$$6CO_2 + 12H_2O + light = C_6H_{12}O_6 + 6O_2 + 6H_2O$$

THE ENERGY BALANCE OF A LEAF

The energy balance of a leaf can be summarized as in Figure 6.1. Inputs include short-wave and long-wave radiation. Outputs include long-wave radiation, conduction and convection, transpiration, transmission, reflectance, and energy stored in carbon compounds (sugars) for export to the

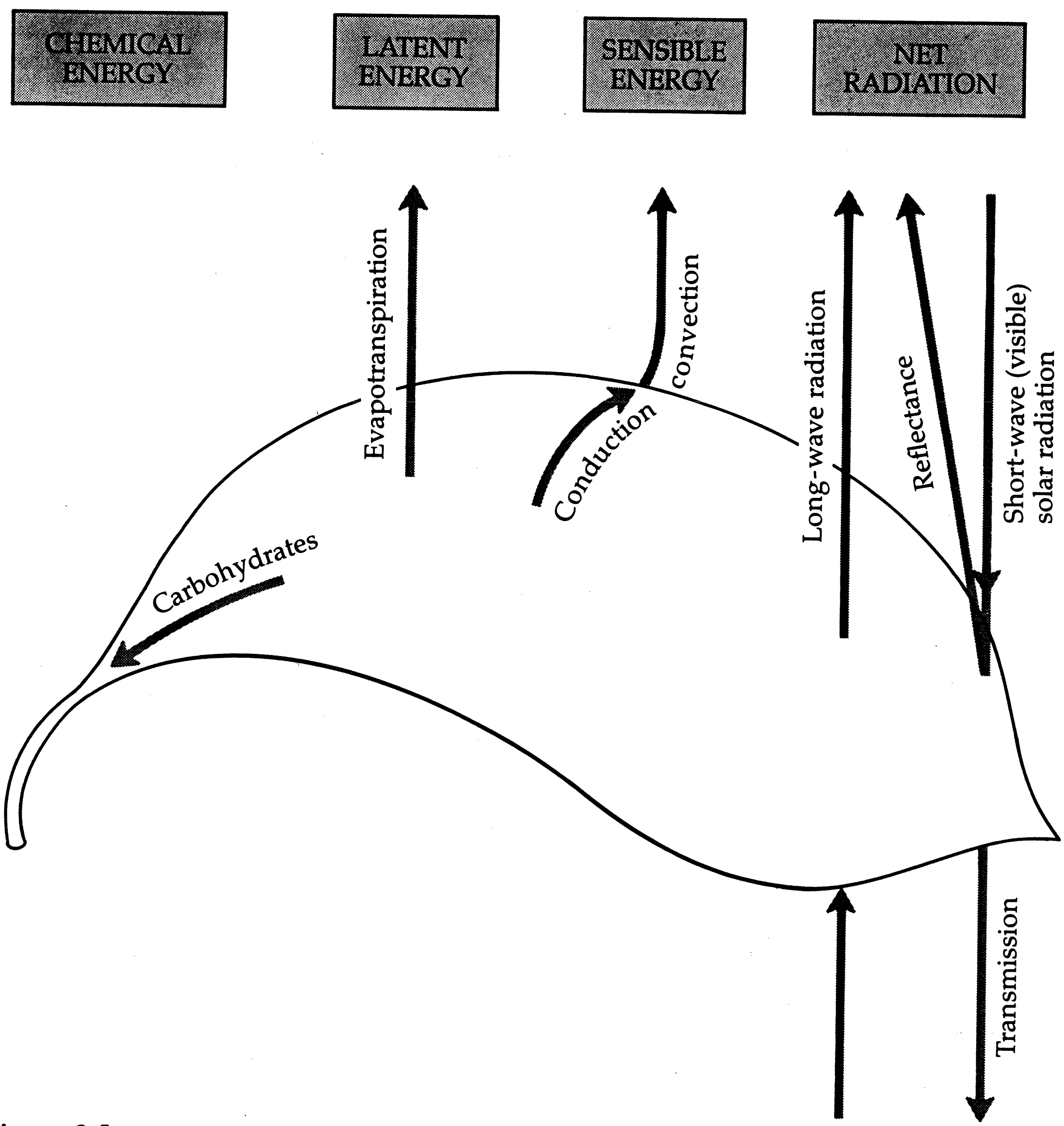
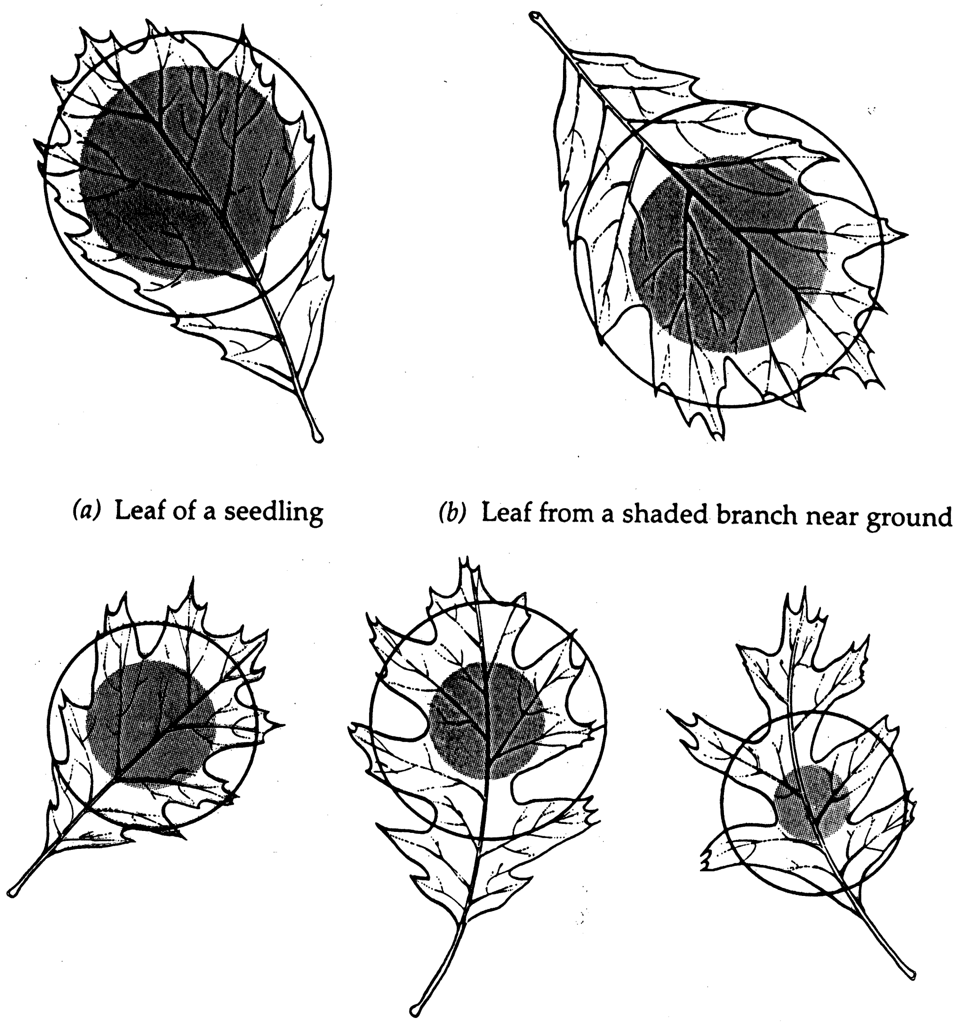


Figure 6.1
Components of the energy balance of leaves.



