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Scaling up of CO₂ fluxes from leaf to canopy in maize-based agroecosystems

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Abstract

Carbon dioxide fluxes are being measured in three maize-based agroecosystems in eastern Nebraska in an effort to better understand the potential for these systems to sequester carbon in the soil. Landscape-level fluxes of carbon, water and energy were measured using tower eddy covariance systems. In order to better understand the landscape-level results, measurements at smaller scales, using techniques promoted by John Norman, were made and scaled up to the landscape-level. Single leaf gas exchange properties (CO₂ assimilation rate and stomatal conductance) and optical properties, direct and diffuse radiation incident on the canopy, and photosynthetically active radiation (PAR) reflected and transmitted by the canopy were measured at regular intervals throughout the growing season. In addition, soil surface CO₂ fluxes were measured using chamber techniques. From leaf measurements, the responses of net CO₂ assimilation rate to relevant biophysical controlling factors were quantified. Single leaf gas exchange data were scaled up to the canopy level using a simple radiative model that considers direct beam and diffuse PAR penetration into the canopy. Canopy level photosynthesis was estimated, coupled with the soil surface CO₂ fluxes, and compared to measured net ecosystem CO₂ exchange (NEE) values from the eddy covariance approach. Estimated values of canopy level absorbed PAR was also compared to measured values. The agreement between estimated and observed values increases our confidence in the measured carbon pools and fluxes in these agroecosystems and enhances our understanding of biophysical controls on carbon sequestration.

Keywords: photosynthetically active radiation, leaf gas exchange, eddy correlation, leaf angle distribution, leaf area index, photosynthesis

1. Introduction

Increased understanding of the role of plant and soil processes is critical for furthering our knowledge of land surface-atmosphere energy, water and gas exchanges. The Carbon Sequestration Program was established in eastern Nebraska by researchers at the University of Nebraska–Lincoln to quantify carbon pools and fluxes in maize-based agroecosystems and to better understand the potential for these production systems to sequester atmospheric carbon in the soil. Program scientists seek to achieve this goal through measures of plant and soil functioning coordinated with year-round landscape-level eddy covariance measurements of energy, water and gas exchanges (Verma et al., 2005).

Leaf area and canopy architecture play an important role in controlling energy, carbon and water vapor exchange between vegetation and the atmosphere (Norman, 1980; Law et al., 2001). Seasonal changes in leaf area as well as diurnal changes

in solar angle and leaf architecture can result in differences in sunlit and shaded leaf and soil areas, as well as radiant flux density, which in turn influence gas exchange and energy partitioning (Baldocchi et al., 2001). Typically, under well-watered conditions, as more light is intercepted by leaves in the canopy, carbon assimilation and water vapor transfer rates increase. As plants develop, leaves age and canopy structure, stomatal conductance and photosynthesis change (Wilson et al., 2001). Water deficits can result in further leaf changes and even leaf drop as a result of prolonged dry conditions. As a result, canopy microclimate changes influence carbon dioxide and water vapor exchanges (Albertson et al., 2001).

The present study investigates effects of leaf area, leaf photosynthetic status and water conditions during plant growth on carbon exchange in maize-based cropping systems using a scaling-up modeling approach. Modeling the plant canopy system can aid in the understanding of the processes controlling exchanges of CO₂, i.e., aid in understanding the interactions of

the atmosphere with the earth's vegetation and soil surfaces. A simple modeling approach extended by Norman et al. (1992b), utilizing many measurement and analysis techniques developed by Norman, was used to better understand the contribution of surface components (measured at smaller scales) to landscape-level fluxes. The modeling approach combined measures of leaf gas exchange, leaf optical properties, canopy structure and soil gas exchange with meteorological measurements to scale these measurements from the leaf-level to the landscape-level on seasonal and diurnal bases. The basis for the simple approach used here is to separate the canopy leaf area into sunlit and shaded classes. Scaling approaches that separate sunlit and shaded leaf classes are receiving increased attention in the literature (e.g., Wang and Leuning, 1998a; De Pury and Farquhar, 1997). In general, good agreement has been found between these simplified models and other, more detailed, scaling models (e.g., Thornley, 2002); however, fewer studies (e.g., Wang and Leuning, 1998b) have focused on comparing the predictions from simple sunlit and shaded leaf models to independent measurements of relevant fluxes. The objective of this paper was to compare the scaled up estimates of net ecosystem CO₂ exchange (NEE) using this relatively simple approach to concurrent measurements of surface-atmosphere CO₂ exchange using the eddy covariance technique. In addition, we compared the canopy absorbed photosynthetically active radiation fluxes (APAR) estimated from canopy structure data with APAR measured using quantum sensors.

2. Methods

2.1. Study site

The study was conducted during the growing seasons of 2001 through 2004 in two irrigated production fields (Sites 1 and 2) and one rainfed production field (Site 3) at the University of Nebraska Agricultural Research and Development Center near Ithaca, Nebraska as part of the Carbon Sequestration Program (CSP; Verma et al., 2005). Site 1 (41°09'54.2"N, 96°28'35.9"W, 361 m) is 47 ha in size, has a center pivot irrigation system, and is planted to continuous maize. Site 2 (41°09'53.5"N, 96°28'12.3"W, 362 m) is 52.4 ha, also has a center pivot irrigation system and is under a maize-soybean rotation. Site 3 (41°10'46.8"N, 96°26'22.7"W, 361 m) is a 65.4-ha rainfed field under a maize-soybean rotation. In the maize-soybean rotation fields, maize was planted in 2001 and 2003 and soybean was planted in 2002 and 2004. The three sites are within 1.6 km of each other. The soils are deep silty clay loams consisting of Tomek, Yutan, Filbert, and Filmore soil series.

Prior to initiating the study, Sites 1 and 2 had a 10-year history of maize-soybean rotation under no-till management. Site 3 had a variable cropping history of primarily wheat, soybean, oats, and maize grown in 2–4 ha plots with tillage. All three sites were uniformly tilled by disking prior to initiating the CSP in 2001. The sites have been under no-till management since that time. Seed was planted below the crop residue from previous years and standard best management practices were followed. The amount of N fertilizer applied was adjusted in the spring before planting to account for nitrate already in the soil, according to recommended guidelines (Shapiro et al., 2001). Cultural data for the crops and growing seasons utilized in the study are listed in Table 1.

Sites 1 and 2 were irrigated to maintain a minimum of 50% available soil moisture in the root zone. Soil water content in the root zone was monitored continuously using Theta probes (model ML2x, Delta-T Devices Ltd., Cambridge, UK) at four depths (0.10, 0.25, 0.5, and 1.0 m) at three locations within each irrigated site and at four locations within the rainfed site.

