

# A comparative study of mass and energy exchange rates over a closed C<sub>3</sub> (wheat) and an open C<sub>4</sub> (corn) crop: II. CO<sub>2</sub> exchange and water use efficiency

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## Abstract

Major differences exist between the photosynthetic and transpiration rates of C<sub>3</sub> and C<sub>4</sub> leaves as a result of biochemical and physiological factors. Whether or not differences between CO<sub>2</sub> and water vapor exchange rates of C<sub>3</sub> and C<sub>4</sub> species scale from leaf to field dimensions is poorly known. The aim of this work is to improve our understanding on how environmental, architectural and physiological variables affect the flux densities of CO<sub>2</sub> and water vapor over C<sub>3</sub> and C<sub>4</sub> crop stands during day and night periods. Experimental data were obtained over a closed wheat and an open corn stand using the eddy correlation method. Interpretation of the field measurements is aided by the use of a canopy photosynthesis/evaporation model.

The flux density of absorbed photosynthetically active radiation ( $Q_a$ ) had a disproportionate influence on CO<sub>2</sub> flux densities measured over a closed C<sub>3</sub> and an open C<sub>4</sub> crop. Variations in  $Q_a$  explained over 88% of the variance in daytime CO<sub>2</sub> flux densities,  $F_c$ . At night, canopy radiative temperature was the main environmental factor controlling the respiratory CO<sub>2</sub> efflux by the two crops.

Leaf area index and growth stage were the plant variables that affected  $F_c$  most. Incremental increases in leaf area index enhanced the corn crop's ability to absorb incident solar radiation and enlarged the corn's sink strength for CO<sub>2</sub>. Heading by the wheat caused rates of daytime CO<sub>2</sub> gains to decrease and rates of night-time CO<sub>2</sub> losses to increase.

Water use efficiency of the wheat crop improved as the absolute humidity deficit of the atmosphere decreased. Water use efficiency of the corn, on the other hand, was relatively insensitive to humidity deficits.

With regard to canopy CO<sub>2</sub> exchange and water use efficiency, differences in canopy structure between the wheat and corn overwhelmed physiological differences. The closed C<sub>3</sub> wheat crop assimilated CO<sub>2</sub> at a higher rate than the sparse C<sub>4</sub> corn canopy, even though corn uses a more efficient photosynthetic pathway. Consequently, water use efficiency of the corn was not greater than values measured over the wheat. Instead, water use efficiencies of the two crops were similar. The corn crop assimilated CO<sub>2</sub> at a lower rate than wheat because the corn's canopy quantum yield was lower and because its sparse canopy absorbed less photosynthetically active radiation than the closed wheat stand.

## 1. Introduction

Agricultural crops use either the C<sub>3</sub> or C<sub>4</sub> photosynthetic pathway to gain carbon. Over the years, a host of physiological studies have been conducted on

leaf photosynthesis, water use efficiency and stomatal conductances of  $C_3$  and  $C_4$  species (Jones, 1983; Pearcy and Ehleringer, 1984). Leaf photosynthetic rates and water use efficiencies of  $C_4$  species are greater than those of  $C_3$  species, while stomatal conductances of  $C_4$  species are less than those of  $C_3$  species (Jones, 1983; Pearcy and Ehleringer, 1984).

A farmer is more interested in the integrated performance of a standing crop than in the performance of its constituent leaves. Growers want to know what conditions allow a  $C_4$  crop to gain more carbon and lose less water than a  $C_3$  crop. To address these needs, agricultural scientists must be able to assess if or how physiological differences between  $C_3$  and  $C_4$  leaves scale from leaf to field dimensions.

Micrometeorological methods offer a non-intrusive means of studying canopy-scale gains and losses of carbon and water. Because of their non-intrusive attribute, micrometeorological methods have been a popular means of exploring daytime  $CO_2$  uptake and water losses of individual  $C_3$  or  $C_4$  crops, such as wheat and corn ( $C_3$ : wheat: Denmead, 1976; Anderson and Verma, 1986; Dunin et al., 1989;  $C_4$ : corn: Lemon, 1960, 1967; Uchijima, 1976; Desjardins, 1985; Held et al., 1990; McGinn and King, 1990). Comparative micrometeorological measurements of carbon and water exchange rates over  $C_3$  and  $C_4$  crops, however, are rare (Held et al., 1990; McGinn and King, 1990). This author is an advocate of comparative micrometeorological studies because they possess the potential to yield new and unexpected findings on the control of canopy-scale carbon and water exchange. Results from the studies by McGinn and King (1990) and Held et al. (1990) illustrate this point. Under benign environmental conditions, a  $C_4$  crop achieved greater rates of net carbon uptake than a  $C_3$  crop (Held et al., 1990; McGinn and King, 1990), as expected. Under non-ideal environmental conditions, there were cases when the integrated photosynthetic rate of a  $C_4$  crop was less than or equal to the photosynthetic rate of a  $C_3$  crop. One example involved the differential sensitivities of  $C_3$  and  $C_4$  photosynthesis to air temperature. When air temperature was cool ( $T_a$  less than  $7^\circ C$ ), canopy  $CO_2$  uptake rates of a  $C_4$  crop were less than  $CO_2$  uptake rates experienced by a  $C_3$  crop (McGinn and King, 1990).

A thought experiment provides another example of unexpected leaf to canopy scaling among  $C_3$  and  $C_4$  crops. Photosynthetic rates of  $C_3$  and  $C_4$  leaves are linear functions of photosynthetically active radiation (PAR) ( $Q_p$ ) when  $Q_p$  is less than  $100 \mu mol m^{-2} s^{-1}$  (Ehleringer and Bjorkman, 1977). Because the quantum yields of  $C_3$  and  $C_4$  leaves are similar (Ehleringer and Bjorkman, 1977), the integrated  $CO_2$  exchange rates of  $C_3$  and  $C_4$  crops should be equal when  $Q_p$  is less than the cited threshold and both canopies absorb the same amount of quanta. Such instances can occur when sun angles are low and both crops are immature and sparse.

Comparing daytime and nocturnal measurements of canopy  $CO_2$  exchange

enables an investigator to examine the relative roles of photosynthetic uptake and respiratory losses by crop canopies. Unfortunately, few nocturnal studies of CO<sub>2</sub> and water vapor exchange have been conducted using micrometeorological methods (wheat: Denmead, 1976; corn: Desjardins, 1985). The paucity of nocturnal CO<sub>2</sub> efflux data stems from the reliance of past micrometeorological studies on aerodynamic or energy balance, or flux-gradient techniques. Flux-gradient methods are susceptible to large errors at night because of low wind speeds or low radiation flux densities (Verma and Rosenberg, 1975). The eddy correlation technique is a micrometeorological method that does not suffer from the problems just identified. Until recently, experimentalists have been reluctant to employ expensive and fragile eddy correlation instrumentation at night (Anderson and Verma, 1986). Now, eddy correlation instrumentation is robust enough to allow continuous operation in the field.

From the above discussion, it is obvious that extrapolation of leaf scale differences between C<sub>3</sub> and C<sub>4</sub> species to the canopy dimension is not linear, nor straightforward. The goal of this paper is to bridge gaps in our knowledge about how environment, physiology, plant architecture and crop phenology interact to control the CO<sub>2</sub> and water vapor exchange rates of C<sub>3</sub> and C<sub>4</sub> crops during the day and night. To accomplish this goal, CO<sub>2</sub> and water vapor flux densities were measured over a closed C<sub>3</sub> crop (wheat) and an immature C<sub>4</sub> crop (corn). This paper presents and discusses the field measurements of CO<sub>2</sub> exchange rates and water use efficiency and uses a canopy photosynthesis/evaporation model, based on micrometeorological and physiological theory, to synthesize and interpret data.

## 2. Materials and methods

### 2.1. Site and crop characteristics

The field experiment was a component of the Boardman ARM Regional Flux experiment (Doran et al., 1992) and was performed on a 4500 ha farm near Boardman, OR (latitude 45° 40' N; longitude 119° 40' E). Wheat (*Triticum aestivum*) and corn (*Zea mays*) were planted on individual circular (800 m diameter) plots, of about 64 ha. The two fields were separated by about 7 km.

Wheat was planted on 15 February and was sown in 0.15 m wide rows. Corn was planted on 13 April and was planted in 0.75 m wide rows. Field measurements were made between 2 June (D153) and 20 June (D171) 1991.

The soil was sandy (Quincy soil series) and contained negligible soil organic matter (less than 0.5%). The soil's classification name is mixed, mesic, xeric, Torripsamments. Its bulk density was 1.4 g cm<sup>-3</sup>. Soil moisture was supplied

every 1–3 days by irrigation, so neither crop suffered from water deficits; the volumetric water content ranged between 0.1 and 0.2 cm<sup>3</sup> cm<sup>-3</sup> (Baldocchi, 1994).

Over the course of the experiment, the wheat crop was closed and green. Its phenological status passed through vegetative, heading and anthesis stages. The height of the wheat increased from 0.75 to 0.85 m and its leaf area index (LAI) increased from 2.7 to 3.3 during the experiment.

The corn was vegetative throughout the experiment, but its canopy architecture varied markedly with time. Qualitatively, the corn canopy varied from being sparse to nearly closed. Quantitatively, corn height increased from 0.35 to 0.75 m and its LAI changed from 1.3 to 3.0. Additional information on temporal variations in crop height and LAI is presented by Baldocchi (1994).

### *2.2. Eddy flux density measurements*

The eddy correlation method was used to measure flux densities of CO<sub>2</sub> and water vapor over both crops. CO<sub>2</sub> flux density measurements over the crop canopies represent the net difference between gains from leaf photosynthesis and losses from leaf, root, and soil respiration. Water vapor exchange rates are the sum of soil evaporation and plant transpiration rates. Negative flux densities symbolize uptake by the surface and positive values denote the loss of mass and energy by the crop.

In theory, flux densities of mass and energy between a crop and the atmosphere are proportional to the mean covariance between vertical velocity ( $w'$ ) and scalar ( $c'$ ) fluctuations. In practice, several conditions must be met before the eddy correlation method can be applied over a crop canopy. First, the site must be flat. Second, vertical velocity must be measured normal to the surface streamlines. Third, the crop should be homogeneous and extensive. Fourth, environmental conditions need to be steady. Finally, no intermediate sources or sinks can exist for the scalar under investigation (see Baldocchi et al., 1988). These cited prerequisites were met through proper site selection, experimental design and data processing.

