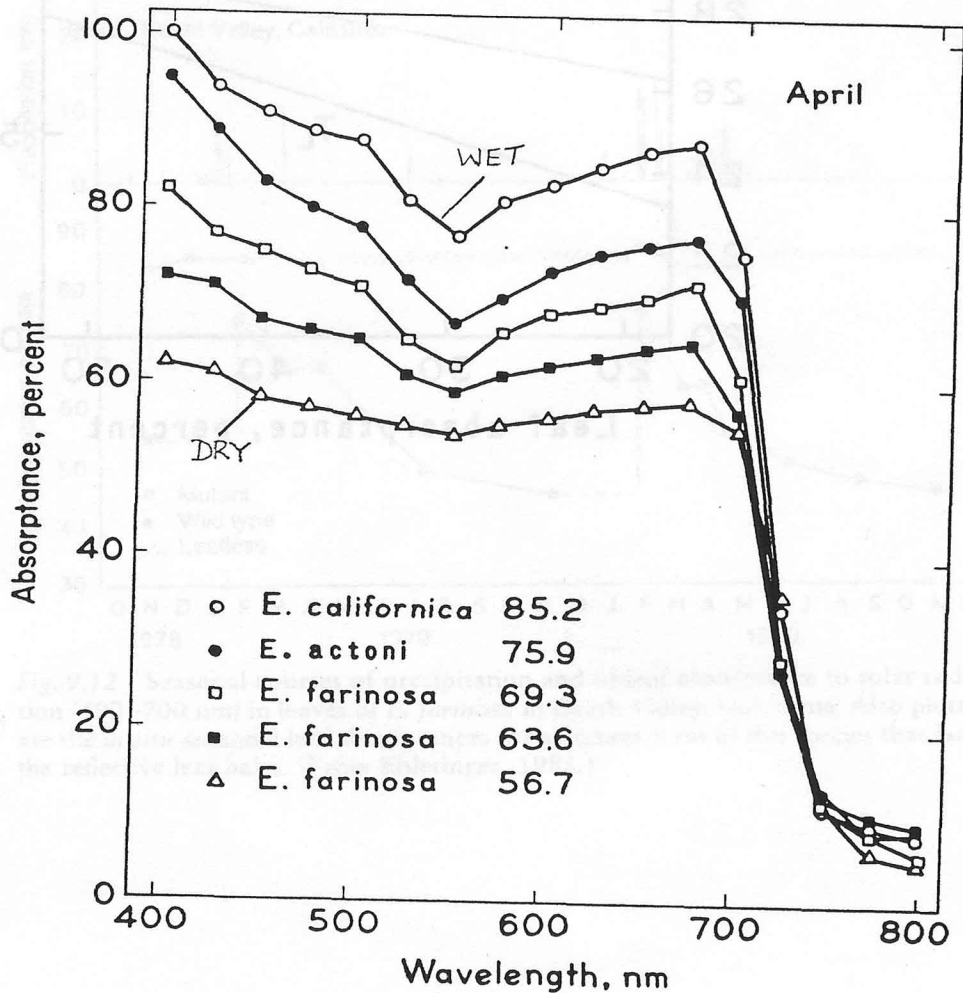


Fig. 9.11 Leaf absorbance spectra of intact leaves of *E. californica*, *E. actoni* and *E. farinosa* along an aridity gradient during April. The value adjacent to each species represents the leaf absorbance to solar radiation between 400–700 nm. (From Ehleringer, 1980.)



