5

Scaling-Up Gas Exchange and Energy Balance from the Leaf to the Canopy Level

1. Introduction

Having discussed the gas exchange and energy balance of individual leaves in previous chapters, we are now in a position to "scale up" to the canopy level. In moving between scales, it is important to determine which interactions are strong enough to be considered and which can be ignored. The water relations of plant canopies differ distinctly from what would be predicted from the study of individual leaves, because each leaf modifies the environment of adjacent leaves by reducing irradiance and wind speed, and either decreasing or increasing vapor pressure deficit, depending on transpiration rates. These changes within the canopy reduce transpiration from each leaf more than would be predicted from an individual leaf model, based on the atmospheric conditions above the canopy. For example, **irradiance** declines more or less exponentially with leaf area index within the canopy (Box 5.1), reducing the energy that each leaf absorbs. Friction from the canopy causes **wind speed** to decline close to the canopy, just as it declines close to the ground surface. Wind speed, generally, declines exponentially within the canopy, and individual leaves within a canopy have lower boundary layer conductance than expected from leaf dimensions and the meteorological conditions of the bulk air. Finally, transpiration by each leaf increases the **water vapor concentration** around adjacent leaves, as does evaporation from a wet soil surface. As stomatal conductance increases, the increasing water vapor concentration within the canopy reduces the driving force for transpiration, so that transpiration increases less than expected from the increase in stomatal conductance alone (Jarvis & McNaughton 1986).

Mathematical functions can be used to describe the effects of variables and their interactions in a model of the system. A good model for scaling will be based on mechanistic processes at a lower scale. Can we treat the canopy simply as one big leaf to arrive at the gas exchange and energy balance of a canopy, or do we need to sum up the gas exchange and energy balance of each leaf and its individual microclimate? These questions will be addressed in the following sections.

2. Canopy Water Use

In Sect. 2.2 of Chapter 2A on photosynthesis, we discussed leaf transpiration as measured on a single leaf in a well ventilated and environmentally controlled gas-exchange cuvette. In such cuvettes, the boundary layer is minimal, and transpiration has little effect on the conditions inside and around the leaf. For leaves in a canopy, however, boundary layers significantly affect the transpiration rate, and the air in the boundary layer contains more water

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Box 5.1

Optimization of Nitrogen Allocation to Leaves in Plants Growing in Dense Canopies

A theoretical optimum distribution of N over the leaves of a plant that maximizes whole plant photosynthesis per unit leaf N can be calculated (Field 1983, Hirose & Werger 1987, Pons et al. 1989, Evans 1993, Anten et al. 1995). Such an optimum distribution pattern depends on the distribution of light over the leaves of a plant growing in a dense canopy. The approach chosen here is for plant stands consisting of one species of even-sized individuals. Hence, the performance of the stand is identical to the performance of individual plants growing in the stand. The calculations consist of five parts that describe mathematically: (1) the distribution of irradiance in the leaf canopy where the plant is growing, (2) the dependence of photosynthetic rate on irradiance of leaves, (3) the relationships with leaf N of the parameters of the photosynthesis–irradiance relationship, (4) canopy photosynthesis by summation of photosynthetic rates in different canopy layers, and (5) the distribution of leaf N at maximum canopy photosynthesis per unit leaf N.

Following the approach discussed in Box 2A.3 on gradients in leaves, we can use the Lambert–Beer law to calculate the light absorption profile in the canopy. An extension of that equation gives the mean irradiance (I_L, µmol m^{-2} s^{-1}) incident on a leaf at a certain depth in the canopy expressed as cumulative leaf area index from the top of the canopy [F, m^2 (leaf area) m^{-2} (ground surface)]:

$$I_L = \frac{I_o K_L}{1-t} \exp^{(-K_L F)} \qquad (1)$$

where I_o (µmol m^{-2} s^{-1}) is the irradiance above the canopy, and the dimensionless parameters K_L, t, and F are the canopy extinction coefficient, leaf transmission coefficient, and leaf area index, respectively (Hirose & Werger 1987). I_o is multiplied by K_L to account for the deviation of leaf angle from horizontal transmission of light by leaves.