Closure of the surface energy balance is the ultimate test of any micro-meteorological flux measurement method. The surface energy balance was closed within 5%, thereby confirming the validity of the method; information on energy balance closure is presented in the companion paper (Baldocchi, 1994).

### *2.3. Instrumentation and data acquisition*

Instrument masts were located on the north end of each field. Measurement sensors were placed 4.0 m above the ground, so that adequate fetch (up to 800 m) was achieved when the wind direction was between 120 and 240 degrees.

Three-dimensional, orthogonal wind velocities ( $u$ ,  $v$  and  $w$ ) and virtual temperature ( $T_v$ ) were measured with a sonic anemometers (Applied Technology, model SWS-211/3K, Boulder, CO, USA). The pathlength between transducers was 0.15 m. Transducer shadowing effects were corrected using sensor software.

Water vapor and CO<sub>2</sub> concentrations were measured with an open-path infrared absorption spectrometer. Details and performance characteristics of the spectrometer are discussed by Auble and Meyers (1992). To aid the reader, the salient characteristics of this instrument are reviewed. The infrared beam was reflected three times between mirrors, creating an 0.80 m absorption path. The response time of the sensor was less than 0.1 s and its noise was less than 300  $\mu\text{g m}^{-3}$ . CO<sub>2</sub> calibration was performed with three standard CO<sub>2</sub> gases mixed in air. Calibration coefficients were steady, varying less than  $\pm 3\%$  through the experiment. Water vapor calibration was referenced to a wet-bulb psychrometer.

Voltages from the sonic anemometer and infrared spectrometer were sampled and digitized at 10 Hz by an analog to digital converter. Digital signals were then transmitted from the field to a personal computer. The computer software transformed the data, computed flux covariances, stored raw data and displayed raw sensor signals on the video display for real-time quality control. A summary of the software data processing follows. The eddy flux measurement system captured most flux-containing eddies by sampling the sensors rapidly and by averaging velocity-scalar fluctuation products for 30 min; this averaging period was sufficient for second moments based on criteria established by Sreenivasan et al. (1978). Turbulent fluctuations were computed as the difference between instantaneous and mean quantities. Mean values were determined, in real-time, using a digital recursive filter with a 400 s time constant. The coordinate system of the three orthogonal wind vectors was rotated to obtain a mean vertical velocity of zero and to orient the longitudinal component ( $u$ ) along the mean wind. Scalar flux covariances were computed in reference to the new coordinate system. Virtual temperature heat flux densities were converted to sensible heat flux densities using algorithms described by Kaimal and Gaynor (1991). The infrared spectrometer measures fluctuations in scalar density, not mixing ratio. Consequently, CO<sub>2</sub> and water vapor flux densities were corrected for density fluctuations imposed by temperature and humidity fluctuations (Webb et al., 1980). Finally, data were rejected when winds were not coming from the field, when it was raining or when the irrigation system passed through the upwind fetch.

#### *2.4. Ancillary meteorological and plant measurements*

Soil heat flux was measured at each site. Three soil heat flux plates (REBS model HFT-3, Seattle, WA, USA) were buried 0.08 m below the surface. Soil

heat flux measurements were corrected for soil heat storage in the upper soil layer. Soil heat storage was calculated by measuring the time rate of change of the mean soil temperature ( $T_s$ ) profile and using the Fowier equation for soil heat transfer (Campbell, 1977). Soil temperature was measured with a thermocouple probe. Sensors were spaced logarithmically at 0.02, 0.04, 0.08, 0.16 and 0.32 m below the surface.

Shortwave radiation ( $R_s$ ), photosynthetic photon flux density ( $Q_p$ ) and the net radiation balance ( $R_n$ ) were measured above each crop with an Eppley pyranometer (model 0-48, Newport, RI, USA), a LICOR quantum sensor (model LI-190S, Lincoln, NA, USA) and a Swissteco net radiometer (Model S-1, Melbourne, Australia), respectively. An infrared radiometer (Everest Interscience, model 4000, Fullerton, CA, USA) sensed the radiative temperature of each canopy. The radiometer pointed downward at a 45 degree angle above nadir. Air temperature and relative humidity were measured with appropriate sensors (Campbell Scientific, model 207, Logan, UT, USA). Wind speed and direction were measured with a wind monitor (RM Young, model 05701, Traverse City, MI, USA). Ancillary meteorological variables were sampled at 1 Hz with a Campbell Scientific (model CR-21x, Logan, UT, USA) data logger and the data were averaged over 30 min periods.

Absorbed photosynthetic photon flux density ( $Q_a$ ) was computed as the difference between incoming ( $Q_I$ ), reflected and transmitted ( $Q_T$ ) components (Hipps et al., 1983)

$$Q_a = Q_I(1 - \alpha_c - Q_T + \alpha_s)$$

$$Q_T = \exp\left(\frac{-0.5L}{\sin\beta}\right) \quad (1)$$

where  $\beta$  is the solar elevation angle and  $L$  is LAI. The PAR transmission computations assumed that each canopy had a spherical leaf inclination angle distribution (Ross, 1981). Computations of PAR absorption assumed that wheat albedo ( $\alpha_c$ ) equalled 0.05 (Denmead, 1976; Ross, 1981). Albedo of the sparse corn crop was assumed to be a function of LAI (Uchijima, 1976). Using an algorithm reported by Uchijima (1976), corn albedo values decreased from 0.064 to 0.052 as LAI increased from 1.3 to 3.0. Soil albedo ( $\alpha_s$ ) was assigned a value of 0.3 (Campbell, 1977).

Stomatal resistances ( $r_s$ ) of the wheat and corn leaves were measured with a LICOR steady-state porometer (model LI-1600, Lincoln, NA, USA). Wheat and corn leaves are amphistomatous, so stomatal measurements were made on the upper and lower sides of leaves. Leaf resistances were computed by combining the upper and lower measurements in parallel. Typically, six to eight sunlit leaves were studied during the sampling period. This sampling strategy was limited by the unavailability of laborers. It is preferable to measure  $r_s$  in proportion to the contribution of sunlit and shaded leaves at

Table 1

A summary of submodels and literature sources used to develop the canopy micrometeorology model (CANWHT) for computing CO<sub>2</sub> exchange fluxes densities over wheat. The model divides the canopy into 30 layers. Details on the model are provided in Baldocchi (1992)

Submodel	Attributes	Reference
Environmental inputs	Time, photosynthetic photon flux density, air and soil temperature, humidity, wind speed	
Photosynthesis/ respiration model	Biochemical/physiological	Farquhar et al. (1980)
Stomatal conductance model	Dependent on photosynthesis, relative humidity and [CO <sub>2</sub> ]	Collatz et al. (1991)
Radiative transfer model	Random spatial and spherical leaf angle distributions	Norman (1979)
Turbulent transfer model	Lagrangian random walk model	Thomson (1987)
Surface energy balance model		Bristow (1986)
Photosynthesis parameters		Kreidemann and Anderson (1990)
Stomatal conductance parameters	$g_s = g_1 Arh/C_s + g_0$ ; $g_1 = 10, g_0 = 0.01 \text{ mol m}^{-2} \text{ s}^{-1}$	Collatz et al. (1990)
Soil/root respiration parameters		Rochette et al. (1991)

various levels in the canopy. In view of the limited sampling strategy these data are only used as an index of potential physiological control by the plants and to derive leaf model parameters.

### 2.5. Modelling canopy photosynthesis and evaporation

A canopy photosynthesis and evaporation model (CANWHT) is used in this paper to calculate and interpret CO<sub>2</sub> and water flux densities measured over the crops. The model is based on micrometeorological, biochemical and physiological theory. Computations of water vapor and CO<sub>2</sub> flux densities were made by linking: 1) a Lagrangian random-walk, turbulent diffusion model; 2) a Poisson radiative transfer model; 3) a C<sub>3</sub>, leaf photosynthesis model; 4) a stomatal conductance model; and 5) a leaf energy balance model. Attributes of the canopy photosynthesis and evaporation models are summarized in Table 1. A complete description and test of the model is presented by Baldocchi (1992). The original model was developed for a soybean canopy and has been modified to consider the attributes of a wheat canopy.

The model, CANWHT, computes stomatal conductance differently from the original soybean model. Present calculations of stomatal conductance are based on the algorithm of Collatz et al. (1991). This algorithm links stomatal conductance to leaf photosynthesis, leaf relative humidity and leaf surface CO<sub>2</sub> concentration.

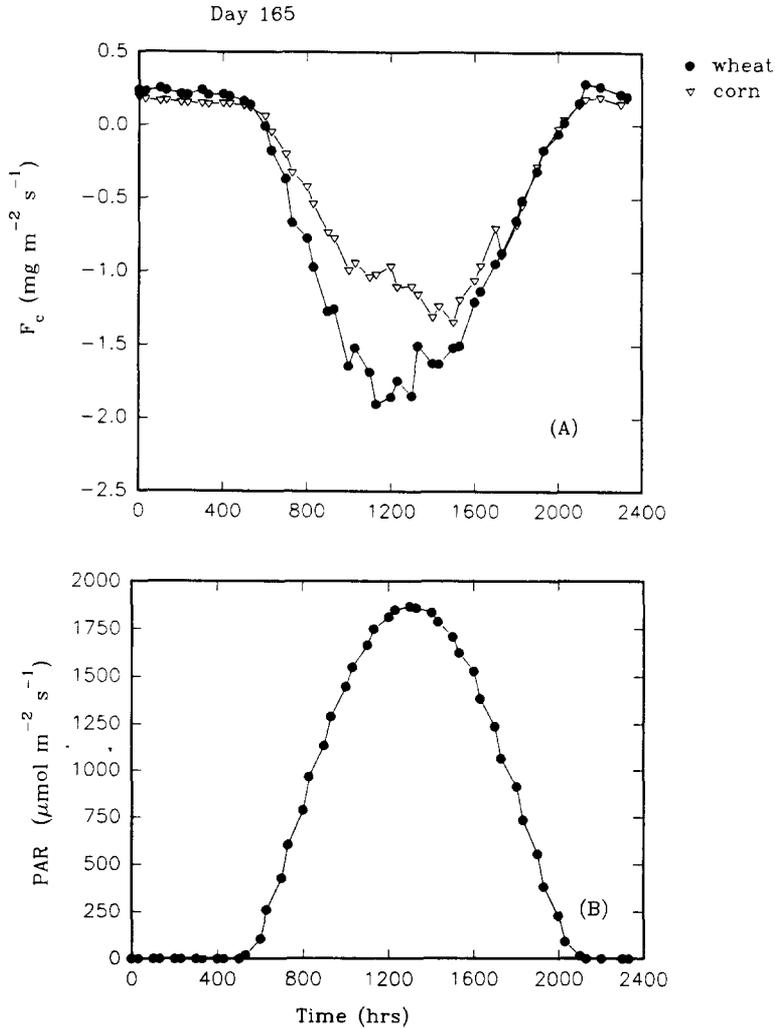


Fig. 1. (a) Diurnal variation of canopy  $\text{CO}_2$  flux densities ( $F_c$ ) measured over a closed wheat and an open corn canopy. (b) Diurnal variation of incident PAR. These data are from a typical clear day (Day 165) with moderate temperatures ( $10\text{--}20^\circ\text{C}$ ) and brisk winds ( $u > 4 \text{ m s}^{-1}$ ). The leaf area indices of the wheat and corn were about 3.0 and 1.8, respectively.

