Predicted versus measured photosynthetic water-use efficiency of crop stands under dynamically changing field environments

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Abstract

Water-use efficiency (WUE) is critical in determining the adaptation and productivity of plants in water-limited areas, either under the present climate or future global change. Data on WUE are often highly variable and a unifying and quantitative approach is needed to analyse and predict WUE for different environments. Hsiao has already proposed a set of paradigm equations based on leaf gas exchange for this purpose, calculating WUE (ratio of assimilation to transpiration) relative to the WUE for a chosen reference situation. This study tests the validity and applicability of these equations to cotton and sweet corn stands with full canopies in the open field. Measured were evapotranspiration and downward flux of atmospheric CO2 into the canopy, soil CO2 efflux, canopy temperature, and CO2 and vapour pressure of the air surrounding the canopy. With the measured mean WUE and conditions at midday serving as the reference, WUE for other times was predicted from the air CO2 and water vapour data, intercellular water vapour pressure calculated from canopy temperature, and an assumed ratio of \( C_i/C_a \) based on leaf gas-exchange data. Provided that the stomatal response to humidity as it affected the \( C_i/C_a \) ratio was accounted for, the equations predicted the moment-by-moment changes in canopy WUE of cotton over daily cycles reasonably well, and also the variation in midday WUE from day-to-day over a 47 d period. The prediction for sweet corn was fairly good for most parts of the day except the early morning. Measurement uncertainties and possible causes of the differences between predicted and measured WUE are discussed. Overall, the results indicate that the equations may be suitable to simulate changes in WUE without upscaling, and also demonstrate clearly the importance of stomatal response to humidity in determining stand WUE in the field.

Key words: Canopy, \( C_i/C_a \) ratio, scaling, stomatal response to humidity, transpiration ratio.

Introduction

In water-limited environments, plant productivity is determined jointly by the amount of water available and the efficiency by which the water is used by the plant. With the continuous rise in atmospheric CO2 and global climate change, to predict the associated changes in productivity and distribution of plant species, it is essential to know how water-use efficiency (WUE) of different species would change with the environment and CO2 levels. At the physiological level, WUE may be defined as the ratio of photosynthesis to transpiration, also referred to in the literature as transpiration efficiency. Photosynthetic WUE is difficult to monitor over long periods, however. More conveniently and for agronomic assessment, WUE has been expressed as the ratio of biomass produced to water consumed, referred to as biomass WUE. Biomass WUE is known to be relatively constant for a given crop under a given climate and the prevailing air CO2 concentration (Hanks, 1983), regardless of whether water supply is ample or deficient (de Wit, 1958). For different climates, biomass WUE is conservative only if normalized for variations in evaporative demand (de Wit, 1958). Because increases in air CO2 concentration generally enhance photosynthesis and reduce stomatal opening, WUE, either in terms of photosynthesis or biomass accumulation, is expected to increase with rising levels of CO2 in the atmosphere, and this has

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almost universally been observed. The increases in WUE for a given increase in CO₂, however, are highly variable among different studies (Eamus, 1991; Morison, 1993; Hsiao and Jackson, 1999). In view of the varied responses, a systematic and conceptual approach is needed to analyse the experimental results and to quantify and predict the impact of environmental changes. Such an approach, general and not restricted to a given species and accounting for all the important variables affecting WUE, was proposed by Hsiao (1993) as a set of paradigm equations. The equations are simple, based on the fundamentals underlying leaf gas exchange, and express WUE under new sets of conditions relative to WUE under a set of reference conditions. Of the environmental factors, temperature, humidity, and air CO₂ concentration are accounted for explicitly, and radiation and wind are accounted for implicitly. In this study, the validity of the equations was tested on cotton and sweet corn growing in large fields as environmental factors varied naturally through the diurnal and seasonal course. This paper reports the first set of the apparently promising results.

Conceptual framework

The basic unit of photosynthesis and transpiration is the single leaf and the two processes are well described by gas exchange equations. In the framework proposed by Hsiao (1993), the complexity of metabolic processes underlying photosynthesis, lumped together as mesophyll resistance ($r'_m$) or conductance ($g'_m$) in the gas exchange equation, was by-passed by considering the rate of CO₂ transport from the bulk air only to the leaf intercellular space, which equals the rate of CO₂ assimilation ($A$) under steady-state conditions. Transpiration shares that segment of transport pathway with photosynthesis. Two equations of identical form may be written, one for the basic unit of photosynthesis and transpiration is the single leaf and the two processes are well described by gas exchange equations. In the framework proposed by Hsiao (1993), the complexity of metabolic processes underlying photosynthesis, lumped together as mesophyll resistance ($r'_m$) or conductance ($g'_m$) in the gas exchange equation, was by-passed by considering the rate of CO₂ transport from the bulk air only to the leaf intercellular space, which equals the rate of CO₂ assimilation ($A$) under steady-state conditions. Transpiration shares that segment of transport pathway with photosynthesis. Two equations of identical form may be written, one for the basic unit of photosynthesis and transpiration is the single leaf and the two processes are well described by gas exchange equations. In the framework proposed by Hsiao (1993), the complexity of metabolic processes underlying photosynthesis, lumped together as mesophyll resistance ($r'_m$) or conductance ($g'_m$) in the gas exchange equation, was by-passed by considering the rate of CO₂ transport from the bulk air only to the leaf intercellular space, which equals the rate of CO₂ assimilation ($A$) under steady-state conditions. Transpiration shares that segment of transport pathway with photosynthesis. Two equations of identical form may be written, one for the basic unit of photosynthesis and transpiration is the single leaf and the two processes are well described by gas exchange equations. In the framework proposed by Hsiao (1993), the complexity of metabolic processes underlying photosynthesis, lumped together as mesophyll resistance ($r'_m$) or conductance ($g'_m$) in the gas exchange equation, was by-passed by considering the rate of CO₂ transport from the bulk air only to the leaf intercellular space, which equals the rate of CO₂ assimilation ($A$) under steady-state conditions. Transpiration shares that segment of transport pathway with photosynthesis. Two equations of identical form may be written, one for

$$A = \frac{1}{r'_s + r'_e} (C_a - C_i) = \frac{1}{r'_s + r'_e} \Delta C$$

$$T = \frac{1}{r_s + r_e} (W_i - W_o) = \frac{1}{r_s + r_e} \Delta W$$

where the resistance to gas transport to the air boundary layer and leaf epidermis are denoted respectively by $r'_s$ and $r'_e$, with $r_e$ being the resistance made up of two parallel resistances, that of the stomata and of the cuticle. The resistances for CO₂ are indicated by a prime, and for water vapour without the prime. Due to its lighter molecular mass, water vapour diffuses faster than CO₂ and encounters a lower resistance in the diffusion path, with $r_e=0.625 r'_e$ for both boundary layer and epidermal parts of the pathway (Farquhar and Sharkey, 1982). The driving force for $A$ and $T$ is, respectively, the difference in CO₂ concentration ($\Delta C$) between the bulk air ($C_a$) and the intercellular space ($C_i$), and the difference in the water vapour concentration ($\Delta W$) between the intercellular space ($W_i$) and the bulk air ($W_o$). The impact of metabolism on $A$ is not dealt with directly but is reflected in the value of $A$, $C_i$, and $C_a$ relative to $C_i$. Because the leaf intercellular space is essentially saturated with water vapour and saturation water vapour pressure is a function of temperature, leaf temperature must be measured or estimated in order to calculate $W_i$ and hence $\Delta W$. Since only physical processes are involved in the gaseous phase of photosynthesis, all terms in equations 1a and b are well defined and can be experimentally determined for single leaves.

