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# Modeling canopy stomatal conductance in a temperate grassland ecosystem\*

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## ABSTRACT

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Field measurements of stomatal conductance were used to develop a leaf stomatal conductance model for major  $C_4$  grass species in a temperate grassland ecosystem. Employing data on incoming photosynthetically active radiation, vapor pressure deficit, green leaf area index and extractable water, the stomatal conductance model was scaled up from a leaf to a canopy level. Values of canopy stomatal conductance, estimated employing this approach, were compared with those of canopy face conductance computed from measured fluxes using the Penman–Monteith equation. Diurnal patterns and magnitudes of the two estimates were in good agreement under well-watered conditions. Under moisture stress conditions, the agreement was poor. Possible reasons are discussed. We substituted the daily extractable soil water input with the hourly measurements of leaf water potential. Although the model with the leaf water potential input did not produce any significant improvement in predicting the magnitude of canopy stomatal conductance under moisture stress conditions, it did simulate the diurnal patterns (e.g. morning peak) adequately.

The estimates of canopy stomatal conductance from the model were used to calculate evapotranspiration and compared against the fluxes measured with the micrometeorological eddy correlation technique.

## INTRODUCTION

Several studies have evaluated canopy conductance on the basis of leaf stomatal response to environmental conditions (Monteith et al., 1965; Szilagyi and Long, 1969; Tan and Black, 1976; Jarvis, 1981; Monteith, 1981; Baldocchi et al., 1987). Information on canopy conductance can be useful for the estimation of evapotranspiration ( $ET$ ) and in developing a better understanding of the processes controlling the exchange rates of trace gases in various terrestrial ecosystems.

Estimation of canopy conductance has generally involved two approaches:

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serially integrating the stomatal conductance of individual leaves, weighted by leaf area; (b) using measured values of latent heat flux and other relevant variables in a stand-level equation (e.g. Penman–Monteith). Recently, Baldocchi et al. (1991) presented an excellent overview of the strengths and weaknesses of different approaches for estimating canopy stomatal conductance. As also discussed in their paper, the above-mentioned approaches do not yield the same results. The former is primarily a physiological parameter, whereas the latter involves additional non-physiological factors (e.g. net radiation budget, aerodynamic conductance) within the canopy (Thom, 1975; Littleworth, 1976; Finnigan and Raupach, 1987; Raupach and Finnigan, 1988; Paw U and Meyers, 1989). The latter also includes the contribution from soil evaporation (Denmead, 1984; Baldocchi et al., 1991). The difference between the two canopy conductances has also been discussed by Baldocchi et al. (1987). They developed a multilayer canopy stomatal conductance model in which the spatial variation of canopy structure and the radiation transfer within the canopy were taken into account. They tested their model against the canopy surface conductance computed from the flux measured in a soybean field and found that the differences between two canopy conductances were of the order of 30–50%. They attributed some of the difference to possible errors in field measurements and the assumptions made in the model.

Here we describe the development and testing of a one-layer canopy stomatal conductance model in a temperate grassland ecosystem. The basic concepts employed are similar to those in Baldocchi et al. (1987). The data were obtained in a micrometeorological study in a tall grass prairie field in northern Kansas during the First ISLSCP (ISLSCP, International Satellite Land Surface Climatology Project; for details, see Sellers et al., 1988), Field Experiment (FIFE) in 1987. The objectives of this paper are: (a) to model the dependence of the leaf stomatal conductance on relevant meteorological, soil and plant variables; (b) to scale up the model from a leaf to a canopy level; (c) to compare modeled canopy stomatal conductance against the values of canopy surface conductance computed from the measured latent heat flux. The  $ET$  rates estimated from the modeled canopy stomatal conductance values are compared against those measured with the micrometeorological eddy correlation technique.

## MATERIALS AND METHODS

### *Site and vegetation*

The study was conducted on tallgrass prairie at a site ( $39^{\circ}3' \text{ N}$ ,  $96^{\circ}32' \text{ W}$ , 10 m above mean sea level) near Manhattan, Kansas. The soil is predominantly Dwight silty clay loam (Typic Natrustolls). The soil bulk density av-

TABLE 1

Species composition (%) at the experimental site during the flowering stage in 1987 (after Kin Verma, 1990b)

Species	%
<i>Andropogon gerardii</i> (Big bluestem) (C <sub>4</sub> )	27.1
<i>Sorghastrum nutans</i> (Indiangrass) (C <sub>4</sub> )	22.2
<i>Panicum virgatum</i> (Switchgrass) (C <sub>4</sub> )	16.6
<i>Sporobolus asper</i> (Tall dropseed) (C <sub>4</sub> )	7.0
<i>Schizachyrium scoparium</i> (Little bluestem) (C <sub>4</sub> )	4.7
<i>Bouteloua gracilis</i> (Blue grama) (C <sub>4</sub> )	4.3
<i>Dichanthelium oligosanthes</i> (Scribner panicum) (C <sub>3</sub> )	4.0
<i>Agropyron smithii</i> (Western wheatgrass) (C <sub>3</sub> )	1.2
Other grasses	2.4
Sedges	6.3
Forbs and woody plants	4.2

