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Modeling canopy stomatal conductance in a temperate grassland ecosystem*

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ABSTRACT

Kim, J. and Verma, S.B., 1991. Modeling canopy stomatal conductance in a temperate grassland system. Agric. For. Meteorol., 55: 149–166.

Field measurements of stomatal conductance were used to develop a leaf stomatal conduct model for major C_4 grass species in a temperate grassland ecosystem. Employing data on incor 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 ca stomatal conductance, estimated employing this approach, were compared with those of canopy face conductance computed from measured fluxes using the Penman–Monteith equation. Diu patterns and magnitudes of the two estimates were in good agreement under well-watered condit Under moisture stress conditions, the agreement was poor. Possible reasons are discussed. We su tuted the daily extractable soil water input with the hourly measurements of leaf water pote. Although the model with the leaf water potential input did not produce any significant improver in predicting the magnitude of canopy stomatal conductance under moisture stress conditions, i simulate the diurnal patterns (e.g. morning peak) adequately.

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

INTRODUCTION

Several studies have evaluated canopy conductance on the basis of leaf matal response to environmental conditions (Monteith et al., 1965; Sz and Long, 1969; Tan and Black, 1976; Jarvis, 1981; Monteith, 19 Baldocchi et al., 1987). Information on canopy conductance can be usefu estimation of evapotranspiration (ET) and in developing a better un standing of the processes controling the exchange rates of trace gases in ious terrestrial ecosystems.

Estimation of canopy conductance has generally involved two approac

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

Iere we describe the development and testing of a one-layer canopy sto-
tal conductance model in a temperate grassland ecosystem. The basic con-
ts employed are similar to those in Baldocchi et al. (1987). The data were
ained in a micrometeorological study in a tall grass prairie field in north-
ern Kansas during the First ISLSCP (ISLSCP, International Satellite Land
face Climatology Project; for details, see Sellers et al., 1988), Field Exper-
nt (FIFE) in 1987. The objectives of this paper are: (a) to model the
endence of the leaf stomatal conductance on relevant meteorological, soil
plant variables; (b) to scale up the model from a leaf to a canopy level;
to compare modeled canopy stomatal conductance against the values of
opy surface conductance computed from the measured latent heat flux.
ET rates estimated from the modeled canopy stomatal conductance val-
are compared against those measured with the micrometeorological eddy
elation technique.

TERIALS AND METHODS

and vegetation

he study was conducted on tallgrass prairie at a site (39°3′ N, 96°32′ W,
m above mean sea level) near Manhattan, Kansas. The soil is predomi-
tly 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 Kim and Verma, 1990b)

| Species	%
Andropogon gerardii (Big bluestem) (C_4)	27.1
Sorghastrum nutans (Indiangrass) (C_4)	22.2
Panicum virgatum (Switchgrass) (C_4)	16.6
Sporobolus asper (Tall dropseed) (C_4)	7.0
Schizachyrium scoparium (Little bluestem) (C_4)	4.7
Bouteloua gracilis (Blue grama) (C_4)	4.3
Dichanthelium oligosanthes (Scribner panicum) (C_3)	4.0
Agropyron smithii (Western wheatgrass) (C_3)	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 sp of 1987 to improve the botanical composition of grasses and forbs. The perimental area had been lightly grazed for several years by domestic l stock, but was not grazed in 1986 and 1987.

Percent species composition at the study site was estimated by emplo; the modified step point method (Owensby, 1973). The vegetation (Tabl is dominated by three C_4 grass species: *Andropogon gerardii, Sorghastrum tans* and *Panicum virgatum*.

Plant and soil measurements

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

The surface soil water content (0–0.1 m) was monitored gravimetric almost every day and subsurface soil water content (0.1–1.4 m) was n
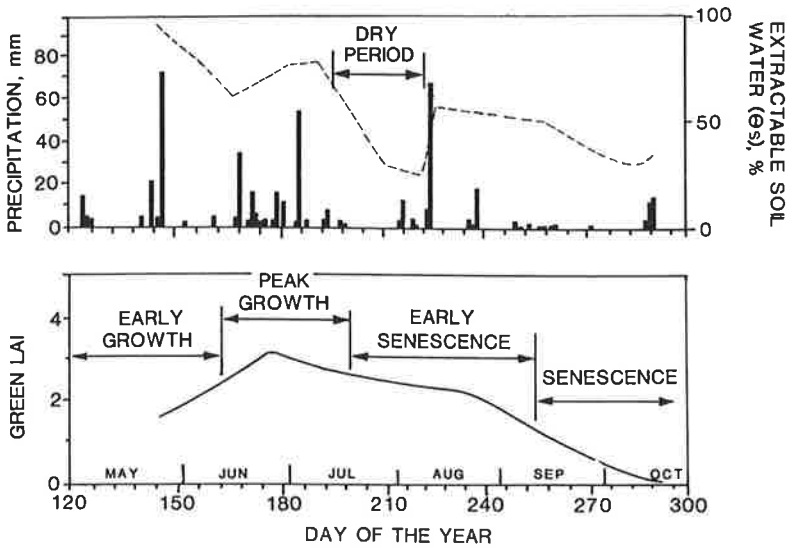
1. Seasonal precipitation, extractable soil water (0–1.4 m) and green leaf area index in