Hsiao (1993) proposed that when conditions change, WUE under the new set of conditions ($WUE_n$) is evaluated in relation to the WUE under the original or reference conditions ($WUE_o$). Expressing photosynthetic WUE as the ratio of $A$ (equation 1a) to $T$ (equation 1b), and cancelling out first the resistances and then the factor 0.625, the ratio of the new WUE to the reference WUE becomes

$$\frac{WUE_n}{WUE_o} = \frac{A_o}{T_o} = \frac{\Delta C_o \Delta W_o}{\Delta C_o \Delta W_o}$$

where the subscript $n$ designates the parameters under the new conditions, and the subscript $o$, the parameters under the original or reference conditions. Equation 2 is fundamental and should hold regardless of whether the plant is $C_3$ or $C_4$, with or without a change in leaf photosynthetic capacity with the change in conditions, whether the leaf is under high or present levels of CO₂, under low or high temperature, and well watered or water deficient. The equation should also hold for conditions of nutrient deficiency and pest infestation, as long as they are not extreme.

As environmental conditions vary, $C_i$ tends to remain constant at a given $C_a$ (Wong et al., 1979). As $C_a$ changes, $C_i$ tends to change in proportion. That is, the ratio of $C_i$ to $C_a$, designated as α, is nearly constant. This conservative behaviour of $C_i$ and α appears to hold, within limits, for variations in photosynthetic active radiation (PAR), temperature, and leaf age (Hsiao and Jackson, 1999). The exception is variations in humidity. In plants with stomata which respond to humidity (more specifically, to $\Delta W$), stomatal conductance decreases and $C_i$ tends to decrease linearly with increases in $\Delta W$ (Morison, 1987).

In view of the conservative nature of $\alpha$, it is advantageous to express the relative changes in $WUE$ in terms of $\alpha$. Thus, to evaluate changes in $WUE$ due to changes in $C_a$, equation 2 is rewritten in terms of $C_a$ by recognizing that $C_i=\alpha C_a$,

$$\frac{WUE_n}{WUE_o} = \frac{(1 - \alpha_o) C_o \Delta W_o}{(1 - \alpha) C_a \Delta W_a}$$

Equation 3 shows that as $C_a$ rises or falls, relative $WUE$ would change in proportion to the $C_a$ ratio modified by the $(1-\alpha)$ ratio and $\Delta W$ ratio. In cases where $\alpha$ does not change
with the changes in conditions, \( \alpha_n \approx \alpha_o \), and equation 3 is reduced to:

\[
\frac{WUE_n}{WUE_o} \approx \frac{C_{a,n}}{C_{a,o}} \frac{\Delta W_o}{\Delta W_n}
\]

with the change in relative \( WUE \) being the product of the \( C_a \) ratio by the \( \Delta W \) ratio.

Theoretically, it is the ratio of \( C_1 \) to \( CO_2 \) concentration at the leaf epidermal surface (\( C_e \)) that behaves conservatively (Ball and Berry, 1982), and the ratio \( C_j/C_a \) is an approximation of the ratio \( C_j/C_e \). This would be true if the air is highly turbulent and \( r_c \gg r_a \). To arrive at equation 4 from equation 3, however, it is not necessary that \( \alpha \) remains constant as long as \( \alpha_n \approx \alpha_o \).

Equations 3 and 4, being derived from equations for gas exchange of single leaves, in principle need to be scaled up when applied to a population of leaves or plants. No upscaling was attempted in this study, but the equations are apparently applicable to canopies of monocultured crops, as will be shown in the Results.

Materials and methods

Gas exchange characteristics of leaves grown in environment chambers

To determine the basic gas exchange parameters of single leaves, cotton (Gossypium hirsutum L., cv. Acala GC 510) and maize (Zea mays L., cv. FR27×FRMO17) were grown in cylindrical tubes (7.4×10^{-3} m^3 in volume) in a well-fertilized Yolo clay loam soil/peat moss (2:1 v:v) mixture in controlled environment chambers under nominally 360 and 720 ppm of \( CO_2 \) and a 14 h photoperiod (0.75–0.82 mmol m^{-2} s^{-1} PAR) for about 1 month. Day/night temperatures and relative humidities were, respectively, 29/20 °C and 45/80%. Pots were watered to a predetermined weight daily.

One or two pots were taken from the growth chamber on measurement days to determine the photosynthetic response of recently matured leaves to \( C_a \), \( PAR \), and \( \Delta W \) in a steady-state open gas exchange system described earlier (Bolaños and Hsiao, 1991). Humidity response curves were obtained by varying \( W_a \) of the incoming air and adjusting the air flow rate into the chamber. \( C_i \) and related gas exchange parameters were calculated according to von Caemmerer and Farquhar (1981).

Stand canopy photosynthesis, evapotranspiration, and water-use efficiency

In the field crop (cv. Sure-Grow 404) was grown in 1997 and maize (sweet corn, cv. Silverrado F1) in 1998 under irrigation on a soil of high fertility (Yolo silty clay loam) and well fertilized with nitrogen (200 kg ha^{-1}), in large fields (3–6 ha) in Davis to provide a fetch of more than 130 m in the prevailing wind directions. The downward flux of \( CO_2 \) to the canopy and the upward flux of water vapour (evapotranspiration, \( ET \)) were measured simultaneously with a Bowen ratio/energy balance/CO2 gradient (BREB+) system (Held et al., 1990) capable of resolving the fluxes for 5 min intervals (Steduto and Hsiao, 1998a). The BREB+ with its data logger (model CR 21X or 23X, Campbell Scientific, Logan, Utah, USA) measured air temperature, water vapour, and \( CO_2 \) concentration at two selected heights above the canopy, as well as net radiation and soil heat flux.

The measurements were taken once per second and averaged over each 5 min interval, and the averages were stored by the logger. The results were used to calculate the \( ET \) rate (\( ET \)) as:

\[
ET = \frac{-R_n - S}{(1 + \beta)}
\]

where \( R_n \) is net radiation flux and \( S \) is soil heat flux in energy units, \( l \) is latent heat of vaporization, and \( \beta \) is the Bowen ratio (ratio of sensible to latent heat flux) calculated from the difference in temperature and vapour pressure between the selected upper and lower heights above the canopy. The downward \( CO_2 \) flux to the canopy was calculated from the \( ET \) rate and the differences in air \( CO_2 \) and water vapour pressure between the two heights (Steduto and Hsiao, 1998a). The drift in the null point of the infrared gas analyser (IRGA, model LI-6252 or 6262, Li-Cor, Lincoln, Nebraska, USA) used for measuring \( CO_2 \) in the BREB+ method was corrected for by automatically stopping the measurements every 30 min for 5 min to determine the IRGA zero. Thus, every sixth data point involving \( CO_2 \) presented in the figures was interpolated from the two adjacent points. Also measured and logged were \( PAR \) (model LI-191SB, Li-Cor) and wind velocity (cup anemometer) about 2 m above the canopy. More details on the BREB+ instruments and techniques is found in Asseng and Hsiao (2000).