### 3. Results

#### 3.1. Canopy $\text{CO}_2$ exchange rates

##### 3.1.1. Diurnal patterns

Diurnal patterns of canopy  $\text{CO}_2$  flux densities ( $F_c$ ) and incident photosynthetic photon flux density ( $Q_p$ ) are shown in Figs. 1(a) and 1(b), respectively, for the wheat and corn crops. This figure presents typical data from a clear day

with moderate air temperature (air temperature ranged between 10 and 20°C) and brisk winds ( $u$  less than 4 m s<sup>-1</sup>). Both crops gained carbon between 06:30 and 20:00 h and lost carbon during the remainder of the day.

The temporal courses and magnitudes of  $F_c$  measured over the wheat and corn crops differed distinctly. During sunlit hours, CO<sub>2</sub> flux densities measured over the wheat canopy were in phase with the daily trend of  $Q_p$ . The daytime trend for both variables was parabolic and peaked near noon. Over the corn crop, CO<sub>2</sub> flux densities lagged the morning trend of  $Q_p$  and peaked 3 h after  $Q_p$  peaked. Larger CO<sub>2</sub> flux densities ( $F_c$ ) were observed over the closed wheat canopy until mid-afternoon, even though wheat uses the less efficient C<sub>3</sub> photosynthetic pathway. As mid-afternoon passed and evening approached, CO<sub>2</sub> flux densities measured over the two crops converged and became nearly equal. During the night, CO<sub>2</sub> efflux densities from the crops were invariant with time and the wheat canopy lost CO<sub>2</sub> at a slightly greater rate than the corn crop.

Maximal rates of CO<sub>2</sub> uptake approached  $-2.0 \text{ mg m}^{-2} \text{ s}^{-1}$  ( $-45 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) over the wheat stand and  $1.5 \text{ mg m}^{-2} \text{ s}^{-1}$  ( $-34 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) over the corn crop. Nocturnal CO<sub>2</sub> efflux rates from the two crops ranged between 0.15 and 0.2 mg m<sup>-2</sup> s<sup>-1</sup> ( $3.4\text{--}4.5 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). These efflux densities were about 10% of peak daytime CO<sub>2</sub> uptake rates.

Daytime CO<sub>2</sub> flux densities measured over the wheat canopy compare favorably with maximum flux densities measured over other closed wheat crops (Puckridge, 1971; Dunin et al., 1989; Wall and Kanemasu, 1990; Whitfield, 1990; Gent and Kiyomoto, 1992). Peak CO<sub>2</sub> flux densities of the wheat crop also approach the upper limit observed for C<sub>3</sub> field crops in toto (Mooney and Field, 1989). Such high rates of CO<sub>2</sub> exchange were possible because neither water nor nitrogen was limited and because benign environmental conditions were encountered during the experiment.

Measurements of peak  $F_c$  over the corn canopy agree with data from partial corn canopies (Held et al., 1990). However, maximum  $F_c$  values from the open corn stand are smaller than data from studies over closed corn canopies. CO<sub>2</sub> flux densities measured over closed corn canopies are often twice the values reported here (Desjardins, 1985; Jones et al., 1986); they can approach  $-3 \text{ mg m}^{-2} \text{ s}^{-1}$  ( $-68 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) (Lemon, 1960, 1967; Uchijima, 1976).

Integration of diurnal CO<sub>2</sub> exchange curves yields information on net CO<sub>2</sub> uptake and growth rates of a crop canopy (Bugbee and Monje, 1992). Daily integration of the  $F_c$  measurements generated values of 29.0 and 49.1 g(CO<sub>2</sub>) m<sup>-2</sup> day<sup>-1</sup> for the corn and wheat crops, respectively. These integrated values of  $F_c$  exceed data from other micrometeorological studies. For example, Denmead (1976) reported 25.1 g m<sup>-2</sup> day<sup>-1</sup> for the daily CO<sub>2</sub> exchange of a closed wheat stand. Desjardins (1985) measured daily rates of CO<sub>2</sub> uptake between 10 and 12 g m<sup>-2</sup> day<sup>-1</sup> over a sparse corn crop.

The daily CO<sub>2</sub> exchange measured over the wheat, while large, was much

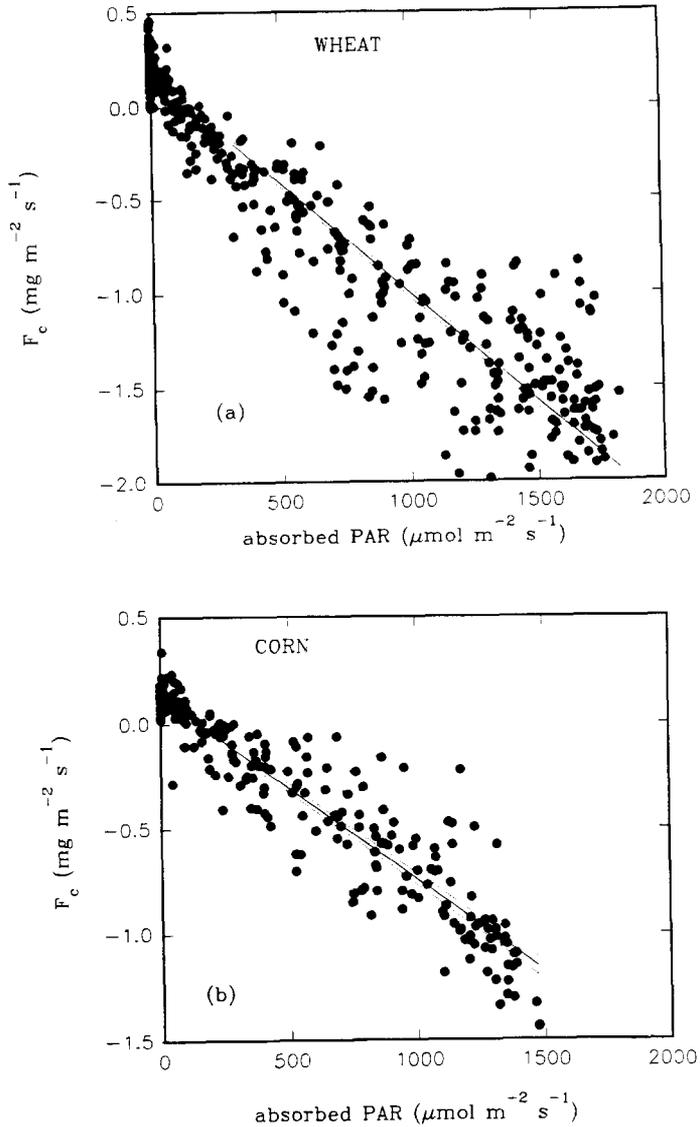


Fig. 2. The relationship between canopy CO<sub>2</sub> flux density ( $F_c$ ) and absorbed PAR for a closed wheat (a) and an open corn (b) stand. These data encompass a wide range of solar energy, temperature, wind and humidity and growth stage conditions.

smaller than its potential maximum. Bugbee and Monje (1992) cultivated wheat in an environmental chamber, grew it in a soil with optimal moisture and nutrients, and exposed the crop to a fourfold input of summertime PAR. Under these ideal conditions, daily CO<sub>2</sub> uptake exceeded 100 g m<sup>-2</sup> d<sup>-1</sup>!

Table 2

Statistics for linear regression of absorbed photosynthetically active radiation ( $Q_a$ ) on canopy  $\text{CO}_2$  flux density. The intercept,  $a$ , is expressed in units of  $\text{mg m}^{-2} \text{s}^{-1}$  and the slope,  $b$ , is expressed in units of  $\mu\text{g} (\text{CO}_2) \mu\text{mol} (\text{quanta})$ .  $r^2$  is the coefficient of determination. Quantum yield is the slope between  $\text{CO}_2$  uptake rates and absorbed PAR, in molar units (moles  $\text{CO}_2$ ) moles (quanta) $^{-1}$ . The  $Q_a$  compensation point is defined as the absorbed photon flux density when  $\text{CO}_2$  flux density equalled zero. Regressions for the corn are based on 239 samples. Regressions for the wheat crop involved 544 data points

Case	Intercept	Slope	$r^2$	Quantum yield	$Q_a$ at $F_c = 0$
$F_c$ , corn	0.137	-0.95	0.882	0.021	146
$F_c$ , wheat	0.162	-1.15	0.906	0.026	141

### 3.1.2. Photosynthetically active radiation

From an energetic standpoint, leaf photosynthesis is a non-linear function of absorbed PAR (Jones, 1983). On a canopy scale a different relationship held between  $\text{CO}_2$  uptake rates and absorbed PAR. Canopy  $\text{CO}_2$  exchange rates of the wheat and corn crops were linear functions of absorbed photosynthetic photon flux density,  $Q_a$  (Fig. 2). Regression statistics are presented in Table 2 and they reveal that 88–90% of the variation in  $\text{CO}_2$  flux densities ( $F_c$ ) was caused by variations in  $Q_a$ .