2.2. Carbon dioxide flux, LAI and supporting measurements

Landscape-level fluxes of carbon dioxide, water vapor and energy were measured using the eddy covariance technique. Measurements began around planting time in 2001 and have run continuously thereafter. Details are provided in Suyker et al. (2003) and Verma et al. (2005). Hourly averages of radiant fluxes of direct and diffuse photosynthetically active radiation (PAR), and reflected and transmitted PAR were measured near the eddy covariance tower throughout the growing season using quantum sensors (models LI-190 and LI-191, Li-Cor, Inc., Lincoln, NE, USA). Transmitted PAR was characterized at each site with two sets of three line quantum sensors (each 1 m in length) placed across crop rows below the canopy near the soil surface at a NE and SW azimuthal orientation (rows ran E-W). These sets were located 4–5 m away from the radiation tower and from each other. An additional line quantum sensor was placed between the two transmitted PAR line quantum sensor sets, near the soil surface and face down (for soil reflected PAR measurements). Incident and reflected PAR were measured with quantum sensors mounted on the radiation tower.

Leaf area index (LAI) was measured with a plant canopy analyzer (model LAI-2000 Li-Cor, Inc., Lincoln, NE, USA) following the standard procedure described by the manufacturer to determine any row structure bias and the number of below canopy measurements needed. In all cases the canopies had grown to a point where the provision to account for row structure bias was not needed. The number of below can-

Table 1. Cultural data for the crops grown in the University of Nebraska-Lincoln Carbon Sequestration study at the UNL Agricultural Research and Extension Center farm during 2001–2004.

Year	Site	Crop	Hybrid/cultivar	Planting date	Seeding rate (seeds ha ⁻¹)	Final plant population (plants ha ⁻¹)	Peak LAI
2001	1	Maize	Pioneer 33P67	May 10	88,900	81,500	6.0
	2	Maize	Pioneer 33P67	May 11	83,300	82,400	6.0
	3	Maize	Pioneer 33B51	May 14	62,200	52,300	3.9
2002	1	Maize	Pioneer 33P67	May 10	84,000	71,300	6.0
	2	Soybean	Asgrow 2703	May 20	370,000	333,000	5.5
	3	Soybean	Asgrow 2703	May 20	370,000	304,000	3.0
2003	1	Maize	Pioneer 33B51	May 15	84,000	76,900	5.6
	2	Maize	Pioneer 33B51	May 14	86,600	78,000	5.6
	3	Maize	Pioneer 33B51	May 13	61,800	57,500	4.3
2004	1	Maize	Pioneer 33B51	May 5	84,000	79,700	5.2
	2	Soybean	Pioneer 93B09	June 2	370,000	296,000	4.4
	3	Soybean	Pioneer 93B09	June 2	370,000	265,000	4.5

opy measurements varied from six to eight for each LAI measurement sampling suite and varied over the years. The below canopy measurements were made over a three row area. Five sampling suites were measured in each of six Intensive Management Zones (IMZ), at the radiation tower location, at the PAR measurement location, and at the location of the leaf-level measurements (described below) in each site. Mean tip angles and associated statistics were also determined. LAI was also calculated using destructive samples of plants harvested from 1 m row lengths at each IMZ. Leaf areas of the harvested plants were then measured with a leaf area meter (model LI-3100C, Li-Cor, Inc., Lincoln, NE, USA) and converted to LAI using plant population counts. Total and green LAI (GLAI) were calculated. The destructive LAI were determined at each site every 10–14 days throughout the growing season.

2.3. Leaf-level gas exchange and optical properties

Single leaf gas exchange properties (CO_2 assimilation rate) were measured with a portable gas exchange system (model LI-6400, Li-Cor, Inc., Lincoln, NE, USA) approximately every 2 weeks during the growing season. Four to six leaves were sampled at each site during each measurement time; usually these leaves were the most recently fully expanded leaves near the top of the canopy. Responses of net CO_2 assimilation rate to relevant biophysical controlling factors were quantified. The photosynthetic rate as a function of incident light [$A(\text{PPFD})$] was described using a non-rectangular hyperbola (Prioul and Chartier, 1977):

$$A(\text{PPFD}) = \frac{(a\text{PPFD} + A_{\max}) - [(a\text{PPFD} + A_{\max})^2 - 4a\text{PPFD} A_{\max} \theta]^{1/2}}{2\theta} - R_d \quad (1)$$

where PPFD is the photon flux density incident on the leaf, A_{\max} is the maximum rate of photosynthesis (the asymptote), and R_d is the respiration rate. A_{\max} , R_d , a , and θ are parameters fit to the gas exchange data using a nonlinear least squares procedure. In addition to the light response curve fits, exponential curves were fit to leaf respiration data (i.e., the net CO_2 assimilation rate in the dark) as a function of temperature. These data sets came from measurements taken over the course of the growing season as ambient temperatures varied.

Leaf optical properties were determined for four leaves per site per measurement day using a spectral radiometer (model SE-590, Spectron Engineering, Denver, CO, USA) mounted with an integrating sphere (model LI-1800, Li-Cor, Inc., Lincoln, NE, USA). Leaves remained intact on the plant during the measurements and were, whenever possible, the same leaves used for leaf gas exchange measurements. Reflectance and transmittance from 400 to 700 nm, at 5 nm intervals, were determined for each leaf sampled. Integration over the PAR wavelengths yielded leaf-level PAR reflectance (ρ_{PAR}) and PAR transmittance (τ_{PAR}) from which PAR leaf absorptance (α_{PAR}) was calculated. Results were averaged from four leaves per site and used to represent the leaf PAR absorptance for that site and day.