(a) Leaf of a seedling

(b) Leaf from a shaded branch near ground

(c) Leaves from progressively higher on the tree

Figure 6.5
The "critical dimension" (inner circle) as a fraction of total surface area (outer circle) for leaves of black oak at different heights in the canopy. (Horn 1971)

rotated 90 degrees from the plane of the leaf blade (Figure 6.7). A breeze will cause the blade to turn or rotate to present the smallest area to the wind; when the leaf has turned, the petiole is then struck, causing the leaf to turn back to its original position. This happens very rapidly, so that the leaf "trembles." This also increases turbulent airflow and decreases the boundary layer, increasing heat loss. It should also increase rates of water loss and CO_2 gain.

Chemical and Latent Energy Exchanges

Photosynthesis

Although photosynthesis never accounts for a large proportion of total energy removed from leaves, there is still a good deal of variation in the

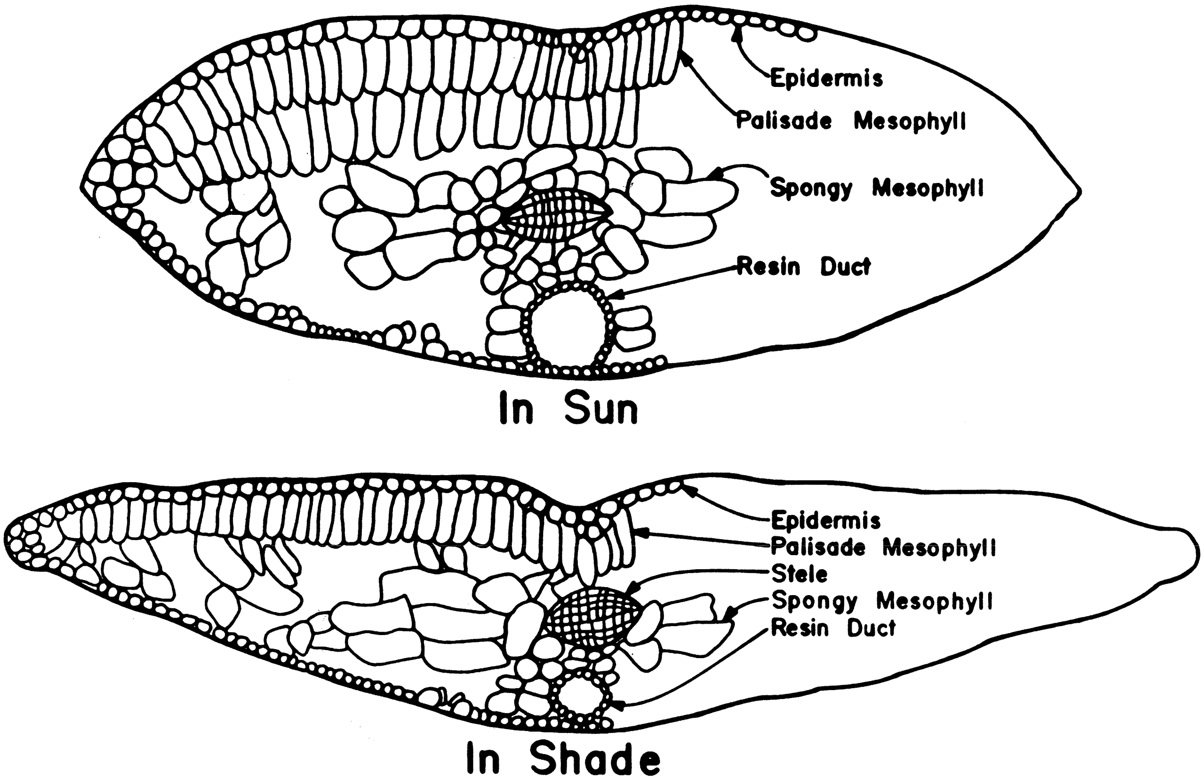


Fig. 2.4. Cross-sectional drawings of western hemlock (*Tsuga heterophylla*) leaves grown in the sun (upper) and in the shade (lower) illustrate that the volume of mesophyll tissue containing chloroplasts is more than twice as large for a comparable surface area in the former than in the latter. (From Tucker and Emmingham, 1977.)

the light compensation point, uptake increases linearly until the amount of carboxylation enzyme or available CO_2 limits the process.