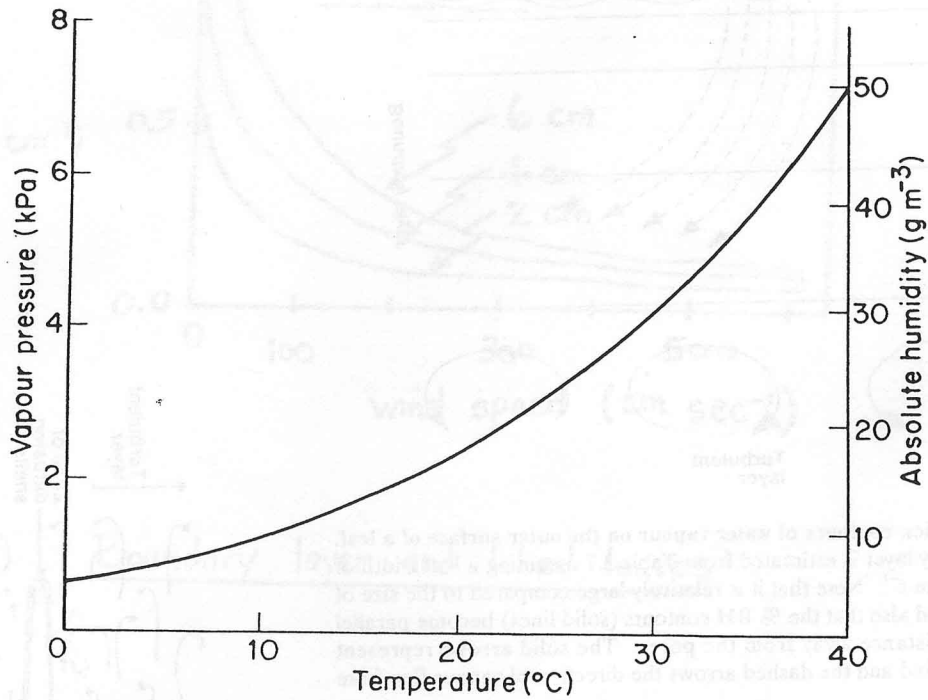


Fig. 2.1 The relation between saturation vapour pressure, absolute humidity, and temperature.

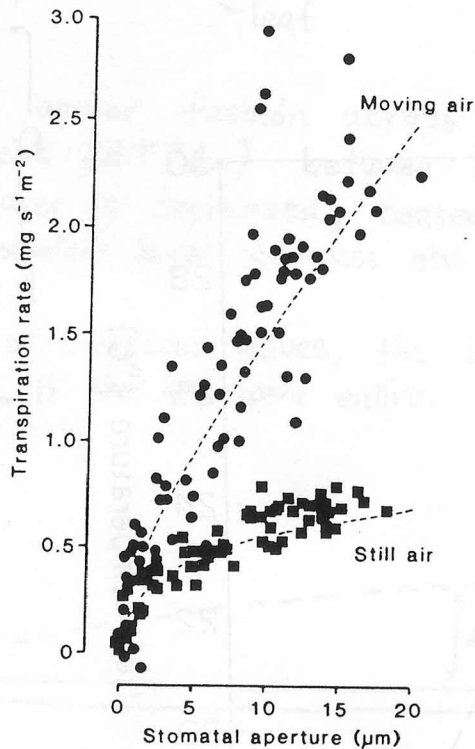


Fig. 3.5 Transpiration rate of *Tradescantia zebrina* leaves at different stomatal apertures in still and windy conditions. Adapted from Bange (1953). The data are based on gravimetric determinations of water loss over 1 - 5 min from leaf discs placed in a special holder to eliminate water loss from the edges and minimise changes in disc temperature. The VPD was 1% and the temperature  $23 \pm 2$  °C (i.e. RH about 90 %). Stomatal apertures were estimated from 25 light microscope measurements and transpiration rates were corrected for stomatal frequency and cuticular water loss. Dashed lines are predictions based on a theoretical analysis analogous to that presented in 3.5.

