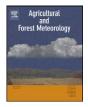
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ABSTRACT

Decreased water uptake closes stomates, which reduces transpiration and increases leaf temperature. The leaf or canopy temperature has long been used to make an empirical estimate of plant water stress. However, with a few supplemental measurements and application of biophysical principles, infrared measurement of canopy temperature can be used to calculate canopy stomatal conductance (g_c) , a physiological variable derived from the energy balance for a plant canopy. Calculation of g_c requires an accurate measurement of canopy temperature and an estimate of plant height, but all of the other measurements are available on automated weather stations. Canopy stomatal conductance provides a field-scale measurement of daily and seasonal stomatal response to prevailing soil water and atmospheric conditions, and facilitates a comparison of models that scale conductance from single leaves (measured with porometers) to canopies. A sensitivity analysis of the input measurements/ estimates showed g_c is highly sensitive to small changes in canopy and air temperature, and less sensitive to the other required measurements (relative humidity, net radiation, wind speed, and plant canopy height). The measurement of g_c becomes increasingly sensitive to all of the component factors as the conditions become cloudier, cooler, and more humid. We determined g_c for alfalfa and turfgrass by making the necessary environmental measurements and coupling them with a two-source (plant canopy layer and soil layer) energy balance model. We then compared these g_c values to maximum single leaf values scaled-up to the canopy level (g_{CP} , defined as potential canopy stomatal conductance herein) for the two crops. For both crops, g_c matched g_{CP} within approximately 10% after irrigation. The turfgrass g_{C} measurements were also compared to mean single leaf values measured with a porometer. At mid-day, $g_{\rm C}$ values were typically about double the single leaf values. Because this approach for determining g_c allows continuous, non-contact measurement, it has considerable potential for coupling with measurements of soil moisture to better understand plant-soil water relations. It also has potential for use in precision drought stress and irrigation scheduling.

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1. Review of measurement approaches for plant canopy water stress

Plant temperature is a widely measured variable because it is a major determining factor in surface energy fluxes and provides insight into plant water status. Monteith and Szeicz (1962) and Tanner (1963) were the first to use infrared thermometry to measure plant temperature, and Tanner (1963) proposed that

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plant temperature be used to quantify water stress. Since then, multiple indices have been proposed and used to quantify plant water stress (Jones, 2004). Plant temperature indicates plant water status because stomates respond to soil and plant water status, and prevailing meteorological conditions, and control evaporative cooling of leaves. As stomates close in response to soil water depletion and a decrease in water uptake, plant temperature increases. Convective energy transfer increases to balance the decrease in transpiration. As stomates close, photosynthesis is reduced because CO₂ absorption is reduced. Several studies have demonstrated correlations between plant stress indices and yield (Smith et al., 1985; Irmak et al., 2000; Ajayi and Olufayo, 2004; Wang et al., 2005). Other studies have related stress indices to available soil water (Jackson et al., 1981; Hatfield, 1983; Colaizzi et al., 2003; Payero and Irmak, 2006) and leaf water potential (O'Toole et al., 1984; Jackson, 1991; Wang et al., 2005). The most

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common application of stress indices has been in irrigation scheduling (Pinter and Reginato, 1982; Reginato and Howe, 1985; Nielsen and Gardner, 1987; Garrot et al., 1994; Alves and Pereira, 2000; Irmak et al., 2000).

Idso et al. (1981) developed an empirical crop water stress index (CWSI) related to air vapor pressure deficit (VPD) and Jackson et al. (1981) derived a theoretically based CWSI from the energy balance for a plant canopy. Both CWSI methods provide a relative indication of plant stress by comparing the measured canopy to air temperature difference to lower (non-water-stressed) and upper (water-stressed) limits of the canopy to air temperature difference. Jackson et al. (1981) showed that the limits, or baselines, are dependent on meteorological and plant factors. Multiple studies (Jackson et al., 1988; Jones, 1999; Alves and Pereira, 2000; Wang et al., 2005; Payero and Irmak, 2006; Payero et al., 2005) have been conducted to refine the calculation/estimation of the baselines and improve the CWSI.

Most temperature-based plant water stress indices have provided only a relative indication of water stress and have relied on empirical measurements. For this reason, Campbell and Norman (1990) suggested abandoning the use of empirically established indices in favor of a direct determination of canopy stomatal resistance calculated from environmental measurements and energy balance principles. Hatfield (1985) and Amer and Hatfield (2004) showed that calculation of canopy stomatal resistance can indicate plant response to available soil water and prevailing meteorological conditions. However, some of the methods for calculation of canopy stomatal resistance still rely on empirical measurements (Jones, 1999; Leinonen et al., 2006). Here we derive an equation to calculate canopy stomatal conductance from measured meteorological and plant variables, review the advantages of conductance versus resistance measurements, analyze the sensitivity of each of the component measurements, and compare canopy stomatal conductance to scaled-up maximum single leaf conductance in alfalfa and turfgrass.

