

Estimating Canopy Light-use And Transpiration Efficiencies From Leaf Measurements

Application Note #105

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Introduction

Light and water are two essential quantities that plants must have in adequate supply if they are to grow and flourish. Although other factors also may be important such as carbon dioxide, reasonable temperatures, oxygen, nutrients and an appropriate rooting medium, frequently these other factors do not limit growth or can be manipulated so as to have minimal impact. However the supply of light or water to leaves can be highly variable and often either one or the other may limit growth. Understanding this interaction between plants and their environment is difficult because of the inherent complexity associated with living organisms. Therefore an appreciation of the importance of these complex biophysical relations by scientists in the numerous disciplines that may benefit from such knowledge requires relatively simple methodologies that emphasize only the factors of major importance.

Sunlight is the source of radiant energy that plants convert into stored chemical energy to support life-sustaining processes. Therefore the efficiency of conversion of light into stored chemical energy and essential carbon compounds provides a method for estimating potential plant productivity. Water is essential for all life and in plants it is not only a “universal” solvent, but it may be required in large quantities to maintain leaf cells in a viable condition as they absorb essential carbon dioxide from air that simultaneously removes water from the leaf tissue. Furthermore, the absorption of light, which also is required for photosynthesis, heats the leaf and may further enhance the loss of water. One of the major accomplishments of terrestrial vegetation is the maintenance of favorable cell water status in the presence of heating by absorbed light and desiccation by air that is supplying carbon dioxide. Plants routinely accomplish this balancing of carbon dioxide uptake with water loss through the extraordinarily elegant structures that we refer to as stomata.

From the perspective of food production and environmental impact, we are interested in the functioning of a community of plants, and we refer to the aerial portion of this community as a canopy. Rates of photosynthesis, respiration and transpiration for plant canopies can be measured

directly using chamber (Garcia et al., 1990; Reicosky, 1990) or micrometeorological methods (Verma, 1990). However, canopy fluxes are the result of many component processes and separating effects of ambient environment, canopy architecture, soil exchanges and plant physiological characteristics can be difficult. Therefore our greatest insight into the functioning of plant communities is likely to arise from measurements at the canopy level combined with measurements on individual leaves (Field, 1989). Using both leaf and canopy measurements to understand plant-environment relations requires a means of combining them.

This note describes a method for using simple measurements of gas exchange on individual leaves to estimate transpiration and light-use efficiencies on a canopy-wide basis for broadleaf, full-cover vegetation.

Transpiration and Light-Use Efficiencies

Transpiration efficiency can be defined in many ways depending on the time scale (instantaneous, daily or seasonal), spatial scale (leaf, plant or field) and the kind of measurement (carbon dioxide assimilation, total biomass, yield, transpiration or evapotranspiration)(Sinclair et al., 1984). For our purposes we shall define transpiration efficiency (ϵ_E) as the ratio of canopy carbon dioxide assimilation ($A_c - \mu\text{mol m}^{-2}\text{s}^{-1}$) and canopy transpiration ($E_c - \text{mol m}^{-2} \text{s}^{-1}$) on the time scale from instantaneous to hourly:

$$\epsilon_E = \frac{A_c 10^{-6}}{E_c} 100 \quad [1]$$

so that the units of ϵ_E are mol CO₂ per mol H₂O expressed as percent (%).

Canopy light-use efficiency can also be defined in many ways depending on time scale (instantaneous, daily or seasonal), kind of carbon measurement (carbon dioxide assimilation, total dry matter, above-ground dry matter, or carbon content of total or above-ground dry matter) and kind of radiation measurement (intercepted or absorbed photosynthetically active radiation, or intercepted or absorbed solar radiation) (Norman and Arkebauer, 1991).

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We shall define canopy light-use efficiency (ϵ_Q) as the ratio of CO₂ assimilation to intercepted photosynthetically active radiation (Q_i - $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$)

$$\epsilon_Q = \frac{A_c}{Q_i} 100 \quad [2]$$

so that the units of ϵ_Q are $\mu\text{mol CO}_2$ per μmol intercepted quanta expressed in percent (%). For our purposes the time scale is instantaneous to hourly.

Measurements

Characterizing canopy light-use-efficiency and transpiration efficiency from leaf measurements requires leaf gas exchange measurements, some environmental measurements, and some measurements of canopy architecture.

Leaf Chamber Measurements

Leaf gas exchange measurements can be done with an LI-6200 so that CO₂ uptake and stomatal conductance are measured along with PAR incident on the leaf, leaf temperature, humidity, air temperature and CO₂ concentration of the air in the chamber. One procedure for acquiring these data is to obtain leaf assimilation and stomatal conductance at a range of light flux densities with other conditions remaining approximately constant. This can be done by measuring on leaves at various angles to the direct solar beam on a clear day or using a neutral-density filter on a single leaf. Using many leaves provides a better sampling of mean leaf assimilation rates for the canopy, but measurements with neutral density filters on a single leaf provide more reliable curves of the relative dependence of assimilation on light.

The scaling procedure outlined in this article requires leaf assimilation rate, at each quantum flux density, as a function of internal CO₂ concentration (C_i) over a range of concentrations near normal ambient conditions for the leaf. Leaf assimilation draws chamber CO₂ concentration down so that after flow rate has been adjusted in the LI-6200 to stabilize humidity, CO₂ concentration is well below ambient. To obtain measurements near ambient CO₂, a small syringe can be used to inject a small amount of high concentration CO₂ into the chamber to elevate CO₂ 20 to 30 $\mu\text{mol mol}^{-1}$ so that, by the time humidity is stabilized, CO₂ is near ambient. By continuously logging data, leaf assimilation is obtained as a function of C_i as the leaf draws chamber CO₂ down (LI-COR Application Note #103). When the leaf assimilation rate declines to about 2/3 of the initial rate, high CO₂ may again be injected to raise the chamber concentration to about 450 $\mu\text{mol mol}^{-1}$. Leaf assimilation rate can then be determined at elevated C_i . If chamber CO₂ is elevated to 450 $\mu\text{mol mol}^{-1}$ initially, stomata tend to close rapidly from the combined effect of lowered boundary layer resistance (since the leaf was just moved from relatively still air to the well mixed chamber) and higher CO₂ causing difficulty in determining A vs C_i .

Allowing draw-down initially may cause stomatal opening so that when CO₂ is suddenly increased, stomata close more slowly in response to elevated CO₂. Since C4 plants saturate at a relatively low C_i , obtaining assimilation at elevated C_i is critical to using the scaling method described in this paper because high boundary layer conductances in chambers often cause stomatal closure. This closure means that leaf assimilation and C_i in the chamber can be lower than the same leaf in a canopy. The CO₂ saturated assimilation rate must also be known to scale to the canopy.

The incident PAR measurements made with an LI-190 quantum sensor, attached to the leaf chamber of the LI-6200, are not appropriate for the leaf because of chamber transmittance τ_c . A value of 0.9 is typical for τ_c for both PAR and NIR spectral regions, although transmission of PAR through chamber walls depends on the angle between the chamber wall and the sun.

Light-versus-assimilation relations are of more general use if light is expressed on the basis of absorbed quanta (Q_a). Leaf absorptivity to PAR can be obtained by two methods, both involving the LI-1800-12S integrating sphere. An LI-190 can be used with the integrating sphere to obtain an approximate absorptivity that is integrated over PAR wavelengths (α_{PAR}). Using a broadband sensor to measure reflectance or transmittance can result in errors because the light source is not spectrally flat, and longer wavelengths are weighted more heavily. However, the relative error associated with using a quantum sensor with the integrating sphere to measure leaf absorptivity is less than 5%. A more accurate absorptivity can be obtained with an LI-1800 spectroradiometer and the integrating sphere to measure the wavelength dependence of absorption in the PAR and near-infrared (α_{NIR}) as well. Software in the LI-1800 permits easy integration of the 400 to 700 nm wavelength band. Typical values for α_{PAR} and α_{NIR} are 0.8 and 0.1, respectively.

Environmental Measurements

The LI-6200 can provide measurements of environmental conditions within the canopy, but additional measurements are required to obtain canopy light-use and transpiration efficiencies. The additional measurements depend on the methods used to estimate canopy light-use and transpiration efficiencies. Methods and instruments for obtaining these environmental measurements are discussed in Goel and Norman (1990).