Again following the approach in Box 2A.3, we calculate the photosynthetic rate in each canopy layer by using the light-response curve. For this purpose, we use the equation introduced in Sect. 3.2.1 of Chapter 2A on photosynthesis:

$$A = \frac{\Phi I + A_{max} - \surd\{(\phi I + A_{max})^2 - 4\Theta I \phi A_{max}\}}{2\Theta} - R_{day} \qquad (2)$$

where A_n (µmol CO$_2$ m^{-2} s^{-1}) is the actual rate of net photosynthesis, ϕ is the apparent quantum yield at low irradiance [mol CO$_2$ mol^{-1} (quanta)], I is irradiance (µmol quanta m^{-2} s^{-1}), A_{max} (µmol CO$_2$ m^{-2} s^{-1}) is the light-saturated rate of (gross) photosynthesis, and Θ (dimensionless) describes the curvature on the A–I relationship.

Parameters of the light-response curve (Equation 2) can be related to leaf N per unit leaf area (N_{LA}). Linear relationships give a satisfactory description of the increase of A_{max} and R_{day} with N_{LA}:

$$A_{max} = a_a(N_{LA} - N_b) \qquad (3)$$

$$R_{day} = a_r(N_{LA} - N_b) + R_b \qquad (4)$$

where a_a and N_b are the slope and intercept of the A_{max}–N_{LA} relation. N_b is the amount of N still present in leaves that have no photosynthetic capacity left. R_b is R_{day} in leaves with $N_{LA} = N_b$. The quantum yield, ϕ, depends on chlorophyll concentration which may also be true for the curvature, Θ. These two parameters may thus also depend on the leaf N concentration, N_{LA}, for which mathematical relationships can be formulated.

Canopy photosynthesis can now be calculated using Equations 1–4 and the leaf N distribution in the canopy. For that purpose distribution functions may be used (Hirose & Werger 1987). Photosynthetic rates are summed over the different canopy layers and over a day or other time interval with varying irradiance. Daily course of irradiance may be described by a sinusoidal curve, or in any other way.

Maximum canopy photosynthesis at constant total leaf N of the plant is reached when at everydepth in the canopy a change in leaf N (δN_{LA}) will result in the same change in daily photosynthesis (δA_{day}) (Field 1983):

$$\frac{\delta A_{day}}{\delta N_{LA}} = \lambda \qquad (5)$$

continued

Box 5.1 *Continued*

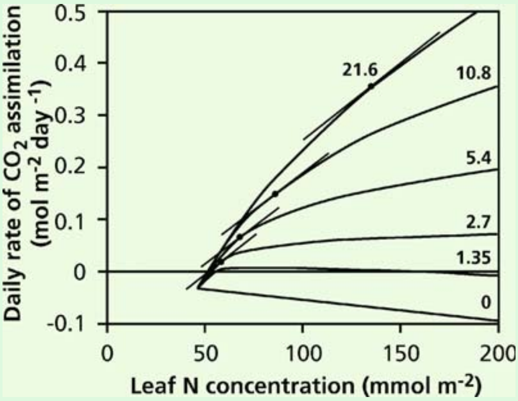

FIGURE 1. Calculated daily photosynthesis as a function of leaf N for different depths in a canopy with concomitantly different levels of irradiance (expressed as mol m^{-2} day^{-1}). The points of contact of the parallel tangents to the curves represent the optimal distribution pattern of N at a given total amount of leaf N (after Hirose & Werger 1987).