2. Theoretical considerations

2.1. Scaling single leaf stomatal conductance to canopies

Canopy stomatal conductance (g_c) [mol m⁻² ground area s⁻¹] is defined as the parallel combination of stomatal conductances of individual leaves weighted by leaf area:

$$g_{\mathcal{C}} = \sum_{i=1}^{l=n} g_{Li} LAI_i \tag{1}$$

where g_{Li} is mean single-leaf stomatal conductance $[mol m^{-2} leaf area s^{-1}]$ for layer *i*, LAI_i is leaf area index $[m^2 leaf area m^{-2} ground area]$ for layer *i*, and *n* is the number of layers in the canopy. A value of g_C is obtained by dividing the canopy into layers and measuring g_{Li} and LAI_i for each layer. Measurements of g_{Li} are made with porometers and multiple measurements must be averaged at each layer to obtain a representative value.

A simple way to scale g_{Li} to g_C is to separate the leaves in a canopy into sunlit and shaded groups. Sunlit leaves are the major contributors to g_C , whereas shaded leaves typically have low conductances, but both groups contribute to g_C according to the sunlit and shaded LAI values:

$$g_{C} = g_{LSun} LAI_{Sun} + g_{LShade} LAI_{Shade}$$
⁽²⁾

where LAI_{Sun} and LAI_{Shade} are sunlit and shaded leaf area indexes, respectively, and g_{LSun} and g_{LShade} are sunlit and shaded single leaf stomatal conductances, respectively. The value of LAI_{Sun} is calculated from total LAI and a canopy radiation extinction

coefficient (K):

$$LAI_{Sun} = \frac{1 - e^{-K \cdot LAI}}{K}$$
(3)

where $K = 1/2 \cos \theta$ for a spherical leaf angle distribution and θ is solar zenith angle. The value of LAI_{Shade} is $LAI - LAI_{Sun}$. More detail on scaling g_{Li} to g_C is given in Baldocchi et al. (1991). Models to scale single leaf conductance to the canopy have been proposed and tested (Rochette et al., 1991; Furon et al., 2007).

2.2. Canopy stomatal conductance model

The energy balance equation for an evaporating plant canopy is:

$$R_{nC} = H_C + \lambda E_C + A_n \tag{4}$$

where R_{nC} is net radiation divergence in the canopy, H_C is sensible heat flux, λE_C is latent heat flux, A_n is net assimilation, and all terms are in W m⁻². The subscript *C* attached to R_n , *H*, and λE indicates these are canopy values and do not include contributions from the underlying soil. Under well-watered conditions plants transpire at or near the potential rate and the canopy remains cool due to λE_C (evaporative cooling) largely balancing R_{nC} in Eq. (4). As water becomes limiting plants begin to close stomates, λE_C decreases, and canopy temperature increases, making H_C more dominant in Eq. (4). When plants use all available soil water, stomates close and $\lambda E_C = 0$. Under these conditions the canopy temperature increases to a point where the available energy is balanced by H_C .

The terms H_C and λE_C can be expressed as (Campbell and Norman, 1998):

$$H_{\rm C} = g_H C_P (T_{\rm C} - T_{\rm A}) \tag{5}$$

$$\lambda E_C = g_T \lambda \left(\frac{e_{SC} - e_A}{P_B} \right) \tag{6}$$

where C_P is heat capacity of air (29.17 J mol⁻¹ C⁻¹), T_C is aerodynamic canopy temperature [°C], T_A is air temperature [°C], λ is latent heat of vaporization [J mol⁻¹], e_{SC} is saturated vapor pressure [kPa] at T_C , e_A is vapor pressure [kPa] of air, P_B is barometric pressure [kPa], g_H is boundary layer heat conductance [mol m⁻² s⁻¹], and g_T is total water vapor conductance g_T is a series combination of boundary layer water vapor conductance (g_V) [mol m⁻² s⁻¹] and canopy stomatal conductance to water vapor (g_C) [mol m⁻² s⁻¹] because water vapor must diffuse through stomates and the boundary layer:

$$g_T = \frac{1}{(1/g_V) + (1/g_C)}.$$
(7)

Combining Eqs. (4)–(7) and rearranging to solve for g_C yields:

$$g_{C} = \frac{g_{V} P_{B}[(R_{nC} - A_{n}) - g_{H} C_{P}(T_{C} - T_{A})]}{g_{V} \lambda(e_{SC} - e_{A}) - P_{B}[(R_{nC} - A_{n}) - g_{H} C_{P}(T_{C} - T_{A})]}.$$
(8)

The required measurements or estimates to calculate g_C from Eq. (8) are canopy temperature, air temperature, barometric pressure, relative humidity, net radiation, wind speed, and plant canopy height (wind speed and canopy height are necessary for g_H and g_V estimation, see Appendix A).

Eq. (8) provides a fundamental link between prevailing meteorological conditions (radiation, temperature, humidity, and wind speed) and plant physiological response, g_C , assuming g_C is a purely physiological variable. Eq. (8) treats the canopy as a "big-leaf" and is a top-down approach (Baldocchi et al., 1991) for estimating g_C . Monteith (1981) indicated that canopy stomatal conductance or resistance calculated from big-leaf equations (e.g. Penman–Monteith equation) may contain a significant aerody-

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