Estimates of canopy light-use efficiency require the following environmental measurements: 1) direct and diffuse incoming PAR flux density above the canopy with an LI-190 and a shading device, 2) intercepted PAR below the canopy with an LI-191S line quantum sensor, and 3) zenith angle of the sun.

Estimates of transpiration efficiency require some additional environmental measurements; 1) net radiation, 2) soil heat conduction flux and 3) wind speed. Net radiation

can be measured with a net radiometer (for example Fritschen or Swissteco). Although net radiation can be estimated from solar radiation, air temperature, air vapor pressure, canopy temperature and canopy albedo, the additional measurements and associated errors result in a direct measurement of net radiation being more desirable than estimation from other measurements. This of course assumes the net radiometer is properly maintained and calibrated.

The soil heat conduction flux can be estimated from soil heat flux plates (ERB) buried at 5-cm depth with thermocouples above the plates to account for heat storage changes (Clothier et al., (1986)). Alternatively, soil heat conduction flux can be estimated from the net radiation and canopy characteristics. For full cover canopies, the soil heat conduction flux is approximately 10% of the net radiation above the canopy between 0900 and 1500 local standard time (Clothier et al., (1986)). Considering the relatively small magnitude of the soil heat conduction flux below full cover canopies, estimation from net radiation is a reasonable choice.

Wind speed measurements are relatively easy to make with cup anemometers placed several meters above the top of the canopy.

Measurements of Canopy Architecture

Estimates of light-use and transpiration efficiency require the same measurements of canopy architecture; height, leaf area index (F), leaf size and some measure of leaf inclination angle such as extinction coefficient K. Canopy height is a simple measurement that is used to estimate canopy roughness and displacement height, which are used to calculate the resistance to heat and water transport between the canopy and the atmosphere. The LAI-2000 can be used to estimate F and radiation extinction coefficients for full cover canopies. Leaf size refers to the distance the wind travels in crossing a leaf. For grasses, use two times the width.

Model

The simple method proposed to calculate canopy photosynthetic rate and conductance has two parts:

- 1) Adjust the leaf chamber light responses of photosynthesis and conductance to the environmental conditions found in the canopy.
- 2) Use a simple canopy radiation model to compute average assimilation and conductance for each layer of the canopy, based on sunlit and shaded irradiances, their area fractions, and the adjusted light response curves. Summing over the layers provides total canopy photosynthetic rate and conductance.

where Q_a gives absorbed quanta per unit leaf area in the chamber, ϕ is the photochemical efficiency at low light levels, A_{max} is the assimilation rate at light saturation, A_o is

Adjusting Chamber Measurements

Leaf gas exchange measurements are made in chambers that usually have intensive mixing and leaf boundary layer conductances g_b that are systematically higher than those found in canopies g_x . For example, a typical 6000-11 one-liter chamber for the LI-6200 may have a boundary layer conductance of $2 \text{ mol m}^{-2} \text{ s}^{-1}$ for a 10-cm wide leaf, whereas in a canopy such a leaf may have a conductance of $0.4 \text{ mol m}^{-2} \text{ s}^{-1}$. This decreased boundary layer conductance tends to decrease leaf photosynthetic rate and internal CO_2 concentration; however, this may be more than offset by an increase in stomatal conductance because of a higher surface humidity adjacent to the stomata (Ball et al., 1987).

An LI-6200 gas exchange system provides measurements of leaf assimilation (A), stomatal conductance (g_s), internal and ambient CO_2 concentrations (C_i and C_a respectively) and ambient relative humidity of the air (H_a). These measurements are typically obtained at several CO_2 concentrations slightly below ambient levels, because the closed system draws down CO_2 concentrations during measurement.

In addition to boundary layer conductance g_x and C_a , chamber H_a and T_a may differ from canopy conditions during the measurement.

Adjustments to A and g_s for changes in H_a , T_a , C_a , and g_x can be made with the following model. First, we assume that the relationship of g_s to A found by Ball et al. (1987) will hold, so that

$$g_s = b_1 \frac{A H_s}{C_s} + b_2 \quad [3]$$

where leaf surface humidity H_s and leaf surface CO_2 concentration C_s are given by

$$H_s = 1 - \frac{E P}{e_s(T_1) g_s} \quad [4]$$

$$C_s = C_a - \frac{A}{f g'_x} \quad [5]$$

P is atmospheric pressure (kPa), T_1 is leaf temperature, and $e_s(T)$ is the saturation vapor pressure (kPa) at temperature T ($^{\circ}\text{C}$) given by Buck (1981),

$$e_s(T) = 0.6136 e^{\left[\frac{17.52 T}{240.97 + T} \right]} \quad [6]$$

Boundary layer conductance to CO_2 g'_x is related to that for H_2O by

$$g'_x = \frac{g_x}{1.35} \quad [7]$$

and f adjusts the boundary layer conductance for the presence of stomata. $f=1$ for hypostomatus leaves and $f=2$ for amphistomatus leaves. In general,

$$f = \frac{(k+1)^2}{(k^2+1)} \quad [8]$$

where k is the ratio of stomatal conductance of the two sides of the leaf (the LI-6200 STOMRAT parameter).

In addition, we assume a linear $A-C_i$ relationship for the leaves in the region in which adjustments are to be made.

$$A = a_1 C_i + a_2 \quad [9]$$

This assumption is usually justified and simplifies the calculations, but is not absolutely necessary.

Eq. [4] requires leaf temperature T_l . When adjusting to conditions significantly different than those of the chamber (especially when g_x is different than g_b), chamber measured T_l will not suffice, since T_l out of the chamber will be different. It is the experience of one of the authors (Norman) that this adjustment method works best when the temperature of the air near the leaf is used in Eq. [4], rather than leaf temperature. Thus, we assume

$$T_l \cong T_c \quad [10]$$

Mean canopy temperature T_c can be measured with an infrared temperature sensor by viewing the canopy at about 55° nadir angle and averaging over the four cardinal directions (Huband and Monteith, 1986). T_c can also be calculated aerodynamically (Appendix C) once canopy conductance g_c and transpiration E_c are known. Thus, make a first guess of T_c , follow this procedure through to the calculation of T_c , and repeat again if the calculated T_c is more than a few degrees different than the assumed T_c .

The model for adjusting A and g_s for non-measurement conditions requires measurements over a range of conditions (especially H_a and to some extent C_a) on a number of leaves to obtain constants b_1 and b_2 . Also, the segment of an $A-C_i$ curve for C_a near ambient is required for obtaining a_1 and a_2 for each light level. Then

1. Compute g_T (Eq. 11) from the measured g_s and the new g_x

$$g_T = \frac{1}{\frac{1}{g_s} + \frac{1}{fg_x}} \quad [11]$$

2. Compute transpiration

$$E = g_T \left(\frac{e_s(T_l) - e_a}{P} \right) \quad [12]$$

3. Compute A by combining Eq. [9] with $A = (C_a - C_i)g'_T$ to

yield the relation

$$A = \frac{a_1 C_a + a_2}{1 + \frac{a_1}{g'_T}} \quad [13]$$

where

$$g'_T = \frac{1}{\frac{1.6}{g_s} + \frac{1.35}{fg_x}} \quad [14]$$

4. Compute H_s (Eq. 4) and C_s (Eq. 5).
5. Compute g_s (Eq. 3).
6. Compare the new g_s to the previous g_s . If they differ by more than 0.01, repeat steps 1 through 5 until g_s converges.

This procedure provides A and g_s values adjusted to canopy conditions at a series of light levels.

To illustrate the importance of these calculations, refer to the example at the end of this note. Canopy assimilation calculated with adjusted light curve data is 12% higher compared to that calculated with chamber light curve data. Similarly, canopy conductance is 24% higher, and canopy transpiration is 7% higher. The chamber data in this example was taken with a reduced fan speed and lower than normal g_x , or the corrections would have been even larger. Clearly, scaling chamber measurements to infer canopy fluxes requires considerable care.

Canopy estimates of assimilation and transpiration will depend on the boundary layer conductance that is implicit in light response curves used in Eqs. [18] and [19]. If chamber light response curves are used then chamber boundary layer conductance is assumed to be appropriate in the canopy. The example above shows that such an assumption can lead to significant errors.