The constant λ is called the *Lagrange multiplier*. This is illustrated in Fig. 1, where the points of contact of the tangents to the lines for daily photosynthesis at different canopy depths as a function of N_{LA} represent the optimal distribution of leaf N. Different total amounts of leaf N will result in different values for λ. In this way optimal leaf N distribution for maximum canopy photosynthesis of a plant per unit leaf N (photosynthetic nitrogen-use efficiency, PNUE) can be calculated. Photosynthetic rates at actual distribution of leaf N in plants growing in leaf canopies have been compared with theoretically derived ones as described earlier, and with plants that have a uniform distribution. For instance, in the study of Pons et al. (1989), the performance of *Lysimachia vulgaris* (yellow loosestrife) at uniform and optimal distribution was 73 and 112%, respectively, of that at actual distribution. Hence, plants tend to distribute their leaf N optimally over leaf area.

A submodel of the model developed above is a canopy photosynthesis model. This is a simplified one because both the light distribution and leaf photosynthesis use simplifications that are valid for the purpose of the above calculations, but not when we are interested in the quantitative outcome of canopy photosynthesis itself. The distribution of light as described here gives the average irradiance incident on leaves at a particular depth in a canopy with unidirectional light coming from straight overhead. It provides a reasonable approximation for diffuse light, but not for directional sunlight because spatial variation due to sunflecks and varying angle of incident sunlight are not accounted for. For the leaf photosynthesis module, the Farquhar et al. (1980) model could be used which accounts not only for varying conditions of irradiance, as in this model, but also for variation in temperature and stomatal conductance. This model is described in Box 2A.1.

vapor than the bulk ambient air. In a canopy, more than in leaves measured in a leaf cuvette, transpiration is therefore affected by both stomatal and **boundary layer conductance**. In effect, the boundary layer provides a **negative feedback** to transpiration. As a result, stomatal conductance has much less effect on canopy water loss than would be expected from study of single leaves (Jarvis & McNaughton 1986).

While transpiration from individual leaves in a leaf cuvette can be adequately described by the diffusion equation, transpiration from leaves in a canopy requires consideration of both diffusion and the leaf energy balance. The dual processes of **vaporization** and **diffusion** were first considered in an evaporation model by Penman (1948). This work was extended to include evaporation from vegetation by incorporation of a canopy conductance (Monteith 1963, 1965). This line of thinking, which leads to "**single-layer**" models, is to determine the evaporation if the plant canopy were simply a partially wet plane at the lower boundary of the atmosphere. This conceptual plane, which is often referred to as a "big leaf", is ascribed a physiological and aerodynamic resistance to water vapor transfer (Fig. 1). In an analogy with an individual leaf, a **canopy conductance** is introduced which implicitly assumes that the conductances of individual leaves act in parallel, so that this canopy conductance can be determined by the leaf-area-weighted sum of leaf conductances (Monteith 1973). This approach ignores details of the canopy profile and simplifies the canopy to one single layer ("big leaf"; Field 1991). The "big-leaf" models are applicable only in circumstances where the detailed and complete spatial structure of the