2.4. Soil surface CO_2 fluxes

Soil surface CO_2 fluxes were measured with a portable gas exchange system (LI-6200, Li-Cor, Inc., Lincoln, Nebraska, USA) connected to a cylindrical steel chamber (Norman et al., 1992a). The chamber volume was approximately 1 l with a diameter of about 10 cm. Surface fluxes were typically measured at six locations (three within-row and three between-row positions) in each of six IMZ at all three sites; i.e., a total of 36 measurements were used to characterize site-level mean soil surface CO_2 fluxes. At each location a PVC collar was installed in the soil; the

collar was a ring about 5 cm tall. Previous research (e.g., Amos et al., 2005) has demonstrated the influence of proximity to the row on surface CO_2 fluxes in maize-based cropping systems; for this study we used an average of within-row and between-row measurements at all six IMZ to obtain mean field-scale fluxes. Fluxes were determined as close to ambient CO_2 concentrations as practical by drawing down the CO_2 concentration in the chamber immediately prior to the measurement and letting the CO_2 concentration rise through the ambient value during the measurement itself. For each flux measurement soil temperatures at 0.1 m were recorded and gravimetric soil water content was determined for a 0–0.1 m soil sample. Gravimetric soil water contents were converted to volumetric water contents (θ_v) using measured bulk densities. In order to interpolate between sampling dates, mean field-scale fluxes were fit to an empirical equation based on Norman et al. (1992a) to describe soil CO_2 flux (C_s) as a function of soil temperature (T_{soil}):

$$C_s = (a + b \text{LAI})\theta_v \exp[c(T_{\text{soil}} - d)] \quad (2)$$

where LAI is the leaf area index, θ_v is the volumetric soil water content, T_{soil} is the 0.1 m soil temperature and a , b , c , and d are parameters fit to the data using a nonlinear least squares technique. This equation was parameterized using values of soil temperature measured near the eddy covariance tower and soil water content measured at the time of surface flux measurement. This allowed us to utilize the continuous data measured at these locations, along with our fitted equation, to estimate soil surface CO_2 fluxes on an hourly basis throughout the study periods. All data from each site for each year were used to parameterize Equation (2), i.e., one set of parameters was obtained for each site for each year.

2.5. Landscape-level model

Single leaf gas exchange data were scaled up to the canopy level using a relatively simple one-layer radiative transfer model (Norman et al., 1992b) that considers direct beam and diffuse PAR penetration into the canopy. Using this model, canopy level photosynthesis was estimated; net ecosystem exchange (NEE) was calculated as the sum of the canopy photosynthetic rate (A_c) and the soil surface CO_2 flux (C_s):

$$\text{NEE} = (A_c + C_s) \quad (3)$$

This scheme considers fluxes toward the surface as positive; that is, canopy photosynthesis is positive, canopy respiration is negative and soil surface CO_2 fluxes are negative. Note that, in Equation (3), A_c is the net CO_2 assimilation rate of the aboveground portions of the plant canopy (i.e., root respiration is not implicit in A_c). An advantage of using this formulation is that no separation of C_s into autotrophic and heterotrophic components is required as would be the case when using estimates or measurements of net primary production (NPP) and heterotrophic respiration (R_h) and setting $\text{NEE} = \text{NPP} - R_h$ [e.g., Wang and Polglase (1995)]. The transition between daytime and nighttime was assumed to occur at a solar zenith angle of 80° . The leaf light response curves were used to estimate A_c during daytime (Equation (1)) and the leaf respiration versus temperature curves were used to estimate A_c (based on air temperatures) during nighttime. In addition, the model was used to estimate values of hourly canopy level absorbed PAR (APAR). Simulations were made for days when measurements of leaf optical properties and soil CO_2 fluxes were available on average within 7 days of leaf-level and canopy CO_2 measurements, regardless of sky condition.

The angular distribution of leaves in the canopy was determined using output from the LAI-2000 (mean tip angle, standard error and the number of samples). The Beta distribution in terms of the Gamma function (Γ), as described by Goel and

Strebel (1984), was employed to calculate the leaf angle distribution [$g(\theta_L, \varphi_L)$], the fraction of leaves per unit leaf zenith angle, θ_L , per unit leaf azimuth angle, φ_L] from which the extinction coefficient (horizontal projection) was determined (Ross, 1975; Campbell and Norman, 1989).

$$g(\theta_L, \mu, \nu) = \left[\frac{1}{360 \times 90} \frac{\Gamma(\mu + \nu)}{\Gamma(\mu)\Gamma(\nu)} \left(1 - \frac{\theta_L}{90}\right)^{\mu-1} \left(\frac{\theta_L}{90}\right)^{\nu-1} \right] \quad (4)$$

The two parameters, μ and ν , are related to the average leaf inclination angle (the mean tip angle, θ_i), its second moment and its variance (see Goel and Strebel, 1984, for details). The leaf angle distribution was assumed azimuthally symmetrical, thus, the distribution was described in ten leaf angle classes.

The extinction coefficient in the direction of the direct beam was calculated as

$$G(\theta_i) = \frac{1}{2\pi} \iint g'(\theta_L) \cdot |\cos\theta_i \cos\theta_L + \sin\theta_i \sin\theta_L \cos\varphi_i| d\theta_L d\varphi_L \quad (5)$$

where the distribution is normalized so that $\int_0^{\pi/2} g(\theta_L) d\theta_L = 1$.

The amounts of sunlit and shaded leaf areas and estimates of the average PAR on sunlit and shaded leaves (Q_{sunlit} and Q_{shade}) are needed to estimate the contribution of shaded and sunlit leaves to the intercepted light in the canopy. The sunlit leaf area index is calculated for a given solar zenith angle θ_i , assuming leaves to be randomly distributed in the canopy GLAI values were used]:

$$F_{\text{sun}} = \left[1 - \exp\left(\frac{-G(\theta_i) \text{GLAI}}{\cos\theta_i}\right) \right] \frac{\cos\theta_i}{G(\theta_i)} \quad (6)$$

The fraction of leaves which are shaded (F_{shade}) is $\text{LAI} - F_{\text{sun}}$. The sunlit fraction of leaves (F_{sun}) was calculated for times when the solar zenith angle was less than or equal to 80° ; for all other times F_{sun} and F_{shade} were set to 0. The photon flux density on sunlit (Q_{sunlit}) and shaded (Q_{shade}) leaves (Norman et al., 1992b) is dependent on the incoming PAR direct beam and diffuse photon flux (Q_D and Q_d , respectively) and canopy architecture [as represented with the extinction coefficient at the appropriate solar zenith angle, $G(\theta_i)$]:

$$Q_{\text{shade}} = Q_d \exp(-0.5 \text{GLAI}^{0.7}) + [0.07 Q_D (1.1 - 0.1 \text{GLAI}) \exp(-\cos\theta_i)] \quad (7a)$$

$$Q_{\text{sunlit}} = Q_D \left(\frac{G(\theta_i)}{\cos\theta_i} \right) + Q_{\text{shade}} \quad (7b)$$

Using the light response curve for the day of interest (Equation (1)), the photosynthesis rates for sunlit and shaded leaves for times when the solar zenith angle was less than or equal to 80° were determined as a function of the average absorbed photon flux densities of sunlit and shaded leaves, $A_c(Q_{\text{sunlit}})$ and $A_c(Q_{\text{shade}})$, respectively.

