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 (CO₂ 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 (Tₗ) 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, Sabia) (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

\[ E = \frac{(e_l - e_a)}{(r_b + r_t)} = (e_l - e_a) \cdot g \]

where: \( g \) = total leaf conductance to water vapor; \( r_b \) = stomatal resistance; \( r_t \) = air boundary layer resistance; \( (e_l - e_a) \) = 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)*

<table>
<thead>
<tr>
<th>life form</th>
<th># of species</th>
<th>upper surface</th>
<th>lower surface</th>
</tr>
</thead>
<tbody>
<tr>
<td>trees</td>
<td>26</td>
<td>0</td>
<td>223</td>
</tr>
<tr>
<td>shrubs</td>
<td>29</td>
<td>0</td>
<td>196</td>
</tr>
<tr>
<td>shade herbs</td>
<td>40</td>
<td>7</td>
<td>86</td>
</tr>
<tr>
<td>sun herbs</td>
<td>110</td>
<td>20</td>
<td>145</td>
</tr>
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</table>

**Crop species**

<table>
<thead>
<tr>
<th>Species</th>
<th>upper surface</th>
<th>lower surface</th>
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<tbody>
<tr>
<td>Avena sativa</td>
<td>51</td>
<td>45</td>
</tr>
<tr>
<td>Hordeum vulgare</td>
<td>72</td>
<td>85</td>
</tr>
<tr>
<td>Triticum vulgare</td>
<td>50</td>
<td>40</td>
</tr>
<tr>
<td>Zea mays</td>
<td>98</td>
<td>108-200</td>
</tr>
<tr>
<td>Helianthus annuus</td>
<td>120</td>
<td>175</td>
</tr>
<tr>
<td>Medicago sativa</td>
<td>169</td>
<td>188</td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>50</td>
<td>190-235</td>
</tr>
</tbody>
</table>

**Tree Species**

<table>
<thead>
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<th>Species</th>
<th>upper surface</th>
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</thead>
<tbody>
<tr>
<td>Pinus strobus</td>
<td>28</td>
<td>121</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>66</td>
<td>182</td>
</tr>
<tr>
<td>Acer negundo (male)</td>
<td>65</td>
<td>189</td>
</tr>
<tr>
<td>Acer negundo (female)</td>
<td>59</td>
<td>255</td>
</tr>
<tr>
<td>Populus fremontii</td>
<td>26</td>
<td>310</td>
</tr>
<tr>
<td>Salix alba</td>
<td>111</td>
<td>128</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>9</td>
<td>144</td>
</tr>
<tr>
<td>Banksia pyninoides</td>
<td>22</td>
<td>92</td>
</tr>
<tr>
<td>Eucalyptus regnans</td>
<td>76</td>
<td>134</td>
</tr>
<tr>
<td>Eucalyptus marginata</td>
<td>109</td>
<td>105</td>
</tr>
</tbody>
</table>
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,

$$h_c = \frac{c_p \rho}{r_a}$$

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):

$$\text{Energy in} = \text{Energy out (@ equilibrium)}$$

$$\alpha \cdot \cos(i) \cdot S_{\text{direct}} + [a \cdot S_{\text{diffuse}}] + \varepsilon \cdot R = \varepsilon \cdot \sigma \cdot (T_l+273)^4 + h_c \cdot (T_l-T_a) + k \cdot L \cdot (e_l-e_a) \cdot g_{\text{tot}}$$

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)
- $T_l$ - temperature of leaf (°C)
- $T_a$ - temperature of air (°C)
- $e_l$ - water vapor pressure of leaf (mbar)
- $e_a$ - water vapor pressure of air (mbar)
constants:
- $\sigma$ - Stephan Boltzmann 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):
- $\cos(l)$ - cosine of leaf orientation to the sun's direct beam (last lecture)
- $a$ - absorption coefficient to solar radiation (300-4,000 nm)
- $\varepsilon$ - 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:
   \[ R_1 = \varepsilon \sigma T^4 \]
   \[ R_1 = \text{energy emitted (W m}^{-2}\text{)} \]
   \[ \varepsilon = \text{emissivity (0.99; dimensionless)} \]
   \[ \sigma = \text{Stephan-Boltzman constant (5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-1})} \]
   \[ T = \text{temperature (°K)} \]
3. Weins Displacement Law - wavelength (\(\lambda\)) of maximum emission (\(\lambda_{\text{MAX}}\) in nm) is:
   \[ \lambda_{\text{MAX}} = \frac{2,897,000}{T} \]
   e.g. sun 6000 K 480 nm
   earth 283 K 10,200 nm
4. Emissivity (\(\varepsilon\)) is a measure of how close an object is to being a perfect blackbody. HINT: compare the \(\varepsilon\) values for polished metals to the oxidized values; an oxidized metal will have high \(\varepsilon\) because of the presence of oxygen (O2) and the O2 allows the bonds to rotate more freely, thereby emitting more heat at a range of wavelengths and increasing the metals \(\varepsilon\) (below):