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

rometeorological measurements

luxes of water vapor (LE), sensible heat (H) and momentum were mea- d with eddy correlation sensors mounted at 2.25 m above the ground. ails on the instrumentation and procedure can be found in Kim and Verma 90a,b). Photosynthetically active radiation (PAR) was measured with a ntum sensor (LICOR, LI-190SB) at 2.0 m above the ground. Mean air perature and humidity were measured with an aspirated ceramic wick chrometer. Net radiation (R_n) and soil heat flux (G) were measured with radiometers (Radiation Energy Balance System, Beaverton, OR) and soil t flow transducers (REBS, Model HFT-1), respectively.

oretical considerations

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

pressure deficit (D), soil/plant water status (e.g. water potential, Ψ) and
a lesser extent, of ambient carbon dioxide concentration (C_a). Jarvis (197
proposed a multiplicative model for the computation of stomatal cond
tance (g_s) as the product of the functional relationships for PAR, D, Ψ, T a
C_a:

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

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

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

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

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

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

$$f_1(D) = 1/(1 + a_3 D) \qquad ($$

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

Soil water and leaf water potential have been proposed as measures of pl;
water status (Turner et al., 1985; Gollan et al., 1985; Kramer, 19
Baldocchi et al., 1991). To examine the role of soil water in controlling g_s
this study, we first used daily values of extractable soil water (computed
the ratio of actual to total soil moisture held with a water potential betwe
$-1/30$ and -1.5 MPa), (θ_s) obtained over the primary root zone (0–
m). The response of g_s to θ_s was estimated using a negative exponential re
tionship (e.g. Jarvis, 1976; Gollan et al., 1986):

$$f_2(\theta_s) = 1 - \exp(-a_4 \theta_s) \qquad ($$

where a_4 is a constant. Also, to estimate the response of g_s to leaf water stat
hourly measurements of leaf water potential (Ψ_L) were used. Based on t
observations of Norman and Polley (1989) and Polley et al. (1990) the (
pendence of g_s on Ψ_L was approximated by a discontinuous linear relationsh

$$f_2(\Psi_L) = 1 \qquad \text{for } \Psi_L > -1 \text{ MPa}$$
$$f_2(\Psi_L) = 1 + a_4' \Psi_L \quad \text{for } \Psi_L < -1 \text{ MPa}$$

where a_4' is a constant.

*Modeling canopy stomatal conductance (g_c): scaling up from a leaf to
...opy level*

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

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

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

$$...I_{\text{sun}} = [1 - \exp(-0.5\text{LAI}/\cos\theta)] \, 2\cos\theta \tag{7}$$

...ere θ is the zenith angle of the sun. The shaded leaf area index was obtained

$$...I_{\text{shade}} = \text{LAI} - \text{LAI}_{\text{sun}} \tag{8}$$

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

$$...R_{\text{sun}} = 0.5\text{PAR}_{\text{dir}}/\cos\theta + \text{PAR}_{\text{shade}} \tag{9}$$

...ere PAR_{dir} is the flux density of direct PAR above the canopy. The flux
...sity of PAR on shaded leaves was computed using a relationship given by
...rman (1982):

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

...ere PAR_{diff} is the flux density of diffuse PAR on a horizontal surface above
... canopy. To obtain PAR_{dir} and PAR_{diff}, the measured incoming PAR was
...arated into direct and diffuse components of PAR using the procedure of
...iss and Norman (1985).