In the analysis described in this paper, assimilation rates measured in the leaf chamber at each light level are adjusted to canopy conditions with respect to boundary layer conductance, air temperature, humidity and CO_2 mole fraction. A light curve is then constructed using the adjusted assimilation rates and absorbed PAR measured in the chamber. Such a light response curve can be described by

$$A = \frac{\phi Q_a}{\left[1 + \left(\frac{\phi Q_a}{A_{max}} \right)^p \right]^{1/p}} + A_o \quad [15]$$

where Q_a gives the absorbed quanta per unit leaf area in the chamber, ϕ is the photochemical efficiency at low light levels, A_{\max} is the assimilation rate at light saturation, A_o is the dark assimilation rate, and p is a curvature parameter. ϕ is typically 0.06 for C4 plants and 0.05 for C3 plants, so one can either assume a value for ϕ or allow a curve-fitting program to find it along with the other parameters. Q_a is given by

$$Q_a = \alpha_{\text{par}} \tau_c Q \quad [16]$$

The resulting light response curve is valid for the environmental conditions that exist in the canopy.

Stomatal conductance for sunlit and shaded leaves can be computed from a linear regression of adjusted g_s vs adjusted A , using the light curve data set.

$$g_s = c_1 A + c_2 \quad [17]$$

Calculating Canopy Fluxes

The procedure for estimating canopy conductance and photosynthetic rate from leaf rates involves dividing the canopy into several layers. Within each layer, consider sunlit and shaded leaves separately; then the contributions of sunlit and shaded leaves are summed separately within each layer. The final canopy values are obtained by summing over the layers. Thus, we need to know the amount of leaf area that is sunlit and the amount shaded in each layer, and an estimate of the mean illumination levels on both sunlit and shaded leaves. This is necessary because of the nonlinear dependence of leaf conductance and photosynthetic rate on light.

The canopy photosynthesis rate per unit ground area for each layer i is estimated from

$$A_{c,i} = A_{\text{sun},i} F_{\text{sun},i} + A_{\text{shade},i} (F_i - F_{\text{sun},i}) \quad [18]$$

where, $A_{\text{sun},i}$ and $A_{\text{shade},i}$ are assimilation rates of sun and shade leaves per unit leaf area, $F_{\text{sun},i}$ is sunlit leaf area index for layer i , and F_i is total leaf area index for layer i . $A_{\text{sun},i}$ and $A_{\text{shade},i}$ are obtained from the mean quantum flux densities for sun and shade leaves, and the light response curve given by Eq. [15]. Similarly, a canopy conductance per unit ground area can be computed for each layer i from the sum of contributions of sunlit and shaded leaves according to

$$g_{c,i} = g_{\text{sun},i} F_{\text{sun},i} + g_{\text{shade},i} (F_i - F_{\text{sun},i}) \quad [19]$$

where $g_{\text{sun},i}$ and $g_{\text{shade},i}$ are calculated from Eq. [17] using $A_{\text{sun},i}$ and $A_{\text{shade},i}$.

The leaf area index for the i^{th} layer F_i is obtained either by dividing total leaf area index F by the number of layers, or

by the difference of leaf area index at the heights bounding the layers using an LAI-2000. Thus, $F_i = F'_i - F'_{i-1}$, where F'_i is the LAI-2000 measurement beneath the i^{th} layer. For n layers, $F'_n \equiv F$.

The sunlit leaf area index in layer 1 (top layer of the canopy) can be calculated for a sun zenith angle θ , if leaves are assumed to be randomly distributed,

$$F_{\text{sun},1} = [1 - \exp(-K F_1 / \cos\theta)] \cos\theta / K \quad [20]$$

where K = the extinction coefficient of light in the canopy, which depends on the leaf inclination angle distribution. Physically K is the fraction of leaf area index projected in the direction θ . For the second layer ($i=2$)

$$F_{\text{sun},2} = \left[\exp\left(\frac{-K F_1}{\cos\theta}\right) - \exp\left(\frac{-K(F_1 + F_2)}{\cos\theta}\right) \right] \frac{\cos\theta}{K} \quad [21]$$

and for a third layer ($i=3$),

$$F_{\text{sun},3} = \left[\exp\left(\frac{-K(F_1 + F_2)}{\cos\theta}\right) - \exp\left(\frac{-K(F_1 + F_2 + F_3)}{\cos\theta}\right) \right] \frac{\cos\theta}{K} \quad [22]$$

The extinction coefficient (K), which usually depends on the sun zenith angle, can be estimated from the contact values calculated from the LAI-2000 measurement (Appendix B).

Clearly, the leaf area index exposed to direct sunlight can vary widely with canopy architecture and sun zenith angle. In fact, a canopy with a leaf area index of 1.0 can have more sunlit leaf area at midday than a canopy with a leaf area index of 3.0 has in morning or evening.

The canopy photosynthetic rate (conductance) depends on a weighted sum of sunlit and shaded leaf photosynthetic rates (conductance) represented by Eq. [18] (Eq. [19]). The photosynthetic rate (conductance) for the entire canopy is calculated from the sum of the contributions of individual layers.

$$A_c = \sum_{i=1}^n A_{c,i} \quad [23]$$

$$g_c = \sum_{i=1}^n g_{c,i} \quad [24]$$

Note that both A_c and g_c are expressed on a ground area basis, rather than a leaf area basis.

To obtain the mean leaf photosynthetic rate and conductance, we must estimate the average incident PAR for both sunlit and shaded leaves. The average PAR received by all

shaded leaves (Q_{shade}) in a canopy was estimated by Norman (1982), assuming a spherical leaf angle distribution. Although this will depend on the leaf angle distribution, no simple equation is presently available for predicting the mean shaded illumination on leaves as a function of leaf inclination. We expect the results from spherical-distribution calculations to be reasonable for many canopies. Therefore, we will use the equation from Norman (1982) to estimate the shaded illumination in the top layer ($i=1$);

$$Q_{\text{shade},1} = Q_d \exp(-0.5 F_1^{0.7}) + C_1 \quad [25]$$

where

$$C_1 = 0.07 Q_D (1.1 - 0.1 F_1) \exp(-\cos\theta) \quad [26]$$

and Q_d and Q_D are the incident sky diffuse and direct solar beam PAR on a horizontal plane above the canopy, respectively. C_1 represents the direct beam scattered by leaves in the canopy. The direct beam flux density Q_D is $Q_{\text{TOT}} - Q_d$. Because Eqs. [25] and [26] represent an average shaded-leaf illumination over the leaf area index (in this case F_1), the shaded illumination for a second layer is given by

$$Q_{\text{shade},2} = 2Q_{\text{shade},1+2} - Q_{\text{shade},1} \quad [27]$$

where $Q_{\text{shade},1+2}$ is evaluated by using Eqs. [25] and [26] and substituting F_1+F_2 for F_1 . Similarly, the shaded flux density for a third layer is given by

$$Q_{\text{shade},3} = 3Q_{\text{shade},1+2+3} - 2Q_{\text{shade},1+2} \quad [28]$$

where $Q_{\text{shade},1+2+3}$ is evaluated by replacing F_1 in Eqs. [25] and [26] by $F_1+F_2+F_3$. Clearly this method can be extended to any number of layers.

The PAR received by sunlit leaves is the sum of that from the direct beam along with the diffuse given by Eqs. [25] and [26]:

$$Q_{\text{sun},i} = Q_D \left(\frac{K_i}{\cos\theta} \right) + Q_{\text{shade},i} \quad [29]$$

Predicting Light-Use and Transpiration Efficiency

The canopy light-use efficiency [Eq. 2] depends on canopy photosynthesis (A_c) and intercepted PAR. The latter is measured directly and A_c is calculated from Eqs. [18] and [23].

Canopy transpiration efficiency requires an estimate of A_c and an estimate of canopy transpiration E_c ($\text{mol m}^{-2} \text{s}^{-1}$), which is calculated from Monteith (1965)

$$E_c = \frac{s(R_n - G) + C_m g_a [e_s(T'_a) - e'_a]}{L_e \left[s + \gamma \left(1 + \frac{g_a}{g_c} \right) \right]} \quad [30]$$

where R_n (W m^{-2}) is the net all-wave radiation above the canopy, G (W m^{-2}) is the soil heat conduction flux, C_m is the mole specific heat of air (J mole^{-1}), g_a is the aerodynamic conductance of the canopy, γ is the psychrometer constant (0.066 kPa K^{-1}), T'_a is air temperature above the canopy, and e'_a is vapor pressure above the canopy.