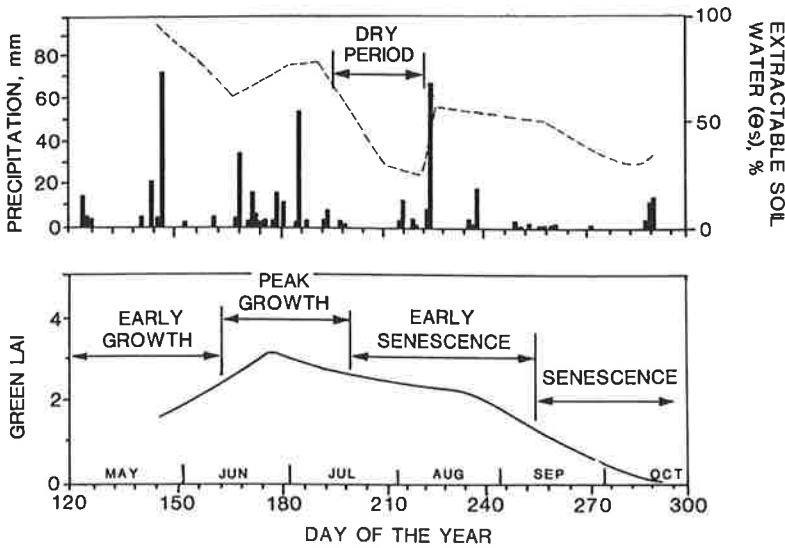
eraged about  $1.15 \text{ Mg m}^{-3}$  for the top 0.3 m. The prairie was burned in spring of 1987 to improve the botanical composition of grasses and forbs. The experimental area had been lightly grazed for several years by domestic livestock, but was not grazed in 1986 and 1987.

Percent species composition at the study site was estimated by employing the modified step point method (Owensby, 1973). The vegetation (Table 1) is dominated by three C<sub>4</sub> grass species: *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum*.

### *Plant and soil measurements*

Stomatal conductance was measured hourly with a steady-state porometer (LICOR, Model LI-1600) on four fully expanded, sunlit leaf blades of tillers of *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum* during June–August 1987. Both adaxial and abaxial conductances were measured. Total leaf conductance was computed assuming that adaxial and abaxial conductances act in series. Incident photosynthetically active radiation (PAR) on these leaf blades was measured with a quantum sensor (LICOR, Model LI-190SB) attached to the porometer. Leaf water potential was also measured with a pressure chamber (Precision Engineering, Lincoln, NE) on similar leaf blades, which were bagged at sampling to prevent tissue water loss. The green leaf area index (LAI) of each grass species was measured with a LiCor area meter (LICOR, Model LI-3000). The total green LAI reached its maximum of about 3.2 at the end of June (during the peak growth stage), and gradually decreased later in the season (Fig. 1).

The surface soil water content (0–0.1 m) was monitored gravimetrically almost every day and subsurface soil water content (0.1–1.4 m) was n



1. Seasonal precipitation, extractable soil water (0–1.4 m) and green leaf area index in

ed with a neutron probe (Campbell Pacific Nuclear Corp., Model 503) on weekly basis. Precipitation was ample from May to September, except during the dry period in late July–early August. During this period the extractable soil water (0–1.4 m) dropped to 25% (Fig. 1) and moisture stress conditions prevailed.

#### *Micro-meteorological measurements*

Fluxes of water vapor ( $LE$ ), sensible heat ( $H$ ) and momentum were measured with eddy correlation sensors mounted at 2.25 m above the ground. Details on the instrumentation and procedure can be found in Kim and Verma (1990a,b). Photosynthetically active radiation (PAR) was measured with a quantum sensor (LICOR, LI-190SB) at 2.0 m above the ground. Mean air temperature and humidity were measured with an aspirated ceramic wick psychrometer. Net radiation ( $R_n$ ) and soil heat flux ( $G$ ) were measured with radiometers (Radiation Energy Balance System, Beaverton, OR) and soil heat flow transducers (REBS, Model HFT-1), respectively.

#### *Theoretical considerations*

##### *Modeling leaf stomatal conductance ( $g_s$ )*

The stomatal conductance of a leaf is considered to be primarily a function of photosynthetically active radiation (PAR), air temperature ( $T$ ), vapor

pressure deficit ( $D$ ), soil/plant water status (e.g. water potential,  $\Psi$ ) and a lesser extent, of ambient carbon dioxide concentration ( $C_a$ ). Jarvis (1976) proposed a multiplicative model for the computation of stomatal conductance ( $g_s$ ) as the product of the functional relationships for PAR,  $D$ ,  $\Psi$ ,  $T$  and  $C_a$ :

$$g_s = g_s(\text{PAR})f_1(D)f_2(\Psi)f_3(T)f_4(C_a) \quad (1)$$

Values of the stress functions,  $f_1(D)$ ,  $f_2(\Psi)$ ,  $f_3(T)$  and  $f_4(C_a)$  range from 0 to 1. There appears to be a wide range of temperature optima for the grass species studied here (Knapp, 1985) and, therefore, the effect of changes in  $T$  was assumed to be negligible (i.e.  $f_3(T) \approx 1$ ). The effect of changes in  $C_a$  was also considered to be negligible (i.e.  $f_4(C_a) \approx 1$ ).

The response of  $g_s$  to PAR was estimated using a hyperbolic relationship (e.g. Monteith, 1965a):

$$g_s(\text{PAR}) = a_1 \text{PAR} / (a_2 + \text{PAR}) \quad (2)$$

where  $a_1$  and  $a_2$  are empirically derived constants with units of  $\text{mm s}^{-1}$  and  $\mu\text{Ei m}^{-2} \text{s}^{-1}$ , respectively. The parameter  $a_1$  represents the asymptotic value of  $g_s$  when  $\text{PAR} \rightarrow \infty$ , and can be considered as the maximum stomatal conductance under optimal condition; and  $a_2$  defines the curvature of the response to PAR.

A curvilinear reduction in  $g_s$  with increasing vapor pressure deficit ( $D$ ) was assumed (e.g. Lohammar et al., 1980; Turner et al., 1984):

$$f_1(D) = 1 / (1 + a_3 D) \quad (3)$$

where  $a_3$  ( $\text{kPa}^{-1}$ ) is a constant.