...ince the prairie vegetation mainly consisted of *Andropogon gerardii, Sor-*
...strum nutans and *Panicum virgatum*, the canopy stomatal conductance
...s weighted by the fractions of leaf areas[a] of these three grass species. Fi-
...ly, the effective canopy stomatal conductance (g_c) of the prairie was ob-

---

...e sum of the leaf area index of *Andropogon gerardii, Sorghastrum nutans* and *Panicum vir-*
...um accounted for 70–85% of the total LAI throughout the season. The LAI of each grass
...cies was, therefore, adjusted such that the sum of LAI of three grass species was equal to the
...l LAI.

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

$$g_c = \{[LAI_{sun}g_s(PAR_{sun}) + LAI_{shade}g_s(PAR_{shade})]f_1(D)f_2(\theta_S \text{ or } \Psi_L)\}_{AG}$$

$$+ \{[LAI_{sun}g_s(PAR_{sun}) + LAI_{shade}g_s(PAR_{shade})]f_1(D)f_2(\theta_S \text{ or } \Psi_L)\}_{SN}$$

$$+ \{[LAI_{sun}g_s(PAR_{sun}) + LAI_{shade}g_s(PAR_{shade})]f_1(D)f_2(\theta_S \text{ or } \Psi_L)\}_{PV}$$

where subscripts AG, SN and PV represent *Andropogon gerardii, Sorg-trum 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 assume that $f_1(D)$ and $f_2(\theta_S \text{ or } \Psi_L)$ are constant for different layers of canopy.

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

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

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

$$1/g_a = r_{am} + r_b$$

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

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

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

values of β for the tallgrass prairie studied here were typically about 0.25
er well-watered conditions and around 1.0 under moisture stress condi-
s (Kim and Verma, 1990a). The values of r_b were of the order of 10 s
. Thus, the second term on the right hand side of eqn. (14) was of the
er of 5 s m^{-1} under well-watered conditions and about 50 s m^{-1} under
ssed conditions. Since the canopy resistance was about 50–200 s m^{-1} un-
well-watered conditions and about 300–1000 s m^{-1} under stressed con-
ons, the difference between the values of $g_{c(PM)}$ and $1/r_{ST}$ was generally
than 10% throughout the season for the prairie vegetation studied here.
is worth noting that $g_{c(PM)}$ also includes the contribution from the soil
poration as well as the transpiration through the stomates. Previous stud-
suggested that the ratio of transpiration to potential ET in most mesophy-
vegetation (e.g. grasslands) well supplied with water increases with leaf
a to an LAI of about 3 (Ritchie and Burnett, 1971; Ritchie et al., 1976;
senberg et al., 1983). On the other hand, Denmead (1984) found that soil
poration in the forest with an LAI ≥ 4 could be 10–40% of the total. There-
e, caution should be exercised in interpreting $g_{c(PM)}$ when LAI is small
ause the soil evaporation may not be negligible.

ULTS AND DISCUSSION

ermination of parameters

y combining eqns. (1)–(4) we obtain:

$$= g_s (PAR) f_1(D) f_2(\theta_S)$$
$$= [a_1 PAR/(a_2 + PAR)][1/(1+a_3 D)][1 - \exp(-a_4 \theta_S)]$$

(15)

ere extractable soil water, θ_S has been used to describe the response of g_s to
water status. The parameters (a_1, a_2, a_3 and a_4) in eqn. (15) were deter-
ned for each grass species by fitting (non-linear least squares) the mea-
ed g_s to the values of PAR, vapor pressure deficit and extractable soil water.
e values of the parameters with their asymptotic standard errors and r^2 are
ed in Table 2(a). Equation (15) accounted for about 71–77% of the vari-
on in data for the three grass species.
igures 2(a)–(c) show the form of the dependence of the stomatal conduc-
ce of *Andropogon gerardii* (which was the most dominant grass species)
PAR, D and θ_S using the parameters given in Table 2(a). The dashed lines
w the uncertainties in relationships owing to a ± 1 standard error in the
ameter values. The horizontal lines represent the range of each variable
d in derivation of the parameters.