The slope s (kPa K^{-1}) of the saturated vapor pressure versus temperature curve can be evaluated from

$$s = \frac{L_e e_s(T)}{R(T + 273)^2} \quad [31]$$

where L_e is the latent heat of water ($44,200 \text{ J mol}^{-1}$ @ 20°C) and R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{K}^{-1}$). The canopy conductance g_c is given by Eq. [24]. The aerodynamic conductance (g_a) is evaluated in Appendix C.

Discussion

The model makes a number of stringent assumptions that enhance simplicity but are not absolutely necessary.

1. Eq. [9] presents A as a first-order function of C_i . This allows Eq. [13] to take a simple form, but Eq. [9] could be represented by a quadratic, hyperbolic, or other function without introducing serious difficulty.
2. The same is true of Eq. [15]. Or, a light curve for g_s could be constructed directly from g_s vs Q_a .
3. It is not necessary that the Ball-Berry model be first order, as long as some tractable functional form exists.

We have not been very clear about the number of layers that may be necessary.

1. The number of layers will depend upon the situation. Perhaps identifying sun leaves and shade leaves in one layer is enough in monospecific culture. In that case, the empirical coefficients for the Ball-Berry model (b_i), the g_s vs A curve (c_i), and the light response curve might characterize the whole canopy considered as one layer.
2. Even within a monospecific canopy, there may be sufficient physiological differentiation between sun and shade leaves in different layers to prevent one light response curve, for example, from characterizing the canopy. This will probably vary among cases, but more layers require more empirical data, of course.
3. Multispecific canopies in which upper story and lower story species can be identified should be divided into at least two layers, as in the example presented here. The number of layers will be a matter of judgement in individual cases.

Summary of Procedure

Measurements

1. Reduce chamber fan speed to about 5.5V. An easy way to do that is described in Application Note #103. Make chamber measurements on a variety of leaves in the canopy, at a range of vapor pressures and small range of CO₂ concentrations (near ambient). These data will be used to determine b_1 and b_2 , the slope and intercept of the conductance vs Ball-Berry index. This data set should include only those cases in which the stomata were equilibrated with the chamber conditions.
2. Use filters, or work on leaves at varying angles to the sun, to measure a chamber light response curve. At each light level, allow the CO₂ to draw down sufficiently to provide an estimate of the slope of A vs C_i at that light level. Use at least 4 light levels. Finally, for C4 species, raise the CO₂ to give an estimate of the maximum photosynthetic rate at each light level.
3. Measure the micrometeorological parameters: net radiation, wind speed above the canopy, air temperature and vapor pressure above the canopy, incident total and diffuse PAR, and below-canopy spatially averaged PAR. If wind speeds can be measured in the canopy, do so. Also measure the air temperature and vapor pressure within the canopy. If an IR gun is available, measure canopy temperature at 55° nadir angle averaged over 4 azimuthal views 90 degrees apart.
4. Measure the canopy structure: canopy height, LAI and extinction coefficients, leaf absorptance to PAR, and leaf size.

Data Processing:

1. Determine b_1 and b_2 from the survey data.
2. Determine a_1 and a_2 for each A-C_i curve light level.
3. For each height corresponding to what you have defined a layer in the canopy to be, compute the boundary layer conductance based on leaf size and wind speed. If wind profile information was not measured within the canopy, compute the wind speeds from the model assuming neutral stability.
4. Adjust the chamber light curve measurements to the canopy conditions (g_x , T_c , C_a , and e_a). Calculate absorbed PAR.
5. Fit the light curve data (adjusted assimilation vs absorbed PAR).
6. Use the adjusted light curve data to compute c_1 and c_2 , the slope and intercept of conductance as a function of assimilation rate.
7. Compute total canopy assimilation and conductance using the layer model (Eq. 18 through 29).

8. Compute the aerodynamic conductance (Eq. C-1) for the canopy, and resulting canopy transpiration (Eq. 30). Solve the energy balance for sensible heat flux (Eq. C-8), and compute stability correction terms (Eqs. C-2 through C-5). Recompute aerodynamic conductance, transpiration, and sensible heat flux. Continue iteration on sensible heat flux.
9. Compute canopy temperature (Eq. C-9). Compare with that assumed in Step 4. Iterate if necessary.
10. Compute canopy efficiencies.

Support Software

A software package is available from LI-COR (3 1/2" disk, part #6200-29, or 5 1/4" disks, part #6200-29a) that will assist in making these calculations. The package includes several programs and the data files required for doing the example at the end of this note. The programs on the disk are:

- a) An editor, for preparing data files for input to the other programs.
- b) A plotting program, including linear (polynomials) and nonlinear regression curve fitting. User-defined equations can be added to the program's repertoire.
- c) A transform program, for general purpose computations, such as those specified in this application note. The program operates on its source file according to instructions (written in a simple BASIC-like language) that reside in a separate text file. These instructions are easily accessed and modified by the user.

Literature Cited

- Ball, J.T., I.E. Woodrow and J.A. Berry. 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. (J. Biggins, ed.) pp. 221-224. Progress in Photosynthesis Research, Vol. 4. Martinus Nijhoff, Dordrecht, The Netherlands.
- Buck, A.L. 1981. New equations for computing vapor pressure and enhancement factor. *J. Appl. Meteorol.* 20:1527-1532.
- Clothier, B.E., K.L. Clawson, P.J. Pinter Jr., M.S. Moran, R.J. Reginato and R.D. Jackson. 1986. Estimation of soil heat flux from net radiation during the growth of alfalfa. *Agric. For. Meteorol.* 37:319-329.
- Field, C.B., J.T. Ball and J.A. Berry. 1989. Photosynthesis: Principles and field techniques. (R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel, editors) pp.209-253. *Plant Physiological Ecology*. Chapman and Hall, N.Y.
- Garcia, R.L., J.M. Norman and D.K. McDermitt. 1990. Measurements of canopy gas exchange using an open chamber system. In: Instrumentation for studying vegetation canopies for remote sensing in optical and thermal infrared regions. (N.S. Goel and J.M. Norman, eds.) pp. 141-162. Harwood Academic Publ., London, England.
- Goel, N.S. and J.M. Norman (eds). 1990. Instrumentation for Studying Vegetation Canopies for Remote Sensing in Optical and Thermal Infrared Regions. Harwood Academic Publ., London, England. 360 pp.
- Grace, J. 1981. Some effects of wind on plants. (J. Grace, E.D. Ford, and P.G. Jarvis, eds.) pp. 31-56. *Plants and their atmospheric environment*. Blackwell Scientific Publishers.
- Huband, N.D.S. and J.L. Monteith, 1986. Radiative surface temperature and energy balance of a wheat canopy. *Boundary-Layer Meteorology* 36:1-17.
- Kanemasu, E.T., M.L. Wesely and B.B.Hicks. 1979. Techniques for calculating energy and mass fluxes. In: Modification of the aerial environment of crops. (B. J. Barfield and J. F. Gerber, eds.) pp.156-182. Amer. Soc. Agric. Engineers, St. Joseph, Mich.
- Monteith, J. L. 1965. Evaporation and environment. *Symp. Soc. Exp. Biol.* 19, 205-234.
- Norman, J. M. 1982. Simulation of microclimates. In: *Biometeorology and Integrated Pest Management*. (J.L. Hatfield and I. J. Thomason, eds.) pp. 65-99. Academic Press, New York.
- Norman, J.M. 1992. Scaling processes between leaf and canopy levels. eds. J. Ehleringer and C. Field. In: *Scaling processes between leaf and landscape levels*. Academic Press, New York (in press).
- Norman, J.M. and T.J. Arkebauer. 1991. Predicting canopy light-use efficiency from leaf characteristics. (J.T. Ritchie and J. Hanks, editors) *Modeling Plant and Soil Systems*. Agron. Monograph 31, Amer. Soc. Agronomy, Madison, WI.
- Reicosky, D.C. 1990. Canopy gas exchange in the field: closed chambers. In: *Instrumentation for studying vegetation canopies for remote sensing in optical and thermal infrared regions*. (N.S. Goel and J.M. Norman, eds.) pp. 163-178. Harwood Academic Publ., London, England.
- Sinclair, T.R., C.B. Tanner and J.M. Bennett. 1984. Water-use efficiency in crop production. *Bioscience* 34:36-40.
- Thom, A.S. 1971. Momentum absorption by vegetation. *Quar. J. Roy. Meteorol. Soc.* 97:414-428.
- Verma, S.B. 1989. Aerodynamic resistance to transfer of heat, mass, and momentum. (T.A. Black, D.L. Splittlehouse, M.D. Novak, D.T. Price, eds.) pp. 13-20. I.A.H.S. Publication No. 177. I.A.H.S., 2000 Florida Ave. N.W., Washington, D.C. 20009.
- Verma, S.B. 1990. Micrometeorological methods for measuring surface fluxes of mass and energy. In: *Instrumentation for studying vegetation canopies for remote sensing in optical and thermal infrared regions*. (N.S. Goel and J.M. Norman, eds.) pp. 99-115. Harwood Academic Publ., London, England.