In general, the leaves of deciduous tree species have the potential for higher photosynthetic rates than those of evergreens—particularly when the comparison is made on the basis of leaf dry weight. In terms of carbon uptake per unit of leaf surface area, the difference is less but sometimes still apparent, reflecting inherent differences in the diffusion pathway for carbon dioxide. Even within a single tree, significant differences in light response curves are evident between fully exposed foliage and that positioned in the more shaded part of the canopy. Foliage exposed to high illumination contains more layers of palisade mesophyll cells and has higher concentrations of carboxylation enzyme than more shaded leaves (Mooney, 1972; Berry and Downton, 1982). Exposed foliage is heavier per unit area than shaded foliage as a result of this difference in anatomy and the amount of storage reserves (Nygren and Kellomäki, 1983; Kozlowski and Keller, 1966; Fig. 2.4). In spite of these differences, the shade foliage may contribute as much as 40% to the tree's total carbon uptake (Schulze *et al.*, 1977; Schulze, 1981).

periods of weeks or even months (Polster and Fuchs, 1963; Tranquillini, 1979). Similar results are reported for *Pinus radiata* (Rook, 1969) and *Pinus sylvestris* (Troeng and Linder, 1982). Different mechanisms may operate but increased respiration following exposure to cold temperatures suggests the repair of damaged membranes is at least partly involved (Pharis *et al.*, 1972). High temperatures likewise may be injurious and the effects long-lasting (Levitt, 1972).

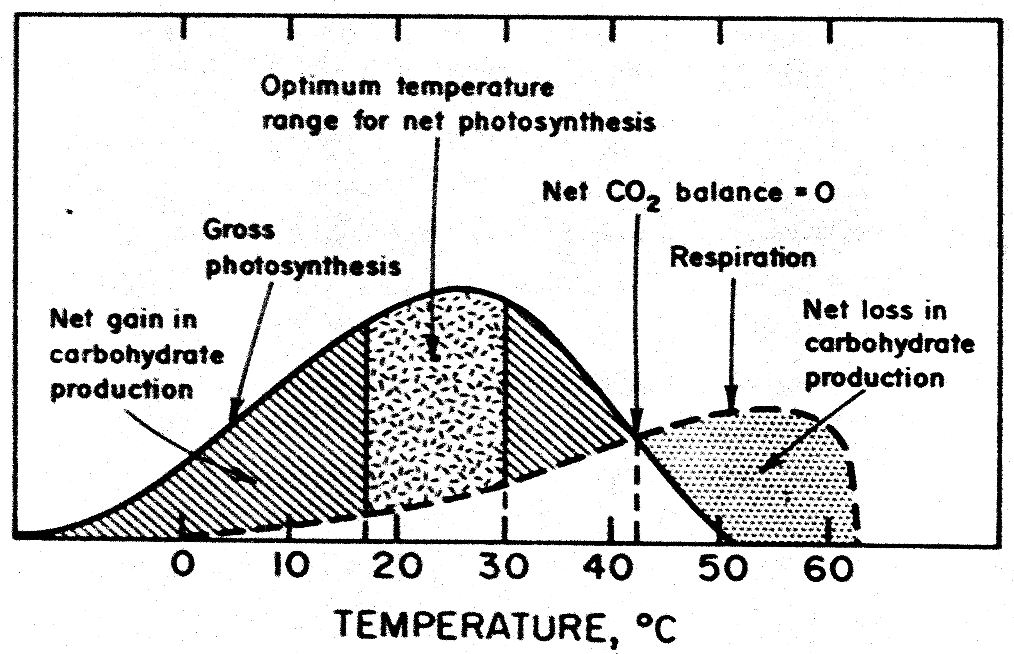


Fig. 2.7. Optimum temperature for net carbon uptake by leaves represents a zone where the difference between gross photosynthesis and losses of CO_2 by respiration are greatest. The optimum temperature varies with species and the season. At high as well as low temperatures, photosynthesis is adversely affected. A large net carbohydrate deficit results at high temperatures because of increasing respiration. Drawing slightly modified to emphasize somewhat greater importance of photosynthesis over respiration at high temperatures. (After Daniel *et al.*, 1979.)