<table>
<thead>
<tr>
<th>materials</th>
<th>emissivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>polished aluminum</td>
<td>.04</td>
</tr>
<tr>
<td>polished copper</td>
<td>.05</td>
</tr>
<tr>
<td>silver</td>
<td>.02</td>
</tr>
<tr>
<td>brass</td>
<td>.22</td>
</tr>
<tr>
<td>copper oxide</td>
<td>.78</td>
</tr>
<tr>
<td>new cast iron</td>
<td>.65</td>
</tr>
<tr>
<td>old cast iron</td>
<td>.80</td>
</tr>
<tr>
<td>asbestos</td>
<td>.96</td>
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<tr>
<td>red brick</td>
<td>.93</td>
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<tr>
<td>glass</td>
<td>.94</td>
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<tr>
<td>water</td>
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<tr>
<td>quartz</td>
<td>.93</td>
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</table>

<table>
<thead>
<tr>
<th>materials</th>
<th>emissivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>soils</td>
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<tr>
<td>sand</td>
<td>.96</td>
</tr>
<tr>
<td>loam</td>
<td>.98</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>leaves</th>
<th>emissivity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gossypium hirsutum (cotton)</td>
<td>.96</td>
</tr>
<tr>
<td>Phaseolus vulgaris (common bean)</td>
<td>.94</td>
</tr>
</tbody>
</table>
5. Sky is not a perfect blackbody; its emittance is a function of gas composition within the air column;
   a. CO₂ and methane are "greenhouse gases" absorbing infrared radiation
   b. Emittance of sky is a function of water vapor content (ξ, mbar of vapor) (Brunt, 1939):
      \[ \xi_{\text{air}} = 0.53 + 0.06 e^{0.5} \]
   c. Over the range of conditions typically found, Swinbank (1963) showed that the amount of IR radiation emitted from the sky (IR_{sky}, W m^{-2}) is:
      \[ IR_{\text{sky}} = 1.2 \sigma T_{\text{air}}^4 - 171 \]
Leaf Energy Balance References:


Gates, D.M., and W. Tantraporn. 1952. The reflectivity of deciduous trees and herbaceous plants in the infrared


Leaf Structure References:

Hanson, H.C. 1971. Leaf structure as related to environment. Amer. J. Bot. 4:533-560.
Wylie, R.B. 1951. Principles of foliar organization shown by sun-shade leaves from ten species of deciduous
26:815-870.
Ceanothus is a shrub widespread throughout California.

from Comstock and Mahall (1985)
Fig. 1.1. Diurnal courses of incident photon flux density on a horizontal surface (--), diapheliotropic leaves (•--•), and paraheliotropic leaves (type I and II) (—).
Fig. 9.7 Leaf absorptance 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.)

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) leaf conductance, 0.02 mol m\(^{-2}\) s\(^{-1}\)

<table>
<thead>
<tr>
<th>Leaf temperature (°C)</th>
<th>Transpiration (mmol m(^{-2}) s(^{-1}))</th>
<th>Photosynthesis (µmol m(^{-2}) s(^{-1}))</th>
<th>WUE (µmol / mmol)</th>
</tr>
</thead>
<tbody>
<tr>
<td>50</td>
<td>1.9</td>
<td>4</td>
<td>2.1</td>
</tr>
<tr>
<td>47</td>
<td>1.7</td>
<td>7</td>
<td>4.1</td>
</tr>
<tr>
<td>43</td>
<td>1.4</td>
<td>10</td>
<td>7.1</td>
</tr>
</tbody>
</table>

○ = some photoinhibition of photosynthesis had occurred

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**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 ± 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 wind speed of 1 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. 11.5 The change of transpiration rate and leaf temperature with wind speed for a Xanthium leaf exposed to radiation of 700 W m⁻² at an air temperature of 15°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

- Air temperature = 25°C
- Green leaf (α = 50%)

- High leaf resistance (20 sec cm⁻¹)
- Low leaf resistance (1 sec cm⁻¹)

Solar radiation (mW cm⁻²)

Effect of leaf size on leaf temperature

- High leaf resistance (20 sec cm⁻¹)
- Low leaf resistance (1 sec cm⁻¹)

Leaf size (cm)
Effect of absorptance on leaf temperature

![Graph showing the effect of absorptance on leaf temperature.](image)

Effect of leaf resistance on leaf temperature

![Graph showing the effect of leaf resistance on leaf temperature.](image)