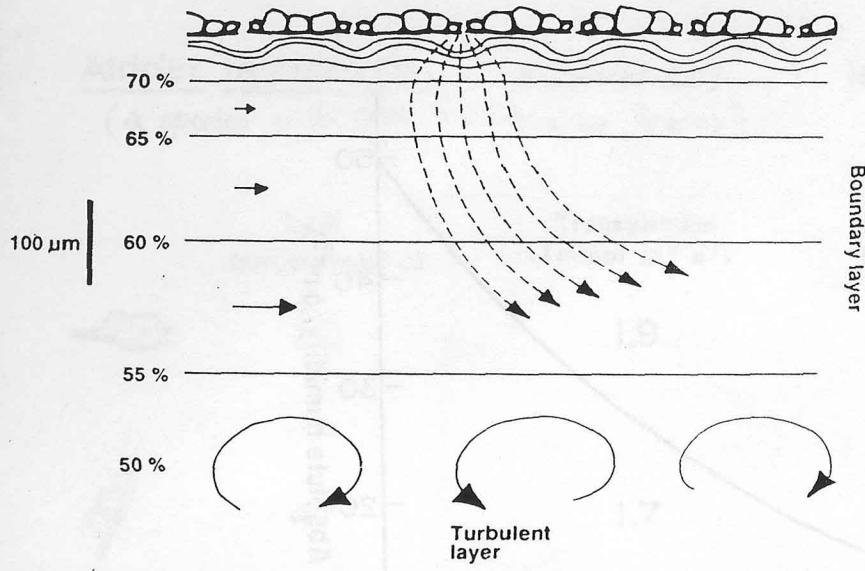


Fig. 3.3 Assumed concentration contours of water vapour on the outer surface of a leaf. The thickness of the boundary layer is estimated from Table 3.7 assuming a leaf width of 10 mm and a windspeed of  $1 \text{ m s}^{-1}$ . Note that it is relatively large compared to the size of the zone of diffusion shells and also that the % RH contours (solid lines) become parallel to the leaf surface a short distance away from the pores. The solid arrows represent direction and magnitude of wind and the dashed arrows the direction of vapour flux from one of the pores only.

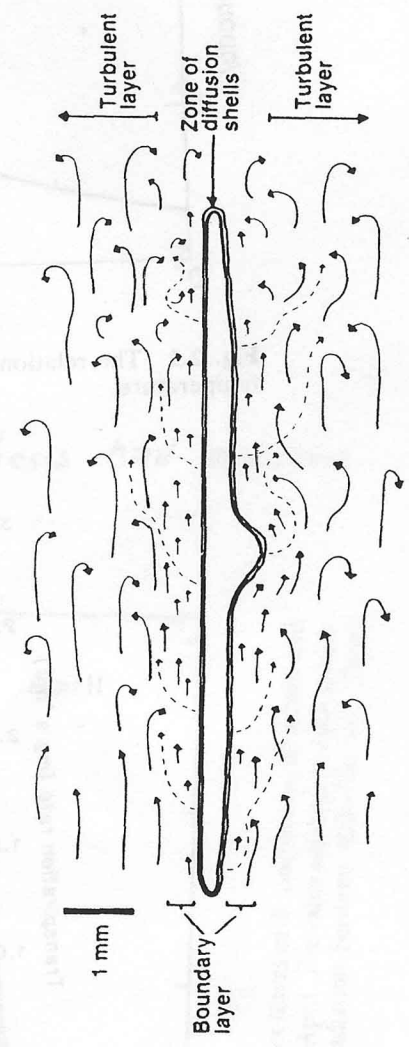


Fig. 3.4 Boundary layers and diffusion shells outside leaves. Representation of air flow pattern over a model leaf; the solid arrows indicate relative wind speed and direction and the dashed arrows the direction of vapour flux. Note laminar flow close to the leaf and turbulent regions downwind from its leading edge. Justification of scaling as in Fig. 3.3.

