Reprinted from the AGRONOMY JOURNAL
Vol. 58:265–268, 1966.

Photosynthesis Under Field Conditions. IX. Vertical Distribution of Photosynthesis Within a Corn Crop[1]

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ABSTRACT

The vertical distribution of the photosynthetic fixation of carbon dioxide within a crop of corn was calculated from carbon dioxide profile data and transfer coefficients obtained by analysis of windspeed measurements. Infrared analyzers were used to measure the carbon dioxide concentration at several heights within and above the crop. The calculated total fixation for the day was approximately 60 g CO_2 m^{-2} (equivalent to 470 pounds of sugar per acre per day). The results demonstrated the importance of the upper leaves in the fixation of carbon dioxide and showed the increased fixation by the lower leaves during periods of high light penetration. There was some indication that a coupling existed between the level of windspeed and fixation under conditions of high light and relatively low windspeed. With refinement in technique the method could be used to obtain more quantitative estimates of the distribution of photosynthesis in other crops.

THE aerodynamic technique has been increasingly used to determine the vertical transfer of molecular quantities between the vegetation at the earth's surface and the atmosphere. Initially it was used to study the vertical flux of heat and water vapor from a vegetated land, or water surface (2, 7, 10, 11, 12). It has more recently been used to estimate the vertical flux of carbon dioxide between the atmosphere and the total plant community of a field (3, 4, 5, 6, 8, 9). Although those who have used the method are not in exact agreement as to its utility or validity, the technique has served as a useful tool for studying the physiological processes occurring at the earth's surface. It offers the desirable feature that processes may be studied under natural field conditions.

Inoue et al. (3, 4) calculated the total photosynthesis for a rice nursery and a wheat field from aerodynamic measurements of windspeed and CO_2 (carbon dioxide) above the crop. Lemon (5, 6) used the aerodynamic method to calculate the turbulent CO_2 exchange from a cornfield. He compared the calculated fluxes with values of fixation obtained from closed canopy studies at the same location as described by Moss, Musgrave and Lemon (10). Monteith has also used the approach and has discussed the measurement and interpretation of CO_2 fluxes in the field (8, 9). In these studies the measurements have been made within the air layer above the vegetated surface where the vertical flux is assumed to be constant. The results therefore deal with the response of the entire plant community.

In addition, however, a need exists for information about the vertical distribution of CO_2 fixation within the plant canopy, the zone above the soil occupied by the plant community. The situation within this plant-air-layer is even more complicated than in the surface-air-layer above. The various portions of the plants are sources and sinks for CO_2 and other molecular quantities as well as drag surfaces which greatly modify the turbulence pattern.

The investigation discussed in this paper was undertaken to gain more detailed information about the photosynthetic fixation of CO_2 layer-by-layer within a crop of corn.

CO_2 concentration profile and windspeed measurements were made within and above a crop of corn during the summer of 1961. The analysis of the windspeed measurements to calculate the transfer coefficients required in calculating the transfer rates of CO_2 has been discussed in the accompanying preceding paper by the authors (14). The vertical flux distribution of CO_2 within the crop was determined by the hour for the afternoon. The divergence of the flux with height was used as a measure of the net photosynthetic fixation of CO_2.

At the time this study was conducted much time and effort was required to analyze the windspeed data. Therefore the results for only one day are presented. Other measurements within the crop have been made since those for this study were completed. The results of the latter studies will be reported separately in the future when the analysis is completed.

[1] Contribution from the Northeast Branch, Soil and Water Conservation Research Division, ARS, USDA, in cooperation with the New York State Agr. Exp. Sta. at Cornell University. The work was supported in part by the Meteorology Dept., U. S. Army Electronics Research and Development Activity, Fort Huachuca, Ariz. Dept. of Agronomy Paper Series No. 679. This paper is a portion of the thesis submitted by the senior author in partial fulfillment of the requirements for the Ph.D. degree at Cornell University. Presented in part by the senior author before Div. S-1, SSSA, Denver, Colo., Nov. 18–21, 1963. Received for publication June 21, 1965.