Soil water and leaf water potential have been proposed as measures of plant water status (Turner et al., 1985; Gollan et al., 1985; Kramer, 1986; Baldocchi et al., 1991). To examine the role of soil water in controlling  $g_s$  in this study, we first used daily values of extractable soil water (computed as the ratio of actual to total soil moisture held with a water potential between  $-1/30$  and  $-1.5$  MPa), ( $\theta_s$ ) obtained over the primary root zone (0–1 m). The response of  $g_s$  to  $\theta_s$  was estimated using a negative exponential relationship (e.g. Jarvis, 1976; Gollan et al., 1986):

$$f_2(\theta_s) = 1 - \exp(-a_4 \theta_s) \quad (4)$$

where  $a_4$  is a constant. Also, to estimate the response of  $g_s$  to leaf water status, hourly measurements of leaf water potential ( $\Psi_L$ ) were used. Based on the observations of Norman and Polley (1989) and Polley et al. (1990) the dependence of  $g_s$  on  $\Psi_L$  was approximated by a discontinuous linear relationship

$$\begin{aligned} f_2(\Psi_L) &= 1 & \text{for } \Psi_L > -1 \text{ MPa} \\ f_2(\Psi_L) &= 1 + a'_4 \Psi_L & \text{for } \Psi_L < -1 \text{ MPa} \end{aligned} \quad (5)$$

where  $a'_4$  is a constant.

### Modeling canopy stomatal conductance ( $g_c$ ): scaling up from a leaf to canopy level

The canopy stomatal conductance ( $g_c$ ) was calculated as a function of PAR weighted by the fractions of sunlit and shaded leaf areas (e.g. Singh and Szeicz, 2000; Norman, 1982; Baldocchi et al., 1987):

$$\text{PAR}) = \text{LAI}_{\text{sun}} g_s(\text{PAR}_{\text{sun}}) + \text{LAI}_{\text{shade}} g_s(\text{PAR}_{\text{shade}}) \quad (6)$$

where  $\text{LAI}_{\text{sun}}$  and  $\text{LAI}_{\text{shade}}$  are sunlit and shaded leaf area indices, respectively, and  $\text{PAR}_{\text{sun}}$  and  $\text{PAR}_{\text{shade}}$  are the flux densities of PAR on sunlit and shaded leaves, respectively. The sunlit leaf area index was estimated from a canopy radiative transfer model (e.g. Norman, 1979). For the prairie studied here, the foliage distribution was relatively uniform and continuous in space. Based on the assumptions that the leaf angle distribution is spherical, and that leaf angle in a canopy is randomly distributed, the sunlit leaf area index in a canopy was computed as:

$$\text{LAI}_{\text{sun}} = [1 - \exp(-0.5\text{LAI}/\cos\theta)] 2\cos\theta \quad (7)$$

where  $\theta$  is the zenith angle of the sun. The shaded leaf area index was obtained

$$\text{LAI}_{\text{shade}} = \text{LAI} - \text{LAI}_{\text{sun}} \quad (8)$$

The flux density of PAR on the sunlit leaves was estimated as:

$$\text{PAR}_{\text{sun}} = 0.5\text{PAR}_{\text{dir}}/\cos\theta + \text{PAR}_{\text{shade}} \quad (9)$$

where  $\text{PAR}_{\text{dir}}$  is the flux density of direct PAR above the canopy. The flux density of PAR on shaded leaves was computed using a relationship given by Norman (1982):

$$\text{PAR}_{\text{shade}} = \text{PAR}_{\text{diff}} \exp(-0.5\text{LAI}^{0.7}) + 0.07\text{PAR}_{\text{dir}} (1.1 - 0.1\text{LAI}) \exp(-\cos\theta) \quad (10)$$

where  $\text{PAR}_{\text{diff}}$  is the flux density of diffuse PAR on a horizontal surface above the canopy. To obtain  $\text{PAR}_{\text{dir}}$  and  $\text{PAR}_{\text{diff}}$ , the measured incoming PAR was separated into direct and diffuse components of PAR using the procedure of Norman and Norman (1985).

Since the prairie vegetation mainly consisted of *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum*, the canopy stomatal conductance was weighted by the fractions of leaf areas<sup>a</sup> of these three grass species. Finally, the effective canopy stomatal conductance ( $g_c$ ) of the prairie was ob-

<sup>a</sup> The sum of the leaf area index of *Andropogon gerardii*, *Sorghastrum nutans* and *Panicum virgatum* accounted for 70–85% of the total LAI throughout the season. The LAI of each grass species was, therefore, adjusted such that the sum of LAI of three grass species was equal to the total LAI.

tained by combining eqns. (2), (3), (4) and (6), or by combining eqns. (3), (5) and (6):

$$g_c = \{ [LAI_{\text{sun}} g_s(\text{PAR}_{\text{sun}}) + LAI_{\text{shade}} g_s(\text{PAR}_{\text{shade}})] f_1(D) f_2(\theta_s \text{ or } \Psi_L) \}_{\text{AG}} \\ + \{ [LAI_{\text{sun}} g_s(\text{PAR}_{\text{sun}}) + LAI_{\text{shade}} g_s(\text{PAR}_{\text{shade}})] f_1(D) f_2(\theta_s \text{ or } \Psi_L) \}_{\text{SN}} \\ + \{ [LAI_{\text{sun}} g_s(\text{PAR}_{\text{sun}}) + LAI_{\text{shade}} g_s(\text{PAR}_{\text{shade}})] f_1(D) f_2(\theta_s \text{ or } \Psi_L) \}_{\text{PV}}$$

where subscripts AG, SN and PV represent *Andropogon gerardii*, *Sorghum nutans* and *Panicum virgatum*, respectively. The canopy stomatal conductance using the extractable soil water data (eqn. (4)) was termed  $g_{c1}$  that using the leaf water potential data (eqn. (5)) was termed  $g_{c2}$ . Here we assume that  $f_1(D)$  and  $f_2(\theta_s \text{ or } \Psi_L)$  are constant for different layers of the canopy.