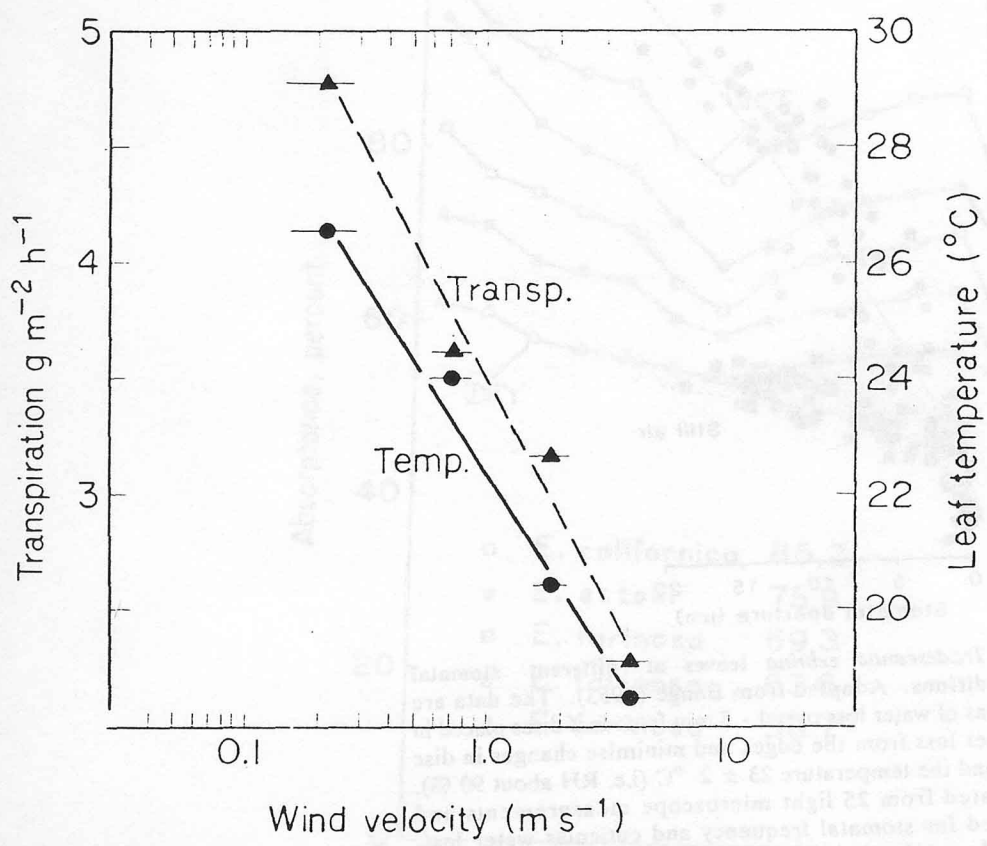
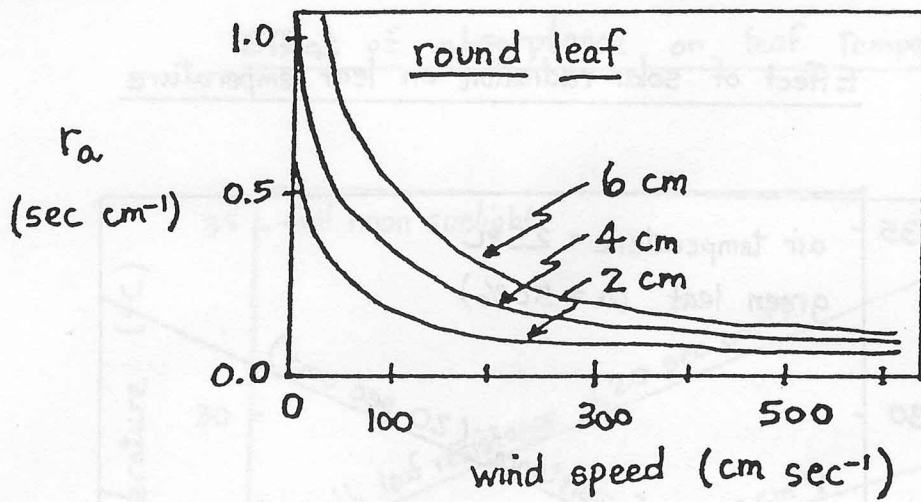
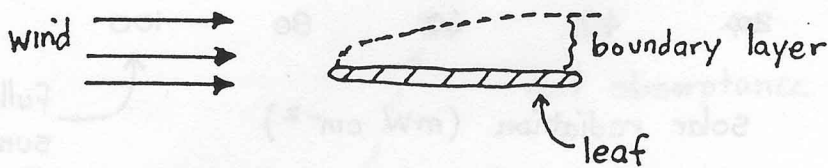


Fig. 11.5 The change of transpiration rate and leaf temperature with windspeed for a *Xanthium* leaf exposed to radiation of  $700 \text{ W m}^{-2}$  at an air temperature of  $15^{\circ}\text{C}$  and 95% relative humidity (from Mellor *et al.*, 1964).