Residual scatter in Fig. 2 was a result of a host of physiological and micrometeorological factors. Simultaneous variations in air and soil temperature, humidity and wind speed influence  $F_c$  independently of  $Q_a$  by altering soil respiration, through the soil's energy balance, and by modifying leaf photosynthesis and respiration through stomatal conductance, enzyme kinetics and leaf boundary layer conductances. This point is illustrated in by model calculations of the relationship between  $F_c$  and  $Q_a$ , driven by environmental conditions encountered over the course of Day 165 (Fig. 3). Measurements of  $\text{CO}_2$  flux densities also have finite sampling errors, which can contribute to the residual scatter observed in Fig. 2. Under the best of conditions, intermittent turbulence can cause 10% run-to-run variation in flux covariances (Sreenivasan et al., 1978).

The slope between  $\text{CO}_2$  uptake rates and absorbed flux density of PAR defines the quantum yield (Ehleringer and Bjorkman, 1977). Corn had a canopy quantum yield of 0.021 moles  $\text{CO}_2$  per mole of quanta, while the canopy quantum yield of wheat was 0.026 moles  $\text{CO}_2$  per mole of absorbed quanta (Table 2). For comparison, quantum yields of  $\text{C}_3$  and  $\text{C}_4$  leaves are similar and range between 0.052 and 0.053 moles  $\text{CO}_2$  per mole of absorbed quanta (Ehleringer and Bjorkman, 1977). Two factors explain why the crops had lower quantum yields than leaves. First, canopy  $\text{CO}_2$  exchange rates encompass additional losses of  $\text{CO}_2$ , via soil and root respiration. Second, quantum yields of leaves are derived from the linear portion of the photosynthesis- $Q_a$  relationship, while quantum yields of canopies are derived from leaves, whose photosynthesis is saturated with respect to absorbed PAR.

Wheat D165

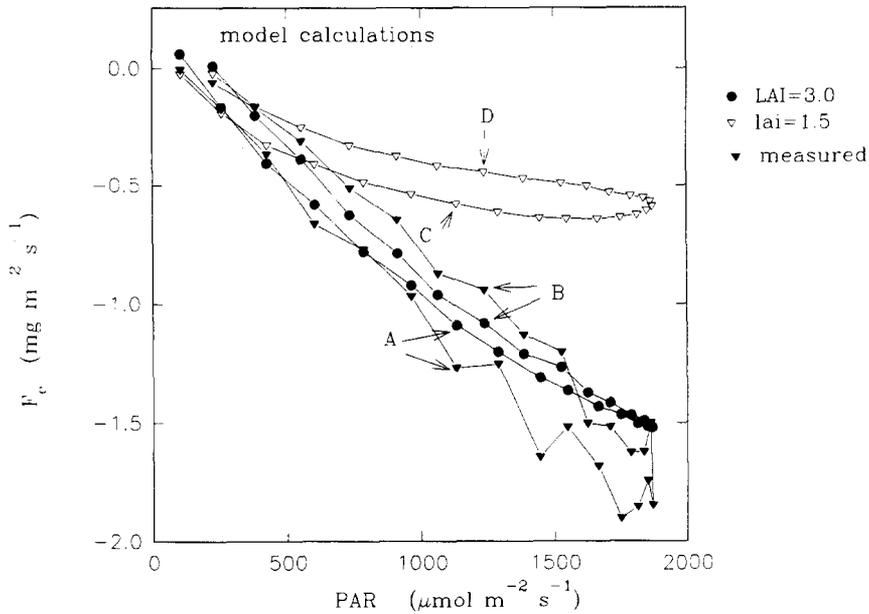


Fig. 3. Calculations of the relationship between canopy  $\text{CO}_2$  flux densities and incident PAR ( $Q_p$ ) for hypothetical wheat canopies with leaf area indices equal to 3.0 and 1.5. The calculations are based on data from Day 165. For cases A and C, time was 09:00 h, air temperature was  $13.2^\circ\text{C}$ , wind speed at 4 m was  $5.9 \text{ m s}^{-1}$  and  $\rho_v$  was  $7.8 \text{ g m}^{-3}$ . For cases B and D, time was 17:00 h, air temperature was  $20.7^\circ\text{C}$ , wind speed at 4 m was  $5.0 \text{ m s}^{-1}$  and  $\rho_v$  was  $7.5 \text{ g m}^{-3}$ . Calculations of canopy photosynthesis ( $\text{mg m}^{-2} \text{ s}^{-1}$ ), soil/root respiration ( $\text{mg m}^{-2} \text{ s}^{-1}$ ) and soil temperature (C) are listed in the following table:

Case	Canopy photosynthesis	Soil/root respiration	Soil temperature
A	1.45	0.198	14.9
B	1.58	0.333	21.7
C	0.79	0.229	16.8
D	0.90	0.460	26.3

The capacity of a plant canopy to capture solar energy and convert this energy into carbohydrate is described by its photosynthetic energy conversion efficiency (Bugbee and Monje, 1992). Efficiencies of  $\text{CO}_2$  acquisition and conversion equalled 2.51 and 1.98% for the wheat and corn crops, respectively; these efficiencies were computed on the assumption that 1 mole of carbohydrate equals 479 kJ of energy (Bugbee and Monje, 1992). For comparison, other studies report that photosynthetic conversion efficiencies of corn range between 2.75 and 3% and photosynthetic efficiencies of wheat range between 1.2 and 1.93% (Denmead, 1966, 1969; Lemon, 1967).

The photosynthetic energy conversion efficiencies observed for the wheat and corn crops underlie theoretical estimates for  $C_3$  and  $C_4$  plant stands growing under natural conditions. For instance, Beadle and Long (1985) calculated that photosynthetic energy conversion efficiencies range between 3.7 and 4.4% for  $C_3$  plant stands and range between 5.0 and 5.8% for plant stands of  $C_4$  species. Furthermore, the measured efficiencies reported in this document do not approach optimal or maximal photosynthetic efficiencies. Optimal efficiencies range between 14 and 17% (Lemon, 1967; Bugbee and Monje, 1992) and maximal efficiencies equal 34% (Beadle and Long, 1985; Bugbee and Monje, 1992). Improving practical photosynthetic efficiencies of crops to optimal levels remains a challenge for agronomists and geneticists.

### 3.1.3. Leaf area index

LAI has two effects on  $CO_2$  exchange rates of a plant canopy. First, leaf area controls the amount of PAR that is absorbed and available to a plant canopy for photosynthesis (Hodges and Kanemasu, 1977; Hipps et al., 1983). Second, leaf area is linked, theoretically, to the vegetation's diffusive source/sink strength, which in turn regulates the mass and energy exchange rates of a plant canopy (Finnigan and Raupach, 1987).

Field measurements documented that more PAR ( $Q_p$ ) transmitted through the sparse corn crop than through the closed wheat stand. The transmission of  $Q_p$  ( $Q_T$ ) through the corn crop ranged between 45 and 50% while  $Q_T$  through the wheat stand was less than 3% (Baldocchi, 1994).

Consequently, the corn canopy absorbed less PAR than the wheat crop under identical  $Q_p$  loads (see Eq. 1). Because canopy  $CO_2$  uptakes rates were a linear function of  $Q_a$  (Fig. 2), differences in  $Q_a$  explain, partly, why the sparse corn crop assimilated  $CO_2$  at a lower rate than the wheat crop, on a ground area basis.

Biases between the integrated  $CO_2$  sink strength of the corn and wheat crops also arise from differences in leaf area. This bias is investigated by comparing  $F_c$  (from a confined range of  $Q_a$ : 1000–1300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) against LAI. Figure 4 shows that the greater LAI of the wheat canopy helped it to overcome its biochemical handicap and assimilate  $CO_2$  at a greater rate than the sparse corn canopy, on a ground area basis.

As the growing season progressed, gradual increases in leaf area improved the corn crop's ability to assimilate  $CO_2$ . A 57% increase of the corn's LAI (LAI increased from 1.4 to 2.2 between Days 154 and 165) caused  $F_c$  to more than double (the magnitude of  $F_c$  increased from  $-0.53$  to  $-1.23 \text{ mg m}^{-2} \text{s}^{-1}$ ).  $CO_2$  exchange rates over the wheat canopy, on the other hand, were more or less independent of LAI variations through the duration of this study.

### 3.1.4. Phenology

Because the temporal increases in  $CO_2$  flux densities over corn were dis-

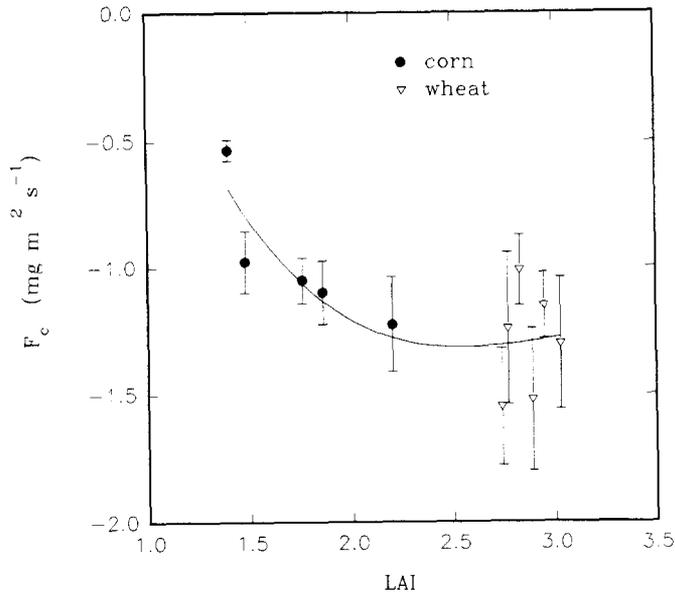


Fig. 4. The relationship between canopy  $\text{CO}_2$  flux density and LAI. Data were obtained from periods when the flux density of absorbed PAR were similar;  $Q_a$  was confined to the range between 1000 and 1300  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

proportional to temporal changes in LAI, one can argue that other controlling processes may have been at work. Two factors can be identified readily. First, the photosynthetic capacity of corn leaves change with age (Pattey et al., 1991). Second, temporal changes in canopy architecture can cause canopy assimilation and soil/root respiration rates to diverge as leaf area increases. This divergence will occur if canopy closure reduces the soil energy balance and thereby cause soil temperatures and soil/root respiration to be lower (Buyanovsky et al., 1986; Rochette et al., 1991). Experimental data prove

Table 3

Soil temperature profiles measured simultaneously under the closed wheat and open corn canopies. These data are from noon on Day 159. The leaf area indices of the wheat and corn crops were 2.8 and 1.5, respectively