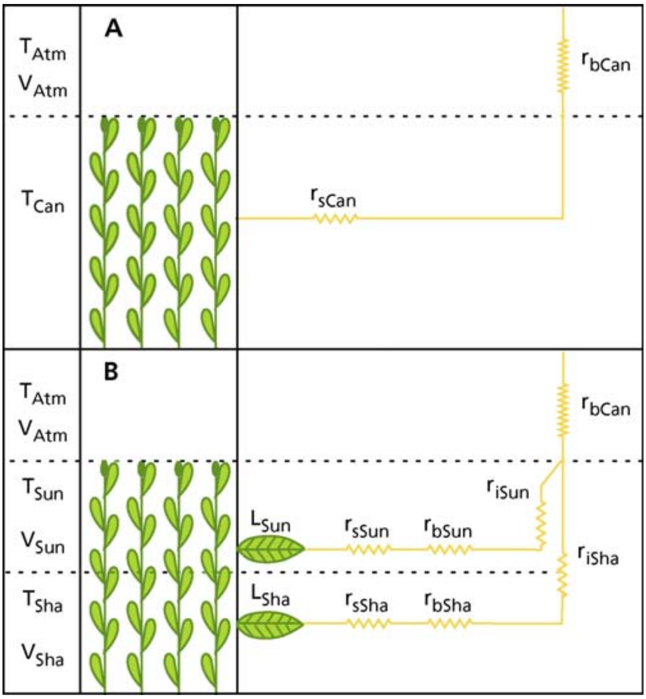

Figure 1. Schematic representation of (A) a single-layer ("big-leaf") model and (B) a multilayer model used for calculation of canopy evapotranspiration [modified after Raupach & Finnigan (1988)]. The model includes temperatures (T), vapor pressures (V), and resistances (r). Subscripts refer to the canopy (Can), the atmosphere (Atm), sunlit leaves (Sun), and shaded leaves (Sha). Resistances are stomatal (s), boundary layer (b), and in the air within the canopy (i).

actual canopy microclimate and difference in light-response curves of individual leaves that make up the canopy are irrelevant (Fig. 1).

Whenever details within the canopy (e.g., the interaction between microclimate and physiology) are important to estimate canopy gas-exchange, big-leaf models are insufficient. "**Multilayer**" models have therefore been developed (Cowan 1968, 1988). These models describe both the evaporation of the entire canopy and the partitioning of evaporation among various components (e.g., soil, understory, and crown) together with other aspects of the canopy microclimate, such as profiles of leaf and air temperature and humidity of the air (Fig. 1).

Single-layer models are appropriate when one is concerned with vegetation essentially as a permeable lower boundary of the atmosphere or upper boundary of the soil, in systems with a length scale much larger than that of the vegetation itself. They are useful in hydrological modeling of large-scale or medium-scale catchments (e.g., areas where water is collected for urban use). On the other hand, multilayer models are appropriate when necessary to resolve details within the canopy, either because the detail is important in its own right or because the height scale is comparable with that of the system under investigation. They are relevant when dealing with interactions between microclimate and plant physiology or with hydrology in small catchments (Raupach & Finnigan 1988).

Water loss from communities includes both transpiration of leaves and evaporation directly from the soil. Evaporation from the soil accounts for about 40% of the water used by a wheat crop in a Mediterranean environment (Siddique et al. 1990). The soil component is affected by the level of radiation that penetrates through the canopy to the soil surface and hence by the canopy leaf area index (LAI). Evaporation from the soil is also affected by wetness of the soil surface, hydraulic conductivity of the soil, and wind speed beneath the canopy. The rate of soil evaporation is high when the surface is wet. As the soil dries out, the point of evaporation moves deeper into the soil and the surface layer offers a greater impedance, thus dramatically reducing soil evaporation. When the canopy intercepts most of the incident radiation, soil evaporation is probably a minor component of the total evaporation. If rain is infrequent and the soil surface dry, then soil evaporation tends to be insignificant. When the canopy is sparse, with a projected foliage cover of less than 1, as occurs on 70% of terrestrial vegetation (Graetz 1991), soil evaporation cannot be ignored, and it should be included in multilayer evaporation models.

Canopies differ in the extent to which the behavior of individual leaves is "coupled" to the atmosphere. In **rough canopies**, such as those of forest trees or of small plants in complex terrain, the complex surface structure creates large eddies of air that penetrate the canopies. As a result, the air that surrounds each leaf has a temperature and humidity similar to that of bulk air, so that single-leaf models predict the behavior of leaves in canopies. On the other hand, individual leaves in **smooth canopies** such as in crops or grasslands, are poorly coupled to the atmosphere. Because of the dimensions of their leaves, their higher stomatal conductances, and their tendency to form smooth canopy surfaces, broad-leaf canopies are less coupled than coniferous forests, and considerable vertical gradients of temperature and humidity can develop over just a few meters. Leaf resistances are in series with the canopy boundary layer resistance (Fig. 1). Therefore, where boundary layer resistance is high, such as in smooth canopies, particularly at low wind speeds, variation in leaf resistance does not play a critical role in determining canopy evaporation.