The canopy absorbed photon flux density (APAR_c) and canopy photosynthesis rate (per unit ground area) (A_c) were calculated as:

$$\text{APAR}_c = \alpha_{\text{PAR}} (Q_{\text{sunlit}} F_{\text{sun}} + Q_{\text{shade}} F_{\text{shade}}) \quad (8a)$$

$$A_c = A(Q_{\text{sunlit}}) F_{\text{sun}} + A(Q_{\text{shade}}) F_{\text{shade}} \quad (8b)$$

where $A(Q_{\text{sunlit}})$ and $A(Q_{\text{shade}})$ are from Equation (1).

Net ecosystem exchange (NEE) was calculated (Equation (3)) considering estimated canopy photosynthetic rate (Equation (8b)) and the soil surface CO₂ flux (C_s) according to Equation (2).

2.6. Analysis

The strength of the model performance was evaluated by comparing the predicted hourly average values of APAR_c and

NEE to the observed hourly averages; linear regressions between observed and measured values, the coefficient of determination (R^2), and the root mean square error (RMSE; Willmott, 1981) were computed.

3. Results and discussion

Single leaf light response curves were parameterized using Equation (1). In general, A_{max} was larger in maize (average $49.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) than soybean (average $20.8 \mu\text{mol m}^{-2} \text{s}^{-1}$). Differences in A_{max} between irrigated and rainfed sites were small. The A_{max} values typically decreased late in the season (following DOY 230) for all crops at all sites. The initial slope of the light response curve (α) was near $0.054 \mu\text{mol } \mu\text{mol}^{-1}$. Systematic differences between maize and soybean or between irrigated and rainfed treatments were not apparent nor were there any apparent change in α through the growing season. The fitted values of θ were more variable than A_{max} or α . Values of θ for maize were near zero and for soybean near 0.24. R_d averaged $3.10 \mu\text{mol m}^{-2} \text{s}^{-1}$ for maize and $2.89 \mu\text{mol m}^{-2} \text{s}^{-1}$ for soybean. The values of R_d decreased slightly for both crops as the growing season progressed.

The soil surface CO₂ flux measurements were fit to Equation (2) for each site for each year. Parameter values were quite variable both between sites and between years. There were no consistent differences in parameter values between maize and soybean nor between irrigated and rainfed sites. The average values for the “ a ” parameter was 0.1710 (standard error of 0.0266); Norman et al. (1992a) reported a value of 0.13

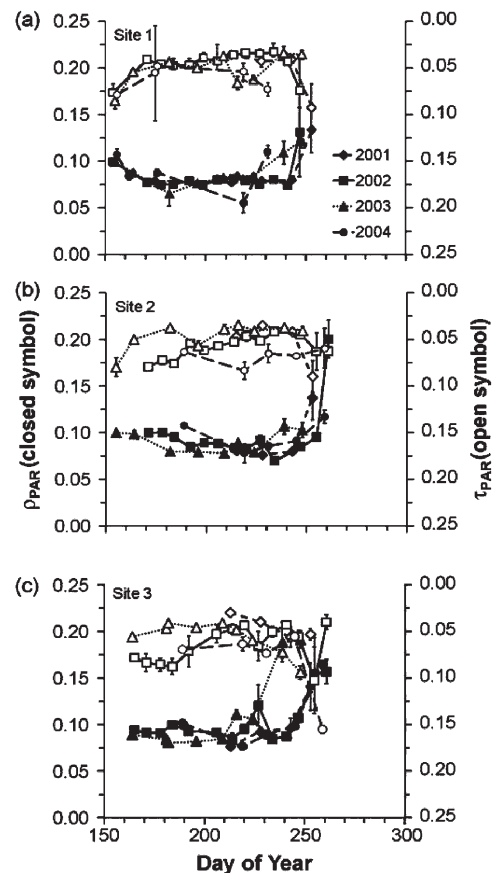


Figure 1. Average photosynthetically active radiation leaf reflectance (ρPAR , closed symbols) and transmittance (τPAR , open symbols) and associated standard error bars for the days simulated for the three research sites for the 4 years of study: (a) irrigated maize, Site 1, (b) irrigated maize-soybean, Site 2, and (c) rainfed maize-soybean, Site 3.

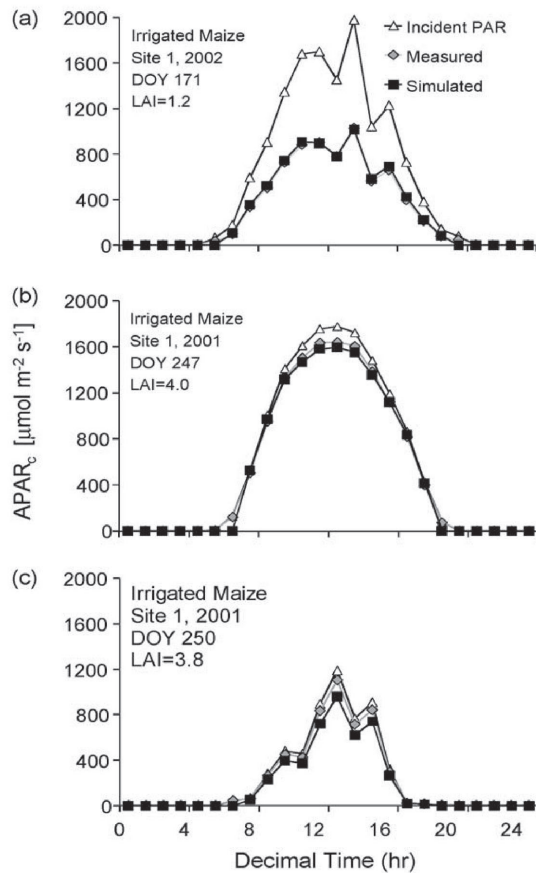


Figure 2. Hourly values of measured incident photosynthetically active radiation flux (PAR), measured canopy absorbed PAR ($APAR_c$) and simulated $APAR_c$ for three different days at the irrigated maize site (Site 1): (a) DOY 171, 2002; (b) DOY 247, 2001; and (c) DOY 250, 2001. Days differ in LAI and sky conditions.

for the grassland FIFE site in eastern Kansas. The average “*b*” parameter was 0.0056 (standard error of 0.0063) in this study; Norman et al. (1992a) obtained a value of 0.054 for the FIFE study. The average “*c*” parameter was 0.0842 (standard error of 0.0210) for this study in contrast to the Norman et al. (1992a) result of 0.069. For the “*d*” parameter, Norman et al. (1992a) set a fixed value of 25.0 while for this study the average was 28.68 (standard error of 3.64).