*Canopy surface conductance ( $g_{c(\text{PM})}$ ) computed from the measured flux*

If the latent heat flux and other meteorological components are known, canopy surface conductance,  $g_{c(\text{PM})}$ , can be calculated by rearranging the Penman–Monteith equation (Monteith, 1965b) as:

$$1/g_{c(\text{PM})} = [(s/\gamma)\beta - 1]/g_a + (\beta + 1)(\rho C_p/\gamma)(D/A) \quad (1)$$

where  $s$  is the slope of the saturated vapor pressure–temperature curve,  $\gamma$  is the psychrometric constant,  $\beta (= H/LE)$  is the Bowen ratio,  $\rho$  is the density of air,  $C_p$  is the specific heat of air,  $D$  is vapor pressure deficit, and  $A (= R_n + G)$  is available energy, and  $g_a$  is the aerodynamic conductance. The value of  $g_a$  was computed from friction velocity ( $u_*$ ) and mean wind speed ( $\bar{U}$ ) measured with a three-dimensional sonic anemometer (see Kim and Verweij, 1990a) as:

$$1/g_a = r_{\text{am}} + r_b \quad (2)$$

where  $r_{\text{am}} (= \bar{U}/u_*^2)$  is the aerodynamic resistance for momentum transfer and  $r_b (\approx (2/ku_*)(\kappa/D_v)^{2/3})$  is the excess resistance, where  $k$  is von Karman constant,  $\kappa$  is the thermal diffusivity and  $D_v$  is the molecular diffusivity of water vapor.

Thom (1975) argued that  $g_{c(\text{PM})}$  obtained from the Penman–Monteith equation does not equal the reciprocal of bulk stomatal resistance ( $1/r_{\text{ST}}$ ), which is the serial, area-weighted sum of the stomatal conductance of individual leaves in the canopy. He showed that  $g_{c(\text{PM})}$  can be an accurate measure of  $1/r_{\text{ST}}$  only when the air vapor pressure and temperature at a reference height above the canopy provide good enough estimates of the actual mean conditions on the transpiring leaf surfaces. The difference between  $g_{c(\text{PM})}$  and  $1/r_{\text{ST}}$  can be expressed (Thom, 1975) as:

$$1/g_{c(\text{PM})} = r_{\text{ST}} + (1 - s\beta/\gamma)r_b \quad (3)$$



values of  $\beta$  for the tallgrass prairie studied here were typically about 0.25 under well-watered conditions and around 1.0 under moisture stress conditions (Kim and Verma, 1990a). The values of  $r_b$  were of the order of  $10 \text{ s m}^{-1}$ . Thus, the second term on the right hand side of eqn. (14) was of the order of  $5 \text{ s m}^{-1}$  under well-watered conditions and about  $50 \text{ s m}^{-1}$  under stressed conditions. Since the canopy resistance was about  $50\text{--}200 \text{ s m}^{-1}$  under well-watered conditions and about  $300\text{--}1000 \text{ s m}^{-1}$  under stressed conditions, the difference between the values of  $g_{c(\text{PM})}$  and  $1/r_{\text{ST}}$  was generally less than 10% throughout the season for the prairie vegetation studied here.

It is worth noting that  $g_{c(\text{PM})}$  also includes the contribution from the soil evaporation as well as the transpiration through the stomates. Previous studies have suggested that the ratio of transpiration to potential  $ET$  in most mesophytic vegetation (e.g. grasslands) well supplied with water increases with leaf area to an LAI of about 3 (Ritchie and Burnett, 1971; Ritchie et al., 1976; Rosenberg et al., 1983). On the other hand, Denmead (1984) found that soil evaporation in the forest with an  $\text{LAI} \geq 4$  could be 10–40% of the total. Therefore, caution should be exercised in interpreting  $g_{c(\text{PM})}$  when LAI is small because the soil evaporation may not be negligible.

## RESULTS AND DISCUSSION

### Determination of parameters

By combining eqns. (1)–(4) we obtain:

$$g_s(\text{PAR})f_1(D)f_2(\theta_s) = [a_1 \text{PAR}/(a_2 + \text{PAR})][1/(1 + a_3 D)][1 - \exp(-a_4 \theta_s)] \quad (15)$$

where extractable soil water,  $\theta_s$  has been used to describe the response of  $g_s$  to soil water status. The parameters ( $a_1$ ,  $a_2$ ,  $a_3$  and  $a_4$ ) in eqn. (15) were determined for each grass species by fitting (non-linear least squares) the measured  $g_s$  to the values of PAR, vapor pressure deficit and extractable soil water. The values of the parameters with their asymptotic standard errors and  $r^2$  are listed in Table 2(a). Equation (15) accounted for about 71–77% of the variation in data for the three grass species.

Figures 2(a)–(c) show the form of the dependence of the stomatal conductance of *Andropogon gerardii* (which was the most dominant grass species) on PAR,  $D$  and  $\theta_s$  using the parameters given in Table 2(a). The dashed lines show the uncertainties in relationships owing to a  $\pm 1$  standard error in the parameter values. The horizontal lines represent the range of each variable used in derivation of the parameters.