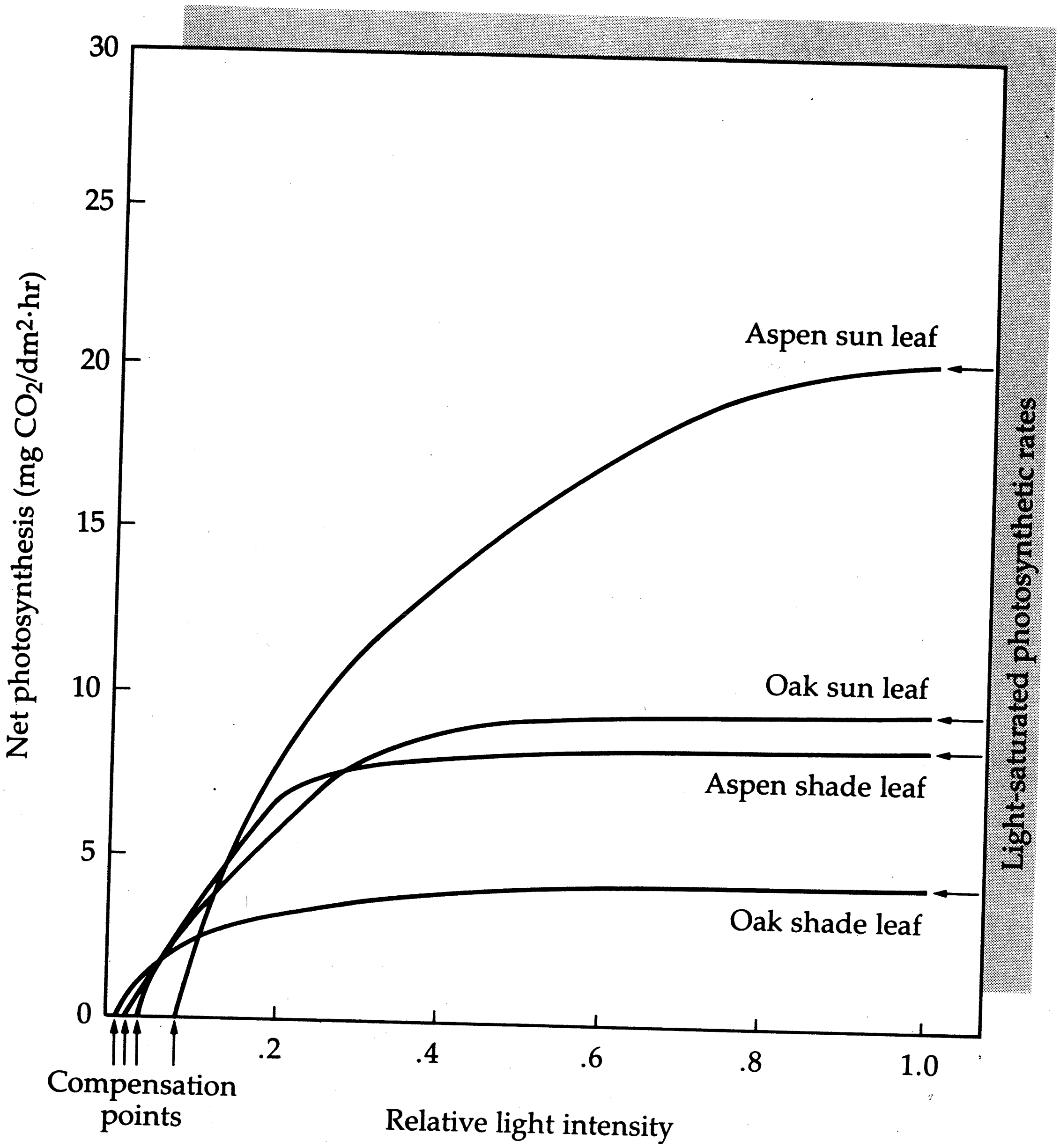


Figure 6.8
Photosynthetic response curves for sun- and shade-grown leaves of trembling aspen and red oak. (After Loach 1967)