Example Calculations

This example is a grass stand whose upper canopy is made up of Switch grass, and whose lower canopy is Big Blue Stem. Therefore, we analyze the canopy in two layers, with separate response curves for each layer. The chamber measurements shown here were made with a 1/4 liter chamber with a reduced fan speed, as reflected by the lower than normal boundary layer conductances of 1.4 mol/m²/s.

Table 1. Meteorological Measurements	
Time and location: 11 Aug. 1987 14:40 CST at 45 °N, 100 °W Solar Zenith angle: 37.5° PAR above canopy: (total + diffuse): $Q_{tot} = 1700 \mu\text{mol m}^{-2} \text{s}^{-1}$ (diffuse): $Q_d = 250 \mu\text{mol m}^{-2} \text{s}^{-1}$ PAR below canopy: 270 $\mu\text{mol m}^{-2} \text{s}^{-1}$ Intercepted PAR: $Q_i = 1700 - 270 = 1430 \mu\text{mol m}^{-2} \text{s}^{-1}$	Wind: 2 m s ⁻¹ at height 4m Net radiation: $R_n = 500 \text{ W m}^{-2}$ Soil Heat Flux: $G = 50 \text{ W m}^{-2}$ Within Canopy: $T_a = 36 \text{ °C}$ $e_a = 2.8 \text{ kPa}$ Above Canopy: $T'_a = 35 \text{ °C}$ $e'_a = 2.7 \text{ kPa}$

Table 2. Canopy Structure Measurements											
Height: 0.6 m Leaf dimension: 0.03 m Leaf absorptance: $\alpha_{PAR} = 0.8$ $\alpha_{NIR} = 0.1$											
(Output from LAI-2000)											
FILE	DATE	TIME	ACHK	PLOT	LAI	SEL	DIFN	MTA	SEM	SMP	
1	11 AUG	06:33:43	11	8	2.80	0.10	0.150	65	3	2	
ANGLES		7.000	23.00	38.00	53.00	68.00					
CNTCT#		0.840	1.031	1.450	1.762	1.360					
STDDEV		0.133	0.063	0.108	0.031	0.011					
DISTS		1.008	1.087	1.270	1.662	2.670					
GAPS		0.430	0.327	0.159	0.054	0.027					
(Output from C2000 program)											
ID#	EXT_7	EXT_23	EXT_38	EXT_53	EXT_68	EXTslope	EXTint				
1	0.300	0.368	0.518	0.629	0.486	4.17E-03	0.302				

Table 3. Survey Data, Switch Grass

$$g_b = 1.43 \text{ mol m}^{-2} \text{ s}^{-1}$$

$$\text{STOMRAT} = 1$$

Q	T _a	T _l	e _a	C _a	C _i	g _s	A	H _a	H _s	C _s	Index*
2163	36.4	39.3	2.26	345	41.1	0.110	19.5	0.37	0.34	335	0.0199
2098	37.7	38.8	2.39	327	55.3	0.129	20.3	0.37	0.37	317	0.0238
329	34.2	34.6	2.08	331	69.6	0.102	15.6	0.39	0.40	323	0.0193
401	35.5	35.0	1.94	339	115	0.061	7.91	0.34	0.36	335	0.0085
331	34.6	34.3	1.95	341	103	0.038	5.32	0.35	0.37	338	0.0058
1840	36.8	37.3	2.89	314	90.3	0.251	32.0	0.47	0.50	299	0.0532
964	38.2	36.9	2.83	342	119	0.223	28.2	0.42	0.50	328	0.0427
332	36.1	35.6	2.39	334	163	0.065	6.3	0.40	0.43	331	0.0081
388	35.7	34.9	2.47	323	147	0.104	10.5	0.42	0.46	318	0.0153
1507	36.1	36.4	3.19	342	105	0.254	34.5	0.53	0.56	326	0.0597
1898	37.5	39.7	3.00	336	88.3	0.154	21.8	0.47	0.44	325	0.0296
1727	38.1	39.5	3.16	339	71.6	0.162	25.1	0.47	0.47	327	0.0359
1813	38.3	40.3	3.24	323	66.7	0.148	21.9	0.48	0.46	312	0.0321
1818	39.2	41.9	3.38	337	64.7	0.093	14.6	0.48	0.43	330	0.0190
1569	39.0	40.1	3.34	322	81.7	0.138	19.1	0.48	0.47	313	0.0289
1886	38.1	40.1	2.84	301	23.3	0.150	23.4	0.43	0.41	289	0.0333
1683	37.7	39.4	2.62	310	36.9	0.115	18.4	0.40	0.39	301	0.0238

$$\text{Index} = \frac{A H_s}{C_s}$$

Table 4. Survey Data, Big Blue Stem

$$g_b = 1.43 \text{ mol m}^{-2} \text{ s}^{-1}$$

$$\text{STOMRAT} = 1$$

Q	T _a	T _l	e _a	C _a	C _i	g _s	A	H _a	H _s	C _s	Index*
1767	35.9	37.8	2.11	335	84.5	0.115	16.6	0.36	0.35	327	0.0176
719	34.5	34.2	2.06	312	104	0.113	13.7	0.38	0.41	305	0.0183
122	38.5	37.7	2.56	344	200	0.033	2.9	0.38	0.40	343	0.0034
2200	37.0	40.2	2.77	332	55	0.143	22.8	0.44	0.40	321	0.0285
1049	40.5	39.5	2.44	334	81	0.139	20.0	0.32	0.37	324	0.0230
457	39.5	39.2	2.56	336	103	0.081	11.0	0.36	0.38	331	0.0127
1301	35.6	36.6	3.18	311	107	0.190	22.3	0.55	0.55	300	0.0406
1866	38.6	40.1	3.12	330	85.2	0.164	22.9	0.46	0.46	319	0.0323
1739	38.4	40.1	3.40	331	101	0.157	20.6	0.50	0.50	321	0.0311
1562	38.2	39.2	3.59	331	136	0.213	23.4	0.54	0.54	320	0.0396
1648	34.1	36.0	2.91	314	115	0.295	33.2	0.54	0.54	298	0.0597
1966	34.4	36.7	3.17	320	112	0.253	29.9	0.58	0.58	306	0.0540
2101	36.1	38.8	3.03	320	66.6	0.182	26.6	0.51	0.51	307	0.0407
2057	37.5	39.7	2.96	311	81.9	0.197	25.6	0.46	0.46	298	0.0381
1838	37.1	38.4	2.50	350	104	0.164	22.9	0.40	0.40	339	0.0272
1804	37.7	38.5	2.47	358	110	0.176	24.7	0.38	0.38	346	0.0285
1762	39.6	39.9	2.46	346	100	0.171	23.7	0.34	0.34	334	0.0264
1746	40.5	40.6	2.55	346	100	0.166	22.9	0.34	0.34	335	0.0254

$$\text{Index} = \frac{A H_s}{C_s}$$

Table 5. Switch Grass A-C _i and Light Measurements							
g _b = 1.43 mol m ⁻² s ⁻¹ STOMRAT = 1							
Q	T _a	T _l	e _a	C _a	C _i	g _s	A
1840	36.8	37.3	2.89	314	90	0.251	32.0
1827	36.9	37.3	2.89	287	72	0.248	30.4
1812	37.0	37.4	2.89	259	60	0.244	28.0
1792	37.0	37.4	2.89	232	53	0.244	25.1
1854	38.0	38.3	2.81	437	154	0.222	35.7
1853	38.1	38.4	2.81	408	136	0.220	34.2
964	38.2	36.9	2.83	342	119	0.223	28.2
942	38.3	37.0	2.81	315	103	0.224	27.0
939	38.3	37.0	2.79	287	84	0.219	25.4
951	38.3	37.0	2.77	260	67	0.219	24.2
947	38.2	37.0	2.76	460	224	0.221	28.3
335	36.1	35.6	2.39	334	163	0.065	6.3
335	36.1	35.6	2.39	301	130	0.066	6.3
129	36.0	35.5	2.50	327	212	0.037	2.4
129	36.0	35.5	2.50	307	192	0.037	2.4