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PROCEDURES

CO_2 concentrations and gradients were measured on a clear day, August 1, 1961, at various heights in a densely planted 10-acre field of corn at Ithaca (Ellis Hollow), N. Y. The location was the same as that described for the wind study (14). The crop had a height of 220 cm and had not yet reached the tasseling stage.

Apparatus

A very sensitive specially designed infrared CO_2 analyzer (Lira M-100, *modified*)[3] was used to measure concentration gradients. The analyzer consisted of two infrared detector cells 40 inches in length arranged so that separate air samples could flow continuously through each cell. The signal from the analyzer represented the difference in the CO_2 concentration of the air passing through the two cells. The analyzer had a high CO_2 to water vapor discrimination eliminating the need to remove water vapor from the airstream when the water vapor concentrations remained within the range normally encountered in the field.

The electronic recorder with the analyzer had a span step-response time rating of 10 seconds, nominal, and a span of 100 millivolts (100 scale divisions on a 10.5 inch strip chart). The recorder was integrated into the feedback servo balancing mechanism which balanced the intensity of the infrared beams in the two cells. The system was relatively free of drift because of its null balancing feature. The recorder range was equivalent to a differential of 25 ppm CO_2 concentration.[4] The system as used gave a center zero on the recorder for a zero concentration difference so that the range was $\pm$ 12.5 ppm with a sensitivity of $\pm$ 0.2 ppm. The amplifier gain and damping controls were set so that 99% of a 10 ppm differential change was recorded in 10 seconds.

The airflow into each cell was adjusted to 1000 cm^3 min^{-1} by flow meters and the air sample was exhausted at ambient pressure. An equal pressure was thus maintained in each cell of the analyzer.

A separate infrared CO_2 analyzer was used to obtain the absolute concentration of one of the air samples passing through the differential analyzer.

[3] Trade names or manufacturers are listed for convenience only and do not imply any endorsement by the U. S. Department of Agriculture.

[4] The CO_2 concentrations are expressed on a ppm (part per million) basis following the convention of representing gas concentrations on a volumetric or mole fraction basis.

Sampling

To facilitate CO_2 sampling, a series of perforated garden hoses (polyvinyl chloride) 25 feet in length were suspended across the rows at heights of 20, 75, 135, 175, 200, 260, and 350 cm within and above the crop. Only two heights were sampled simultaneously. Therefore, the 260 cm height was chosen as a reference height and was sampled continuously. It was connected to one cell of the differential analyzer and to the absolute analyzer as well. The remaining heights were sampled sequentially for 10 minutes once each hour. The first 5 minutes of each 10-minute period was used to change the lead-in hose for each height and to allow sufficient time for the air sample to pass through the analyzers. The last 5 minutes were used for recording. Measurements commenced at near noon and continued for nearly 9 hours.

The continuous air samples were drawn from the sampling hoses and transferred to the analyzers through two garden hoses (polyvinyl chloride) by air pumps. A large airflow of 28 liters per minute was maintained through the sampling hoses which decreased the time lag to less than 1 minute between sampling and measurement. This also decreased any possible error of CO_2 diffusion through the walls of the lead-in hoses. Only a small portion of the airflow was drawn off through the needle valves and flow meters for analysis.

The mean values for each sampling period were calculated from the chart data. Continuous profiles were then constructed for each hour using the differential concentration values between each height and the reference height and the absolute concentration at the reference height.

RESULTS AND DISCUSSION

An example of the trace from the differential CO_2 analyzer showing the fluctuating CO_2 concentration differences between two heights is given in Fig. 1. During the afternoon the absolute concentration at the reference level remained fairly steady so the normalization was simplified for this period. The CO_2 profiles obtained for the period from 1200 to 1800 hours EST (Eastern Standard Time) are presented in Fig. 2. The profile data for 1800 to 2100 hours and for 0500 to 0600 hours on the following day are given in Table 1.