Efflux of \( CO_2 \) from the soil was measured periodically, at various times over the daily course, at five sites in three different areas of the field with a large mobile stirred-chamber (covering 0.44×0.85 m of soil) operating as a closed system. The chamber was placed for less than 1 min on a base frame installed earlier in the soil between crop rows to measure the soil \( CO_2 \) efflux rate, as described by Steduto and Hsiao (1998b). Regression equations fitted to the daily-course data were used to calculate soil \( CO_2 \) efflux for 5 min intervals over the day. Net canopy assimilation rate was calculated as the sum of \( CO_2 \) fluxes into the canopy, from the atmosphere (measured by BREB+), and from the soil. Photosynthetic \( WUE \) was calculated as the ratio of net canopy assimilation rate to \( ET \). The data presented were taken after the canopy was well developed (\( LAI \) given in figure legends), so the soil was mostly shaded and not receiving much energy from radiation. Hence, most of the \( ET \) was attributable to transpiration, and soil evaporation was assumed to be negligible.

\( CO_2 \) and water vapour pressure of air surrounding the canopy, and intercellular water vapour pressure

To predict \( WUE \) under different environmental conditions using equation 3 or 4, data on \( CO_2 \) and water vapour pressure of the air surrounding the canopy are required. \( CO_2 \) and water vapour profiles within and above the canopy were obtained simultaneously with a multiport air sampling apparatus (Xu et al., 1999) that measured \( C_a \) and \( W_a \) for 8 s at a given height and sequentially cycled through six heights in 1 min. The five 8 s measurements taken over a 5 min interval were averaged for each height and stored by the logger. Canopy \( C_a \) and \( W_a \) used in calculation were taken as the weighted average for three heights where most of the photosynthetically active leaves were located. For cotton in 1997 these were 0.6, 1.3 and 1.65 m with a canopy height of 1.4 m on 2 and 3 September, and 0.7, 1.4, and 1.8 m with a canopy height of 1.5 m on 9 and 10 September. For sweet corn in 1998, these were 0.9, 1.65, and 2.4 m with a canopy height of 2.4 m. To estimate intercellular water vapour pressure of the canopy (\( W_i \)), canopy surface temperature was monitored continu-ously using an infrared thermometer with a viewing angle of 15° (Model 4000BL, Everest Interscience, Fullerton, California, USA), positioned toward the north at an angle of approximately 30° from the horizontal, and viewing the upper part of the canopy. \( W_i \) was calculated by assuming water vapour saturation of the intercellular space at the measured canopy temperature.
Calculating and predicting photosynthetic WUE using equations 3 and 4

Although equations 3 and 4 were derived for single leaf gas exchange, they were used without modification to calculate predicted WUE for canopies of the crops consisting of a population of plants in the open field.

To predict WUE of a given species for any given environment using equation 3 or 4, a reference situation must be chosen with its known WUE ($WUE_o$) and the associated pertinent parameters ($a_o$, $C_o$, and $D_o$). For variations of $WUE$ over a diurnal cycle, the midday period of 11.30 h to 12.30 h of that day was chosen as the reference situation. The 12 values of the 5 min measurements over that period were averaged to obtain $WUE_o$, $a_o$, and $D_o$. For sweet corn, whose $a_o$ did not vary with $D_o$, the predicted $WUE$ ($WUE_o$) was calculated with equation 4 from $WUE_{\text{a/o}}$, $a_o$, $W_{\text{a/o}}$, $W_{\text{LO}}$, and the measured $C_o$, $W_{\text{LO}}$, and $W_i$ of each 5 min interval, taken as new situations. For cotton, whose $a_o$ was not constant but changed with $D_o$, an empirical linear relationship between $a_o$ and $D_o$ was obtained from the humidity–response measurements described earlier. The equation for humidity response was $a_o = -0.092 D_o$ (kPa)+0.8718, the result of adjusting the regression equation for data in Fig. 2 of the Results according to the regressions of the other sets of cotton data.

Values of $a_o$ for the reference and new situations were calculated with the response equation from measured $D_o$, and predicted $WUE$ ($WUE_o$) was calculated using equation 3.

For the variation of $WUE$ of cotton over many days, the reference situation chosen was the means for the 11.30–12.30 h period of 16 September 1997. Data were obtained from cotton at the full canopy stage spanning many days, but on some days the canopy photosynthesis data were reliable only for the midday period of a few hours due to the particularity of the BREB+ technique, and on other days the multiport apparatus to measure canopy profile of air CO2 and vapour pressure was either malfunctioning or not yet installed. Thus, the comparison between measured and predicted $WUE$ of cotton from day-to-day over many days using only one day as the reference situation had to be confined to the midday period. In addition, due to the lack of canopy profile data, it was necessary: (i) to assume that air CO2 surrounding the canopy at midday did not vary significantly from one day to the next, and (ii) to use the air vapour pressure measured by the lower unit of the Bowen ratio apparatus in place of the weighted average obtained with the multiport apparatus to calculate $AW$ for the new and reference situations. The validity of these simplifying steps will be considered in the Discussion.

Results

Constancy and variability of $C_i/C_a$ ratio ($\alpha$)

Knowing under what conditions $\alpha$ remains constant and when and how it varies is pivotal to the application of the model. Under conditions favouring good rates of photosynthesis, $C_i$ increased linearly with increases in $C_a$ in cotton and maize (Fig. 1a, c). Nearly identical results were obtained regardless of whether the plants were grown under ambient (360 μmol mol$^{-1}$) or 2× ambient (720 μmol mol$^{-1}$) $C_a$ in the growth chamber (data not shown). Long-term acclimation to elevated $C_a$ did not alter significantly the slope ($\alpha$) of $C_i$ versus $C_a$ curves. Values of $\alpha$, obtained by averaging the slope by linear regression of the data in Fig. 1a and c and similar experiments, were found to be 0.61 and 0.33 for cotton and maize, respectively, similar to values published by Wong et al. (1979).

The response of $C_i$ to PAR was also assessed for cotton and maize. At $C_a=360$ μmol mol$^{-1}$, $C_i$ for both remained essentially constant, at about 230 μmol mol$^{-1}$ for cotton, and 120 μmol mol$^{-1}$ for maize, over a wide PAR range of

Fig. 1. Intercellular CO2 concentration ($C_i$) in relation to air CO2 concentration ($C_a$) (a, c) and to incident PAR (b, d) for recently matured leaves of cotton (a, b) and maize (c, d). Each line represents one leaf of a different plant. Plants were grown in air of nominally 360 ppm of CO2, day/night temperature of 27/20 °C, and 0.77 mmol m$^{-2}$ s$^{-1}$ PAR (14 h light period) in controlled environment chambers. Linear regression of the data in (a) and (c) yielded $C_i=11.1+0.660C_a$ for cotton, with $r^2=0.992$, and $C_i=-11.6+0.337C_a$ for maize, with $r^2=0.967$. Hence, the ratio of $C_i/C_a$ ($\alpha$) was 0.660 for cotton and 0.337 for maize.
0.5–2.0 mmol m\(^{-2}\) s\(^{-1}\) (Fig. 1c, d). \(C_i\) rose as PAR fell below approximately 0.6 mmol m\(^{-2}\) s\(^{-1}\) for maize, and 0.4 mmol m\(^{-2}\) s\(^{-1}\) for cotton. Because the PAR response curves were determined with \(C_a\) held constant, it is obvious that \(\alpha\) remained about the same over the PAR range where \(C_i\) remained constant.