Soil depth	Wheat	Corn
$z$ (cm)	Soil temperature (C)	Soil temperature (C)
2	21.4	25.49
4	19.68	24.22
8	17.54	21.95
16	15.71	19.7
32	15.32	18.81
$1/Z \int_0^z T_{\text{soil}}(z) dz$	16.34	20.18

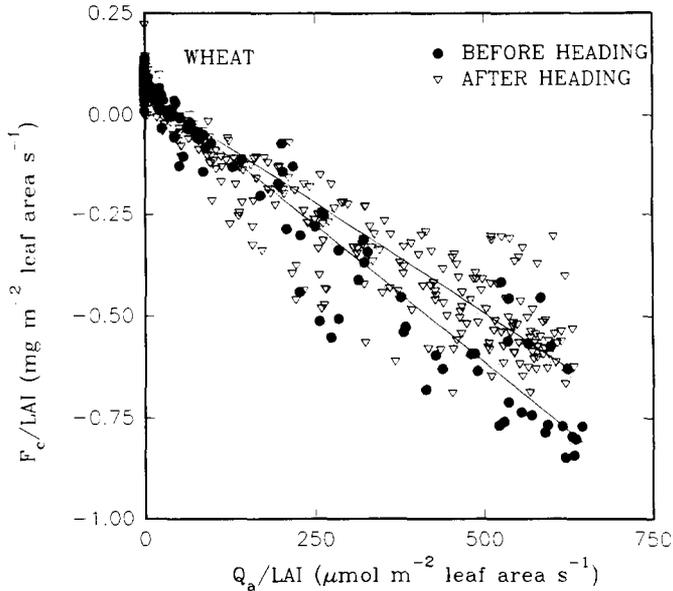


Fig. 5. The relationship between canopy  $\text{CO}_2$  flux density ( $F_c$ ) and absorbed PAR ( $Q_a$ ) for a closed wheat stand during pre- and post-heading vegetative stages. Both variables are normalized by LAI.

that soil temperatures were cooler under the closed canopy than under the sparse one. When environmental forcing was similar mean soil temperature, integrated between 0 and 32 cm, was  $3.84^\circ\text{C}$  lower at midday under the closed wheat canopy than under the sparse corn canopy (Table 3). Model calculations also support this hypothesis. The ratio between canopy photosynthesis and soil/root respiration flux densities was calculated to range between 4.75 and 7.3 under a closed crop stand ( $L = 3.0$ ) and to range between 1.96 and 3.45 under a sparse crop stand ( $L = 1.5$ ); calculations were based data presented in Fig. 3. Although these theoretical calculations support my hypothesis, the reader must recognize that these calculations are based on a simplistic, temperature-dependent root respiration model. Root biomass multiplies as the crop grows, so root maintenance respiration must increase accordingly (Jones, 1983; Buyanovsky et al., 1986). Greater maintenance respiration will counteract, to some degree, the down regulation in soil/root respiration rates that would otherwise occur as canopy closure modifies the soil energy balance and diminishes soil temperature.

Most seasonal studies on wheat photosynthesis conclude that seasonal changes in  $F_c$  are a result of varying leaf area (Puckridge, 1971; Puckridge and Ratkowsky, 1971; Dunin et al., 1989; Wall and Kanemasu, 1990). Other scientific evidence indicates that phenological growth stage impacts canopy  $\text{CO}_2$  flux densities of wheat independently of LAI (Hodges and Kanemasu, 1977; Gent and Kiyomoto, 1992). Data obtained from this experiment sup-

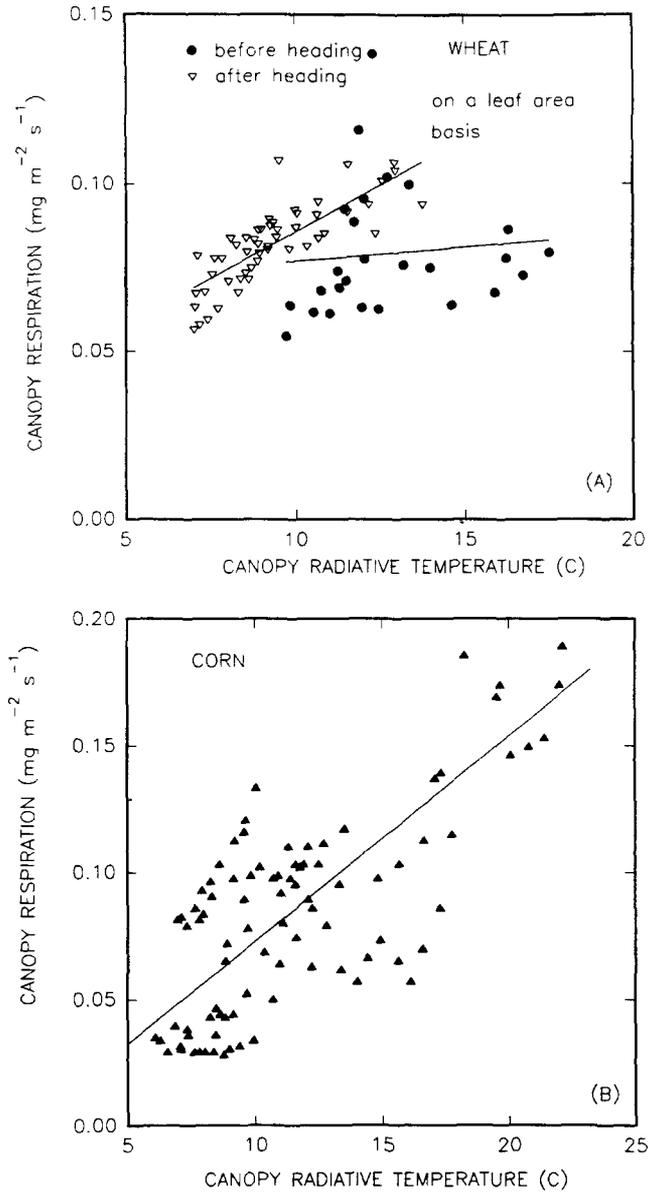


Fig. 6. The relationship between nocturnal  $\text{CO}_2$  flux density, normalized by LAI ( $F_c/\text{LAI}$ ), and canopy radiative temperature for a closed wheat stand, during pre- and post-heading vegetative stages (a) and a sparse corn crop (b). The nocturnal measurements of canopy  $\text{CO}_2$  flux density represent respiratory losses of  $\text{CO}_2$  by the crop, roots and soil. Data are from windy periods when the canopy aerodynamic resistance was less than  $50 \text{ s m}^{-1}$ . This selection criterion was used to minimize measurement uncertainties that occur when winds were light and unsteady.

port the observations of Gent and Kiyomoto (1992) and Hodges and Kanemasu (1977). Figure 5 shows that the slope of the relationship between canopy CO<sub>2</sub> flux density and  $Q_a$  (normalized by LAI) changed significantly after the wheat headed. Before heading the slope of the relationship between  $F_c/LAI$  and  $Q_a/LAI$  was  $-1.35 \mu\text{g}(\text{CO}_2) \mu\text{mol}(\text{quanta})^{-1}$  and after heading it was  $-1.09 \mu\text{g}(\text{CO}_2) \mu\text{mol}(\text{quanta})^{-1}$ . The timing of this phenological switch agrees with data from Hodges and Kanemasu (1977). However, this phenological switch occurs earlier than the observations of Gent and Kiyomoto (1992), who report that  $F_c$  becomes reduced between the anthesis and grain fill stages.

### 3.1.5. Canopy dark respiration

Canopy respiration rates consist of CO<sub>2</sub> losses from plant, root and soil components. Here, nocturnal measurements of CO<sub>2</sub> flux densities are used to investigate the control of environmental and phenological variables on canopy respiration.

Theoretically, crop respiration rates increase with temperature in an exponential manner (Collatz et al., 1991). Experimentally, respiration flux densities of the wheat canopy (normalized by LAI) were functions of the canopy's radiative temperature and its growth stage (Fig. 6(a)). Before heading, the wheat canopy respiration rates were independent of canopy's radiative temperature, whereas after heading canopy respiration rates were sensitive to radiative temperatures. These results are supported by data from Denmead (1976), who also observed that respiration rates of wheat increased markedly after heading. This increase in respiration rates, after heading, seems to explain the coincident decrease in canopy CO<sub>2</sub> flux densities, noted in Fig. 5.

Respiration flux densities from the corn canopy were also functions of the canopy radiative temperature (Fig. 6(b)). It is impossible to comment on whether corn respiration rates changed with growth stage because the corn was vegetative throughout this experiment.

A functional relationship between canopy respiration rates and temperature can be defined from the Arrhenius equation

$$\ln \frac{k_2}{k_1} = \frac{E_a}{R} \left( \frac{1}{T_1} - \frac{1}{T_2} \right) \quad (2)$$

where  $k_1$  and  $k_2$  are canopy respiration flux densities at absolute temperatures  $T_1$  and  $T_2$ ,  $E_a$  is the activation energy and  $R$  is the universal gas constant. Estimates of activation energy ( $E_a$ ) quantify the sensitivity of canopy respiration rates to temperature. After heading, canopy CO<sub>2</sub> uptake rates of wheat (normalized by LAI) increased from 0.058 to 0.116 mg m<sup>-2</sup> s<sup>-1</sup> as canopy radiative temperature increased from 7 to 15°C. This temperature response corresponds to an activation energy of 58 089 J mol<sup>-1</sup> K<sup>-1</sup>. Corn canopy

