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1. INTRODUCTION

Net canopy photosynthesis (P_n) has been defined by Brisco et al. (1975) as

$$P_{n} = \sum (P_{a} + R_{s}) - \sum (R_{a} - R_{s})$$
(1)

where P_a is the photosynthesis attributed to CO_2 from the atmosphere, R_a is sum of respiration from the soil (R_s), roots (R_r), and canopy (R_c). P_a is greater than zero only during the daylight hours. R_s , R_r and R_a are greater than zero 24 hours a day. At an open-path infrared gas analyzer (IRGA) properly installed in the field, $P_a - R_a$ is measured during the daylight hours, and includes any of the carbon from R_s that escapes from the canopy. However in this instance, it is assumed that all R_s during the daylight hours is fixed by canopy photosynthesis, and during the dark hours, assuming adequate mechanical mixing, R_s is released into the atmosphere.

Observations of CO_2 fluxes from corn (*Zea mays* L.) canopies have been used to estimate the net ecosystem productivity (NEP) during a growing season. Comparisons of carbon fixation from an open path IRGA and periodic biomass sampling has revealed an underestimate of the carbon fixed as measured by the IRGA (Hollinger and Meyers, 2002). In earlier work Hollinger and Meyers (2002) showed that accumulating the mean 30-minute night R_s with the daylight CO_2 accumulation obtained from the IRGA resulted in a reasonable estimate of NEP (Figure 1). R_s was estimated using the mean dark hours R_a measured by eddy covariance methods.

 CO_2 profile measurements made in a canopy show an accumulation of CO_2 in the canopy during the night. During the daylight hours, CO_2 is depleted from the mid-canopy (Prueger et al. 2004). Near the soil surface the CO_2 concentration $[CO_2]$ is greater than at mid-canopy. Such a profile suggests R_s may be inferred from profile measurements of $[CO_2]$.

The objective of this paper is to examine the contribution to NEP of R_s , measured with a CO_2 profile system located in a corn canopy.



Figure 1. Comparison between NEP estimated from biomass samples and eddy-covariance fluxes.

2. METHODS

 CO_2 profiles were monitored in a no-till corn canopy, at the AmeriFlux tower located near Champaign, Illinois during the summer of 2003. The profile system consisted of a Li-Cor 820 CO_2 Analyzer** (LI-COR Incorporated, Lincoln, Nebraska), with four switchable ports, allowing for the monitoring of three levels, and one calibration port. The sampling lines were purged for 30 seconds before sampling began. Each night at midnight local standard time (LST) the gas analyzer was calibrated by purging the line of CO_2 and then a CO_2 standard was sampled. The three sample inlets were located at 0.05 m above the soil, at mid-canopy height, and at 10 m above the soil, the elevation of the open path IRGA on the AmeriFlux tower.

Measurements from AmeriFlux tower included CO_2 and H_2O_v eddy covariance measurements, solar components (incoming and outgoing long and short wave radiation, net radiation, incoming and outgoing

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^{**}Mention of specific brand names is for convenience only and does not imply endorsement of a specific instrument or company or other comparable instruments or equipment.

photosynthetic flux density), soil heat flux, surface temperature, air temperature and humidity, precipitation, soil moisture and temperature to depths of 1.0 m and 1.28 m, barometric pressure, and wind speed and direction. All variables were accumulated to 30 minute means.

Biomass measurements were collected once per week. These measurements included wet biomass of leaves, stems, sheaths, husks, cobs, and grain and leaf area index by two methods. The leaf area was measured optically with a LI-2000, and by manual measurement of the length and width of each leaf on three plants. Dry biomass for each of the plant compartments were obtained by drying the biomass samples in an oven at 50°C for two days. Three samples were collected from the field each week and the means and standard errors computed.

The CO₂ profile and AmeriFlux data were used to compute fluxes of CO₂ in the canopy. The flux from the 0.05 m level to the mid-canopy level was accumulated during the daylight hours to estimate the contribution of R_s to canopy photosynthesis.