By contrast with the conservative nature of \(\alpha\) in the face of varying \(C_a\) and PAR, \(\alpha\) decreased linearly as the difference in vapour pressure between the leaf intercellular space and the air (\(\Delta W\)) increased for cotton leaves (Fig. 2a). For maize leaves, however, there was no obvious trend as \(\Delta W\) increased (Fig. 2b). The results indicate that cotton stomata became less and less open as \(\Delta W\) increased, but maize stomata did not close significantly in response to increases in \(\Delta W\). Others (Held, 1991; Dai et al., 1992) have reported a lack of stomatal response to \(\Delta W\) for maize leaves. In terms of the equations to predict relative changes in WUE, it appears that predictions for cotton under different \(\Delta W\) needs to take changes in \(\alpha\) into account by using equation 3, whereas equation 4 is sufficient for maize as its \(\alpha\) does not show a clear response to changes in \(AW\).

### Prediction of WUE for single leaves

WUE of single leaves of cotton and maize were measured in a gas exchange chamber, taking the ratio of CO\(_2\) assimilation to transpiration (\(A/\overline{F}\)) as the measured WUE. The experiments were performed under different \(C_a\) and \(\Delta W\), yielding a wide range of measured WUE. The results are compared in Fig. 3 with the WUE predicted by equation 3 for cotton and equation 4 for maize. The reference WUE \(WUE_0\) used for the calculation was determined under \(C_a\) of 360 \(\mu\)mol mol\(^{-1}\) and \(\Delta W\) of 1.8 kPa. The comparison shows a near 1:1 relationship between the predicted and the measured WUE over the wide ranges of \(C_a\) and \(\Delta W\). The slopes of the predicted values versus measured values were not significantly different from 1.0 for both cotton and maize. The good agreement between the predicted and measured leaf WUE is obviously expected, as equations 3 and 4 are simply variants of the fundamental equations used in all leaf gas exchange calculations.

### Prediction of diurnal trends in WUE for cotton stand in open field

Strictly speaking, the paradigm equations are for single leaves and upscaling would be necessary for application to the canopy made up of numerous leaves on a population of plants. Nonetheless, the paradigm equations for predicting canopy WUE of the two crops in the open field was tested. \(C_a\) and \(W_a\) surrounding the canopy were measured as given under Materials and methods. Canopy temperature, continuously sensed with an infrared thermometer, was used to calculate \(W_i\) and hence \(AW\).

The predicted diurnal pattern of WUE was compared with the measured WUE for cotton on four days in Figs 4 and 5. In both figures, measured \(PAR\) and canopy assimilation rates are presented in the top pair of panels. Comparison of the predicted and measured WUE are given.
Fig. 4. Comparison of predicted with measured canopy photosynthetic WUE for cotton (LAI=5.7) in an open field over the daily cycle, on a day of variable clouds (b, c) and of clear sky (f, g). Predictions were made by either assuming the ratio of \( C_i/C_a \) (\( \alpha \)) to be constant (b, f) or to change with changes in \( \Delta W \) (c, g). Variation in \( \alpha \) was calculated from \( \Delta W \) determined for each 5 min interval, as \( \alpha = -0.092 \Delta W \) (kPa)+0.8718. Also given are the measured PAR and canopy assimilation rates (a, e, note the displaced origin of the y-axis for PAR), relative humidity and wind speed at, respectively, about 1.5 m
in the middle two pairs of panels, together with air temperature (2nd panel pair) and mean CO₂ concentration of the air surrounding the photosynthetically active part of the canopy (3rd panel pair). The trends in air relative humidity and wind speed are given in the bottom panel pair. Comparison of predicted with measured WUE is made first by assuming α to be constant (using equation 4) in the 2nd panel pair, then by taking the variation in α with changes in ΔW into account (using equation 3) in the 3rd panel pair. For the prediction, the reference situation was taken as the 11.30 h to 12.30 h and the values of $WUE_o$, $C_o$, $ΔW_o$, and $α_o$ were the means for that period.

On 3 September 1997 (Fig. 4, right panels), with the sky clear all day, measured WUE (Fig. 4f, g) declined from early morning to midday, then remained nearly constant until mid-afternoon, before increasing slightly toward sunset. WUE predicted by assuming α to be constant ($α_o$), shown in Fig. 4f, was much higher than the measured value in the early morning and somewhat lower than the measured value in the afternoon. As expected, the predicted WUE was very similar to the measured WUE in late morning and early afternoon since the chosen reference situation is the mean for the midday 1 h period.

To be more accurate in the prediction, as stomata of cotton respond to humidity and $α$ changes with $ΔW$ (Fig. 2a), the changes in $α$ need to be taken into account. The value of $α$ was calculated from $ΔW$ as derived from canopy temperature and $W_o$, using the linear regression equation of $α$ versus $ΔW$ (Fig. 1a gives an example of such regressions). Based on these changing values of $α$, WUE was then predicted using equation 3. The results (Fig. 4g) show that the predicted WUE now matched the measured WUE closely. Not only was the difference between the measured and predicted values for the morning period in Fig. 4f essentially eliminated, the difference in the afternoon was also reduced to a minimum. A remarkable fact is that the function of $α$ versus $ΔW$ used in the calculation was not based on measurements made on field-grown plants, but measurements made on plants grown in growth chambers.

The data in the right panels of Fig. 4 were collected on a clear day (3 September 1997). On the day before (2 September 1997) radiation was highly variable, with periods of sunshine alternating with periods of clouds. The clouds cut solar radiation and $PAR$ by more than half and caused canopy assimilation to fluctuate widely, mostly in synchrony with the fluctuation in $PAR$ (Fig. 4a). The sudden reductions in $PAR$ caused the canopy (not shown) and the air to cool (Fig. 4b). Measured WUE (Fig. 4b, c) was also higher in the morning and lower in the afternoon. As clouds obscured the sun, measured WUE usually increased noticeably. Both CO₂ assimilation and transpiration were reduced markedly by the clouds, but the proportion of reduction was apparently larger for transpiration, causing WUE to rise. By assuming $α$ to be constant, WUE was also over-predicted in the early morning and under-predicted in the afternoon (Fig. 4b). By treating $α$ as a variable dependent on $ΔW$ and using equation 3 (Fig. 4c), the prediction was made nearly perfect for the major portion of the middle of the day. Improvement was also substantial in the late afternoon and early morning (07.30–08.00 h, see Discussion regarding a complication caused by dew before 07.30 h). For the period between 08.00 h and 09.30 h, using variable $α$ actually made the prediction worse. Overall, it is notable that the general pattern is reasonably predicted, particularly the increases in measured WUE during the cloudy periods.