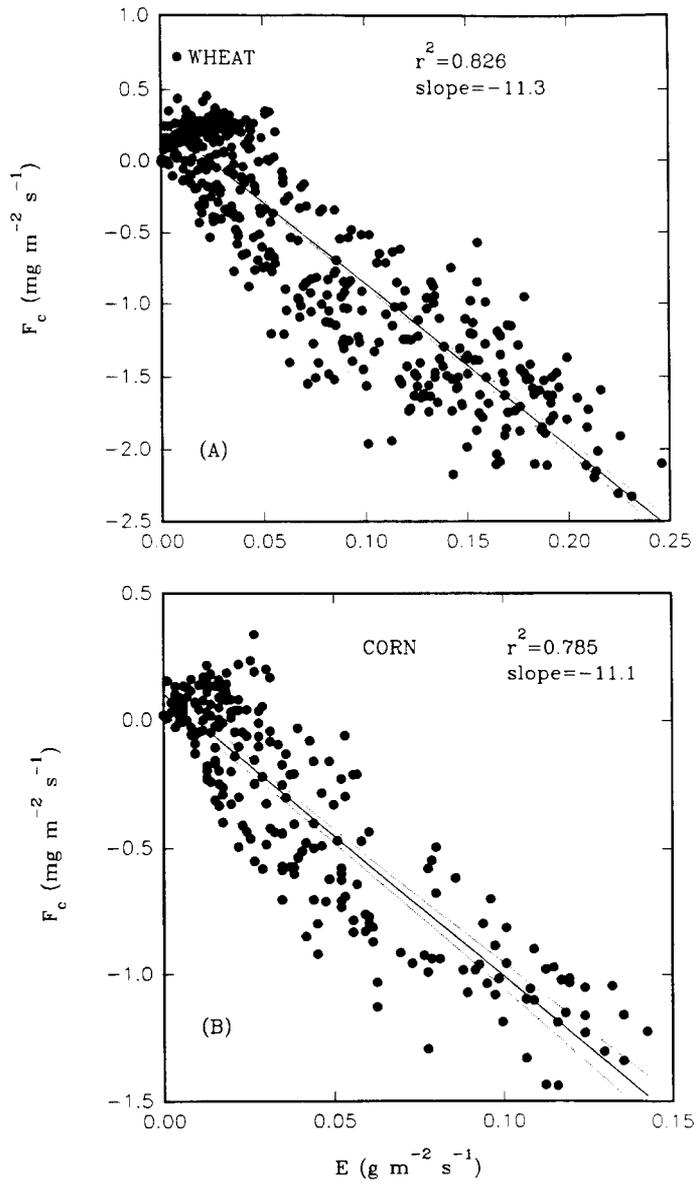


Fig. 7. A comparison between canopy CO<sub>2</sub> ( $F_c$ ) and water vapor flux densities ( $E$ ) measured over the closed wheat (a) and the sparse corn (b) crops. These data are from daylight periods and encompass a wide range of solar energy, temperature, wind and humidity conditions.

respiration rates increased from 0.025 to 0.15 mg m<sup>-2</sup> s<sup>-1</sup> (on a leaf area basis) as surface temperature increased from 5 to 23°C. These data yield an activation energy of 68 101 J mol<sup>-1</sup> K<sup>-1</sup>. On comparing respiration rates between the corn and wheat crops, greater respiration sensitivities to temperature ( $E_a$ ) were associated with the C<sub>4</sub> corn crop (68 101 vs. 58089 J mol<sup>-1</sup> K<sup>-1</sup>). It is unclear why the temperature coefficients for canopy respiration differed between the C<sub>3</sub> and C<sub>4</sub> crop because respiration rates of C<sub>3</sub> and C<sub>4</sub> leaves do not differ (Jones, 1983). However, the greater sensitivity of corn respiration to temperature helps explain why the sparse corn crop possessed a lower canopy quantum yield than the C<sub>3</sub> wheat crop (see Table 2).

The temperature coefficient for corn canopy respiration agrees with data from Desjardins (1985) and Moss et al. (1961). Absolute magnitudes of corn canopy respiration, on the other hand, were less than values reported by Desjardins (1985), whose crop had more biomass and was subjected to warmer temperatures.

### 3.2. *Water use efficiency: the ratio between CO<sub>2</sub> gained to water lost*

Plants lose water at the expense of gaining carbon. The ratio between photosynthesis and transpiration ( $A/T$ ) is a measure of water use efficiency. Theoretically, this ratio is a function of a leaf's internal CO<sub>2</sub> concentration ( $C_i$ ) and leaf–air vapor pressure difference (Jones, 1983). Because C<sub>3</sub> leaves maintain higher  $C_i$  values than C<sub>4</sub> leaves, lower water use efficiencies are expected for C<sub>3</sub> leaves under similar environmental conditions (Jones, 1983; Pearcy and Ehleringer, 1984). At the field scale, it is difficult to measure canopy photosynthesis and transpiration rates directly. Canopy CO<sub>2</sub> ( $F_c$ ) and water vapor flux densities ( $E$ ), however, are potential surrogates for studying  $A$  and  $T$  at the canopy scale.

Simultaneous measurements of  $F_c$  and  $E$  were coupled tightly over the wheat and corn crops (Fig. 7). Variations in  $E$  accounted for 78–83% of the variation in  $F_c$ . Residual scatter was most likely a result of temporal variations in the ratios between vegetation and soil gas exchange flux densities.

Calculating the slope between changes in CO<sub>2</sub> and water vapor flux densities is one measure of water use efficiency. The corn and wheat crops experienced similar slopes between  $F_c$  and  $E$  despite their biochemical differences. The slope of the linear relationship between  $F_c$  and  $E$  was about  $-11$  mg CO<sub>2</sub> gH<sub>2</sub>O<sup>-1</sup> over each crop.

#### 3.2.1. *Diurnal trends*

The ratio between CO<sub>2</sub> and water vapor flux densities ( $F_c/E$ ) is another index of stand-level water use efficiency (Baldocchi et al., 1985). Figure 8(a)

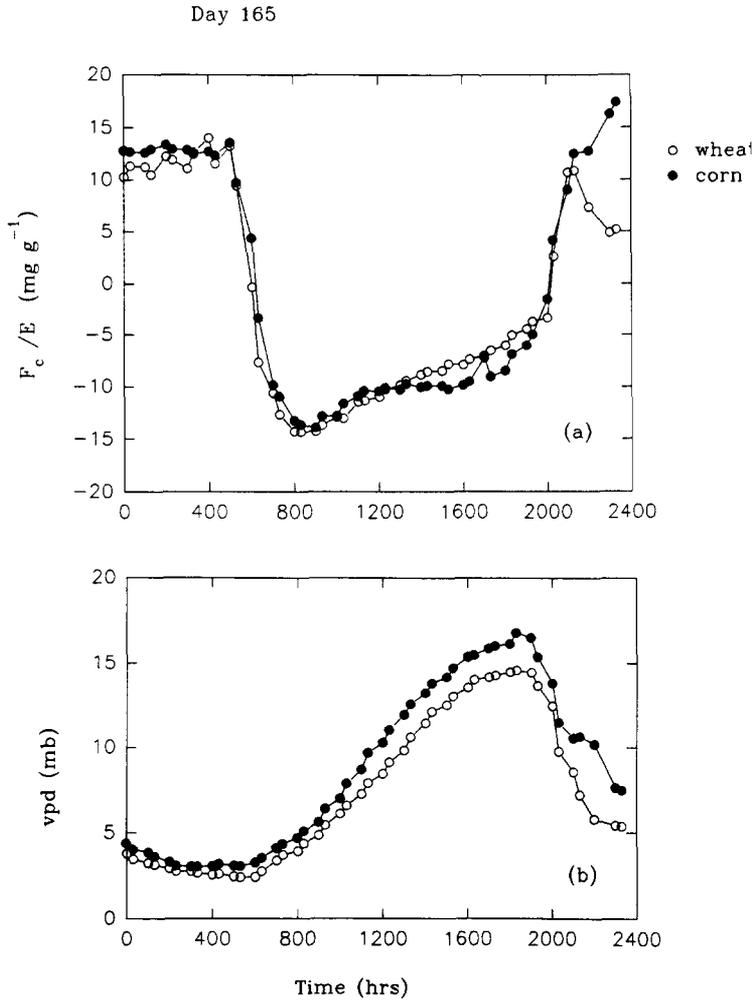


Fig. 8. (a) Diurnal variation of a water use efficiency index ( $F_c/E$ ) measured over a closed wheat and an open corn canopy.  $F_c$  is the canopy  $\text{CO}_2$  flux density and  $E$  is the canopy water vapor flux density. (b) Diurnal variation of vapor pressure deficit ( $D$ ) measured over the corn and wheat crops. These data are from a typical clear day (Day 165) with moderate temperatures and brisk winds.

shows that  $F_c/E$  values for the wheat and corn crops were nearly identical throughout a clear day. Values of  $F_c/E$  peaked near  $-15 \text{ mg } (\text{CO}_2) \text{ g}(\text{H}_2\text{O})^{-1}$  before mid-morning (08:00 h). Afterward,  $F_c/E$  decreased linearly with time until sunset. Between mid-morning and mid-afternoon reductions in  $F_c/E$  were correlated with increases in the atmosphere's vapor pressure deficit ( $D$ ) (Fig. 8(b)).

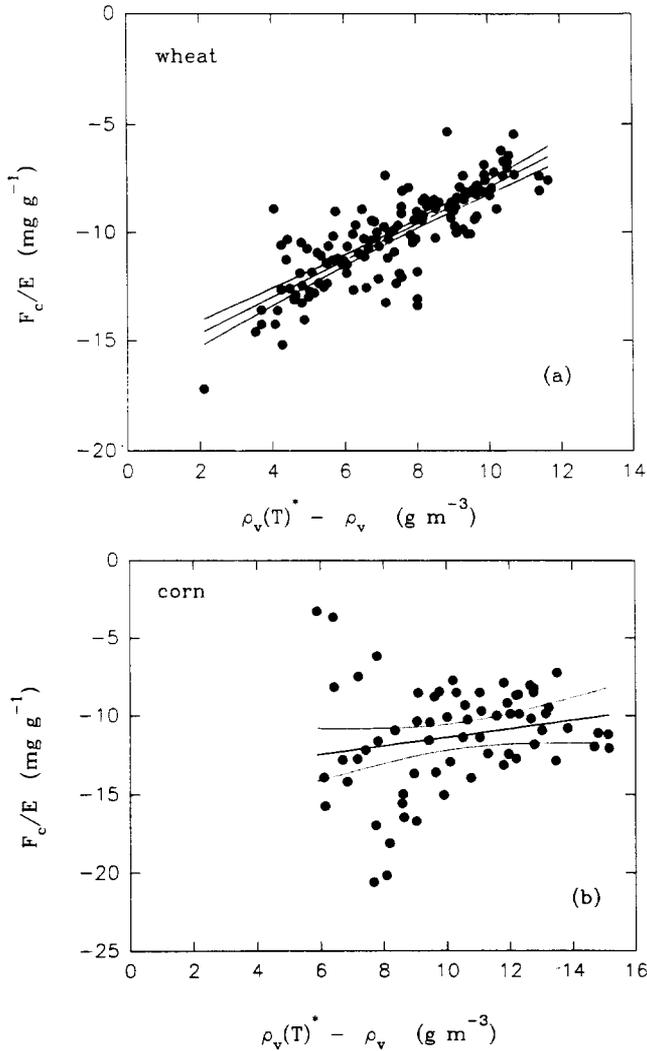


Fig. 9. The relationship between an index of water use efficiency ( $F_c/E$ ) and the absolute humidity deficit of the atmosphere.  $\rho_v^*(T)$  is the saturation absolute humidity at air temperature,  $T$ , and  $\rho_v$  is the absolute humidity of the atmosphere. Data presented in this figure were obtained when the net radiation flux density exceeded  $300 \text{ W m}^{-2}$ . (a) Wheat canopy. Regression statistics: intercept =  $-16.37$ , slope =  $0.848$ ,  $r^2 = 0.666$ . (b) Corn canopy. Regression statistics: intercept =  $-19.37$ , slope =  $0.27$ ,  $r^2 = 0.0361$ .