3. Canopy CO_2 Fluxes

Carbon accumulation in communities involves exchanges of carbon with both the atmosphere and the soil (i.e., photosynthesis, plant respiration, and microbial respiration). **Photosynthesis** of the entire canopy can be approached as discussed in Sect. 2 for water use, using single-layer or multilayer models. Models of canopy gas exchange based on equations developed for single leaves (**big-leaf** approach) are relatively simple but can introduce major errors when averaging gradients of light and photosynthetic capacity. Photosynthesis can also be modeled in a "multilayer" approach (Box 2A.1 and Box 5.1). In big-leaf models of canopy photosynthesis, the Rubisco activity and electron-transport capacity per unit ground area are taken as the sums of activities per unit leaf area within the canopy. These models over-estimate rates of photosynthesis unless they incorporate empirical factors that adjust the response of photosynthesis to irradiance (Mercado et al. 2007).

Canopy photosynthesis can also be measured using large cuvettes that enclose entire plants or several plants in the canopy, or by **eddy covariance**, which is a micrometeorological approach that compares the concentrations of water vapor, CO_2, and heat in upward-moving vs. downward-moving parcels of air. Figure 2 shows the rate of canopy CO_2 assimilation and total stomatal conductance of an entire macadamia tree (*Macadamia integrifolia*). Net CO_2 assimilation and stomatal conductance are related to photon irradiance, but the relationships differ for overcast conditions and clear sky.

The heterogeneity of the canopy complicates model estimates of canopy photosynthesis because the light environment and leaf physiological properties are highly variable (Sect. 3 of Chapter 2A on photosynthesis). The resulting variation in photosynthesis and transpiration modifies the air within the canopy, creating gradients in humidity, temperature, and CO_2 concentration. Errors associated with big-leaf models can be avoided in **multilayer models** that treat the canopy in terms of a number of layers. Thus, by combining a model of **leaf photosynthesis** with a model on **penetration of light** and on transport processes within the canopy, the flux from each canopy layer can de estimated. Such models are essential for analyzing the significance of within-canopy variation in leaf traits. For example, the **allocation of nitrogen** to different leaves within a canopy is determined by the light gradient in a canopy in both single-species and multispecies canopies, but the gradient in leaf N is always less than that in irradiance (Field 1983, Hirose & Werger 1987) (Box 5.1) which is why big-leaf models do not work. When sunlit and shaded leaf fractions of the canopy are modeled separately, such a **single-layer sun/shade model** is much simpler than a multilayer canopy model (de Pury & Farquhar 1997).

There are important interactions among environmental gradients and physiological processes within a canopy. For example, under moist conditions, the leaves at the top of the canopy which have the highest N concentrations and experience the highest light availability account for most of photosynthesis. As the soil dries, particularly for vegetation with tall canopies, the leaves at the top of the canopy may have significantly reduced stomatal conductances compared with those lower down, and the zone of maximum photosynthesis shifts farther down in the canopy (Ryan et al. 2006).

It has been consistently more difficult to model **canopy dark respiration** using simple canopy scaling rules because growth and respiration within the canopy are not a simple function of photosynthesis within the canopy (Sects. 1 and 4 of Chapter 2B on respiration). Complications arise because respiration depends on metabolic activity as well as on carbohydrate status, in a manner that is not readily modeled. Thermal acclimation (Sect. 4.5 in Chapter 2B on respiration) and the extent to which dark respiration continues during photosynthesis (Sect. 4.9 in Chapter 2B on respiration; Mercado