The smooth, gradual inflection of the 1200-hour profile, as contrasted with the sharper inflection of the profiles for

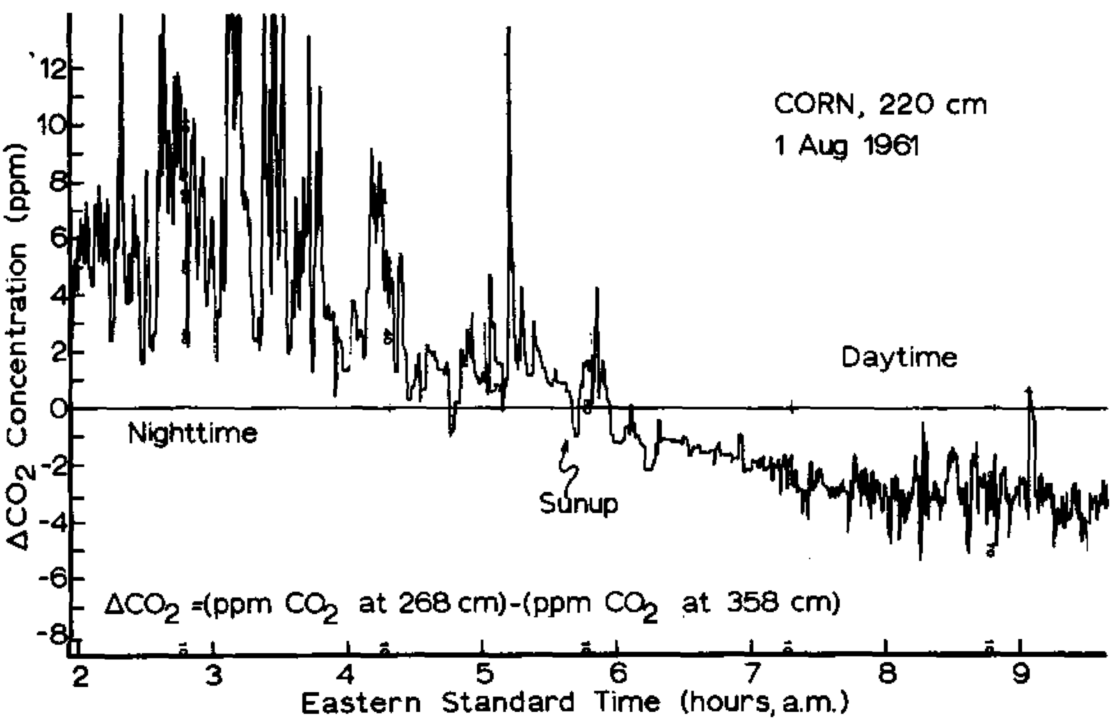

Fig. 1. Trace of ΔCO_2 concentration above the crop showing the nature of the variations, the effects of nighttime atmospheric stability, and daytime CO_2 fixation.

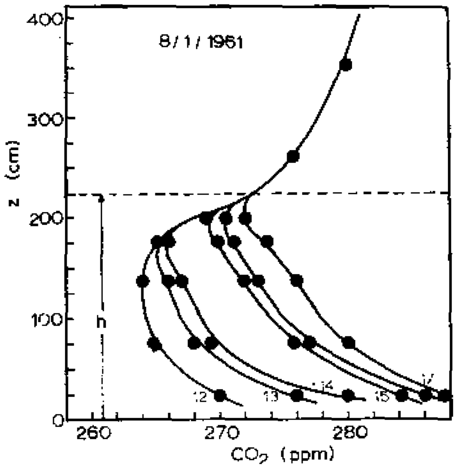

Fig. 2. CO_2 profiles within and above a corn crop for the period 1200–1700 hours EST (Ellis Hollow) where z is height above ground.

Table 1. Concentrations of carbon dioxide at several heights within and above an immature corn crop, 220 cm high, August 1, 2, 1961.

Height cm	CO_2 concentration, ppm			
	EST, hours			
	1800-1900	1900-2000	2000-2100	0500-0600
350	304	348	374	312
260	300	350	376	313
200	295	349	376	314
175	298	355	379	314
135	300	354	378	317
75	305	356	381	326
20	305	358	383	327

the later hours, represents a light effect. (At 1200 hours the sun angle was greatest so that light penetrated with higher intensity into the crop.) This increased the photosynthetic activity of the lower leaves and thus also the sink strength for CO_2. The height of the profile minimum within the crop moved upwards as the afternoon progressed and the sun angle decreased. This corresponds nicely with the results of the radiation mesaurements made by Allen, Yocum, and Lemon (1) on a different date within the same crop. They measured the intensity of the sunlight at several heights within the crop throughout the day.