### 3.2.2. Humidity deficits

A more extensive look at the relationship between atmospheric humidity deficits and water use efficiency is shown in Fig. 9. Over the wheat,  $F_c/E$  responded linearly as absolute humidity deficits diminished (Fig. 9(a)). In other words, more carbon was gained per unit of water lost as absolute

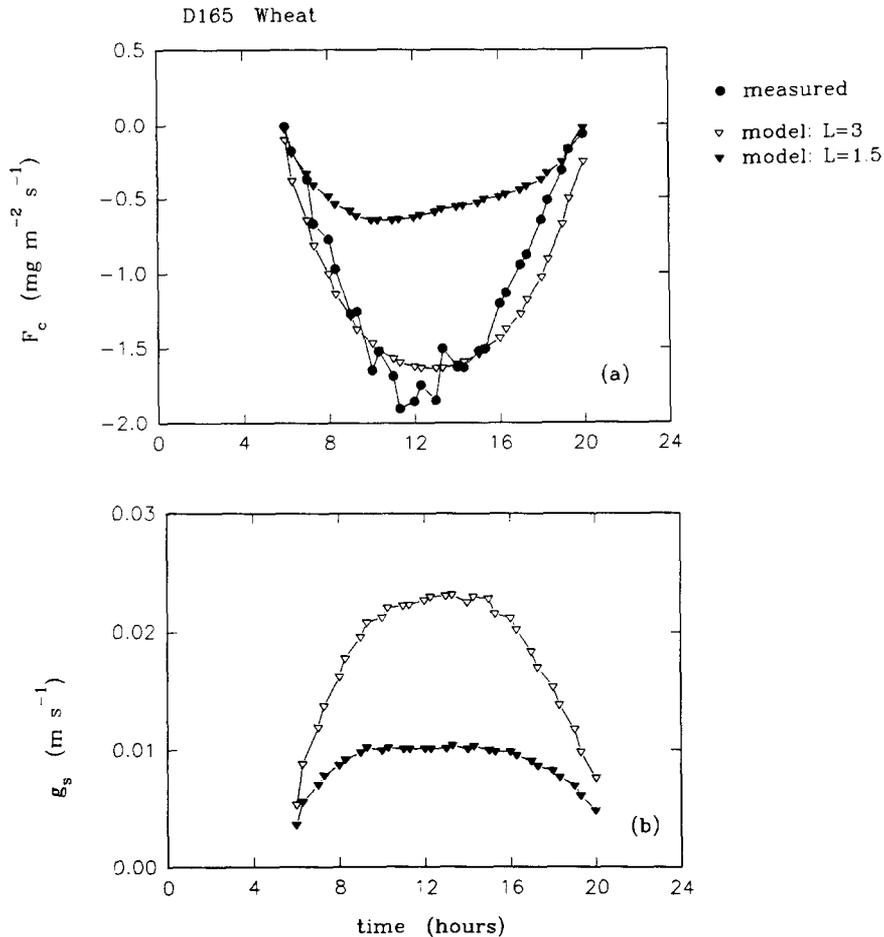


Fig. 10. (a) Model calculation of canopy  $\text{CO}_2$  flux density for hypothetical wheat canopies with leaf area indices ( $L$ ) equal to 3.0 and 1.5. Superimposed on the figure are field measurements of  $F_c$ . The calculations are based on environmental data from Day 165. (b) Model calculation of the integrated canopy stomatal conductance for hypothetical wheat canopies with  $L$  equal to 3.0 and 1.5.

humidity deficits curtailed. Over the sparse corn crop, the relationship between  $F_c/E$  and absolute humidity deficits broke down. In this second case,  $F_c/E$  was statistically independent of absolute humidity deficits (Fig. 9(b)).

## 4. Discussion

### 4.1. $\text{CO}_2$ flux densities

#### 4.1.1. Diurnal patterns

The diurnal course of  $F_c$  is influenced by LAI, stomatal physiology, photo-

synthetic photon flux density and earth–sun–leaf geometry (Duncan et al., 1967; Cowan, 1982; Jones, 1983). Model calculations are presented in Fig. 10 to illustrate the roles of LAI and stomatal conductance on the diurnal course of  $F_c$ . Figure 10(a) shows that calculated (and measured) time courses of  $\text{CO}_2$  flux density are parabolic on sunny day when LAI equals 3. In contrast, calculations of  $F_c$  over a sparse  $\text{C}_3$  crop (Fig. 10(b);  $L = 1.5$ ) suggest that  $\text{CO}_2$  flux densities peak during mid-morning and afterward ramp down with time. The observation and calculation of a parabolic daytime course of  $F_c$  over the wheat (Figs. 1(a) and 10(a)) agree with a plethora of experimental data from closed crops (wheat: Denmead, 1976; Wall and Kanemasu, 1990; Whitfield, 1990; corn: Moss et al., 1961; Desjardins, 1985; Jones et al., 1986; Held et al., 1990). Furthermore, the diurnal behavior of  $F_c$  over the hypothetical sparse wheat crop agrees with data from a sparse wheat crop (Wall and Kanemasu, 1990).  $\text{CO}_2$  flux densities over a sparse  $\text{C}_3$  canopy plateau at mid-morning because most leaves are sunlit. Consequently, the high flux densities of PAR absorbed by these leaves saturate the regeneration of ribulose biphosphate (RuBP) via electron transport, and limit carboxylation (Farquhar et al., 1980). The downward ramping of photosynthesis, later in the day, stems from the daily increase in temperature, which coincidentally increases respiratory losses of  $\text{CO}_2$  from leaves, roots and the soil (see Fig. 3).

Stomatal optimization theory concludes that stomata open and close over the course of a day to maintain a constant ratio between sensitivities of photosynthesis and transpiration to stomatal conductance (Cowan, 1982). When water is limiting, stomata will close at midday to optimize the ratio of carbon gained to water lost (Cowan, 1982), causing temporary depressions in the flux densities of  $\text{CO}_2$  and water vapor. However, stomata remain open and flux densities of  $\text{CO}_2$  and water can follow a parabolic daytime course when soil water is widely available (Cowan, 1982). Calculations presented in Fig. 10(b) (and measurements reported by Baldocchi (1994)) indicate that stomatal conductances were constant at midday, thereby allowing  $F_c$  to peak at midday instead of being restricted.

Biochemical factors may explain why the temporal peak of  $F_c$  measured over the corn lagged the daily peak of  $Q_p$  (Fig. 1(a)).  $\text{C}_4$  photosynthesis is equal to minimum rate of three colimiting processes: a  $Q_p$ -limiting rate ( $J_i$ ), a  $\text{CO}_2$ -limiting rate ( $J_c$ ), and limiting rate imposed by the saturation of RuBP carboxylase/oxygenase in the bundle sheaths ( $J_e$ ) (Collatz et al., 1992). Corn photosynthesis rates will peak when  $Q_p$  is maximal only if biochemical colimitations by rates  $J_c$  or  $J_e$  are not occurring. Calculations of  $\text{C}_4$  photosynthesis rates, using algorithms and parameters from Collatz et al. (1992), can help deduce what factors affected the diurnal course of  $F_c$  over corn. I calculate that  $J_e$  is less than  $J_i$  when  $Q_p$  exceeds  $650 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Incident  $Q_p$  on sunlit leaves typically exceeds  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$  between mid-morning and mid-afternoon (Fig. 1(b)). Because most leaves of the sparse corn canopy were

sunlit, it is reasonable to conclude that RuBP carboxylase/oxygenase saturation ( $J_e$ ) occurred between mid-morning and mid-afternoon. Consequently, it is plausible to conclude that photosynthetic limitation by  $J_e$  prevented  $F_c$  over corn from tracking the daily course of  $Q_p$ , which would have occurred if  $F_c$  was limited solely by  $J_i$ .

The contribution of temperature on the diurnal trend of  $F_c$  measured over corn cannot be discounted. The diurnal variation of air temperature lagged the daily course of incident sunlight by 2–3 h. Consequently, it is plausible to expect the rates of many enzyme reactions associated with photosynthesis and respiration to be maximal at mid-afternoon.

#### 4.1.2. *Photosynthetically active radiation*

A plethora of studies conducted over closed crop canopies report that  $F_c$  is a linear function of  $Q_a$  and that  $Q_a$  accounts for a disproportionate amount of the variation in  $F_c$  (sorghum: Anderson and Verma, 1986; soybeans: Baldocchi et al., 1981; corn: Moss et al., 1961; Desjardins et al., 1984; Jones et al., 1986; wheat: Denmead, 1969, 1976). Another set of studies report that canopy  $\text{CO}_2$  exchange rates over wheat saturate with respect to  $Q_a$  (Puckridge, 1971; Puckridge and Ratkowsky, 1971; Wall and Kanemasu, 1990). These alternative cases of  $F_c$  saturation from  $Q_a$ , however, were from sparse wheat crops, having low leaf area indices (2 and less).