Table 6. Big Blue Stem A-C _i and Light Measurements							
g _b = 1.43 mol m ⁻² s ⁻¹ STOMRAT = 1							
Q	T _a	T _l	e _a	C _a	C _i	g _s	A
2200	37.0	40.2	2.77	332	55	0.143	22.8
1917	37.0	39.0	2.76	308	58	0.145	21.0
1912	37.0	38.8	2.73	283	56	0.148	19.3
1910	37.0	38.7	2.72	259	52	0.151	18.0
1920	37.0	38.8	2.72	236	47	0.154	16.7
1934	37.1	38.8	2.75	212	43	0.159	15.4
1951	38.2	39.4	2.70	441	162	0.178	27.3
1949	38.1	39.4	2.69	416	135	0.174	27.2
1049	40.5	39.5	2.44	334	81	0.139	20.0
1041	40.4	39.4	2.42	310	75	0.139	18.7
1045	40.2	39.1	2.41	286	71	0.142	17.6
1011	39.9	38.8	2.39	263	67	0.147	16.5
1058	39.8	38.8	2.39	240	60	0.149	15.5
1069	39.6	38.6	2.41	217	53	0.155	14.4
1082	39.0	37.9	2.47	478	216	0.172	23.8
457	39.5	39.2	2.56	336	103	0.081	11.0
453	39.4	39.1	2.59	314	90	0.085	11.1
459	39.2	38.8	2.59	292	80	0.091	11.2
458	39.1	38.6	2.62	269	76	0.100	11.1
455	39.1	38.5	2.62	247	70	0.111	11.4
454	39.0	38.3	2.60	224	64	0.118	10.9
456	39.0	38.2	2.58	202	64	0.134	10.6
453	38.9	38.1	2.62	180	56	0.142	10.0
452	38.7	37.8	2.62	158	52	0.154	9.3
466	38.2	37.4	2.54	444	250	0.155	15.4
464	38.0	37.5	2.63	375	161	0.114	13.9
122	38.5	37.7	2.56	344	200	0.033	2.9
122	38.5	37.7	2.56	324	180	0.033	2.9

Step 1

Compute the slopes (b_1) and intercepts (b_2) of the Ball-Berry index functions for the two sets of survey data (Tables 3 and 4).

	b_1	b_2
Switch Grass	4.05	0.026
Big Blue Stem	4.17	0.037

Figure 1. Survey data, Switch Grass

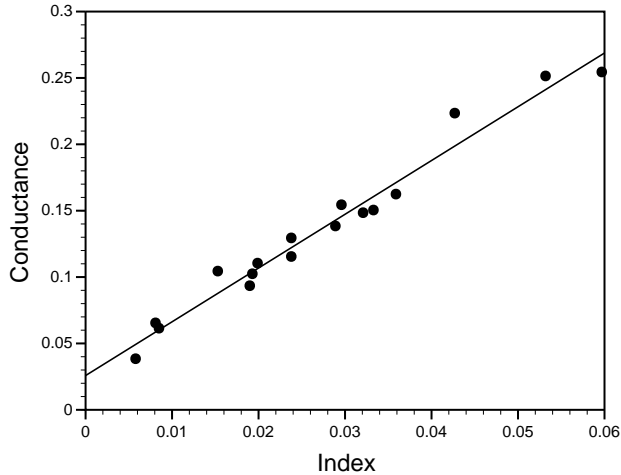
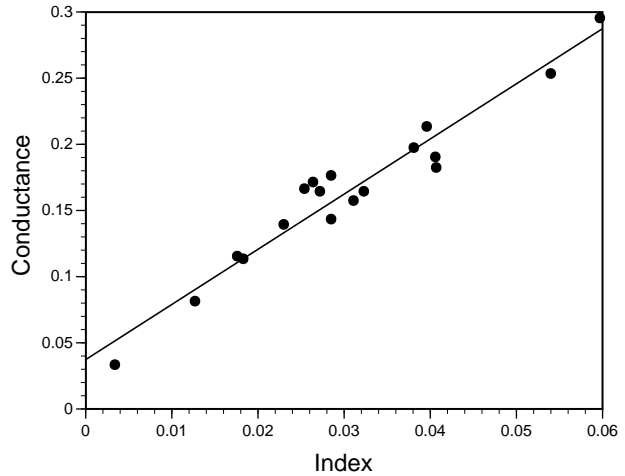


Figure 2. Survey data, Big Blue Stem



Step 2

Determine slope (a_1), intercept (a_2), and A_{\max} for the A- C_i curve at each light level (Tables 5 and 6). The above-ambient C_a data are used only for A_{\max} .

Switch Grass			
Q	a_1	a_2	A_{\max}
1840	0.176	16.8	35.7
964	0.078	18.9	28.3
335	0	6.3	6.3
129	0	2.4	2.4

Big Blue Stem			
Q	a_1	a_2	A_{\max}
2200	0.41	-2.4	27.3
1049	0.20	3.4	23.8
457	0.028	8.7	15.4
122	0	2.9	2.9

Step 3

Assuming neutral stability ($\psi_m=0$), and a canopy openness parameter m of 2.5, compute wind speed u and boundary layer conductance at each layer height in the canopy. Wind is computed from Equations C-7, C-11, and C-12, and leaf boundary conductance from Equation C-10.

Height	Remarks	u (m s ⁻¹)	g_x
0.60	Top of canopy	0.545	—
0.45	Layer 1	0.206	0.57
0.22	Layer 2	0.082	0.36

Step 4

Adjust the light curve measurements (Equations 3 - 14).

Adjusting Switch grass light curve to canopy conditions:

Target $g_x = 0.57 \text{ mol m}^{-2} \text{ s}^{-1}$ Target $C_a = 340 \text{ ppm}$ Target $T_c = 36 \text{ }^\circ\text{C}$ Target $e_a = 2.8 \text{ kPa}$ $b_1 = 4.05$ $b_2 = 0.026$ $\alpha_{\text{PAR}} = 0.8$ $\alpha_{\text{NIR}} = 0.1$ $\tau_c = 0.9$	Chamber Data - Switch Grass									
	Q	T_a	T_l	e_a	C_i	g_s	A	a_1	a_2	A_{max}
	1840	36.8	37.3	2.89	90	0.251	32.0	0.176	16.8	38.1
	964	38.2	36.9	2.83	119	0.223	28.2	0.078	18.9	28.3
	335	36.1	35.6	2.39	163	0.065	6.30	0	6.30	6.30
	129	36.0	35.5	2.50	212	0.037	2.40	0	2.40	2.40

Adjusted to Canopy			
Q_a	g_s	C_i	A
1325	0.309	110	35.7
694	0.228	110	27.5
241	0.064	177	6.30
93	0.040	233	2.40

Adjusting Big Blue Stem light curve to canopy conditions:

Target $g_x = 0.36 \text{ mol m}^{-2} \text{ s}^{-1}$ Target $C_a = 340 \text{ ppm}$ Target $T_c = 36 \text{ }^\circ\text{C}$ Target $e_a = 2.8 \text{ kPa}$ $b_1 = 4.17$ $b_2 = 0.037$ $\alpha_{\text{PAR}} = 0.8$ $\alpha_{\text{NIR}} = 0.1$ $\tau_c = 0.9$	Chamber Data - Big Blue Stem									
	Q	T_a	T_l	e_a	C_i	g_s	A	a_1	a_2	A_{max}
	2200	37.0	40.2	2.77	55	0.143	22.8	0.410	-2.4	27.0
	1049	40.5	39.5	2.44	81	0.139	20.0	0.200	3.4	23.8
	457	39.5	39.2	2.56	103	0.081	11.0	0.028	8.7	15.4
	122	38.5	37.7	2.56	200	0.033	2.90	0	2.9	2.90