concentrations. Look again at Figure 6.6, which shows changes in the structure of American beech leaves in sun and shade. The leaf in sun has two layers of chlorophyll-bearing palisade cells and so a greater density of chlorophyll per unit leaf surface area. There is generally a close relationship between the amount of chlorophyll and the amount of proteins and enzymes required to carry out all the biochemical reactions of photosynthesis. This higher concentration of chlorophyll and enzymes causes both the higher rate of net photosynthesis under full light (it takes more energy to saturate the photosynthetic "machinery") and the higher compensation point (it takes more light to offset the respirational costs of

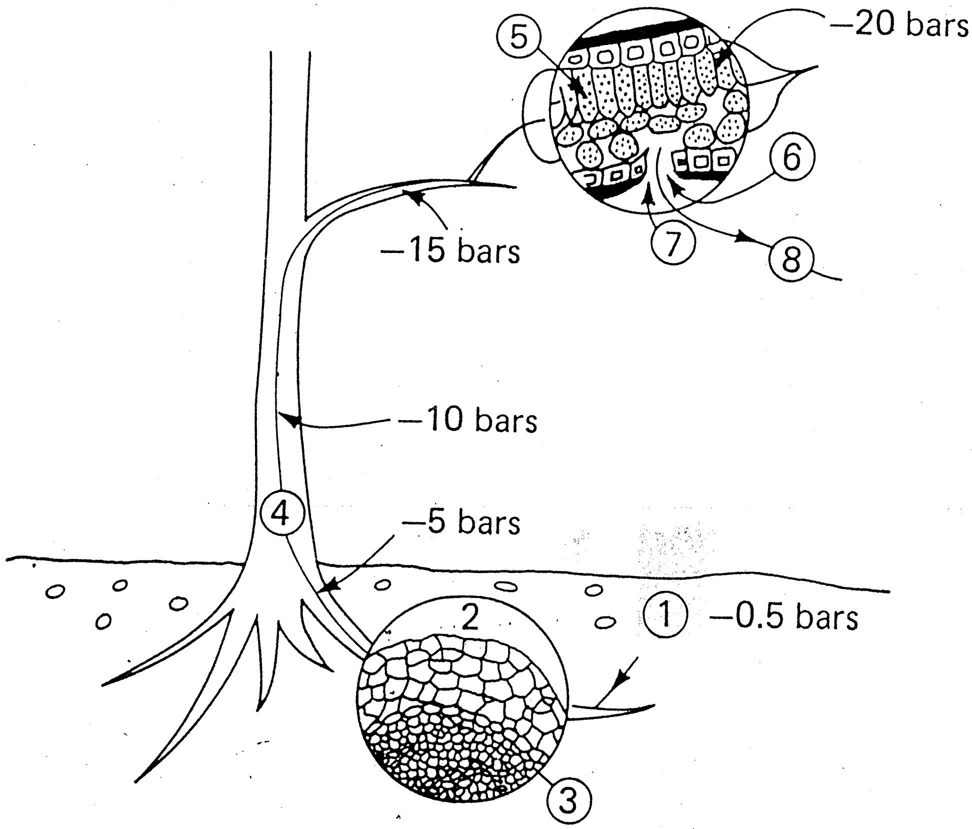


Figure 5-18 Main factors in water transport: (1) capillary size; (2) root bark; (3 dermis; (4) vessels or fibers; (5) leaf parenchyma, mesophyll and intercellular spa stomatal aperture; (7) boundary layer; and (8) vapor-pressure gradient from atmosphere.