Fluxes from the CO_2 profile measurements were computed assuming a logarithmic wind profile above the canopy. Wind speed at the top of the canopy (u_h) was computed by

$$u_{h} = \frac{u^{*}}{0.4} \ln \left[\frac{h - d}{z_{0}} \right]$$
(2)

where h is the height of the canopy, d the zero plane displacement, Z_0 the momentum roughness parameter, and u* the friction velocity. d was estimated using 0.65h and Z_0 was estimated as 0.1h (Campbell and Norman 1997). u* was determined using the momentum flux term (u'w') from the eddy covariance 3-dimensional sonic measurements. In the cases where u'w' was not available (2) was solved for u* using the mean wind speed at 10 m in place of u_h

In the top 90 percent of the canopy, the wind speed was computed by (Campbell and Norman 1997)

$$u_{z} = u_{h} \exp\left[a\left(\frac{z}{h} - 1\right)\right]$$
(3)

where u_z is the wind speed at height z in the canopy, u_h is computed from (2) and a is the attenuation coefficient computed as

$$a = \left(\frac{0.2 L_t h}{l_m}\right). \tag{4}$$

In (4) L_t is the total leaf area index of the canopy, and $I_{\rm m}$ the mean distance between leaves in the canopy given by

$$l_m = \left(\frac{4wh}{\pi L_t}\right) \tag{5}$$

and w is the mean width of the leaves (Campbell and Norman 1997) measured on a weekly basis.

The 0.05 m CO₂ profile inlet was in the lowest 10 percent of the canopy, a height below the level where (3) is applicable (Campbell and Norman 1997). Therefore, to compute the wind speed at 0.05 m, (2) was solved for u* with h replaced by h_i which was equal 0.1h, d was assumed to be zero, and z_0 was assumed to be 0.01 m. Using the new computed u*, (2) was then used to compute the wind speed at 0.05 m.

The flux of R_s to the mid-canopy was computed using K-theory (Campbell and Norman 1997), a log profile estimate, and an estimate from eddy fluxes during the night hours. The K-theory estimate is given by

$$C = -K_c \rho \frac{dC_c}{dz} \tag{6}$$

where K_c , the CO₂ diffusivity, is equal to $0.15\sigma_w$ (Meyers and Paw U 1987). σ_w is the standard deviation of the vertical wind velocity measured by the 3-dimensional sonic anemometer. The log profile flux estimates were computed using

$$\frac{E}{\sigma} = -\left(\frac{k}{\ln(0.05 / z_m)}\right)^2 (\bar{u}_{0.05} - \bar{u}_m) (\bar{c}_{0.05} - \bar{c}_m) (7)$$

where the 0.05 subscript denotes the 0.05 m height of the lowest CO_2 profile inlet, m denotes the midcanopy inlet height. \mathcal{U} and \mathcal{C} are the mean wind speed and $[CO_2]$ at the two heights. The R_s estimated from the eddy covariance measurements was the mean of all 30-minute night time CO_2 fluxes for the period from 20 June through 7 September.

3. RESULTS

Data were collected from the profile beginning on 20 June 2003 (day 171) and continued through the end of the year. For the period of 20 June through 7 September, the profile data show highest $[CO_2]$ of the three levels near the middle of the canopy at 0330LST (Table 1), and the lowest $[CO_2]$ of the three levels near the mid-canopy height at 1330 LST. At sunrise (0600 LST) and sunset (1800 LST) a continuous gradient from the soil surface to the 10 m level is observed.

 $[CO_2]$ at the three profile levels for the period of 16 to 19 August (day 228 to 231) show an example of profile $[CO_2]$ under different turbulent conditions (Figure 2). During the night of 16-17 August (day

Table 1. Mean CO_2 concentration (ppm) at three levels at time of maximum concentration at midcanopy (1.2 m) height, sunrise, minimum concentration at mid-canopy, and sunset.

	Time of Day (LST)			
Height	0330	Sunrise 0600	1330	Sunset 1800
10 m	440.0	438.9	360.5	363.3
1.2 m	495.7	463.0	346.6	368.8
0.05 m	502.1	474.5	358.2	390.1

228-229) the standard deviation of the vertical wind speed (σ_w) was less than 0.1 m s⁻¹ and there was a strong CO₂ gradient between the canopy and the atmosphere at 10 m (Figure 2a). The vertical line in figure 2 is at 0600 on 17 August and shows that the gradient was broken down in approximately two hours. Coincident with the breakdown of the gradient is a spike of CO₂ exiting the canopy as shown in the carbon flux trace (Figure 2b), an increase in the wind speed from <1 m s⁻¹ to approximately 2 m s⁻¹ (Figure 2c), and an increase in σ_w from, <0.1 m s⁻¹ to approximately 0.4 m s⁻¹ (Figure 2d). On the following night (17-18 August, day 229-230), there is only a small increase in canopy [CO2] over that in the atmosphere at 10 m (Figure 2a). This night was characterized by wind speeds between 2 and 3 m s⁻¹ and σ_w greater than 0.2 m s⁻¹. The carbon flux (Figure 2b) also shows a continuous efflux of carbon throughout the night, showing a coupling of the canopy with the atmosphere during the night of 17-18 August.