TABLE 2

The values of the parameters with their asymptotic standard errors and r^2 for (a) the model (eqn. (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^{-1})	a_2 (μEi m^{-2} s^{-1})	a_3 (kPa^{-1})	a_4
Andropogon gerardii	110	18.4 ±3.8	585 ±187	0.188 ±0.083	0.029 ±0.008
Sorghastrum nutans	110	20.2 ±4.4	346 ±103	0.060 ±0.057	0.013 ±0.005
Panicum virgatum	110	20.5 ±7.3	392 ±142	0.030 ±0.062	0.010 ±0.006

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

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

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

$$g_s = g_s(PAR)f_1(D)f_2(\Psi_L)$$
$$= [a'_1 PAR/(a'_2 + PAR)][1/(1+a'_3 D)][1+a'_4 \Psi_L]$$

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 Ψ_L was substituted for θ_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 (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 θ_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 θ_S with the half-hourly values of l
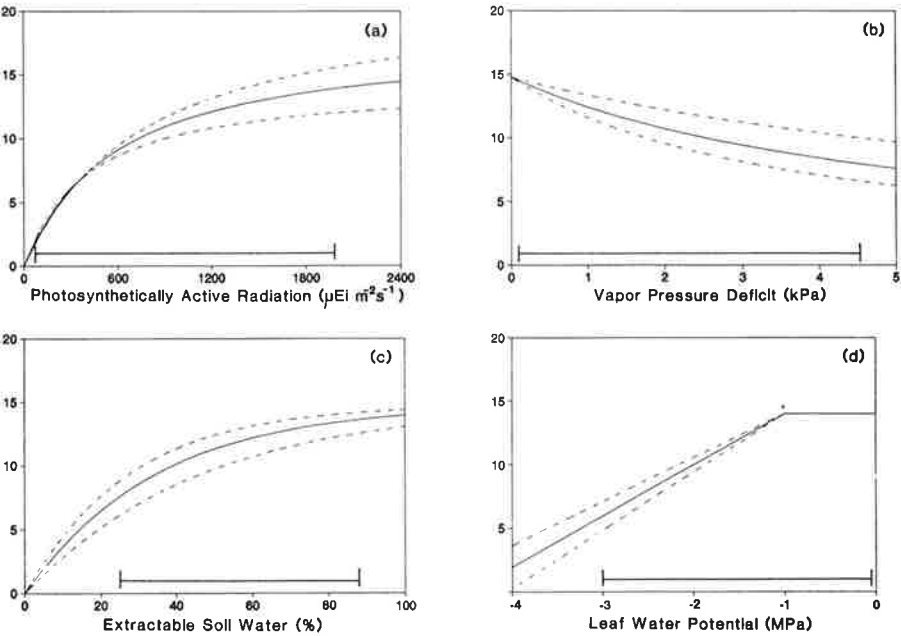
2. The stomatal conductance response functions: (a) $g_s(PAR)$, (b) $f_1(D)$, (c) $f_2(\theta_S)$ and $f_2(\Psi_L)$ for *Andropogon gerardii*. The dashed lines show the uncertainties in relationships g to a ± 1 standard error in the parameter values. The horizontal lines represent the range ch variable used in derivation of the parameters.

er potential, Ψ_L (obtained by interpolating hourly measurements of Ψ_L), btain g_{c2}.

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

arly growth

he two days (June 5 and 6) considered here were mostly clear. Soil water not limiting (Table 3). As would be expected for well-watered vegeta-, g_{c1}, g_{c2} and $g_{c(PM)}$ followed the diurnal pattern of PAR. Values of g_{c1} and greed within 1 mm s^{-1} (Figs. 3(a) and 3(b)). The modeled conductance mates (g_{c1} and g_{c2}) generally agreed with $g_{c(PM)}$ within 2 mm s^{-1}. During midday hours $g_{c(PM)}$ exceeded modeled conductance estimates by 1–2 s^{-1}. Since the prairie was only partially covered by the vegetation
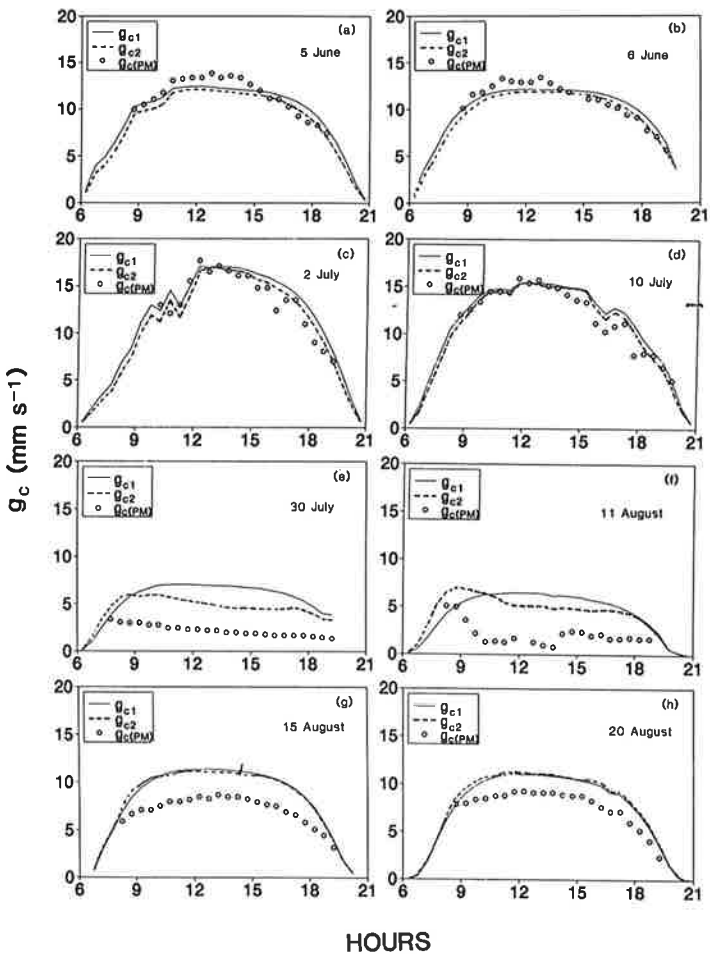
Fig. 3. Comparison of modeled conductances (g_{c1} using extractable soil water and g_{c2} using l water potential) and $g_{c(PM)}$ on selected days in 1987.