The position of the minimum within the crop indicates the height at which the flux direction changes. It does not correspond to the height at which photosynthesis is balanced by respiration. (This height cannot be detected from the concentration profiles alone because there is a net flux of CO_2 upward from the soil itself.) Sundown occurred at approximately 1900 hours so the 1900-hour profile showed only a slight minimum within the crop. The increase in concentration with depth into the crop in the case of the 2000-hour profile showed the reverse role of the crop as a source rather than as a sink for CO_2.

Vertical Flux of Carbon Dioxide

The vertical flux of CO_2 at some height z is given by

$$P_s = \rho_a K_C \, dC/dz \qquad [1]$$

where P_s is the vertical flux taken for convenience to be positive in the downwards direction (g cm^{-2} sec^{-1}), ρ_a is the air density at the prevailing temperature and pressure (g/cm^3), K_C is the CO_2 transfer coefficient (cm^2 sec^{-1}), dC/dz is the CO_2 concentration gradient (g CO_2 per g air per cm), and C is the specific CO_2 concentration (g CO_2 per g air). Equation [1] is an analog of the turbulent momentum transfer equation given by Equation [3] in (14).

Inasmuch as the infrared analyzers measured CO_2 concentrations on a ppm basis, the vertical flux was actually calculated by

$$P_s = K_C \, dC'/dz \qquad [2]$$

where C′ is the CO_2 density in the air[5] (g CO_2 per cm^3 air). As used in this study, this is the transfer equation for CO_2. Under turbulent conditions the bulk of the mixing in the moving air stream is due to turbulent transfer so that molecular diffusion can be neglected.

Inasmuch as turbulence involves the movement of macroscopic parcels of air normal to the mean direction of flow, the transfer of the molecular constituents is quantitatively related to the transfer of momentum. Therefore, the transfer coefficient K_C for CO_2 can be taken without serious error to be equal to the transfer coefficient for momentum K_m. Accordingly, K_C in Equation [1] was set equal to the respective K_m calculated from concurrent windspeed measurements (see Wright and Lemon, Table 2 (14)).

The calculated flux of CO_2 on an hourly basis is shown in Fig. 3. The important effect of the transfer coefficient on the flux is expressed by these results. Even though the concentration gradients were lower during the middle of the afternoon than at 1200 hours, the flux of CO_2 was greater because the transfer coefficients were greater. The negative flux (upward flux) of CO_2 from the soil accounted for only a small part of the total even though the gradients were large within the lower portion of the crop.

Calculated Fixation of Carbon Dioxide

The flux difference between two heights represents the net gain or loss of CO_2 in that height interval. The net

[5] 1 ppm CO_2 = 1 cm^3 CO_2 per 1 × 10^6 cm^3 air. CO_2 density = 0.00179 g cm^{-3} at 20C, 740 mm Hg.

Table 2. Mean hourly fixation of CO_2 calculated from transfer rates obtained above and within a corn crop, 220 cm high, August 1, 1961, Ithaca (Ellis Hollow), N. Y.

Time, hours, EST	CO_2 fixation at height intervals, cm							
	20-175		175-200		200-250		Total	
	g*	%	g*	%	g*	%	g*	%
1200-1300	1.42	28	2.74	53	1.00	19	5.14	100
1300-1400	1.54	35	2.37	54	0.52	12	4.42	100
1400-1500	1.69	27	3.99	64	0.47	8	6.14	100
1500-1600	0.44	7	4.92	83	0.57	10	5.93	100
1600-1700	0.47	16	2.16	73	0.30	11	2.94	100
1700-1800	0.32	12	0.93	35	1.44	54	2.68	100
1800-1900	−0.09	−10	0.35	41	0.60	69	0.85	100
1900-2000	−0.06	−75	0.11	138	0.03	37	0.08	100
2000-2100	−0.02	--	0.03	---	−0.08	--	−0.07	---

* Grams/m²/ hour. Positive values indicate sink for CO_2. Negative values indicate source of CO_2.