Adjusted to Canopy			
Q_a	g_s	C_i	A
1584	.281	133	27.3
755	.239	135	23.8
329	.132	153	13.0
88	.055	250	2.9

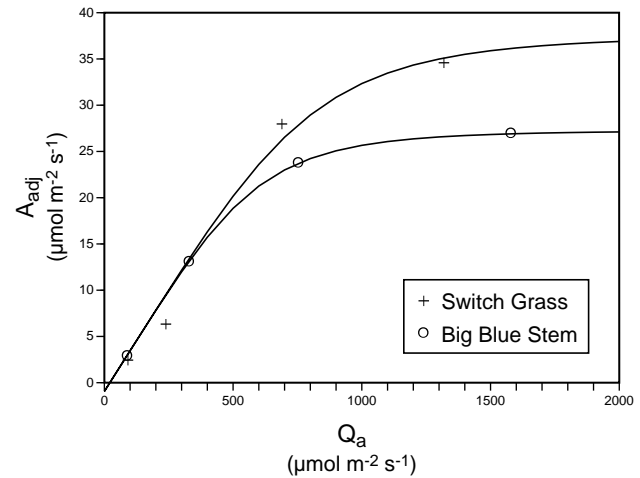
Step 5

Fit the light response curve (Equation 15) parameters using the light curve adjusted to canopy conditions.

Big Blue Stem		Switch Grass	
Q_a	A_{adj}	Q_a	A_{adj}
1584	27.3	1325	35.7
755	23.8	694	27.5
329	13.0	241	6.3
88	2.9	93	2.4

	ϕ	A_{sat}	p	A_0
Switch Grass	0.043	39.9	3.32	-0.91
Big Blue Stem	0.043	28.6	3.32	-0.91

Figure 3. Light curve adjusted to canopy conditions



Step 6

Compute slope (c_1) and intercept (c_2) of adjusted g_s as a function of adjusted A :

	c_1	c_2
Switch Grass	0.00800	0.0165
Big Blue Stem	0.00924	0.0220

Step 7

Use the layer model (Eq. 18 - 29) to compute total canopy conductance and photosynthetic rate:

$$\theta = 37.5^\circ$$

$$Q_{TOT} = 1700 \mu\text{mol m}^{-2} \text{s}^{-1}$$

$$Q_{DIFF} = 250$$

$$Q_{BEAM} = 1450$$

LAYER i	F	F_i	A_{ci}	g_{ci}	$F_{sun,i}$	$Q_{sun,i}$	$A_{sun,i}$	$g_{sun,i}$	$F_{shade,i}$	$Q_{shade,i}$	$A_{shade,i}$	$g_{shade,i}$
1	1.4	1.40	30.9	0.270	0.92	1104	30.8	0.263	0.48	177	5.2	0.058
2	2.8	1.40	11.0	0.132	0.38	1005	24.3	0.247	1.02	77	1.8	0.038

$A_c = 41.9 \mu\text{mol m}^{-2} \text{s}^{-1}$
 $g_c = 0.403 \text{ mol m}^{-2} \text{s}^{-1}$

Step 8

Use aerodynamic conductance (Eq. C-1 thru C-8) to compute canopy transpiration rate:

	g_a (mol m ⁻² s ⁻¹)	$\sqrt{E_c}$ (W m ⁻²)	E_c (mol m ⁻² s ⁻¹)	U (W m ⁻²)	T _c	Ψ _m	Ψ _h
Initial Conditions	0.580	401	9.08 x 10 ⁻³	0	36	0	0
Final Conditions	0.770	408	9.24 x 10 ⁻³	42	36.9	-0.579	-0.579

Step 9

Compare computed and assumed canopy temperature. We assumed 36 °C, and computed 36.9. This will not affect our light response curves, so we don't need to iterate.

Step 10

Compute canopy efficiencies:

$$\epsilon_E = \frac{A_c 10^{-6}}{E_c} 100 = \frac{41.9 \times 10^{-6}}{9.31 \times 10^{-3}} 100 = 0.45\%$$

$$\epsilon_Q = \frac{A_c}{Q_i} 100 = \frac{41.9}{1430} 100 = 2.9\%$$

As a comparison, we calculate canopy fluxes based on unadjusted chamber data:

	Adjusted to canopy	Raw chamber data	% change
A _c	41.9	37.0	12
g _c	0.403	0.305	24
E _c (W m ⁻²)	408	380	7

APPENDIX A

Calculation of Sun Zenith Angle

The sun zenith angle (θ) is usually calculated from latitude (λ), sun declination (δ), local longitude (L), time difference (hours) from GMT (D , earlier > 0 , later < 0), date and local time (t_{loc}), and is given by

$$\cos(\theta) = \sin(\lambda)\sin(\delta) + \cos(\lambda)\cos(\delta)\cos[0.2618(t_{sun} - 12)] \quad [A-1]$$

where t_{sun} is solar time in decimal hours between 0 and 24, and 0.2618 converts solar time in hours to hour angle in radians. The solar time can be calculated from local time t_{loc} (decimal hours), the local longitude (degrees), D , and Equation of Time (EoT-hours and fractions of hours):

$$t_{sun} = t_{loc} + EoT + D - \frac{L}{15} \quad [A-2]$$

The solar declination and Equation of Time are given by (Blackadar, A.K., personal communication)

$$\sin(\delta) = \sin\left(\frac{23.44}{57.30}\right)\sin(S) \quad [A-3]$$

$$EoT = \frac{9.4564 \frac{\sin(2S)}{\cos(\delta)} - (4)(57.30)(V)}{60} \quad [A-4]$$

where

$$S = \frac{(-79.828 + 0.9856Y)}{57.296} + V \quad [A-5]$$

$$V = 0.03348 \sin(M) + 0.02093 \sin(2M) \quad [A-6]$$

$$M = \frac{-1 + 0.9856Y}{57.296} \quad [A-7]$$

$$Y = (\text{year} - 1977) 365 + \text{DOY} + 28124 \quad [A-8]$$

where DOY represents cumulative day-of-year beginning with January 1. In addition to Equation A-8, one day must be added to Y for each leap year between 1977 and the year of interest; therefore three additional days would have to be added if the year of interest is 1990. Leap years are evenly divisible by 4, unless they are evenly divisible by 400, such as the year 2000 (not a leap year).

All angles in the above equation development are in units of radians unless otherwise stated.

APPENDIX B

Calculating Extinction Coefficient From LAI-2000 Measurements

Contact values (c_i) are measured at the five viewing angles of the LAI-2000 and the extinction coefficient (K_i) can be calculated for each of these viewing angles from

$$K_i = \frac{c_i}{F} \quad [B-1]$$

where F is the LAI-2000's LAI estimate. If the extinction coefficient is not known, usually it is set to 0.5 at all angles, which corresponds to the spherical leaf angle distribution.

NOTE: The C2000 program (version 2.14 or later) will compute extinction coefficients, as well as the slope and intercept of extinction coefficient as a function of angle.