Leaf angle distributions and light extinction coefficients for maize and soybean calculated using the approach described by Goel and Strebel (1984) and output from the LAI-2000 (the mean tip angle, standard error and number of samples) were comparable to those cited in the literature (Monsi et al., 1973; Haile et al., 1998; Antunes et al., 2001; Purcell et al., 2007). The average light extinction coefficient for the maize canopies for solar angles of 15–80° over the years of the study ranged from 0.51 to 0.52 with standard errors ranging from 0.0023 to 0.0036 (as compared to an extinction coefficient of 0.5 for a canopy with a spherical leaf angle distribution) (Table 2). The values varied by solar zenith angle (a spherical canopy would yield an extinction coefficient of 0.5, regardless of solar angle); the highest value (for a particular site and solar angle) was 0.67 while the minimum was 0.45. The highest and lowest values were primarily obtained for canopies of LAI less than one and can most likely be attributed to the challenge of using an indirect technique (the LAI-2000) in canopies of low height and non-uniform vegetative cover (i.e., large gaps between rows).

Foliage clumping, as occurs in row crops, influences the accuracy of indirect leaf area index estimates from the LAI-2000;

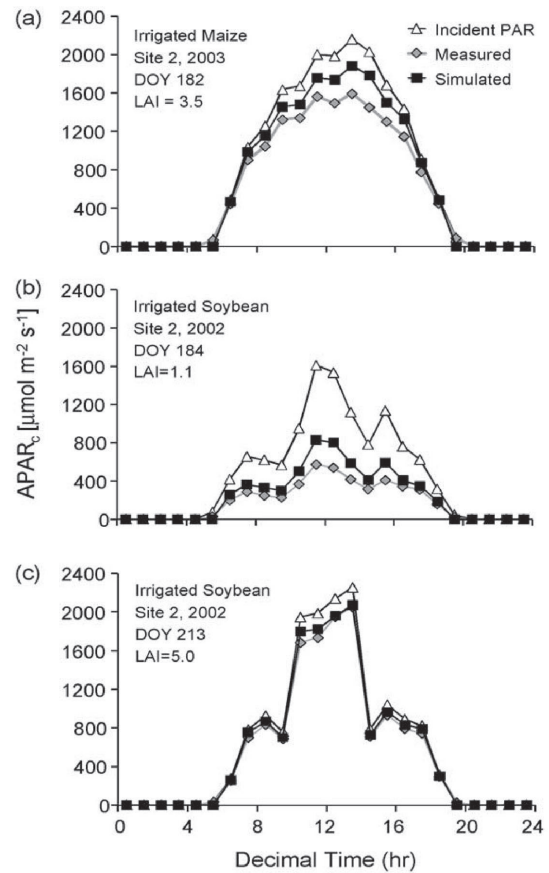


Figure 3. Hourly values of measured incident photosynthetically active radiation flux (PAR), measured canopy absorbed PAR ($APAR_c$) and simulated $APAR_c$ for three different days at the irrigated maize/soybean rotation site (Site 2): (a) DOY 182, 2003; (b) DOY 184, 2002; and (c) DOY 213, 2002. Days differ in crop type, LAI and sky conditions.

the Beer–Lambert law is applied assuming a random distribution of leaves (Kucharik et al., 1998; Kucharik et al., 1999). Thus the determination of the light extinction coefficient would likewise be in error through the violation of the random distribution assumption for which the spatial sampling could not account, especially under low leaf area conditions. The average light extinction coefficients for the soybean canopies were 0.54 for the irrigated site (standard error of 0.0067) and 0.55 for the rainfed site (standard error of 0.0067); maximum and minimum values of 0.75 and 0.43, respectively, were typical of soybean canopies with LAI less than one.

Leaf optical properties were rather consistent over the time period represented in the simulations, especially in the irrigated sites (Figure 1). Properties were more varied in the rainfed site, not only because of the change in crop from maize (odd years) to soybean (even years) but also due to the moisture variability at the site. Variations in values were especially noted for days representing the end of the growing season, as senescence varied from year to year and by crop type.

Table 2. Average extinction coefficients, *G* (a spherical leaf angle distribution yields a *G* of 0.5). Standard errors are given in parentheses.

Site	Average	Maximum	Minimum
1—Irrigated maize	0.51 (0.0023)	0.67	0.45
2—Irrigated maize	0.51 (0.0036)	0.67	0.45
Irrigated soybean	0.54 (0.0067)	0.75	0.43
3—Rainfed maize	0.52 (0.0034)	0.66	0.45
Rainfed soybean	0.55 (0.0067)	0.76	0.43

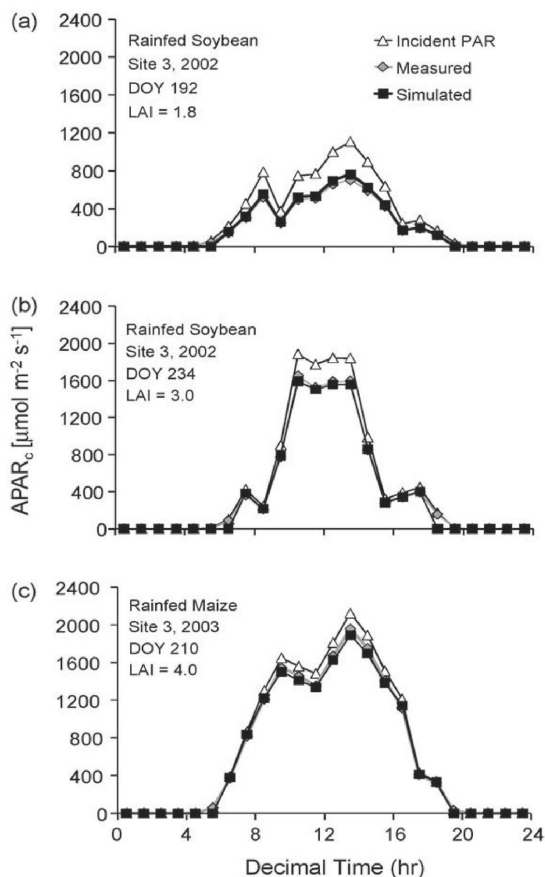


Figure 4. Hourly values of measured incident photosynthetically active radiation flux (PAR), measured canopy absorbed PAR (APAR_c) and simulated APAR_c for three different days at the rainfed maize/soybean rotation site (Site 3): (a) DOY 192, 2002; (b) DOY 234, 2002; and (c) DOY 210, 2003. Days differ in crop type, LAI and sky conditions.