To assess further the consistency of the prediction using the paradigm equations, data obtained on two other days one week later on the same crop are presented in Fig. 5. On the clear day of 10 September (Fig. 5, right panels), temperature was considerably cooler and wind speed higher than on 3 September (Fig. 4, right panels). By assuming $α$ to be constant, the predicted WUE was again too high in the morning and too low in the afternoon (Fig. 5f). Taking the variation of $α$ with $ΔW$ into account, however, made the predicted and measured values nearly coincidental for most of the day except in the late afternoon, when the predicted WUE was slightly lower than the measured WUE (Fig. 5g). On the preceding day (9 September) with variable clouds (Fig. 5, left panels), it was relatively calm in the morning and very windy in the afternoon. Relative humidity of the air declined from morning to afternoon as usual but with more marked up and down fluctuations, and reached a low of only 24%. The WUE predicted with a constant $α$ turned out to agree with the measured values for most of the day except for early in the morning (the deviation starting around 16.30 h was caused by measurement uncertainties, see Discussion). Incorporating variations in $α$ caused by variations in $ΔW$ in the calculations improved the afternoon and very early morning predictions somewhat, but caused significant under-prediction from 08.40 h to 10.30 h (Fig. 5c). Although the deviations are of concern, it is nonetheless notable that the general fluctuating pattern under variable clouds are predicted to a fair degree.

Generally speaking, on most of the days for cotton the predicted WUE appear to deviate considerably from the measured WUE very early in the morning and late in the afternoon even after the variations in $α$ with $ΔW$ were taken into account. The underlying causes may involve measurement errors, particular weather conditions, and certain
Fig. 5. Comparison of predicted with measured canopy photosynthetic WUE for cotton (LAI=6.0) in an open field over the daily cycle, on another day of variable clouds (b, c) and of clear sky (f, g). Predictions were made by either assuming the ratio of $C_i/C_a$ ($\alpha$) to be constant (b, f) or to change with changes in $\Delta W$ (c, g). Also given are the measured PAR and canopy assimilation rates (a, e, note the displaced origin of y-axis for PAR), relative humidity and wind speed at, respectively, about 1.5 m and 2 m above the canopy (d, h), air temperature at about 1.5 m above the canopy (b, f), and CO$_2$ of the air.
underlying assumptions, as will be elaborated in the Discussion.

Prediction of diurnal trends in WUE for a sweet corn stand in the open field

WUE of sweet corn was measured in 1998 over diurnal cycles and compared with the predictions made by the paradigm equation. Data collected on two days are presented as samples in Fig. 6. Compared with the cotton data shown (Figs 4, 5), the days were hotter with afternoon temperature going above 35°C, and the rate of assimilation of the sweet corn was higher than that of cotton. Since for these conditions, maize leaf stomata (data not shown) and ζ (Fig. 2b) do not respond significantly to ΔW, ζ was assumed to be constant over the daily cycle and WUE was predicted simply with equation 4. On the clear day (12 August) the predicted WUE was in reasonably good agreement with the measured WUE for most of the day, except for the period before 09.00 h (Fig. 6b). At 07.00 h the difference between the predicted and measured WUE was very large, and decreased as time progressed toward 09.00 h. The next day (13 August, Fig. 6c, d) there were three brief periods of minor reductions in PAR due to clouds (Fig. 6c). Because of the frequent fluctuation in the measured canopy assimilation rate, only in one of the periods (around 09.00 h) was there a clear reduction in assimilation associated with the reduced PAR. WUE was again over-predicted in the morning on this day, up to 09.30 h, with the greatest deviation in the early morning and during the cloudy period around 09.00 h (Fig. 6d). The possible causes for these deviations will be taken up under the Discussion.

Discussion

Prediction of midday WUE of a cotton canopy in the open field over many days

Although the predictions made over daily cycles using midday values as references are reasonably successful, the question remains whether acceptable predictions can be made for longer periods, over weeks and months, and using only a single reference data set. To make the long-term predictions with the available data, it was necessary to take two simplifying steps: (i) assuming $C_a$ not to vary from midday to midday, and (ii) replacing the weighted mean water vapour pressure with water vapour pressure measured by the lower Bowen ratio unit when calculating $\Delta W$ (see Materials and methods, and Discussion). The comparisons between the measured and predicted results are presented in Fig. 7.

Figure 7a shows that the predicted WUE made with ζ assumed to be constant followed more or less the ups and downs of measured WUE, but was mostly lower than the measured WUE. Comparing Fig. 7a with Fig. 7b, it is seen that accounting for the variations in ζ with changes in $\Delta W$ from day to day reduced the deviation between the predicted and measured on most days. Over a 47 d period the predicted midday WUE followed the measured values reasonably well, except for a few dates (e.g., 92 DAP). Generally speaking, the time trend of cotton WUE at midday was well predicted. As expected, there tended to be an inverse relationship between measured WUE (Fig. 7a, b) and air temperature (Fig. 7c); and conversely, a direct relationship with air relative humidity. This is particularly evident when the fluctuations in WUE from one day to the next are considered. On the other hand, there was no clear long-term trend in WUE for the portion of the life cycle depicted, whereas relative humidity showed a decline over the long term as the season progressed.

Applicability of the paradigm equations to canopies without upscaling

Modelling of canopy photosynthesis and transpiration based on the characteristics of CO2 assimilation and stomatal conductance of leaves (DePury and Farquhar; 1997; Wang and Leuning, 1998) is not straightforward, due to non-linearity in the scaling-up processes (Fannigan and Raupach, 1987; Baldocchi, 1993). Equally difficult has been the modelling of plant water-use efficiency for conditions of elevated CO2 and climate change scenarios (Eamus, 1991; Morison, 1993; Hsiao and Jackson, 1999). This paper reports the results of experimental tests of the WUE paradigm equations (Hsiao, 1993). While the validity of the model at the leaf level (Fig. 3) is fully expected because the model derives from the fundamental equations for gas exchange of single leaves, fairly good agreement between predicted and measured WUE for population of plants in the field over diurnal and long-term courses was surprising as the model was directly applied to the canopy. The results point to the exciting possibility that the equations, without any explicit upscaling, may be applicable to whole plants and crop canopies of many species in surrounding the photosynthetically active part of the canopy (c.g., Air CO2=$C_a$). Reference values used for the prediction were the means (of $WUE_m$, $C_{a,oo}$, $\Delta W_o$, and $\xi_o$) for the 11:30 h to 12:30 h period of each day, and variation in ζ was calculated as in Fig. 4. Gaps in data between 07.30 and 08.30 of 9 September (a, b, c, d) were the result of the Bowen ratio instruments being serviced during that time.
open fields over the period of mid-morning to mid to late afternoon, when most of the CO₂ is assimilated and the water transpired. The reason for not needing upscaling may be the use of a reference and the expression of WUE of the new situation relative to that for the reference situation. Since the upscaling is likely not to change for the new situation relative to the reference situation, calculating WUE relative to a reference situation allows upscaling to be bypassed.

The Cᵢ/Cₐ ratio (α), and its constancy and variability

It is well known that the Cᵢ/Cₐ ratio, α, plays an important role in the determination of WUE. A clear inverse relationship exists, at least for C₃ species, between α and WUE, and between α and carbon isotope discrimination (Farquhar et al., 1989), to the extent that a large number of studies used carbon isotope discrimination either to assess WUE of different genetic material or to breed for improved WUE. The usefulness of the paradigm equations is dependent on the constancy or orderly and regular variations with variation in environmental factors. Early work (Wong, 1979; Wong et al., 1979) showed that leaf CO₂ assimilation was well co-ordinated with stomatal behaviour so that Cᵢ was constant for a given Cₐ for a number of C₃ and C₄ species, under varied levels of PAR, nitrogen and phosphorus nutrition, and slowly imposed water stress. These authors also showed that Cᵢ changed in proportion to changes in Cₐ (α being constant) as Cₐ was varied for Eucalyptus pauciflora and maize. Many subsequent studies demonstrated the conservative nature of α. Notable is the fact the α remained the same in 26 diverse species in 33 studies, regardless of whether the plants were grown under an ambient or elevated level of CO₂ (Drake et al., 1997).