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

Peak growth

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

LE 3

	Annual life cycle stage	PAR (μEi m^{-2} s^{-1})	T (°C)	D (kPa)	g_a (mm s^{-1})	θ_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
ıst 11	period	1844	33.1	3.16	9.3	24.8	2.5
ıst 15	Early	1888	33.7	2.33	36.0	54.4	2.4
ıst 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
ilability of soil water and high atmospheric evaporative demand (Table
July 30 was clear, but August 11 was partly cloudy. The magnitudes of all
ee conductance estimates were significantly smaller on these days (Figs.
) and 3(f)). The magnitudes of g_{c1} and g_{c2} were, however, larger than
t of $g_{c(PM)}$ by 2–5 mm s^{-1}. The diurnal course of g_{c1} followed that of PAR,
a manner similar to what would be expected in well-watered conditions.
e patterns of g_{c2} and $g_{c(PM)}$ showed an early morning peak followed by a
eral decrease during the rest of the day. The patterns of g_{c2} and $g_{c(PM)}$
med to be typical of water-stressed vegetation (e.g. Kim and verma,
90a). On August 11 (Fig. 3(f)) the differences in the diurnal patterns of
, g_{c2} and $g_{c(PM)}$ were more pronounced. The leaf water potential (Ψ_L) of
jor grass species (e.g. *Andropogon gerardii*, *Sorghastrum nutans*) de-
ased very rapidly in the morning and stayed below −2.0 MPa for most of
 day (from 0900 to 1900 h) on July 30 and August 11. The early morning
ık followed by a decrease during the day in g_{c2} was most likely driven by
rresponding rapid decrease in Ψ_L and a rapid increase in D. We speculate
ıt the failure of the g_{c1} model to simulate the diurnal pattern under mois-
e stress conditions was due to the inability of the single daily value of θ_S in
equately representing the rapid changes in water status of the prairie vege-
ion through the day.
Both modeled conductances (g_{c1} and g_{c2}) could have been overestimated
rtly owing to the errors involved in the measurements of green LAI. An
erestimation of the effective green LAI during this dry period could have
ulted because the leaf blades of dominant grass species were either partially
led or folded due to severe water stress. The lack of validity of our assump-
n 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 Denm (1976) and Mogensen (1980) have shown that the critical value of Ψ_L creased for leaves at higher levels in the canopy, suggesting that lower lea close their stomata first under stressed conditions. Since the relationships tween g_s and Ψ_L were derived from data on sunlit leaves in the upper can the effect of Ψ_L might have been underestimated during the moisture st conditions.