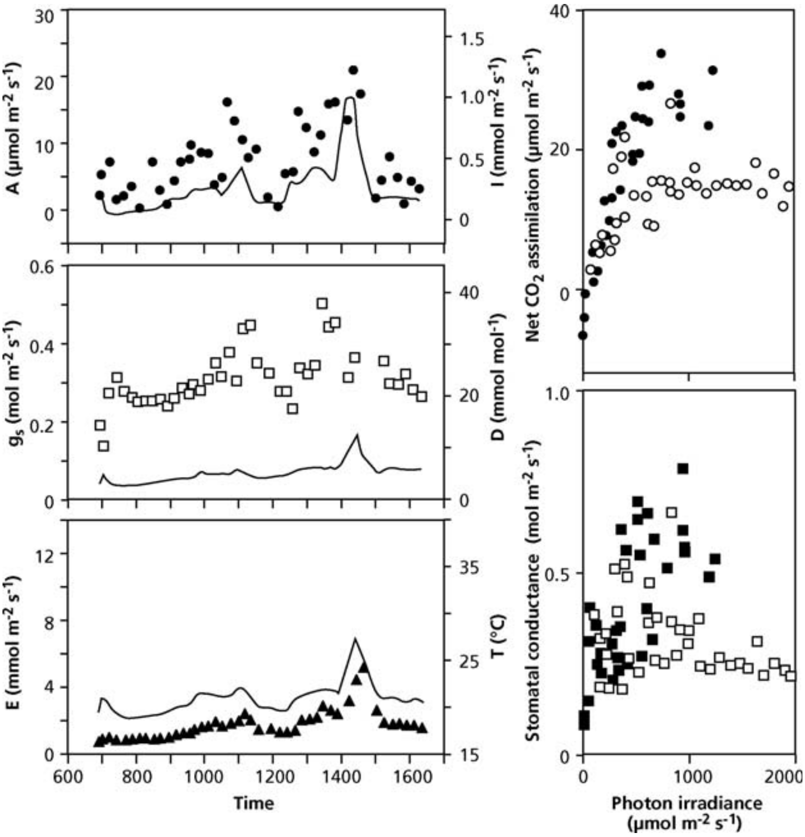

FIGURE 2. (*Left*) The rate of CO_2 assimilation, stomatal conductance, and transpiration (all expressed on a ground area basis) of an entire tree of *Macadamia integrifolia* (macadamia), throughout an entire day. Diurnal changes in irradiance (I), leaf-to-air vapor pressure difference (D) and air temperature (T) are also shown (*solid lines*). (*Right*) The rate of net CO_2 assimilation and stomatal conductance (expressed on a ground area basis) of an entire tree of *Macadamia integrifolia* (macadamia), as dependent on photon irradiance. The solid and open symbols refer to overcast and clear-sky conditions, respectively (Lloyd et al. 1995), *Australian Journal of Plant Physiol.* 22: 987—1000, Copyright CSIRO, Australia).

et al. 2007) represent further uncertainties, with major variation among species. This remains an area of plant physiology where more information is needed to allow scaling from the leaf's CO_2 flux to that of the canopy, especially if canopy scaling is going to be used to address global issues.

4. Canopy Water-Use Efficiency

If canopies affect the gas-exchange properties of individual leaves, then the water-use efficiency (WUE) of the canopy cannot be deduced simply from that of individual leaves measured under the prevailing bulk air conditions. Does this imply that genotypic differences in WUE at the leaf level (Sect. 6 of Chapter 3 on plant water relations) disappear when studied at an ecologically more relevant scale? When dealing with a **rough canopy** (Sect. 2), the differences certainly persist. In a **smooth canopy**, however, such as that of a wheat crop, the differences in conductance are diminished when scaling from the leaf to the canopy level (Fig. 3). For example, a leaf-level difference in photosynthetic water-use efficiency of 24% is

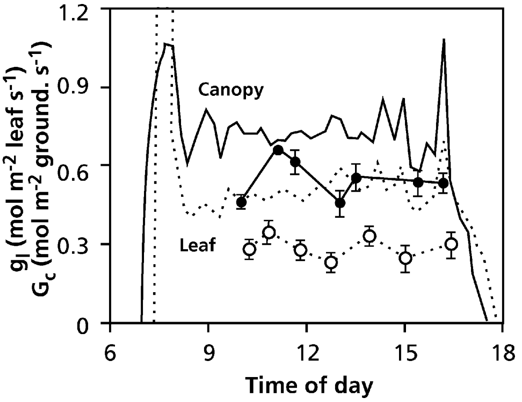

FIGURE 3. Comparison of the diurnal variation of leaf conductance, g_l (*circles connected by lines*) and canopy conductance, G_c (*lines only*) for two cultivars of *Triticum aestivum* (*wheat*), selected on the basis of their contrasting photosynthetic water-use efficiency at the leaf level (de Pury 1995). Reproduced with the author's permission.