The results presented in Fig. 1 add to this extensive database and also illustrate the fact that below a threshold level of PAR, α no longer remains constant but increases as PAR decreases (Fig. 1b, d). Presumably this is the consequence of light limiting photosynthesis more than stomatal opening.

Two other variables affecting α—leaf age and temperature—receive considerably less attention in the literature. Under ambient Cₐ, Cᵢ was apparently relatively constant for cotton leaves of different ages (Constable and Rawson, 1980), and for tomato leaves over a period of 50 d, from the time of rapid leaf expansion to the onset of senescence (Bolaños and Hsiao, 1991). Similar results were obtained

Fig. 6. Comparison of predicted with measured canopy photosynthetic WUE for sweet corn (LAI=4.7) in an open field over the daily cycle, on a clear day (a, b) and a day with occasional clouds (c, d). Predictions were made taking the ratio of Cᵢ/Cₐ (α) to be constant. Also given are the measured PAR and canopy assimilation rates (a,c; note the displaced origin of the y-axis for PAR), and air temperature at approximately 1.5 m above the canopy (b, d). Reference values used for the prediction were the means (of WUEₒ, Cₐₒ, ΔWₒ, and αₒ) for the 11.30 to 12.30 h period of each day.
with maize leaves of different ages in the field (L-K Xu and TC Hsiao, unpublished results). Obviously the insensitivity of $C_i$ and $\alpha$ to leaf age is a prerequisite for the prediction of variations in $WUE$ over many days of a crop’s life cycle. As for temperature, Björkman (1981) showed that $C_i$ of *Larrea divaricata* remained almost constant between 25 °C and 43 °C, but rose gradually when temperature dropped below 23 °C, and more sharply when temperature increased beyond 45 °C. Sage et al. (1990) found that at a constant $C_i$, $C_i$ of *Chenopodium album* remained essentially constant over a range of 15–34 °C. It is not known for certain if $\alpha$ of cotton and sweet corn responds to temperature in a similar way. Preliminary leaf gas exchange data indicate, however, that sweet corn $\alpha$ may be substantially higher at low temperatures. This may be the result of cold temperature also inhibiting photosynthesis more than stomatal opening.

Although variations in a number of external and plant parameters within limits have little or no impact on $\alpha$, one environmental parameter, $\Delta W$, is exceptional. $\alpha$ of many species decreases as $\Delta W$ increases. Ball and Berry (1982) found $\alpha$ to decrease linearly with increases in $\Delta W$ for *Geraea canescens* and *Perityle emoryii*. Morison and Gifford (1983) demonstrated a similar linear relationship for two C$_3$ (*Oryza sativa* L. and *Phalaris aquatica* L.) and two C$_4$ (maize and *Paspalum plicatum* Michx) species grown in controlled environment chambers at moderate temperature and high humidity. $\alpha$ of cotton in this study followed a similar trend (Fig. 2a). For maize, however, there was no clear response of $\alpha$ to $\Delta W$ (Fig. 2b). This could be the result of growing the plants in chambers of lower humidity and higher temperature than that used by Morison and Gifford (1983). For maize grown in the field in the summer in Davis, there is minimum or no stomatal response to $\Delta W$ (Held, 1991), similar to the results of Dai et al. (1992) obtained at a different location.

As illustrated by the results with cotton, the variation in $\alpha$ with changes in $\Delta W$ is all important in the prediction of $WUE$. Before discussing further the role of $\alpha$ in making predictions, however, it is necessary first to assess the uncertainties in this study’s measurements and assumptions.

**Uncertainties in measured $WUE$**

While the predicted $WUE$ matched the measured $WUE$ reasonably well much of the time, there were periods when the predicted and measured values were substantially or even widely apart. These differences could be due to a number of potential causes. The more likely ones are now examined, starting with uncertainties in the measured values.

The experimental $WUE$ data were obtained by combining measurements made in different ways, each with its own potential sources of error or uncertainty. Measured $WUE$ was calculated as the ratio of canopy assimilation to evapotranspiration, the latter determined by the BREB+ technique. Canopy assimilation rate was calculated as the sum of the downward CO$_2$ flux from the atmosphere, measured also by the BREB+ technique, and the upward CO$_2$ efflux from the soil. $ET$ measured by the BREB technique has been found to agree well with $ET$ measured by precision lysimeters (Held et al., 1990) and can apparently be more accurate than $ET$ measured by the eddy covariance technique (Dugas et al., 1991). Nonetheless, it is well known that accuracy of the BREB+ technique is substantially less for the time shortly after sunrise and before sunset, with errors in the CO$_2$ flux measurement being larger than that in the $ET$ measurement (Held et al., 1990). The inaccuracy is partly the result of the net
radiation (\(R_a\)) level being low for that time of the day relative to the sensor error (Pruit et al., 1987); but more importantly, it is rooted in the fundamentals of the technique. As can be seen in equation 5, as Bowen ratio (\(\beta\)) approaches the value of -1 (sensible heat flux downward equals latent heat flux upward), the denominator on the right side of the equation approaches zero and the measurement errors for \(\beta\) become more and more magnified in the calculated \(ET\) (and hence assimilation) rate. Depending on weather conditions, this situation often occurs in late afternoon before sunset. An example can be seen in the cotton data of 9 September (Fig. 5). \(\beta\) (data not shown) fell in late afternoon and reached a value of \(-0.77\) at 16.15 h, \(-0.92\) at 16.30 h, \(-0.94\) at 16.40 h, and \(-1.19\) at 17.00 h. During this period (16.15–17.00 h), canopy assimilation rates were unrealistically high or low (Fig. 5a) and measured \(WUE\) fluctuated wildly (Fig. 5b, c). As a general practice, these obviously erroneous data points would normally be excluded, but here they are shown to illustrate the problem.

Uncertainty in soil CO2 efflux also contributed to the uncertainties in the early morning and late afternoon data. By contrast with the downward CO2 flux from the atmosphere, soil efflux (data not shown) was more steady and changed more slowly with time, with rates ranging from 3 to 9 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) depending on the temperature regime and soil water status. Since limited resources did not permit extensive and very frequent measurements, soil CO2 efflux at 5 min intervals over daily cycles had to be calculated with generalized regression equations. During periods of high \(PAR\) and high assimilation rate, soil efflux contributed a minor portion of the assimilated CO2 and error in its estimation was not important. In the early morning, late afternoon, and heavily clouded periods, however, the situation was reversed and the percentage of uncertainty in the calculated canopy assimilation rate would be large if the estimation error in soil efflux was large.