Early senescence

The soil moisture content increased in mid August due to frequent, an rainfall. The sky was clear on August 15 and 20 and the soil water conditi were favorable (Table 3). The diurnal patterns of the three conductances erally followed that of PAR (Figs. 3(g) and 3(h)). Values of g_{c1} and g_{c2} agr within 1 mm s^{-1} but exceeded that of $g_{c(PM)}$ by 2–3 mm s^{-1}. The over mation by g_{c1} and g_{c2} may have been partly owing to the senescing condit of the leaves, a factor not considered in the present model. Also, the stom responses of the prairie grasses may not have recovered fully after the sev 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 estima latent heat flux (LE) is examined here. The canopy stomatal conducta estimates (g_{c1} and g_{c2}), in conjunction with measurements of R_n, G, D, T g_a, were used to evaluate half-hourly values of latent heat flux employing Penman–Monteith equation. Results are compared with the latent heat (LE_{EC}) measured with the micrometeorological eddy correlation techni on the days discussed above (Fig. 4). The diurnal variations of modeled measured LE are also presented on a day with favorable soil moisture (I 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 ference between LE_1 (obtained from g_{c1}) and LE_2 (obtained from g_{c2}). modeled (LE_1 or LE_2) and measured (LE_{EC}) fluxes were generally wit 5% (a linear regression through the origin gave a slope of 1.05 for LE_1 1.04 for LE_2) (see Table 4). Under moisture stress conditions, however, b LE_1 and LE_2 exceeded LE_{EC} by 50–90% (Figs. 4 and 5(b)). The large dif ences between modeled and measured LE during the moisture stress cor tions are expected because of the overestimation of g_c by the model (cussed above, Figs. 3(e) and 3(f)).
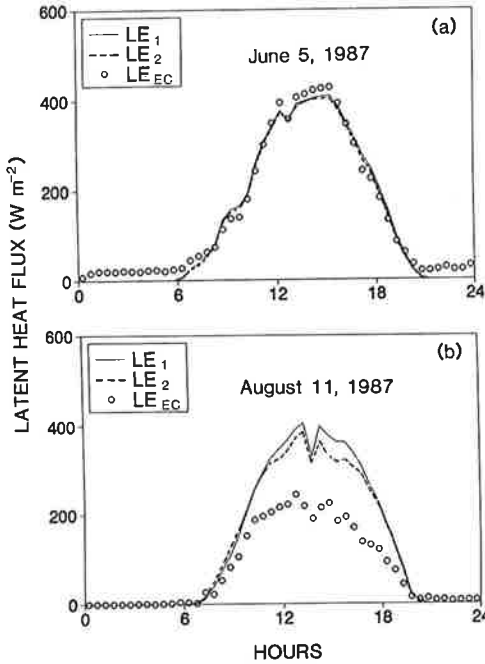
As also described by Jarvis and McNaughton (1986), the response of to small changes in g_c can be written as:

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

The term Ω is a decoupling parameter ($0 < \Omega < 1$) that sets the relative
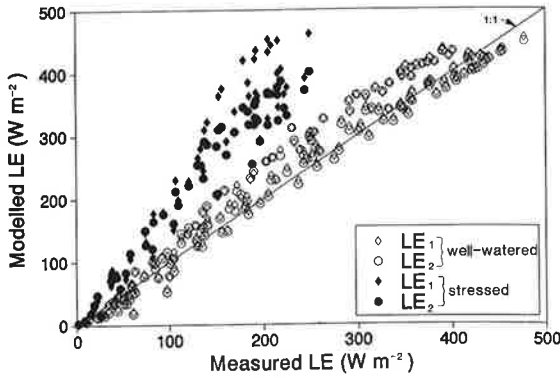
4. Comparison of modeled (LE_1 using g_{c1} and LE_2 using g_{c2}) and measured (LE_{EC}) latent flux on selected days in 1987.

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).

rtance of the 'equilibrium LE' and the 'imposed LE' (McNaughton and rvis, 1983), and is defined by:

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

TABLE 4

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

Model	Plant/soil water conditions	Estimation of		Latent heat flu
		Canopy conductance		
		Slope	r^2	Slope
The g_{c1} model (using θ_S)				
	Well-watered	1.07	0.86	1.05
	Stressed	2.33	0.01	1.89
The g_{c2} model (using Ψ_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 (mm s^{-1})	dg_c/g_c (%)	dLE/LE (%)
Well-watered			
($\Omega \approx 0.72$, $g_c \approx 15.0$ 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			
($\Omega \approx 0.25$, $g_c \approx 3.0$ 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 Ω and g_c for
prairie averaged about 0.72 and 15 mm s^{-1}, respectively (Kim and Ver
1990a). Under these conditions, for example, an error of 2 mm s^{-1} in
estimation of g_c would result in <4% error in the estimation of LE (Table
Under moisture stress conditions, however, values of Ω and g_c would be sn
and similar error in g_c would result in about 50% error in estimating LE (
ble 5). These calculations illustrate that the computation of LE is more s
sitive to errors in g_c under moisture stress conditions. Owing to the non-
earity of the Penman–Monteith equation, as has also been discussed
Finnigan and Raupach (1987), the differences between the modeled a
measured LE were smaller than the corresponding differences in g_c under b
well-watered and moisture-stressed conditions.