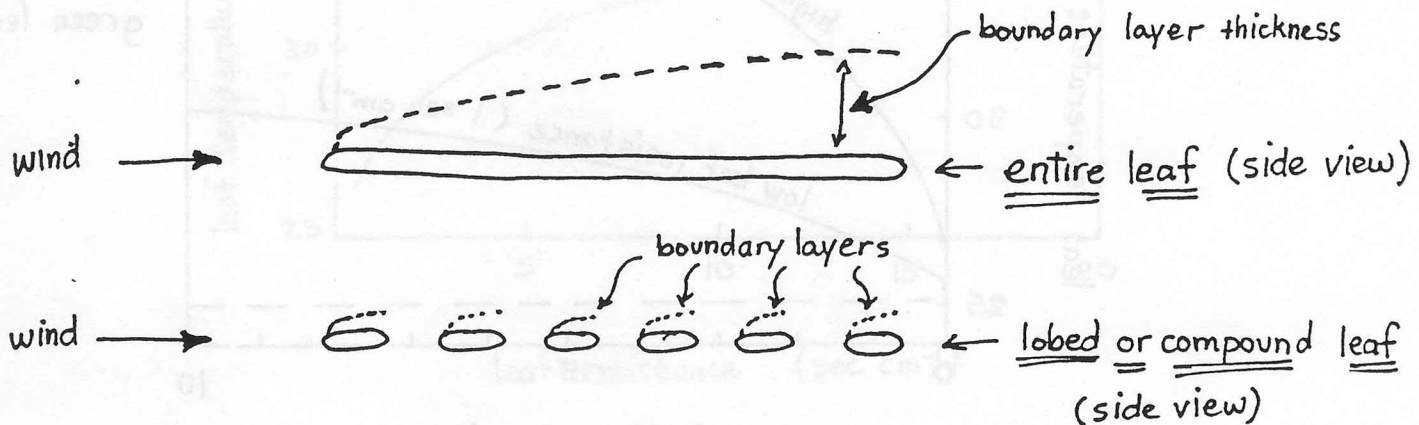


### Boundary layer and lobed leaves



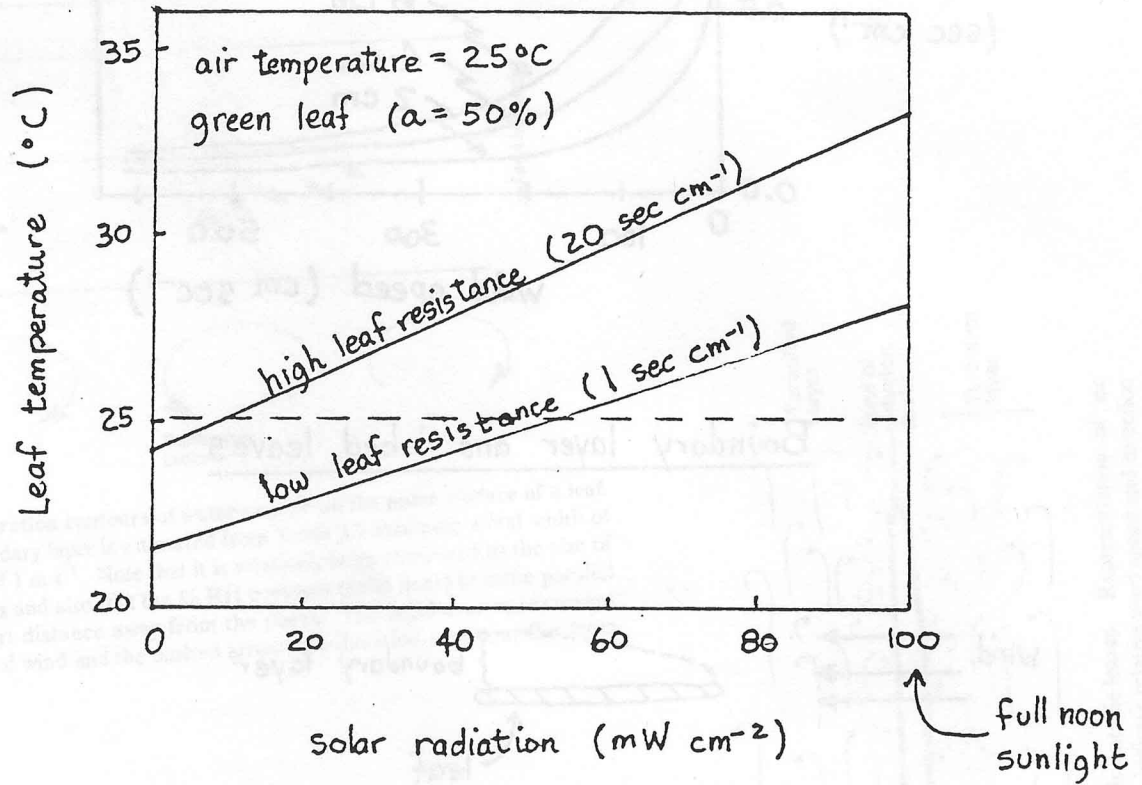
As air moves in laminar fashion across the leaf, the temperature gradient ( $dT/dx$ ) between leaf and the air in the boundary layer is decreased; consequently heat exchange is decreased. Boundary layer thickness also increases across the leaf.

By having lobed or compound leaves, the boundary layer never attains the size it would if the leaf were entire.