During the daylight hours, when carbon is being taken up by photosynthesis, the $[CO_2]$ is lowest in the mid-canopy from approximately 0800 to 1600. Consistent with uptake of carbon from the atmosphere as seen by the carbon flux (Figure 2b). The lower $[CO_2]$ at the mid-canopy compared to the 0.05 m level also indicates a contribution to photosynthesis from R_s .

The total contribution of R_s , including both soil and root respiration, was estimated by summing the day time estimates of the fluxes estimated from the K-theory, the log-profile method, and the night eddy covariance measurements. K-theory produced the largest rate of soil CO₂ fluxes (31.02 µmol m⁻² s⁻¹ during the day light hours, and 13.63 µmol m⁻² s⁻¹ during the night) and the eddy covariance measurements the smallest (3.97 µmol m⁻² s⁻¹). The log profile mean day flux was 10.69 µmol m⁻² s⁻¹ and at night 5.56 µmol m⁻² s⁻¹.



Figure 2. $[CO_2]$ traces at two levels in the canopy and one in the atmosphere (a), carbon flux (b), wind speed (c), and the standard deviation of the vertical wind velocity (σ_w).

The 30 minute K-theory and log profile estimates of C accumulation attributed to R_s were added to the corresponding 30-minute time period of C from the atmosphere. For the eddy flux estimates, the night time estimate of R_s was added to the day light 30-minute flux measurements.

Even with gaps in the data, both the K-theory



Figure 3. Carbon accumulation compared to weekly biomass measurements. The bars associated with the weekly biomass measurements are standard errors of the means.

and log profile overestimated the C assimilated by the canopy (Figure 3). Accumulating C from the observed C fluxes from eddy covariance, backfilling the gaps in the measurements, and including estimates of R_s from the mean night CO₂ fluxes resulted in the best fit to the final biomass C estimate (Figure 3).

4. DISCUSSION

The CO₂ profile measurements clearly show an accumulation of CO₂ in the corn canopy during night hours. However, this accumulation does not occur every night. CO₂ accumulates on nights with little or no turbulent mixing characterized by σ_w less than 0.1 m s⁻¹ and wind speeds less than 2 m s⁻¹. On these nights [CO₂] as great as 1000 ppm may be observed. The fate of these high [CO₂] is of interest, because if these concentrations were to persist into the daylight hours, photosynthesis rates would be stimulated. Comparing the profile concentrations to

the eddy flux measurements and wind speed shows that these elevated concentrations are short lived in, and are generally flushed from, the canopy at sunrise. In fact, any time the 30-minute σ_w exceeds 0.1 m s⁻¹ any accumulation of CO₂ is flushed from the canopy, and is detected by the open-path IRGA at 10 m above the surface. Therefore, we conclude that CO₂ released from the soil and canopy at night is not available for photosynthesis the next day.

On nights when σ_w is greater than 0.1 m s⁻¹ CO₂ flux from the canopy is consistently measured at 10 m. On these nights there is a monotonic gradient from the surface to 10 m, with the highest concentrations occurring at the soil surface.

 $[CO_2]$ are greatest at night (Table 1) at the three levels where measurements were made and begin to decrease at sunrise. By mid-day the middle of the canopy $[CO_2]$ are lower than the 0.05 and 10 m levels, producing a gradient between the 10 m and mid-canopy heights and between the 0.05 m and mid-canopy heights. These gradients support the hypothesis that the atmosphere and soil both contribute CO₂ to the photosynthesis process.

Previous work (Hollinger and Meyers 2002) showed that estimating the R_s from the night eddy covariance measurements resulted in a reasonable estimate of the C accumulated in the biomass of both corn and soybean canopies. This work supports that earlier observation. Intuitively, use of the CO_2 profile measurements should have resulted in a better estimate. However, both estimates using the profile measurements fail to accurately estimate the R_s contribution to canopy C. This failure is due to the application of the K-theory and log-profile methods to measurements and fluxes within a canopy. Both methods apply best to above canopy profiles. This initial analysis demonstrates the need to adapt models and procedures that work within canopies. In the interim, above canopy estimates of R_s may be used to improve estimates of NPP.

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