CLUDING REMARKS

e results indicate that the measurements of leaf stomatal conductance
be used to scale up to a canopy level to provide reasonable estimates of
py stomatal conductance for well-watered vegetation on a short-time (e.g.
hour) basis. The model developed in this study is empirical, yet it ap-
s to provide physiologically and physically realistic results. The evapo-
spiration rates computed from the modeled canopy stomatal conduc-
e were generally in good agreement with those measured with the
ometeorological eddy correlation technique, except in moisture stress
litions. The failure of the model under these conditions could be attrib-
partly to the errors associated with the measurement of effective green
area when leaves were rolled and folded due to severe water stress.

e g_{c2} model seems to provide more realistic diurnal patterns of canopy
atal conductance under moisture stress conditions, but it has a practical
ation due to its dependence on the availability of leaf water potential
. The results with the g_{c1} model seem to indicate that soil moisture mea-
d on one time a day basis may not be sufficient under moisture stress
litions. Also, species-specific relationships between leaf stomatal conduc-
e and relevant controling factors may vary somewhat from site to site and
year to year. Further tests of the present model during different growing
ons and at different locations are needed to make it more applicable.

ERENCES

occhi, D.D., Hicks, B.B. and Camara, P., 1987. A canopy stomatal conductance model for
aseous deposition to vegetated surfaces. Atmos. Environ., 21: 91–101.
occhi, D.D., Luxmoore, R.J. and Hatfield, J.L., 1991. Discerning the forest from the trees:
n essay on scaling canopy stomatal conductance. Agric. For. Meteorol., 54: 197–226.
mead, O.T., 1984. Plant physiological methods for studying evapotranspiration: problems
om telling the forest from the trees. Agric. Water Manage., 8: 167–189.
igan, J.J. and Raupach, M.R., 1987. Modern theory of transfer in plant canopies in relation

to stomatal characteristics. In E. Zeiger, G. Farquhar and I. Cowan (Editors), Ston
Function. Stanford University Press, CA, pp. 385–429.

Gollan, T., Turner, N.C. and Schulze, E.-D., 1985. The responses of stomata and leaf ga:
change to vapor pressure deficits and soil water content, III. In the sclerophyllous wo
species *Nerium oleander*. Oecologia, 65: 356–362.

Gollan, T., Passioura, J.B. and Munns, R., 1986. Soil water status affects the stomatal con
tance of fully turgid wheat and sunflower leaves. Aust. J. Plant Physiol., 13: 459–464.

Jarvis, P.G., 1976. The interpretation of the variations in leaf water potential and stom
conductance found in canopies in the field. Phil. Trans. R. Soc. Lond., Ser. B., 273: 5
610.

Jarvis, P.G., 1981. Stomatal conductance, gaseous exchange, and transpiration. In: J. Gr
E.D. Ford and P.G. Jarvis (Editors), Plants and Their Atmospheric Environment. Black
Scientific, Oxford, pp. 175–204.

Jarvis, P.G. and McNaughton, K.G., 1986. Stomatal control of transpiration: Scaling up f
leaf to region. Adv. Ecol. Res., 15: 1–49.

Kim, J. and Verma, S.B., 1990a. Components of surface energy balance in a temperate grass!
ecosystem. Boundary-Layer Meteorol., 51: 401–417.

Kim, J. and Verma, S.B., 1990b. Carbon dioxide exchange in a temperate grassland ecosyst
Boundary-Layer Meteorol., 52: 135–149.

Knapp, A.K., 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii*
Panicum virgatum in a tallgrass prairie. Ecology, 66: 1309–1320.

Kramer, P.J., 1988. Changing concepts regarding plant water relations. Plant, Cell Environ.,
565–568.

Lohammar, T., Larsson, S., Linder, S. and Falk, S., 1980. FAST-Simulation models of gase
exchange in Scots pine. In: Structure and Function of Northern Coniferous Forests – an I
system Study. Ecol. Bull., 32: 505–523.

McNaughton, K.G. and Jarvis, P.G., 1983. Predicting effects of vegetation changes on trans
ation and evaporation. Water Deficits and Plant Growth, Vol. VII, pp. 1–47.

Millar, B.D. and Denmead, O.T., 1976. Water relations of wheat leaves in the field. Agron
68: 303–307.