where ψ_{cell} is the potential of water in the cell, and ψ_s, ψ_p, and ψ_m are butions to ψ_{cell} by solutes in the cell, wall pressure, and matrix forces of binding colloids and surfaces in the cell. ψ_s and ψ_m are negative, with ψ_m monly being very small and sometimes disregarded. ψ_p may be either p or negative. ψ_{cell} is therefore usually negative and becomes more nega water becomes less available. When the cell is fully turgid, ψ_{cell} approaches

Water uptake occurs because the xylary fluid in the root is common lower potential (more negative value) than is the water in the soil. Due to increasing solute concentrations from the root cortex to mesophyll

OH 2.7

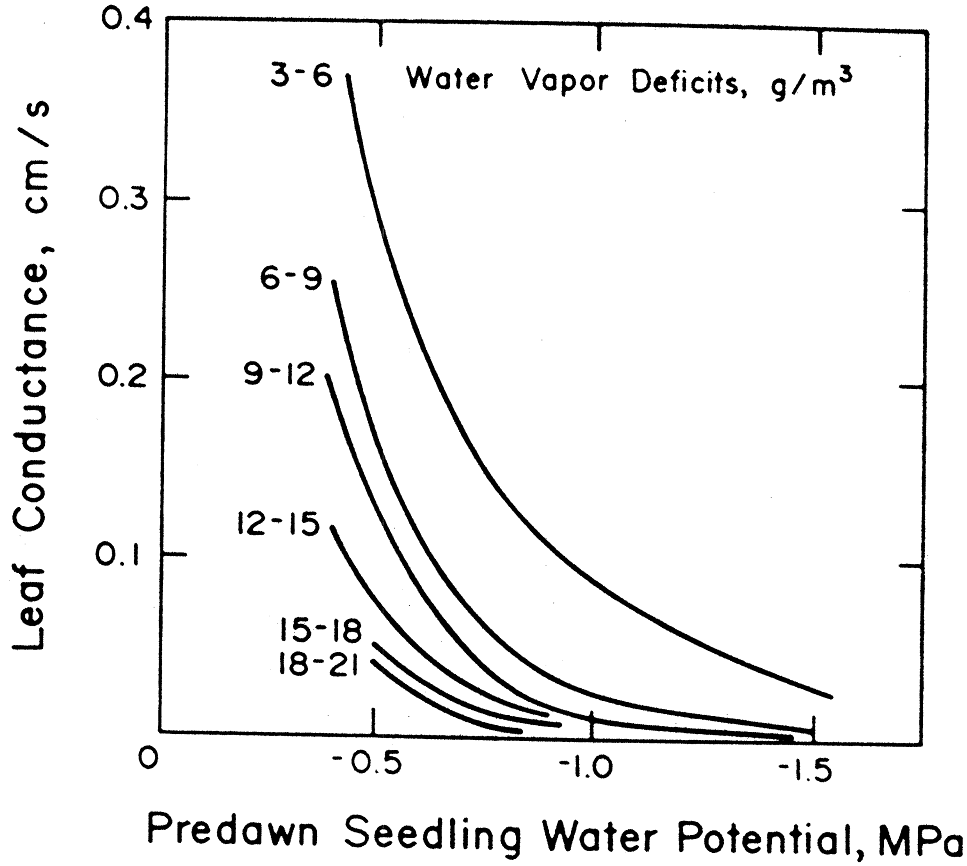
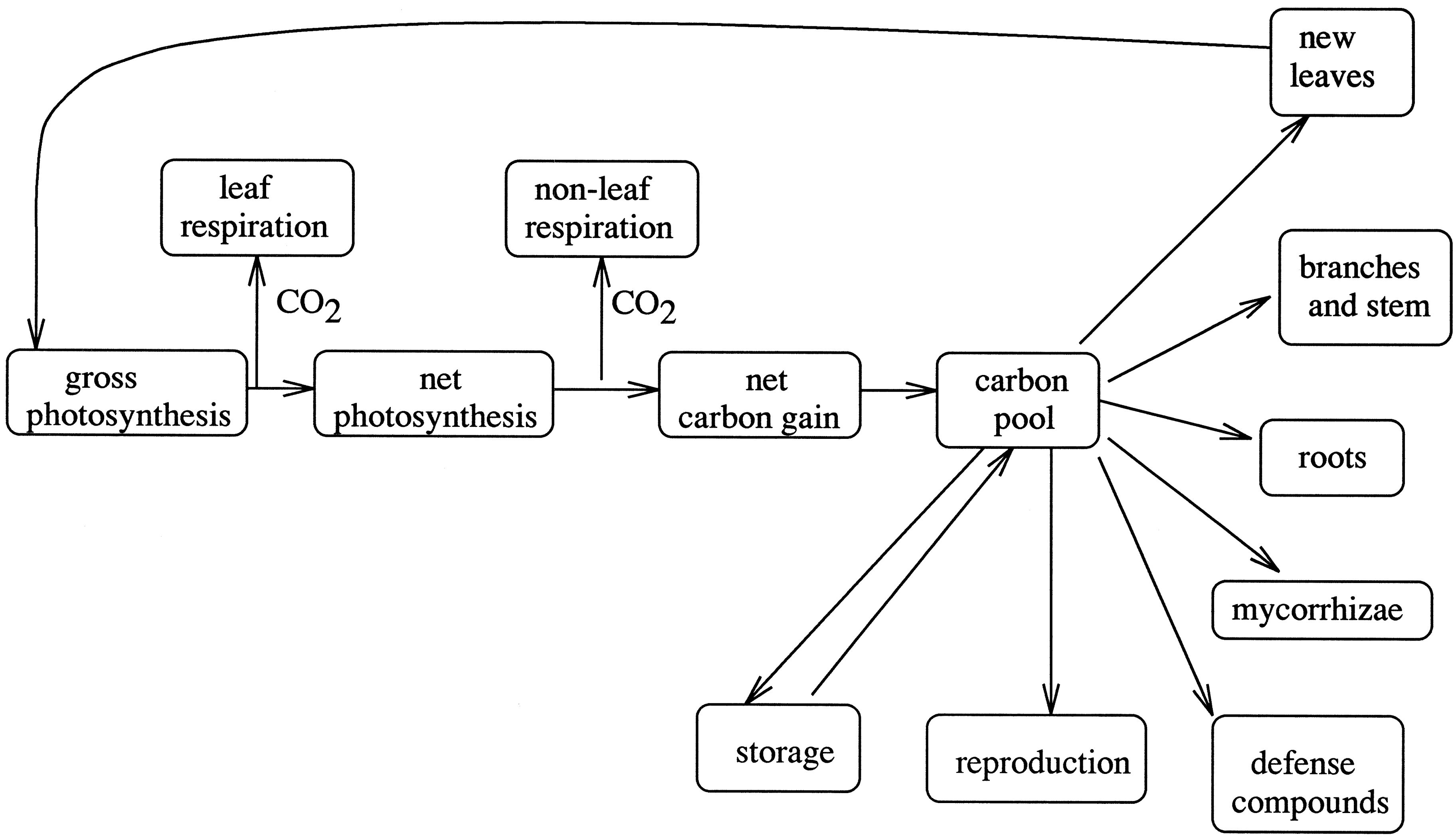


Fig. 4.10. As predawn water potentials decrease, young seedlings of Douglas fir close stomata more at a given water vapor deficit, here expressed in grams of water per cubic centimeter of air. (After Lassoie, 1982.)

become acclimated to dry conditions by increasing osmotic concentrations in cells to maintain turgor, by reducing cell wall rigidity to permit growth, and by increasing membrane permeability to facilitate the diffusion of water (Bradford and Hsiao, 1982). After extended exposure to drought, *Quercus alba*, for example, was able to open stomata to half of maximum at relative water contents and



gross photosynthesis
leaf respiration
CO_2
net photosynthesis
non-leaf respiration
CO_2
net carbon gain
carbon pool
new leaves
branches and stem
roots
mycorrhizae
storage
reproduction
defense compounds