Estimated hourly average APAR_c values were in good agreement with measured values for most days and most conditions (for green LAI, healthy green leaves and solar zenith angle ≤80°). Results from 24-h periods of three selected days at each site (selected to demonstrate the modeling performance for varying LAI, crop type and sky conditions) show the agreement between simulated and measured values (Figures 2–4). Hourly APAR_c values closely followed the pattern of incident PAR flux under clear sky and cloudy to partly cloudy sky conditions. Good agreement was found for all three sites, for maize and for soybean, and for sunny and cloudy days throughout the growing seasons of the 4 years of the study (Figure 5). The agreement was especially good for irrigated conditions, regardless of the crop or rotation with slopes of 1.004 and 1.002, and RMSE of 110 and 80 μmol m⁻² s⁻¹, for the irrigated maize and irrigated maize–soybean rotation, respectively. The agreement was less ideal for simulations for the rainfed maize–soybean rotation site with a slope of 0.96 and an RMSE of 161 μmol m⁻² s⁻¹ (Table 3). Given the simplicity of the model, which assumes randomly distributed leaves (i.e., no foliage clumping), we investigated the impact of low LAI (and potential associated errors in the estimate of extinction coefficients) on simulated APAR_c. Restricting the comparison to canopies of green LAI greater than one (values representing canopies with an LAI < 1 are circled in Figure 5) reduced the error between simulated and measured values (RMSE values of 91, 71 and 158 μmol m⁻² s⁻¹, for the irrigated maize, irrigated maize–soybean and the rainfed maize–soybean sites,

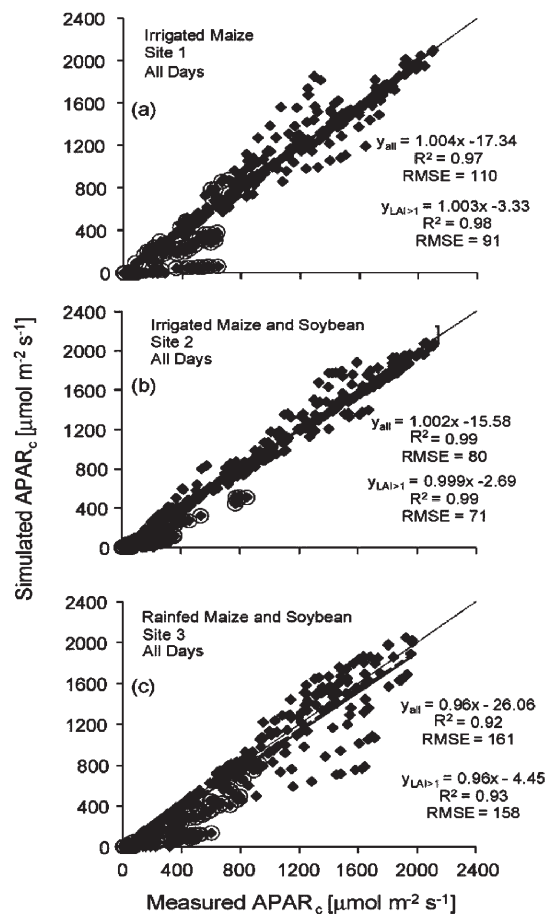


Figure 5. Hourly values of measured and simulated APAR_c for all days at each site of the study in which leaf properties were measured: (a) irrigated maize, Site 1; (b) irrigated maize–soybean, Site 2; and (c) rainfed maize–soybean, Site 3. Two different regressions are presented: (1) all days (solid line) and (2) for all days with green LAI greater than 1 (dashed line). Values for conditions of green LAI less than one are circled.

respectively). The improved agreement between simulated and measured values for canopies of LAI > 1 highlights the error introduced in a simple random leaf distribution model in representing light interaction; an introduction of a clumping index would likely improve the simulations (Anderson et al., 2005). The scatter in the results for the rainfed site is likely due to vegetation response to the periodic dry conditions at the site and the fact that leaf-level measurements were taken at various locations in the field (representing different soil conditions) while APAR_c was measured at a central location near the flux tower. Representative leaf-level measurements for the central location would be more difficult to measure under water limiting conditions. Despite the larger errors for the rainfed site, the results inspire confidence in the validity of the measurements used as input into the model (field measurements of incident PAR, leaf optical properties, green LAI and inferred leaf angle distributions from the LAI-2000) and the radiative transfer representation of the model.

Accurate estimation of the light interaction in the canopy is necessary for adequate estimation of canopy photosynthesis and, thus, NEE. Using a more rigorous approach including a number of canopy layers, foliage clumping index and defining various leaf angle classes (instead of an average PAR) could yield better estimates (Norman, 1980); however, this would come at a cost of more detailed input data (e.g., light transmit-

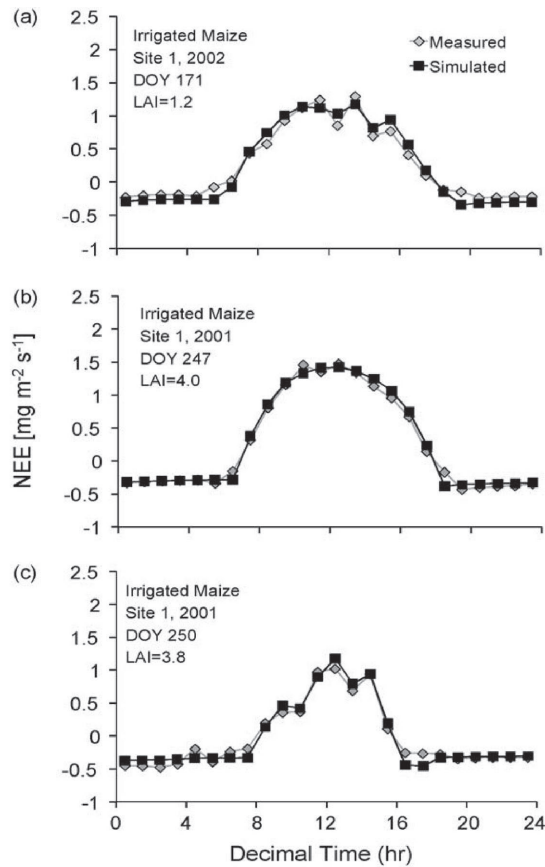


Figure 6. Hourly values of measured and simulated net CO₂ ecosystem exchange (NEE) for three different days at the irrigated maize site (Site 1): (a) DOY 171, 2002; (b) DOY 247, 2001; and (c) DOY 250, 2001. Days differ in LAI and sky conditions.