Mogensen, V.O., 1980. Drought sensitivity at various growth stages of barley in relation to
ative evapotranspiration and water stress. Agron. J., 72: 1033–1038.

Monteith, J.L., 1965a. Light distribution and photosynthesis in field crops. Ann. Bot., N
113: 17–37.

Monteith, J.L., 1965b. Evaporation and environment. In: G.E. Fogg (Editor), The State
Movement of Water in Living Organisms. Academic Press, New York, pp. 205–234.

Monteith, J.L., 1981. Evporation and surface temperature. Q. J. R. Meteorol. Soc., 107: 1–

Monteith, J.L., Szeicz, G. and Waggoner, P.E., 1965. The measurement and control of stom
resistance in the field. J. Appl. Ecol., 2: 345–355.

Norman, J.M., 1979. Modeling the complete crop canopy, In: B.J. Barfield and J.F. Ge
(Editor), Modification of the Aerial Environment of Plants, Am. Soc. Agric. Engr., St.
seph, MI, pp. 249–277.

Norman, J.M., 1982. Simulation of microclimates. In: J.L. Hatfield and I.J. Thompson (I
tor), Biometeorology in Integrated Pest Management. Academic Press, New York, pp.
99.

Norman, J.M. and Polley, H.W., 1989. Canopy photosynthesis. In: W.R. Briggs (Editor), F
tosynthesis. Allan R. Liss, New York, pp. 227–241.

Owensby, C.E., 1973. Modified step-point system for botanical composition and basal cc
estimates. J. Range Manag., 26: 302–303.

Paw U, K.T. and Meyers, T.P., 1989. Investigations with a higher-order canopy turbulence m
into mean source–sink levels and bulk canopy resistance. Agric. For. Meteorol., 47: 2
271.

—

y, H.W., Norman, J.M., Arkebauer, T.J., Walter-Shea, E.A. and Greegor, Jr., D.H., 1990. as exchange of *Andropogon gerardii* Vitman, *Panicum virgatum* L., and *Sorghastrum nu-ns* (L.) Nash in a tallgrass prairie. In preparation.

bach, M.R. and Finnigan, J.J., 1988. 'Single-layer models of evaporation from plant cano-ies are incorrect but useful, whereas multilayer models are correct but useless': Discuss. ust. J. Plant Physiol., 15: 705–716.

hie, J.T. and Burnett, E., 1971. Dryland evaporative flux in a subhumid climate: II. Plant nfluences. Agron. J., 60: 545–549.

hie, J.T., Rhoades, E.D. and Richardson, C.W., 1976. Calculating evaporation from native rassland watersheds. Trans. ASAE, 19: 1098–1103.

enberg, N.J., Blad, B.L. and Verma, S.B., 1983. Microclimate: The Biological Environment. Viley, New York, 495 pp.

rs, P.J., Hall, F.G., Asrar, G., Strebel, D.E. and Murphy, R.E., 1988. The First ISLSCP ield Experiment (FIFE). Bull. Am. Meteorol. Soc., 69: 22–27.

tleworth, W.J., 1976. A one-dimensional theoretical description of the vegetation-atmo-phere interaction. Boundary-Layer Meteorol., 10: 273–302.

h, B. and Szeicz, G., 1980. Predicting the canopy resistance of a mixed hardwood forest. gric. Meteorol., 21: 49–58.

cz, G. and Long, I.F., 1969. Surface resistance of crop canopies. Water Resour. Res., 5: 622–33.

, C.S. and Black, T.A., 1976. Factors affecting the canopy resistance of a Douglas-fir forest. Boundary-Layer Meteorol., 10: 475–488.

m, A.S., 1975. Momentum, mass, and heat exchange of plant communities, In: J.L. Mon-eith (Editor), Vegetation and the Atmosphere. Academic Press, New York, Vol. 1, pp. 57–09.

ner, N.C., Schulze, E.-D. and Gollan, T., 1984. The responses of stomata and leaf gas ex-hange to vapor pressure deficits and soil water content. I. Species comparisons at high soil vater contents. Oecologia, 63: 338–342.

ner, N.C., Schulze, E.-D. and Gollan, T., 1985. The responses of stomata and leaf gas ex-hange to vapor pressure deficits and soil water content, II. In the mesophytic species *He-ianthus annuus*. Oecologia, 65: 348–355.

ss, A. and Norman, J.M., 1985. Partitioning solar radiation into direct and diffuse, visible nd near-infrared components. Agric. For. Meteorol., 34: 205–213.