Some uncertainties are associated with the assumptions made in the calculation of \(WUE\). In the calculation, the rate of transpiration was assumed to be the same as the rate of \(ET\). This is reasonable since the crops had full canopy cover, except when dew is present on the canopy surface on some mornings. With dew on the canopy, evaporation from the wet canopy surface could be much higher than transpiration through stomata, and measured \(WUE\) (\(A/ET\)) would be much lower than its true value (\(A/T\)) because of the inclusion of evaporation as transpiration. Of the data presented, on 2 and 3 September (Fig. 4), canopy temperature was substantially below dewpoint of the air before sunrise (data not shown), indicating the presence of dew. Measured \(WUE\) either started low in the morning and rose to a plateau (2 September), or stayed on a plateau (3 September), and declined with time later. On 9 and 10 September, canopy temperature at sunrise was either above the air dewpoint (9 September), indicating no dew, or very close to dewpoint (10 September), indicating possibly very light dew. On these two days (Fig. 5), measured \(WUE\) started high in the morning and declined continuously with time till noon. Taken together, the results for cotton on these four days are consistent with the idea that on mornings with dew, the measured \(WUE\) are anomalously low and do not reflect the true ratio of assimilation to transpiration. Therefore, it is argued that the prediction of \(WUE\) made with \(a\) as a variable depending on \(\Delta W\) worked fairly well for cotton even in the early morning, as judged by the good agreement with the measured values on 10 September (Fig. 5g) and the small under-prediction on 9 September (Fig. 5c). The apparent over-predictions in the early morning of 2 and 3 September (Fig. 4c, g) were due to the fact that measured \(WUE\) was anomalously low because of dew evaporation. On the other hand, the sweet corn data (Fig. 6) also showed morning plateau in measured \(WUE\), but the canopy and dewpoint data indicated either very light or no dew on the sweet corn on those two days. Other possible causes for the poor prediction of sweet corn \(WUE\) for the morning will be discussed later.

Overall, the measured \(WUE\) in the early morning and late afternoon were associated with greater uncertainties because of the limitations of the BREB+ technique and of the soil efflux estimation, and the probable complication caused dew evaporation. For the more middle part of the day, the uncertainty was also greater during periods of heavy clouds because of limitations of the soil efflux estimate and \(R_n\) measurement, already mentioned earlier.

**Simplifying steps in the prediction of long-term midday \(WUE\)**

In making the long-term prediction of variations in midday \(WUE\) over a part of the season for cotton, it was necessary to use two simplifying steps because of the lack of data on CO2 and water vapour pressure of the air surrounding the canopy on some days. One step was to assume that \(C_a\) did not change from day to day (\(C_{a,n}/C_{a,o}=1\)). Examining the \(C_a\) data (air CO2) in Figs 4 and 5, it is seen that at midday \(C_a\) varied only slightly (between 340 and 350 \(\mu\)mol mol\(^{-1}\)) over the four days. This turned out to be true for the other days when data were available, largely because the high CO2 concentration in the air, built up during some nights when there was inversion, had gradually depleted toward noon, and wind in Davis is usually higher than 1 m s\(^{-1}\) by noon, providing air mixing. For most middays \(C_a\) was within 3% of the average value. Hence, the assumption of midday \(C_a\) being invariant should not introduce substantial error on most days.

The other simplifying step was in the calculation of \(\Delta W\). Water vapour measured by the lower Bowen ratio unit was used in place of the weighted average water vapour measured by the multiport air sampling apparatus. The former, because it was taken at some height (about 0.3 m) above the canopy, would obviously be lower in value than the latter,
How well do the equations predict WUE?

Taking the limitations of the measurement methods and assumptions into account, it may be concluded that the paradigm equation worked surprisingly well in predicting the variations in canopy or stand WUE of cotton from moment to moment in the field (Figs 4, 5), and from one midday to the next over the long term (Fig. 7). There was a slight tendency, however, to underpredict (by 6% according to the regressions of data of 2, 3, and 10 September). The situations covered involved large variations in radiation, temperature, relative humidity, and wind, and small variations in Cₐ and foliage age. The equation, in spite of its simplicity, appears to be adequate to account for all these variations. True, the dependence of α on ΔW had to be incorporated; but it was done using a regression equation derived from data obtained on cotton grown in environment chambers, without any determination of α in the field. Using the same function for α, the ups and downs of WUE under fluctuating radiation caused by moving clouds was reasonably well predicted on one day (2 September, Fig. 4c), and less well predicted on another (9 September, Fig. 5c). How WUE may change between alternating sunny and cloudy periods is not intuitively obvious. The fact that equation 3 predicted many of the measured slight increases in WUE during the cloudy periods can be taken as positive evidence for this approach. It is important to note that radiation is not directly accounted for by the paradigm equations.

As this report is limited to irrigated conditions, questions may be raised on the validity of the equations for crops under water stress. In theory, the equations should be valid with or without stress of different kinds, including water stress (Hsiao, 1993), as long as the stress is not severe enough to cause extreme stomatal closure and the behaviour of α is known. As mentioned, α tends to remain constant under slowly imposed water stress (Wong et al., 1979), although it may decrease under fast developing water stress and increase under very severe water stress (reviewed by Hsiao and Jackson, 1999). Strictly speaking, our data do encompass some periods of modest water stress. As can be seen in Fig. 7b, toward the end the cotton had not been irrigated for up to 17 d (on day 122), yet the WUE predictions appear to be of similar accuracy as for the days very shortly after each irrigation. Also, it is well known that on warm and sunny days leaf water potential undergoes marked diurnal variations (from −0.1 to −1.3 MPa, for well-watered cotton in Davis), but the paradigm equation worked well over the daily cycle in spite of these changes in water status (Figs 4, 5). For the period depicted in Fig. 7, the extremes of mean leaf water potential measured at midday on some days were −0.61 MPa (on 107 DAP) to −1.45 MPa (on 102 DAP). Nonetheless, more direct studies of water-stress effects on the prediction made with the paradigm equations are needed.

Predicting crop water-use efficiency in the field
PAR and before a steady state is reached, calculated C_l often fluctuated, presumably reflecting a time lag in the adjustment of stomatal aperture relative to the adjustment in photosynthetic rate. In the field with PAR varying as well as the associated variations, especially in canopy temperature, such lags presumably also occur. Thus, the assumption of α changing with radiation only through the effect of radiation on ΔW and in strict accordance to the α versus ΔW equation used may be too simplistic to make good predictions for cotton when PAR fluctuated rapidly. A similar conclusion may be drawn regarding the assumption of constant α under fluctuating PAR for sweet corn.

In addition to the uncertainty regarding α when radiation fluctuated rapidly, there is the question of whether the PAR or temperature was too low in the early morning or late afternoon to cause α to deviate from the assumed values. With a couple of exceptions to be noted later, PAR was higher than 0.4 μmol m⁻² s⁻¹ for cotton and 0.5 μmol m⁻² s⁻¹ for sweet corn in the data presented. These levels should be high enough not to cause a substantial increase in α according to the data in Fig. 1b and d, obtained on plants grown in environment chambers. It is possible, however, that the crops in the field, exposed to maximal PAR much higher than in the chambers, may have a higher PAR threshold below which α begins to increase. A higher α (α_l) would yield a lower predicted WUE, as can be seen from equation 4. PAR did fall to 0.315 mmol m⁻² s⁻¹ at 07.55 h and to 0.344 mmol m⁻² s⁻¹ at 08.00 h for cotton on 2 September (Fig. 4a), and to 0.385 mmol m⁻² s⁻¹ around 09.00 h for sweet corn on 13 August (Fig. 6c). With PAR below the threshold, α most likely increased during these periods. Had higher values of α been used for the prediction, the predicted WUE would be lower than shown for those periods in the figures, matching better the measured WUE.