The linear response of  $F_c$  to  $Q_a$  over wheat (Fig. 2(a)) is at odds with photosynthesis– $Q_a$  response curves for individual  $\text{C}_3$  leaves, which saturate when  $Q_a$  exceeds a threshold value (Jones, 1983; Percy and Ehleringer, 1984). Saturation of the wheat canopys  $\text{CO}_2$  exchange rate does not occur because the transmission and intensity of  $Q_p$  increases with solar elevation (Fig. 1(b); Ross, 1981). Consequently, more solar energy becomes available to leaves deep inside the canopy, whose photosynthetic apparatus is not saturated with respect to  $Q_p$  (see Denmead, 1976; Campbell, 1977; Jones, 1983). Linearization of the canopy  $F_c$ – $Q_a$  response relationship by closure of a crop canopy is illustrated theoretically in Fig. 3 by the comparison between  $F_c$  over a hypothetical closed ( $L = 3$ ) and sparse ( $L = 1.5$ ) crop.

The linear response of  $F_c$  to absorbed PAR explains, in part, why Monteith's (1977) method of predicting dry matter production of crops on the basis of absorbed PAR is successful. In addition, results from Fig. 2 can be used to support arguments for estimating of regional  $\text{CO}_2$  exchange rates of cropped systems, under ideal conditions, using satellite-based measurements of absorbed radiation (Sellers, 1985).

#### 4.1.3. *Canopy respiration*

What proportion of canopy respiration came from the soil cannot be assessed with confidence. However, data from Rochette et al. (1991) and Hodges and Kanemasu (1977) give some insight into the magnitude of soil

respiration rates under corn and wheat canopies. Rochette et al. (1991) report that soil respiration rates under a corn canopy ranges between 0.1 and 0.15 mg m<sup>-2</sup> s<sup>-1</sup> when soil temperature is near 30°C and volumetric soil water content is between 13 and 18%. They also reported that soil respiration rates under a wheat crop ranged between 0.05 and 0.10 mg m<sup>-2</sup> s<sup>-1</sup> during dry periods and reached a maximum near 0.3 mg m<sup>-2</sup> s<sup>-1</sup> after a rainfall event. Hodges and Kanemasu (1977) cite soil respiration rates equalling 0.07 mg m<sup>-2</sup> s<sup>-1</sup> in bare soil without roots. Respiration by soil microbes was probably nil at the Oregon field site because the soil organic content was insignificant. If we accept Rochette et al.'s soil/root respiration rate of 0.10 mg m<sup>-2</sup> s<sup>-1</sup> as an upper limit for soil/root respiration, we can conclude (from data in Fig. 1) that plant and root respiration rates were nearly equal.

#### 4.2. Water use efficiency

The similarity between  $\delta F_c/\delta E$  ratios over the corn and wheat (Fig. 7) is an artifact of comparing a sparse C<sub>4</sub> crop and a closed C<sub>3</sub> crop. During this experiment, both CO<sub>2</sub> and water vapor flux densities of the corn crop were, on average, 59% less than the respective flux densities measured over the closed wheat stand (Baldocchi, 1994). Because the relative differences of  $F_c$  and  $E$  between the corn and wheat were identical, water use efficiencies must also be equal. Had the corn canopy been closed, its  $\delta F_c/\delta E$  ratio would have probably exceeded that of the wheat. This conclusion stems from the standpoint that a closed corn crop has a greater potential for CO<sub>2</sub> uptake than a closed wheat stand (Mooney and Field, 1989), while evaporation rates from two closed crops would probably be similar because well-watered crops evaporate at rate proportional to 1.3 times available energy (Jarvis and McNaughton, 1986).

##### 4.2.1. Humidity deficits

A host of experimental studies show a correlation between short-term, crop water use efficiency and atmospheric humidity deficits (Rawson et al., 1977; Zur and Jones, 1984; Baldocchi et al., 1985; Jones et al., 1986; Dunin et al., 1989). Theory, derived from a big-leaf model, defines the form of the relationship between water use efficiency of a crop and humidity deficits (Bierhuizen and Slatyer, 1965; Tanner and Sinclair, 1983)—short-term water use efficiency is inversely related to humidity deficits,  $A/T = -k/\Delta\rho_v$ , where the coefficient,  $k$ , is a function of the intercellular CO<sub>2</sub> concentration.

Figure 11 presents calculations of  $F_c/E$  and  $A/T$  derived from the CANWHT model and the big-leaf model, respectively. Both models predict a similar (inverse) dependency of  $A/T$  (or  $F_c/E$ ) on humidity deficits. On comparing measured and calculated water use efficiency indices, one must conclude that water use efficiency theory needs refinement. The measured

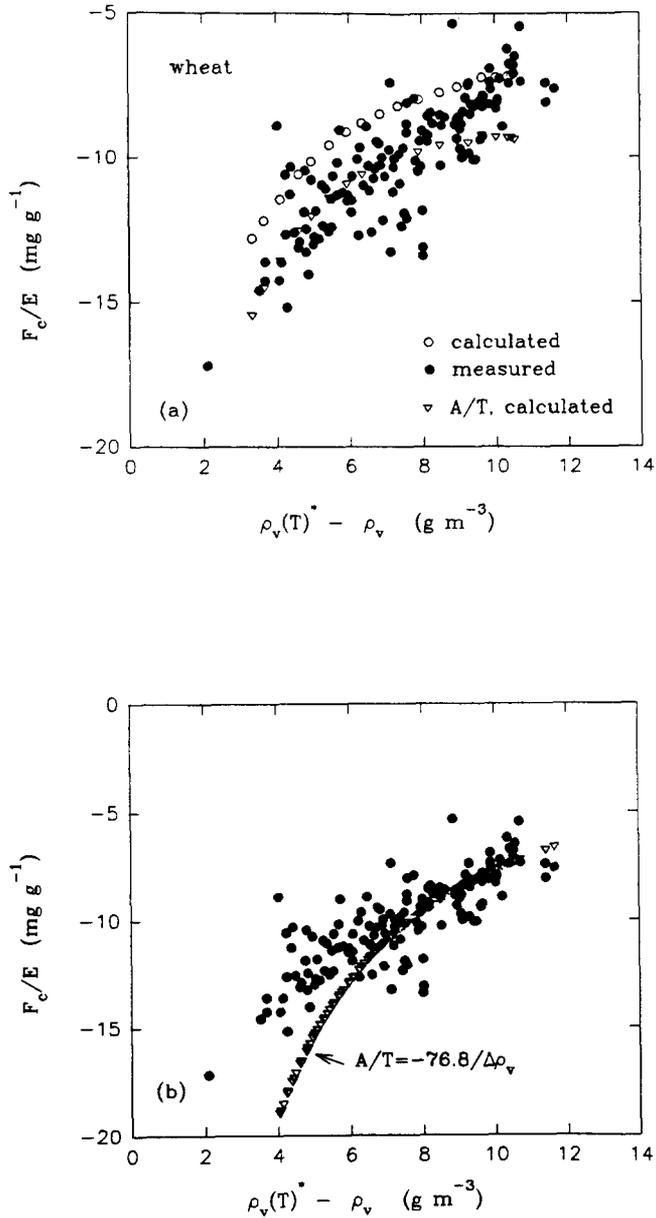


Fig. 11. (a) The response of measured and calculated indices of water use efficiency to variations in absolute humidity deficits. Calculations of water use efficiency are derived from the CANWHT model (Table 1). (b) Relationship between measured and calculated indices of water use efficiency and absolute humidity deficits. Measurements are based on the ratio between  $F_c$  and  $E$ . Calculations are based on the ratio between canopy assimilation and transpiration rates. Calculations of  $A/T$  are from:  $WUE = -k/\Delta\rho_v$ .  $k$  was assigned a value equal to  $78.8 \text{ g m}^{-3}$  ( $10.4 \text{ kPa}$ ), based on data reported by Zur and Jones (1984).

response of water use efficiency to absolute humidity deficits was more linear than theory predicts.

A bias was observed between calculations of  $F_c/E$  and  $A/T$ . This bias, however, occurred because  $F_c/E$  includes additional carbon and water losses from soil evaporation and respiration.

## 5. Summary and conclusion

Canopy scale  $\text{CO}_2$  and water vapor flux densities were measured over a closed wheat and an open corn canopy. The closed wheat crop assimilated  $\text{CO}_2$  at a higher rate than the sparse corn canopy, even though corn uses a more efficient photosynthetic pathway. The  $\text{C}_4$  corn crop assimilated  $\text{CO}_2$  at a lower rate than wheat because the corn's canopy quantum yield was lower and because the sparse corn canopy absorbed less PAR than the closed wheat stand. Water use efficiencies of the two crops, on the other hand, were similar.

How environmental, architectural and physiological variables affect the flux densities of  $\text{CO}_2$  and water vapor over  $\text{C}_3$  and  $\text{C}_4$  crop stands during day and night periods was also examined. The flux density of absorbed PAR ( $Q_a$ ) had a disproportionate influence on  $\text{CO}_2$  uptake rates of a closed  $\text{C}_3$  and an open  $\text{C}_4$  crop. Variations in  $Q_a$  explained over 88% of the variance in daytime  $\text{CO}_2$  flux densities,  $F_c$ . At night, canopy radiative temperature was the main environmental factor controlling the nocturnal respiratory efflux by the two crops. Canopy respiration by the corn crop was more sensitive to temperature than was respiration by the wheat crop. This difference in respiration sensitivity may contribute towards explaining why the sparse corn crop experienced a lower canopy quantum yield than the closed wheat crop.

LAI and growth stage were the plant variables that affected  $F_c$  most. Rates of daytime  $\text{CO}_2$  gains and night-time  $\text{CO}_2$  losses changed dramatically after the wheat headed. Incremental increases in LAI enhanced the corn crop's ability to absorb incident solar radiation and enlarged the crop's sink strength for  $\text{CO}_2$ . However, seasonal changes in LAI probably did not cause all temporal variations in maximum  $\text{CO}_2$  flux densities. From the literature and model calculations, one can conclude that seasonal changes in leaf photosynthetic capacity and root/soil respiration will also modify canopy  $\text{CO}_2$  flux densities. Water use efficiency of the wheat crop improved as the absolute humidity deficit of the atmosphere decreased. Water use efficiency of the corn, on the other hand, was relatively insensitive to humidity deficits.

The measurements of canopy  $\text{CO}_2$  flux densities consist of contributions from root, soil and plant components. Future studies should examine soil evaporation and respiration, separately, to isolate soil effects from plant

effects. Collaborative studies among micrometeorologists and biochemists and physiologists are also needed to address why respiration rates of wheat change so dramatically at heading and why the sensitivity of corn respiration to temperature was greater rate than the wheat.

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