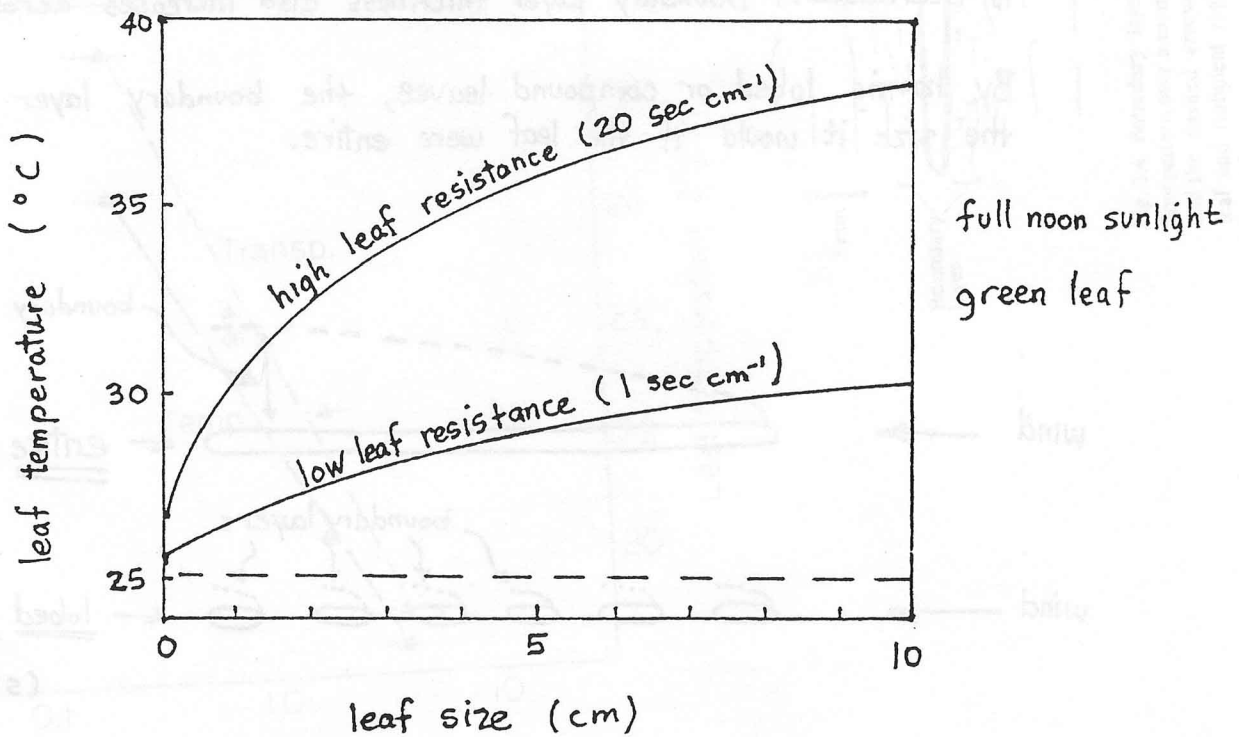


A lobed or compound leaf is a better heat exchanger than is an entire leaf.

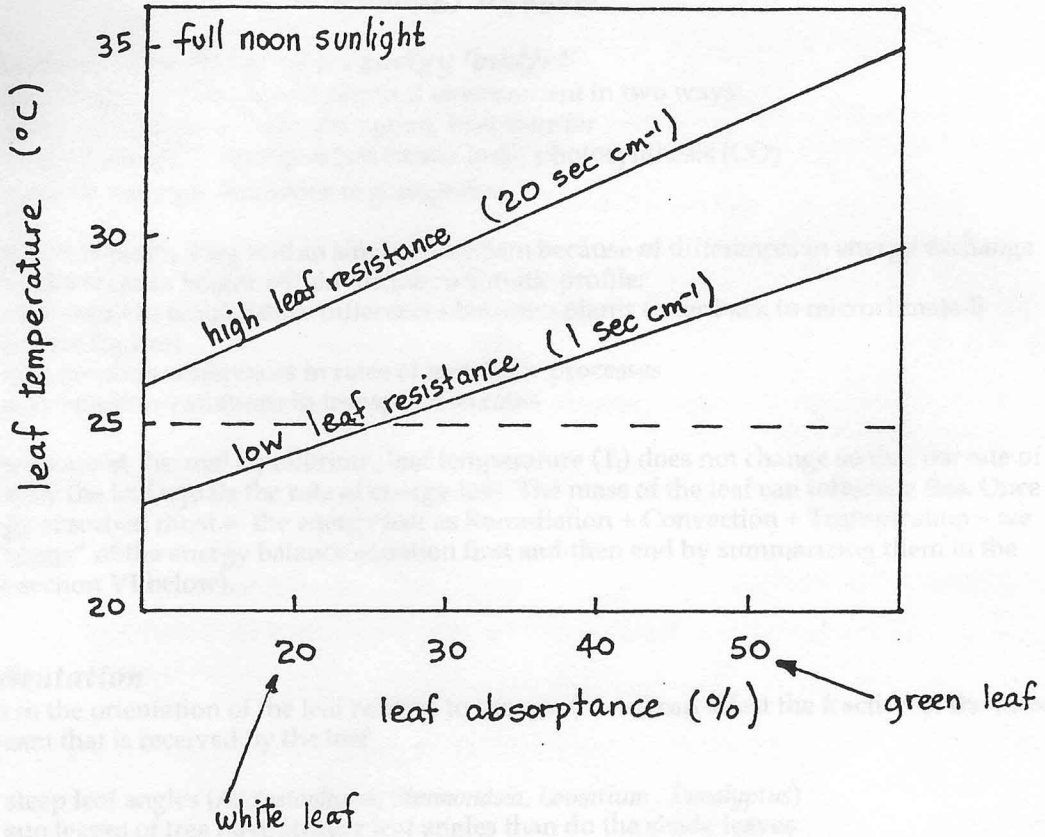
## Effect of solar radiation on leaf temperature



## Effect of leaf size on leaf temperature



## Effect of absorptance on leaf temperature



## Effect of leaf resistance on leaf temperature