APPENDIX C

Calculation of Aerodynamic Conductance and Leaf Boundary Layer Resistance

The aerodynamic conductance g_a ($\text{mol m}^{-2} \text{s}^{-1}$) between the canopy and the height of the wind speed measurement is given by

$$g_a = \frac{0.16 u_z \rho}{\left[\ln\left(\frac{z-d}{z_o}\right) + \psi_m \right] \left[\ln\left(\frac{z-d}{z_h}\right) + \psi_h \right]} \quad [\text{C-1}]$$

where z is the height of the wind speed measurement u_z , ρ is the mole density of air, d is the displacement height ($d = 0.63 H$, where H is the height of the canopy) and z_o is the roughness length for momentum ($z_o = 0.13 H$) and z_h is the roughness length for heat [$z_h = z_o/5$] (Verma, 1989). The diabatic profile correction factor for momentum (ψ_m) is given by (Kanemasu et al., 1979)

$$\psi_m = -5 \xi \quad 0 \leq \xi < 1 \quad [\text{C-2}]$$

$$\ln(\psi_m) = 0.032 + 0.4481 \ln(-\xi) - 0.132[\ln(-\xi)]^2 \quad 0 < -\xi < 2 \quad [\text{C-3}]$$

and the diabatic correction factor for heat (ψ_h) is given by

$$\psi_h = -5\xi \quad 0 \leq \xi < 1 \quad [\text{C-4}]$$

$$\ln(\psi_h) = 0.598 + 0.39 \ln(-\xi) - 0.09 [\ln(-\xi)]^2 \quad 0 < -\xi < 2 \quad [\text{C-5}]$$

where

$$\xi = \frac{0.4gU(1+0.07/B)(z-d)}{\rho C_m T u_*^3} \quad [\text{C-6}]$$

and g is the gravitational constant (9.8 m s^{-2}), B is the ratio of sensible to latent heat fluxes known as the Bowen ratio, u_* is the friction velocity given by

$$u_* = \frac{0.4 u_z}{\ln\left[\frac{(z-d)}{z_o}\right] + \psi_m} \quad [\text{C-7}]$$

and U is the sensible heat flux calculated from the energy balance equation

$$U = R_n - G - E_c \quad [\text{C-8}]$$

The diabatic corrections to the log wind and temperature profile equations involve considerable calculation; in fact, several iterations are required because the diabatic correction factors (ψ_m and ψ_h) depend on the heat flux (U), which is not known until the diabatic correction factors are known. If these diabatic correction factors are ignored, errors of a factor of two or more can occur in aerodynamic conductance.

Canopy temperature is then estimated from

$$T_c = T'_a + \frac{R_n - G - E}{C_m g_a} \quad [\text{C-9}]$$

The boundary layer conductance of a “representative” leaf (including convection from only one side of a leaf and in units of $\text{mol m}^{-2} \text{s}^{-1}$) in the canopy can be estimated from a typical leaf size and “representative” wind speed using

$$g_x = 0.22 \sqrt{\frac{u}{D}} \quad [\text{C-10}]$$

where D is the leaf dimension in meters (for example diameter or width) and u is the wind speed in meters/second in the canopy (Grace, 1981). Eq. [C-7] cannot be used to evaluate the wind speed in the canopy, but it can be used to estimate the wind speed at the top of the canopy H :

$$u_H = \frac{u_*}{0.4} \left(\ln\left[\frac{(H-d)}{z_o}\right] + \psi_m \right) \quad [\text{C-11}]$$

The equation of Thom (1971) can be used to estimate the wind speed with height z within the canopy using a single empirical coefficient m :

$$u = \frac{u_H}{\left(1 + m \left[1 - \frac{z}{H}\right]\right)^2} \quad [\text{C-12}]$$

where m may be about 1.5 for more open canopies such as corn and 2.5 for more dense canopies of wheat.

APPENDIX D

Symbol List

a_1, a_2	slope and intercept of near-ambient A-C _i relation	k	stomatal ratio
A	leaf assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	K	canopy extinction coefficient
A_c	canopy CO ₂ assimilation rate ($\mu\text{mol CO}_2 \text{ m}^{-2}$ ground area s^{-1})	L	longitude (degrees)
A_{max}	maximum photosynthetic rate ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	L_e	latent heat of water ($\cong 44200 \text{ J mol}^{-1}$)
A_o	assimilation rate in the dark ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	M	used in calculation of EoT
b_1, b_2	slope and intercept of g_s vs $A H_s/C_s$	p	light curve fit parameter
B	Bowen ration (E_c/U)	P	atmospheric pressure (kPa)
c_1, c_2	slope and intercept of A vs g_s	Q_a	absorbed quanta ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
c_i	contact value (LAI-2000) for i th angle	Q_d	incident sky diffuse PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
C_a	CO ₂ mole fraction of ambient air ($\mu\text{mol mol}^{-1}$)	Q_D	direct beam PAR ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
C_i	intercellular CO ₂ mole fraction ($\mu\text{mol mol}^{-1}$)	Q_i	PAR intercepted by the canopy ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
C_m	mole specific heat of air ($\cong 29 \text{ J mol}^{-1} \text{ K}^{-1}$)	Q_{shade}	average incident PAR on shaded leaves ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
C_n	scattering of PAR by leaves for the n th layer	Q_{TOT}	total (beam + diffuse) incident PAR at top of canopy ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)
C_s	leaf surface CO ₂ concentration ($\mu\text{mol mol}^{-1}$)	R	universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$)
d	canopy displacement height (m)	R_l	leaf level net radiation (W m^{-2})
D	difference (hours) between local time and GMT. D>0 means west longitude, D<0 means east longitude	R_n	net radiation, all wavelengths, of canopy (W m^{-2})
e_a	vapor pressure (kPa)	s	slope of saturation vapor pressure curve (kPa K^{-1})
e'_a	vapor pressure above canopy (kPa)	S	used in calculation of EoT
$e_s(T)$	saturation vapor pressure (kPa) at temperature T ($^{\circ}\text{C}$)	t_{loc}	local time (decimal hours)
E	leaf transpiration ($\text{mol m}^{-2} \text{ s}^{-1}$)	t_{sun}	solar time (decimal hours)
E_c	canopy transpiration rate ($\text{mol H}_2\text{O m}^{-2}$ ground area s^{-1})	T_a	air temperature ($^{\circ}\text{C}$)
EoT	equation of time (decimal hours)	T'_a	air temperature above canopy ($^{\circ}\text{C}$)
E_Q	canopy light use efficiency (%)	T_c	mean canopy temperature ($^{\circ}\text{C}$)
f	stomatal correction factor for g_x	T_l	leaf temperature ($^{\circ}\text{C}$)
F	leaf area index for canopy (m^2 leaf area/ m^2 ground area)	u	wind speed above canopy (m s^{-1})
F_{sun}	sunlit leaf area index	u_*	friction velocity (m s^{-1})
g	gravitational constant (9.8 m s^{-2})	u_H	wind speed at top of canopy (m s^{-1})
g_a	canopy aerodynamic conductance for H ₂ O ($\text{mol m}^{-2} \text{ s}^{-1}$)	u_z	wind speed (m s^{-1}) at height z above the canopy
g_b	one-sided leaf boundary layer conductance for H ₂ O in a chamber ($\text{mol m}^{-2} \text{ s}^{-1}$)	U	sensible heat flux for canopy (W m^{-2})
g_c	total canopy stomatal conductance for H ₂ O (mol m^{-2} ground area s^{-1})	V	used in calculation of EoT
g_s	leaf stomatal conductance for H ₂ O ($\text{mol m}^{-2} \text{ s}^{-1}$)	Y	used in calculation of EoT
g_T	total (stomatal + boundary layer) leaf conductance for H ₂ O ($\text{mol m}^{-2} \text{ s}^{-1}$)	Z	height above canopy (m)
g'_T	total (stomatal + boundary layer) leaf conductance for CO ₂ ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	z_o	canopy roughness length (m) for momentum
g_x	boundary layer conductance of H ₂ O for a leaf (one-sided) ($\text{mol m}^{-2} \text{ s}^{-1}$)	z_h	canopy roughness length (m) for heat
g'_x	boundary layer conductance of CO ₂ for a leaf (one-sided) ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	α_{NIR}	leaf absorptivity in NIR
G	soil heat flux (W m^{-2})	α_{PAR}	leaf absorptivity in PAR
H	canopy height (m)	δ	solar declination (degrees)
H_a	ambient humidity fraction [$e_a/e_s(T_a)$]	ϕ	photochemical efficiency at low light
H_s	leaf surface humidity fraction	γ	psychrometric constant (0.066 kPa K^{-1})
		λ	latitude (degrees)
		θ	solar zenith angle (degrees)
		ρ	mole density of air ($\cong 37.9 \text{ mol m}^{-3}$)
		ψ_h	adiabatic profile correction factor for heat
		ψ_m	adiabatic profile correction factor for momentum
		ϵ_E	canopy transpiration efficiency (%)
		ϵ_Q	canopy light-use efficiency
		τ_c	chamber transmittance

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