TABLE 2

The values of the parameters with their asymptotic standard errors and  $r^2$  for (a) the model (15) using extractable soil water and (b) the model (eqn. (16)) using leaf water potential

(a) Equation (15): using extractable soil water

Grass species	Number of data points	Parameters			
		$a_1$ (mm s <sup>-1</sup> )	$a_2$ ( $\mu\text{Ei m}^{-2} \text{s}^{-1}$ )	$a_3$ (kPa <sup>-1</sup> )	$a_4$
<i>Andropogon gerardii</i>	110	18.4 $\pm 3.8$	585 $\pm 187$	0.188 $\pm 0.083$	0.029 $\pm 0.008$
<i>Sorghastrum nutans</i>	110	20.2 $\pm 4.4$	346 $\pm 103$	0.060 $\pm 0.057$	0.013 $\pm 0.005$
<i>Panicum virgatum</i>	110	20.5 $\pm 7.3$	392 $\pm 142$	0.030 $\pm 0.062$	0.010 $\pm 0.006$

(b) Equation (16): using leaf water potential

Grass species	Number of data points	Parameters			
		$a'_1$ (mm s <sup>-1</sup> )	$a'_2$ ( $\mu\text{Ei m}^{-2} \text{s}^{-1}$ )	$a'_3$ (kPa <sup>-1</sup> )	$a'_4$
<i>Andropogon gerardii</i>	110	18.7 $\pm 4.3$	781 $\pm 231$	0.180 $\pm 0.073$	0.287 $\pm 0.040$
<i>Sorghastrum nutans</i>	110	14.4 $\pm 2.6$	530 $\pm 142$	0.064 $\pm 0.053$	0.405 $\pm 0.037$
<i>Panicum virgatum</i>	110	15.6 $\pm 4.3$	762 $\pm 287$	0.095 $\pm 0.072$	0.471 $\pm 0.065$

Replacing  $f_2(\theta_s)$  by  $f_2(\Psi_L)$  in eqn. (15) results in:

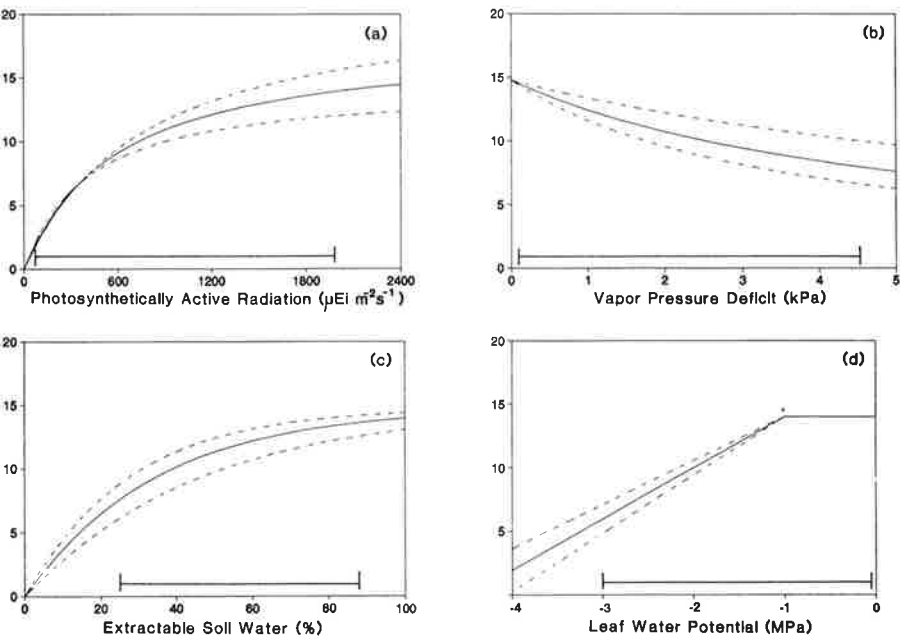
$$g_s = g_s(\text{PAR})f_1(D)f_2(\Psi_L) \quad (1)$$

$$= [a'_1 \text{PAR} / (a'_2 + \text{PAR})] [1 / (1 + a'_3 D)] [1 + a'_4 \Psi_L]$$

The values of the parameters ( $a'_1$ ,  $a'_2$ ,  $a'_3$  and  $a'_4$ ) with their asymptotic standard errors and  $r^2$  are given in Table 2(b). No significant difference in  $r^2$  was apparent when  $\Psi_L$  was substituted for  $\theta_s$  (Table 2). The form of  $f_2(\Psi_L)$  for *Andropogon gerardii* is given in Fig. 2(d). The responses of  $g_s$  to PAR and  $D$  (in eqn. (16)) were similar to those obtained from eqn. (15).

### Test of canopy stomatal conductance model

First, using the derived values of parameters in eqn. (14) ( $a_1$ ,  $a_2$ ,  $a_3$  and  $a_4$ ), the daily values of green LAI (obtained by interpolating biweekly measurements of green LAI) and  $\theta_s$ , and the half-hourly values of above canopy PAR and  $D$ , the canopy conductance ( $g_{c1}$ ) was computed employing eqn. (11). Second, we substituted the daily  $\theta_s$  with the half-hourly values of  $\theta_s$



2. The stomatal conductance response functions: (a)  $g_s(\text{PAR})$ , (b)  $f_1(D)$ , (c)  $f_2(\theta_s)$  and  $f_2(\Psi_L)$  for *Andropogon gerardii*. The dashed lines show the uncertainties in relationships  $g$  to a  $\pm 1$  standard error in the parameter values. The horizontal lines represent the range of each variable used in derivation of the parameters.

er potential,  $\Psi_L$  (obtained by interpolating hourly measurements of  $\Psi_L$ ), obtain  $g_{c2}$ .