only 5% at the canopy level. This decrease in the effect of genotype on WUE, when scaling from a single leaf to the canopy, reflects both the dominance of the **canopy boundary layer conductance** in the total canopy conductance (Sect. 2) and the greater leaf area of the cultivar with lower WUE. This greater leaf area reduces the canopy boundary layer conductance, which counteracts the greater stomatal conductance. In addition, much of the gain made by decreasing stomatal conductance and transpiration can be offset by greater evaporation from the soil when the rate of leaf area development decreases simultaneously.

Wheat genotypes with a low WUE tend to develop their leaf area faster and have a higher leaf area ratio (LAR), in comparison with ones that have a higher WUE, with two important consequences. First, genotypes with a lower WUE transpire more of the available water early in the growing season, when the vapor pressure deficit of the air is relatively low due to low temperatures such as in Mediterranean climates, and, consequently, the WUE is high. Second, transpiration represents a greater fraction of the total crop water use of low-WUE genotypes due to the reduced evaporation from the soil, as mentioned earlier (Condon et al. 1993). A high leaf area ratio (LAR) and vigorous early growth is clearly a major trait determining a crop's water use (Van den Boogaard et al. 1997). This calls for a line of plant breeding, which combines a high WUE (low δ^{13}C-value) with vigorous early growth to reduce soil evaporation.

5. Canopy Effects on Microclimate: A Case Study

As pointed out above, individual leaves in smooth canopies, such as in crops or grasslands, are poorly coupled to the atmosphere. When stomatal conductance declines to low levels, leaves dissipate most heat through convective exchange, warming the air within the canopy. This creates turbulence within the canopy which brings new dry air into the canopy to increase transpiration.

The net loss of radiative energy from a surface exposed to the sky at night is balanced by the flow of heat from the overlying air and the underlying soil. During nights of radiation frost, temperatures of *Eucalyptus* (gum tree) leaves exposed to clear skies may be 1–3°C below those of the air. The resistance to heat transfer between air and grass is less than between air and soil because of the canopy's greater aerodynamic roughness. Because the thermal resistance of air within the grass sward is rather high, air temperatures immediately above the grass are lower than that above bare soil, which conducts heat more easily to the surface. As a result, leaf temperatures of seedlings above grass tend to be lower than those above dry soil which are lower than those above moist soil. This affects the performance of plants growing above a grass canopy, as compared with those above bare patches (Sect. 2 of Chapter 9E on interactions among plants).

6. Aiming for a Higher Level

Scaling of processes from a single leaf to an entire canopy or community is complicated because of complex environmental and physiological gradients and interactions within the canopy. "Big-leaf" models are often a useful simple starting point, especially for estimates of process rates over large geographic areas. However, an understanding of the role of physiology in mediating the exchanges of water, carbon, and heat often benefits from a "multilayer" approach that uses information about these environmental and physiological gradients to model the gas exchange of the entire canopy (Mercado et al. 2007).

When dealing with canopies, we often find that differences (e.g., in water-use efficiency) that are relatively large when studied at the leaf level become smaller or disappear at the canopy level. Scaling from single leaves to communities will become increasingly important when ecophysiologists model effects of global change in temperature and atmospheric CO_2 concentration on primary productivity. Difficulties arise when dealing with the time factor; short-term effects of temperature on rates of processes may differ widely from those in acclimated plants. Temporal and spatial scaling are therefore an important research area for ecophysiologists seeking to develop more effective crops or predict the performance of plants under future conditions.

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