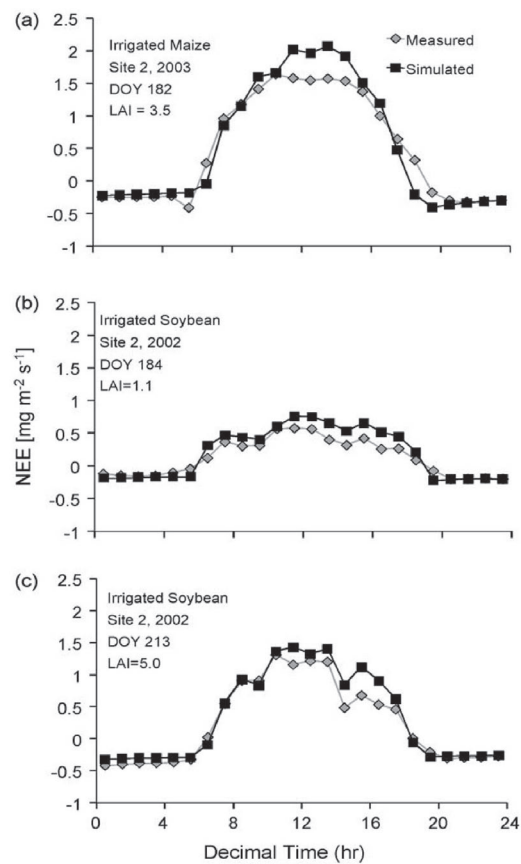


Figure 7. Hourly values of measured and simulated net CO₂ ecosystem exchange (NEE) for three different days at the irrigated maize/soybean rotation site (Site 2): (a) DOY 182, 2003; (b) DOY 184, 2002; and (c) DOY 213, 2002. Days differ in crop type, LAI and sky conditions.

Table 3. Mean observed and modeled values of APAR_c and NEE, standard error, mean bias error, coefficient of variation and RMSE values for all green LAI conditions and those of green LAI greater than one.

Figure	Site	Variable	Means		MBE	R ²	RMSE		
			Obs.	SE				Mod.	SE
4	1	APAR _c { $\mu\text{mol m}^{-2} \text{s}^{-1}$ }							
		All	479	23	463	24	-16	0.97	110
	LAI > 1	521	27	519	27	-2	0.98	91	
	2	All	484	26	469	26	-15	0.99	80
		LAI > 1	544	30	541	30	-3	0.99	71
	3	All	447	24	403	24	-44	0.92	161
LAI > 1		505	30	482	30	-23	0.93	158	
8	1	NEE { $\text{mg m}^{-2} \text{s}^{-1}$ }							
		All	0.296	0.031	0.276	0.030	-0.024	0.89	0.225
	LAI > 1	0.352	0.036	0.342	0.034	-0.028	0.90	0.244	
	2	All	0.265	0.034	0.262	0.033	-0.003	0.90	0.237
		LAI > 1	0.333	0.042	0.374	0.039	0.042	0.92	0.234
	3	All	0.200	0.025	0.153	0.028	-0.047	0.87	0.245
		LAI > 1	0.249	0.029	0.248	0.032	-0.001	0.90	0.216

tance measurements along a transect, leaf-level measurements made at specific heights in the canopy and for specific leaf angle classes). Given the canopies investigated in this study, calculation of the extinction coefficient could be eliminated as an extinction coefficient of 0.5 would suffice [estimates using an extinction coefficient of 0.5 yielded mixed results with only

minor changes in the estimates of APAR_c and associated errors, attributed to the average extinction coefficients derived from the LAI-2000 close to a value of 0.5 (see Table 2)]. However, given the use of the LAI-2000, calculation of the extinction coefficient was only a minor amount of added effort in this study.

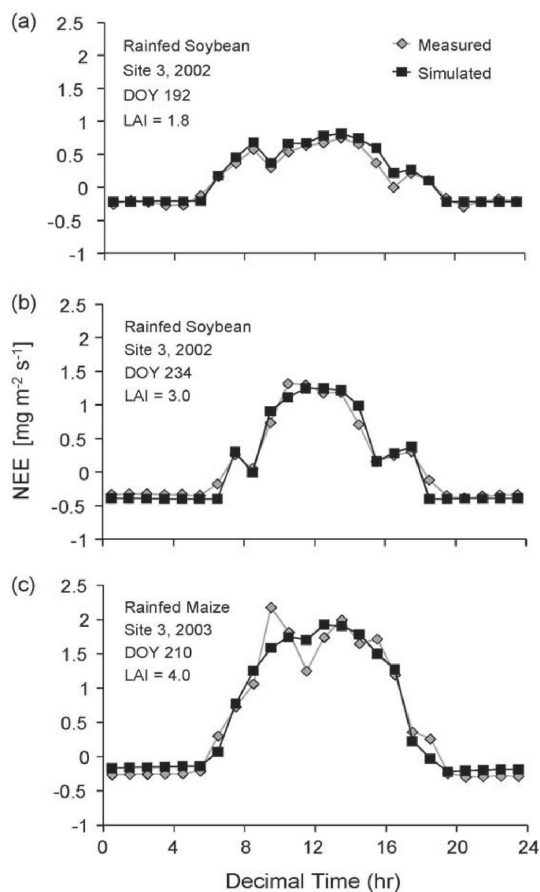


Figure 8. Hourly values of measured and simulated net CO₂ ecosystem exchange (NEE) for three different days at the rainfed maize/soybean rotation site (Site 3): (a) DOY 192, 2002; (b) DOY 234, 2002; and (c) DOY 210, 2003. Days differ in crop type, LAI and sky conditions.

NEE was simulated for days on which the leaf-level light response curves were made. In general, the simulated daytime NEE values also compared favorably with the eddy covariance measurements. Representative diel examples, showing hourly values of measured and simulated NEE from continuous maize and maize/soybean rotations, irrigated and rainfed sites appear in Figures 6–8. The effects of periods of cloudiness on NEE were, in general, adequately simulated. On a diel basis, the simulated and measured NEE differed at times; these discrepancies were most evident in mid- to late-afternoon periods (e.g., Figure 7). A probable reason for these discrepancies is the effect of other environmental factors (e.g., vapor pressure deficit or humidity, CO₂ concentration; Sharkey, 1985) on leaf gas exchange; these factors were not considered in our analysis. Changes in these factors between the time of measurement of the light response curves and the time of the eddy covariance measurements could thus be responsible since the light response curves were typically obtained during the morning hours.