The measurements made in this study were divided into four sub-periods: early growth, peak growth, dry period and early senescence (or post-dry period) (Fig. 1). For each sub-period, we selected 2 days when the micrometeorological flux measurements were available. Values of  $g_{c1}$  and  $g_{c2}$  from the model were compared with those of  $g_{c(\text{PM})}$  calculated from our measured values. The diurnal patterns of  $g_{c1}$ ,  $g_{c2}$  and  $g_{c(\text{PM})}$  on the selected days are presented in Figs. 3(a)–(h). Meteorological and soil water conditions on these days are summarized in Table 3.

### Early growth

The two days (June 5 and 6) considered here were mostly clear. Soil water was not limiting (Table 3). As would be expected for well-watered vegetation,  $g_{c1}$ ,  $g_{c2}$  and  $g_{c(\text{PM})}$  followed the diurnal pattern of PAR. Values of  $g_{c1}$  and  $g_{c2}$  agreed within  $1 \text{ mm s}^{-1}$  (Figs. 3(a) and 3(b)). The modeled conductance estimates ( $g_{c1}$  and  $g_{c2}$ ) generally agreed with  $g_{c(\text{PM})}$  within  $2 \text{ mm s}^{-1}$ . During midday hours  $g_{c(\text{PM})}$  exceeded modeled conductance estimates by  $1\text{--}2 \text{ mm s}^{-1}$ . Since the prairie was only partially covered by the vegetation

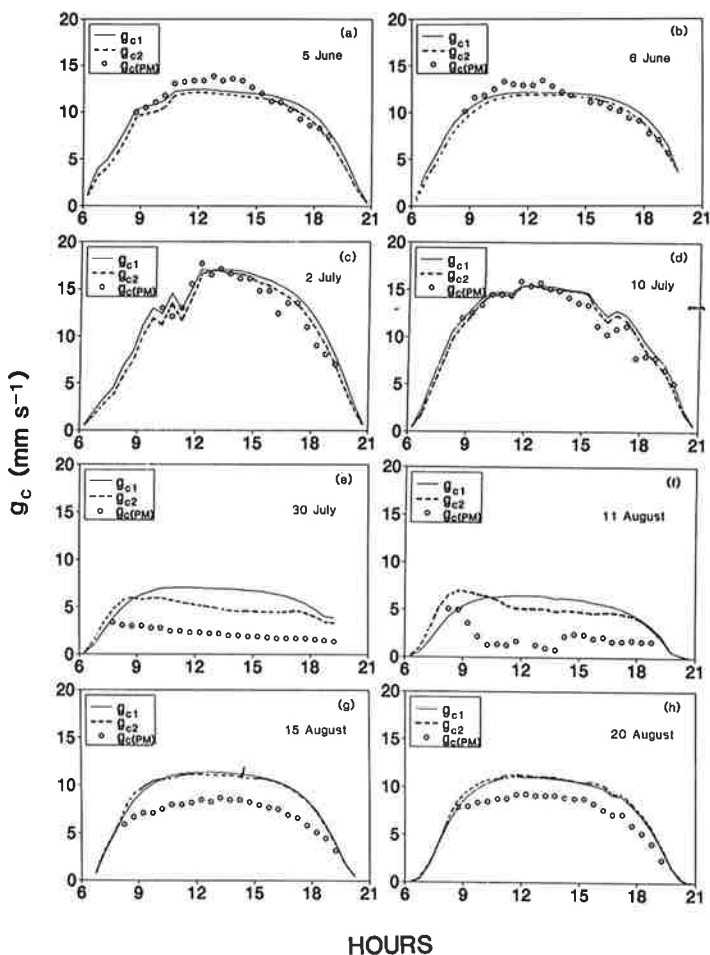


Fig. 3. Comparison of modeled conductances ( $g_{c1}$  using extractable soil water and  $g_{c2}$  using water potential) and  $g_{c(PM)}$  on selected days in 1987.

( $LAI < 2$ , Table 3), this difference could be partly attributed to soil evaporation.

#### *Peak growth*

July 2 and 10 were partly cloudy. Soil water conditions were favorable. Again, the patterns of  $g_{c1}$ ,  $g_{c2}$  and  $g_{c(PM)}$  were quite similar (Figs. 3(c) and 3(d)). The agreement between the modeled and measured conductances was similar (within  $2 \text{ mm s}^{-1}$ ) to that observed in the stage of early growth. The midday overestimation of  $g_{c(PM)}$ , observed earlier, was not found on these days. This may have resulted from a fuller vegetative cover ( $LAI \approx 3$ , see Table 3), which reduced the influence of soil evaporation.

midday (12:30–14:30 h) averages of photosynthetically active radiation (PAR), air temperature ( $T$ ), vapor pressure deficit ( $D$ ) and aerodynamic conductance ( $g_a$ ) on selected days in 1987. Values of extractable soil water (0–1.4 m) ( $\theta_s$ ) and green leaf area index (LAI) are also provided

	Annual life cycle stage	PAR ( $\mu\text{Ei m}^{-2} \text{s}^{-1}$ )	$T$ ( $^{\circ}\text{C}$ )	$D$ (kPa)	$g_a$ ( $\text{mm s}^{-1}$ )	$\theta_s$ (%)	Total green LAI
5	Early	2048	27.1	1.89	24.2	77.7	1.9
6	growth	2050	27.8	2.09	34.8	76.2	1.9
2	Peak	2002	27.5	1.27	26.0	73.1	3.1
10	growth	1900	30.9	1.74	44.1	69.6	2.8
30	Dry	1953	37.1	4.30	37.0	30.1	2.6
August 11	period	1844	33.1	3.16	9.3	24.8	2.5
August 15	Early	1888	33.7	2.33	36.0	54.4	2.4
August 20	senescence	1860	32.8	2.33	40.9	53.4	2.3