The much higher predicted WUE than measured WUE for sweet corn (Fig. 5) in the mornings on days when dew evaporation was not a likely factor could not be the result simply of low PAR causing higher α in the morning, because at similar PAR levels in the afternoon (Fig. 6a, c), there was no over-prediction (Fig. 6b, d). It is possible, however, that low temperature and low PAR interacted synergistically to cause increases in α in the morning. The lowest air temperature on those two days was 22.5 °C at 07.00 h (Fig. 6d) with canopy temperature at 21.2 °C. This is around the temperature threshold for α of L. divaricata (Björkman, 1981). However, the over-prediction of WUE lasted until 08.00 h or later on 12 August, when air temperature had reached 27–28 °C (Fig. 6b). It is unlikely that the temperature threshold for α could be so high, unless confounded by other factors. Clearly, there is a need to determine the α versus temperature function at different levels of PAR for sweet corn. Overall, it may be concluded that, with the possible exception of the early morning period for sweet corn, the paradigm equations worked well enough in making prediction of WUE under different environmental conditions for the major portion of the day.

The broader context

Global change in climate with the rising of CO₂ and other greenhouse gases has received much attention lately, and efforts have been devoted to the prediction of potential future changes in crop productivity and cropping systems under climate change scenarios (Rosenzweig and Parry, 1994; Tubiello et al., 1999). It has long been recognized that for much of the world where water is limiting, primary productivity of crops may be estimated simply from the amount of water available for transpiration, and the efficiency of water use for biomass production (Fisher and Turner, 1978). Some of the crop production models (Stöckle et al., 2003) are beginning to use this relationship as one of the ways to simulate crop productivity. Since biomass production is due mostly to the net accumulation of photosynthetic assimilates, ability to quantify the changes in photosynthetic WUE for different environment and climate change scenarios is crucial for this effort. It is well known that WUE of plants will improve under elevated CO₂, because transpiration is lessened due to reduced stomatal opening and photosynthesis is increased due to higher C_l efficted by higher C_a (Drake et al., 1997; Hsiao and Jackson, 1999). The data in Fig. 3 show that the paradigm equations worked well in predicting changes in WUE of single leaves for different levels of CO₂. In addition, the preliminary publication (Hsiao and Xu, 2000) demonstrated with limited data that the equations worked well in predicting quantitatively the changes in biomass WUE under elevated CO₂ for cotton grown in environment chambers. Additional biomass WUE data (TC Hsiao, Y Kosugi, L-K Xu, unpublished results) also show reasonably good predictions for soybean, sunflower, and bean under different levels of CO₂. Generally, many model simulations of future crop or forest productivity for the scenario of climate changes under higher CO₂ have incorporated the effects of temperature, humidity, and radiation well into the models based on fundamentals. But the effect of elevated CO₂ has usually been empirically based on experimental data and parameterization. An approach grounded in fundamental principles is needed to ensure the general applicability of such simulation models, allowing them to be used for widely different situations with a minimal amount of empirical experimentation. The paradigm equations, although needing further testing and verification, appear to have the potential to fulfill that role.

In addition to predicting and simulating WUE, the equations should prove to be useful as a framework in the analysis and integration of the results of diverse studies on WUE as affected by climate and elevated CO₂. A large number of such studies are available in the literature, but often with divergent results in need of reconciliation (Eamus, 1991; Morison, 1993; Hsiao and Jackson, 1999).
As equation 3 emphasizes, four factors, air CO₂ and water vapour pressure, foliage temperature, and the ratio of \( C_{\text{i}}/C_{\text{a}} \), are central in the determination of WUE. Usually, the information provided in such studies includes some but not all of these factors. Nonetheless, the equations provide a systematic means to assess quantitatively the impact of the factors for which information is available, and make estimates of the magnitude or range of the factors for which information is missing. In doing so, explanations may be found for the divergence in results, and faulty results due to errors in methods or in assumed environmental conditions may be identified.

Another aspect of this study with wide implications is the importance of stomatal response to humidity (more specifically, to \( \Delta W \), the difference in water vapour pressure or concentration between the leaf interior and the bulk air) and the associated changes in \( \alpha \). The humidity response has long been known in a wide range of species (Schulze and Hall, 1982). When stomata close partially under low humidity, photosynthesis and transpiration are both reduced, and usually their ratio (WUE) is improved compared with the situation had stomata not responded. Although this has been shown in studies on leaves in gas exchange chambers (Farquhar et al., 1980), it is difficult to obtain the type of data needed to demonstrate in the field for crop stands. Also, the extrapolation of gas exchange results on WUE to field situations is open to question because leaf temperature is normally kept artificially constant in the gas exchange chamber and the normal changes in leaf temperature and intercellular water vapour concentration (\( W_i \)) dictated by the principle of energy balance are circumvented (Hsiao and Jackson, 1999). Further, canopies with high LAI may be substantially decoupled from the atmosphere in contrast to the close coupling between the leaf and the air in gas exchange chambers, and hence transpiration from the canopy may be relatively insensitive to changes in conductance (Eamus, 1991; Jones, 1992). In the field data on cotton stands, however, the effect of humidity response on WUE can be readily seen with the help of equations 3 and 4. In Fig. 8, the measured WUE data of 10 September are again shown, but the predicted WUE are now calculated using the mean values for the period of 07.30 h to 08.30 h instead of the hour around noon as references. Hence, in Fig. 8a the predicted WUE is based on a constant and high \( \alpha \) (and therefore constant and high stomatal conductance) appropriate for the mean \( \Delta W \) of the early morning (07.30–08.30 h). As the day progressed, it is seen that WUE would have declined to values considerable lower (averaged 37% lower for the period of 13.00 to 17.00 h) than the measured WUE had stomatal conductance and \( \alpha \) remained unchanged. In Fig. 8b, it is seen that by incorporating the change in stomata and \( \alpha \) responses to \( \Delta W \), the predicted WUE is raised and agrees with the measured WUE throughout the day. This constitutes credible evidence for the importance of stomatal response to humidity and the associated change in \( \alpha \) in enhancing WUE of crop stands under conditions of high evaporative demand. On the other hand, there is an associated cost of reduced assimilation rate.

The importance of variations in \( \alpha \) with variations in \( \Delta W \) in improving WUE prediction is clear in all the cotton data, including the daily patterns under sunny or conditions of variable clouds (Figs 4, 5) and the long term trend (Fig. 7). This critical role of \( \alpha \) variation in determining WUE has two broader implications. One is the possible need to fine tune, according to the stomatal humidity response, the widely used crop coefficient approach in the estimation of crop ET for the purpose of irrigation scheduling. The other implication is in terms of canopy photosynthesis in the field. The paradigm equations were derived based on the tight linkage between CO₂ assimilation and transpiration. As may be deduced from equation 2, the equations can be arranged in terms of CO₂ assimilation (Hsiao, 1993; Hsiao and Jackson, 1999) and used to predict variations in canopy photosynthesis in the field where a number of environmental parameters vary naturally. The effects of stomatal response to humidity and the associated change in \( \alpha \) have been
complicated to deal with in quantifying photosynthesis, especially under field conditions (Bunce, 2003). The rearranged equations may provide a systematic framework to facilitate this quantification, or even serve as a part of simulation models.

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