Nighttime NEE estimates were based on soil CO₂ flux measurements and single leaf respiration rates as a function of temperature. The nighttime NEE were simulated fairly well (Figures 6–8). At times, the transition periods between daytime and nighttime showed a difference between simulated and measured values (e.g., DOY 234 Figure 8). This is probably due to the rather arbitrary cutoff that was used to separate daytime and nighttime in the simulations, that is, solar zenith angles greater than 80° were considered nighttime and the

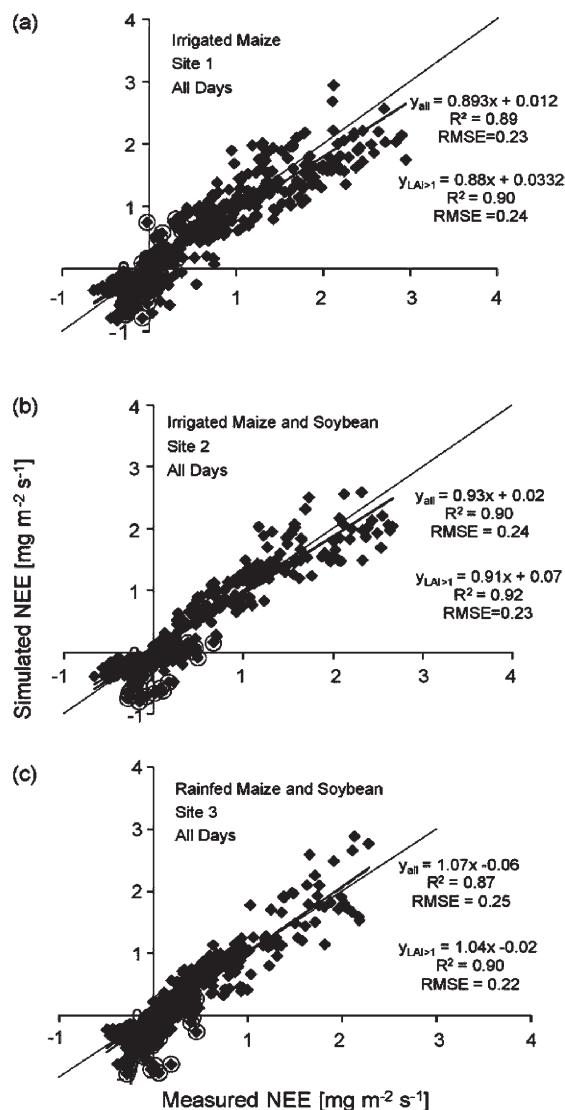


Figure 9. Hourly values of measured and simulated NEE for all days at each site of the study in which leaf properties were measured: (a) irrigated maize, Site 1; (b) irrigated maize–soybean, Site 2; and (c) rainfed maize–soybean, Site 3. Two different regressions are presented: (1) all days (solid line) and (2) for all days with green LAI greater than 1 (dashed line). Values for conditions of green LAI less than one are circled.

canopy was assumed to be respiring. However, it is likely that a small amount of CO₂ assimilation (photosynthesis) was occurring during the transitions and this appears in the eddy covariance data sets since the simulated NEE values are smaller (less positive) than the eddy covariance NEE measurements.

Overall, the good simulation of the canopy light interactions (as evidenced by the APAR_c simulations) yielded fairly good NEE estimates regardless of canopy type and cover (Figure 9). Linear regression slopes varied from 0.88 to 1.07 and RMSE values varied from 0.22 to 0.25 mg m⁻² s⁻¹. There was no apparent difference in the agreement between measured and simulated values at the three sites nor between the maize versus soybean data. At times, relatively large differences occurred at all sites, however, when the green LAI was less than one. In these cases, the simulated values were usually smaller than the measured values (the data cluster beneath the 1:1 line in Figure 9). At low LAI the simulations are more dependent on the estimation of soil surface CO₂ fluxes and, hence, discrepancies at low

LAI may indicate an overestimation of the magnitude of the soil flux. Wang and Leuning (1998b) also used a sun and shade leaf scaling procedure to estimate canopy CO₂ fluxes in wheat and found that uncertainties in the estimates of soil surface fluxes contributed to discrepancies between their simulated and measured values of canopy level fluxes.

Variability in the soil surface CO₂ flux measurements led to a wide range of parameter values in the fitted Equation (2). Uncertainties in the soil surface flux estimates thus lead to uncertainties in the NEE estimates, particularly at low LAI when the canopy contribution to NEE is small. The model that was used (Equation (2)) is undoubtedly an oversimplification of the underlying processes. For example, the sites were under no-till and there was a lot of surface residue present, particularly in the years after maize was grown. The residue often has a different temperature and water content than the soil at 0.1 m (the depth that was used for the soil temperature and water content in Equation (2)). Moreover, the temperature and water content of the residue varies much faster than the soil. Since the residue can be a large component of the total surface flux, Equation (2) is too simple and a multicomponent soil surface flux model may perform better. Further investigation and analyses of this component of the NEE model is currently underway.

Taken as a whole, the results increase confidence in the component measurements that make up the input data for the simulations as well as the representation of the leaf and soil CO₂ flux as a function of incident PAR and soil temperature, respectively. The high degree of correspondence between the eddy covariance measurements and the simulations are especially encouraging considering the simplicity of the underlying model.

4. Conclusions

The relatively good agreement between estimated and measured values of APAR_c and NEE increases our confidence in the measured APAR and carbon fluxes in these agroecosystems as well as the measured input data sets (e.g., soil and air temperatures, LAI, leaf angle distribution) for the simulations. Moreover, the results obtained here support the validity of the underlying model; that is, under many conditions where the assumption of random leaf distribution is approached (such as under conditions of LAI greater than one) a simple approach to modeling APAR_c and NEE adequately represents the behavior of the underlying vegetation. Similar conclusions were reached by other investigators using simplified sunlit and shaded leaf models (e.g., De Pury and Farquhar, 1997; Wang and Leuning, 1998b). The results enhance our understanding of biophysical controls on carbon fluxes further demonstrating the importance of canopy architecture (i.e., leaf area index and leaf angle distribution), canopy light conditions (i.e., sunlit and shaded leaf areas) and leaf responses to light and soil surface CO₂ flux responses to temperature. These data sets are available for many research sites and would be very useful for internal consistency checks on measured APAR_c and NEE values. Less readily available is more detailed knowledge of canopy conditions, for example, the distribution of leaf area with height in the canopy and explicit consideration of the angular distribution of leaf area in the canopy and foliage clumping. These may be necessary to decrease the simulation errors in APAR_c. To increase the correspondence between measured and simulated values of NEE more detailed knowledge of the dependence of leaf gas exchange on other environmental conditions (e.g., CO₂ concentration, vapor pressure deficit) in addition to the detailed canopy condition information, will likely be critical.

Acknowledgments

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