### Dry period

Moisture stress conditions prevailed on July 30 and August 11 owing to low availability of soil water and high atmospheric evaporative demand (Table 1). July 30 was clear, but August 11 was partly cloudy. The magnitudes of all aerodynamic conductance estimates were significantly smaller on these days (Figs. 3(e) and 3(f)). The magnitudes of  $g_{c1}$  and  $g_{c2}$  were, however, larger than that of  $g_{c(\text{PM})}$  by 2–5  $\text{mm s}^{-1}$ . The diurnal course of  $g_{c1}$  followed that of PAR, in a manner similar to what would be expected in well-watered conditions. The patterns of  $g_{c2}$  and  $g_{c(\text{PM})}$  showed an early morning peak followed by a gradual decrease during the rest of the day. The patterns of  $g_{c2}$  and  $g_{c(\text{PM})}$  seemed to be typical of water-stressed vegetation (e.g. Kim and Verma, 1990a). On August 11 (Fig. 3(f)) the differences in the diurnal patterns of  $g_{c2}$  and  $g_{c(\text{PM})}$  were more pronounced. The leaf water potential ( $\Psi_L$ ) of major grass species (e.g. *Andropogon gerardii*, *Sorghastrum nutans*) decreased very rapidly in the morning and stayed below  $-2.0$  MPa for most of the day (from 0900 to 1900 h) on July 30 and August 11. The early morning peak followed by a decrease during the day in  $g_{c2}$  was most likely driven by the corresponding rapid decrease in  $\Psi_L$  and a rapid increase in  $D$ . We speculate that the failure of the  $g_{c1}$  model to simulate the diurnal pattern under moisture stress conditions was due to the inability of the single daily value of  $\theta_s$  in adequately representing the rapid changes in water status of the prairie vegetation through the day.

Both modeled conductances ( $g_{c1}$  and  $g_{c2}$ ) could have been overestimated partly owing to the errors involved in the measurements of green LAI. An overestimation of the effective green LAI during this dry period could have resulted because the leaf blades of dominant grass species were either partially wilted or folded due to severe water stress. The lack of validity of our assumption that  $f_1(D)$  and  $f_2(\Psi)$  are constant for different layers in the canopy may

have also contributed to this discrepancy. For example, Millar and Denmead (1976) and Mogensen (1980) have shown that the critical value of  $\Psi_L$  increased for leaves at higher levels in the canopy, suggesting that lower leaves close their stomata first under stressed conditions. Since the relationships between  $g_s$  and  $\Psi_L$  were derived from data on sunlit leaves in the upper canopy, the effect of  $\Psi_L$  might have been underestimated during the moisture stress conditions.

### *Early senescence*

The soil moisture content increased in mid August due to frequent, abundant rainfall. The sky was clear on August 15 and 20 and the soil water conditions were favorable (Table 3). The diurnal patterns of the three conductances generally followed that of PAR (Figs. 3(g) and 3(h)). Values of  $g_{c1}$  and  $g_{c2}$  agreed within  $1 \text{ mm s}^{-1}$  but exceeded that of  $g_{c(\text{PM})}$  by 2–3  $\text{mm s}^{-1}$ . The overestimation by  $g_{c1}$  and  $g_{c2}$  may have been partly owing to the senescing condition of the leaves, a factor not considered in the present model. Also, the stomatal responses of the prairie grasses may not have recovered fully after the severe stress conditions of late July–early August.

### *Latent heat flux estimates using the canopy stomatal conductance model*

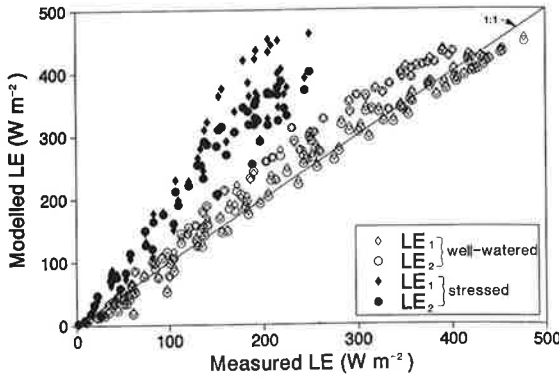
The performance of the canopy stomatal conductance model in estimating latent heat flux ( $LE$ ) is examined here. The canopy stomatal conductance estimates ( $g_{c1}$  and  $g_{c2}$ ), in conjunction with measurements of  $R_n$ ,  $G$ ,  $D$ ,  $T_a$ ,  $T_s$ ,  $g_a$ , were used to evaluate half-hourly values of latent heat flux employing the Penman–Monteith equation. Results are compared with the latent heat flux ( $LE_{\text{EC}}$ ) measured with the micrometeorological eddy correlation technique on the days discussed above (Fig. 4). The diurnal variations of modeled and measured  $LE$  are also presented on a day with favorable soil moisture (Fig. 5(a)) and on a day with moisture stress (Fig. 5(b)).

Under well-watered conditions (Figs. 4 and 5(a)) there was very little difference between  $LE_1$  (obtained from  $g_{c1}$ ) and  $LE_2$  (obtained from  $g_{c2}$ ). The modeled ( $LE_1$  or  $LE_2$ ) and measured ( $LE_{\text{EC}}$ ) fluxes were generally within 5% (a linear regression through the origin gave a slope of 1.05 for  $LE_1$  and 1.04 for  $LE_2$ ) (see Table 4). Under moisture stress conditions, however, both  $LE_1$  and  $LE_2$  exceeded  $LE_{\text{EC}}$  by 50–90% (Figs. 4 and 5(b)). The large differences between modeled and measured  $LE$  during the moisture stress conditions are expected because of the overestimation of  $g_c$  by the model (discussed above, Figs. 3(e) and 3(f)).

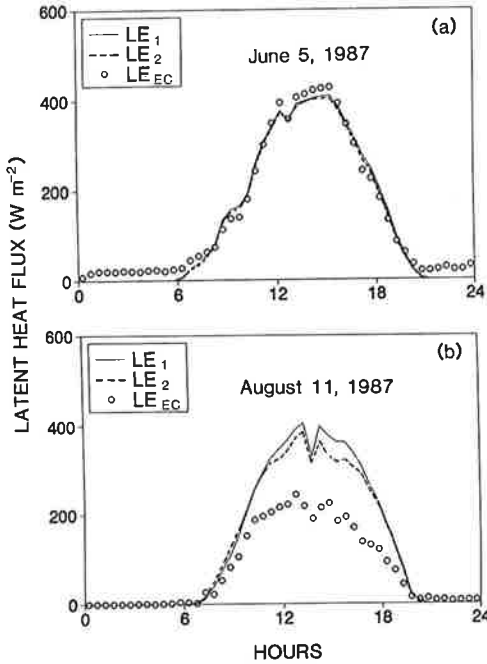
As also described by Jarvis and McNaughton (1986), the response of  $LE$  to small changes in  $g_c$  can be written as:

$$dLE/LE = (1 - \Omega) dg_c/g_c \quad (1)$$

The term  $\Omega$  is a decoupling parameter ( $0 < \Omega < 1$ ) that sets the relative



4. Comparison of modeled ( $LE_1$  using  $g_{c1}$  and  $LE_2$  using  $g_{c2}$ ) and measured ( $LE_{EC}$ ) latent flux on selected days in 1987.



5. Comparison of the diurnal variations in the modeled ( $LE_1$  using  $g_{c1}$  and  $LE_2$  using  $g_{c2}$ ) measured ( $LE_{EC}$ ) latent heat flux on (a) day with ample soil moisture (June 5 1987) and day with moisture stress (August 11 1987).

distance of the 'equilibrium  $LE$ ' and the 'imposed  $LE$ ' (McNaughton and Jarvis, 1983), and is defined by:

$$= [1 + \gamma(g_a/g_c)/(s + \gamma)]^{-1} \quad (18)$$

TABLE 4

The slope and  $r^2$  of regressions (through the origin) between modeled and measured canopy conductance and latent heat flux using two canopy stomatal conductance models

Model	Plant/soil water conditions	Estimation of		
		Canopy conductance		Latent heat flux
		Slope	$r^2$	Slope
The $g_{c1}$ model (using $\theta_s$ )	Well-watered	1.07	0.86	1.05
	Stressed	2.33	0.01	1.89
The $g_{c2}$ model (using $\Psi_L$ )	Well-watered	1.04	0.82	1.04
	Stressed	2.10	0.45	1.71

TABLE 5

Response of  $LE$  to errors in  $g_c$

Conditions	$dg_c$ ( $\text{mm s}^{-1}$ )	$dg_c/g_c$ (%)	$dLE/LE$ (%)
Well-watered ( $\Omega \approx 0.72$ , $g_c \approx 15.0 \text{ mm s}^{-1}$ )	1	6.7	1.9
	2	13.3	3.7
	3	20.0	5.6
	5	33.3	9.3
Moisture stressed ( $\Omega \approx 0.25$ , $g_c \approx 3.0 \text{ mm s}^{-1}$ )	1	33.3	25.0
	2	66.7	50.0
	3	100.0	75.0
	5	166.7	125.0

When the soil water was not limiting, the midday values of  $\Omega$  and  $g_c$  for prairie averaged about  $0.72$  and  $15 \text{ mm s}^{-1}$ , respectively (Kim and Verma 1990a). Under these conditions, for example, an error of  $2 \text{ mm s}^{-1}$  in estimation of  $g_c$  would result in  $<4\%$  error in the estimation of  $LE$  (Table 5). Under moisture stress conditions, however, values of  $\Omega$  and  $g_c$  would be small and similar error in  $g_c$  would result in about  $50\%$  error in estimating  $LE$  (Table 5). These calculations illustrate that the computation of  $LE$  is more sensitive to errors in  $g_c$  under moisture stress conditions. Owing to the non-linearity of the Penman–Monteith equation, as has also been discussed by Finnigan and Raupach (1987), the differences between the modeled and measured  $LE$  were smaller than the corresponding differences in  $g_c$  under both well-watered and moisture-stressed conditions.



## CLUDING REMARKS

The results indicate that the measurements of leaf stomatal conductance can be used to scale up to a canopy level to provide reasonable estimates of canopy stomatal conductance for well-watered vegetation on a short-time (e.g. hour) basis. The model developed in this study is empirical, yet it appears to provide physiologically and physically realistic results. The evapotranspiration rates computed from the modeled canopy stomatal conductance were generally in good agreement with those measured with the meteorological eddy correlation technique, except in moisture stress conditions. The failure of the model under these conditions could be attributed partly to the errors associated with the measurement of effective green area when leaves were rolled and folded due to severe water stress. The  $g_{c2}$  model seems to provide more realistic diurnal patterns of canopy stomatal conductance under moisture stress conditions, but it has a practical limitation due to its dependence on the availability of leaf water potential. The results with the  $g_{c1}$  model seem to indicate that soil moisture measured on one time a day basis may not be sufficient under moisture stress conditions. Also, species-specific relationships between leaf stomatal conductance and relevant controlling factors may vary somewhat from site to site and from year to year. Further tests of the present model during different growing seasons and at different locations are needed to make it more applicable.

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