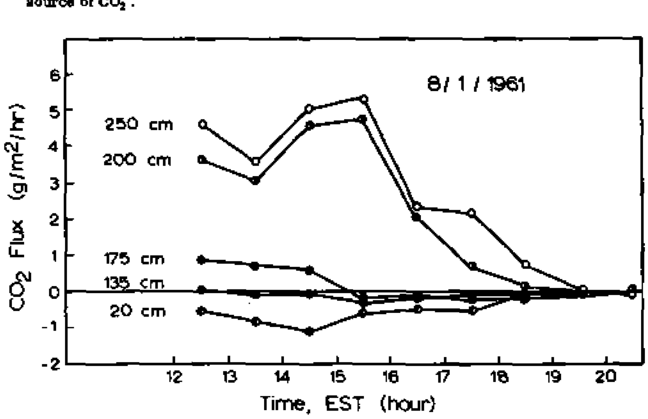

Fig. 3. Hourly mean vertical flux of CO_2 at several heights within and above the corn crop. Positive (+) values indicate downward flux, negative (—) upward flux (crop height = 220 cm, Ellis Hollow).

fixation of CO_2 is a measure of net photosynthesis and the net loss a measure of respiration. (For convenience respiration will be referred to as negative photosynthesis, $-P_s$). In this study an estimation of the net photosynthesis for a given height interval was obtained by taking the difference between the flux into and the flux out of that respective interval. The results are shown in Table 2. The total fixation included the downward flux from the air and the upward flux from the soil. They clearly indicated the active sites of photosynthesis layer by layer within the crop.

The change in air storage of CO_2 represented by the change in the concentration of the air with time was neglected. It was a very small quantity. The maximum hourly change shown in Fig. 2 was less than 10 ppm, which is equivalent to a change in CO_2 concentration of 1.79×10^{-8} g cm^{-3} hr^{-1}. To increase the concentration of an air layer 200 cm deep by 10 ppm would require a flux of 3.59×10^{-6} g cm^{-2} hr^{-1}. This is small compared with a flux of over 5×10^{-4} g cm^{-2} hr^{-1} calculated for photosynthesis.

The 175–200 cm zone accounted for most of the fixation of CO_2 between 53% and 89% of the total depending on the time of day. The percentage contribution of this zone increased as the sun angle decreased while that of the 20–175 cm zone decreased. Even so, the results showed that during the daylight hours even the lower portions of the crop were not a detriment photosynthetically, i.e., they did not reduce the total net fixation of CO_2.

The total fixation for the afternoon was approximately 30 g of CO_2 per m^2. Assuming an equal amount for the morning hours, the total fixation for the day would have been 60 g m^{-2}. This is equivalent to 52 g sugar, which seems like a small amount; however, on an acre basis it amounts to 470 pounds of sugar per acre per day. Sustained production at this rate for 60 days, neglecting all losses such as those due to night-time respiration, would result in a yield of 14.5 tons of sugar per acre.

A comparison of wind intensity, total CO_2 fixation, and total incident radiation, all on an hourly basis, is presented in Fig. 4. The data are shown as percentages of the highest respective intensity. The percentage fixation of CO_2 during the first four-hour period closely paralleled the wind intensity in spite of decreasing incident radiation. The sky was fairly clear throughout most of the afternoon.

By comparison Lemon (6) used wind and CO_2 measurements taken above the crop of the same cornfield during July to calculate the total flux of CO_2. He obtained a peak value for a short time period of 250×10^{-9} g CO_2 cm^{-2} sec^{-1} (9.00 g m^{-2} hr^{-1} compared with the value of 6.18 g m^{-2} hr^{-1} reported here). The highest average for an hourly period was nearly equal to that obtained here.[3] Yocum et al. (15), using the same method, calculated a CO_2 transfer of 0.254×10^{-6} g cm^{-2} sec^{-1} (9.15 g m^{-2} hr^{-1}) for August 16 for the same cornfield. The windspeeds were somewhat higher in their case.

Though only the data for one day have been presented, the results do point to the utility of the technique as a tool for studying the distribution of photosynthesis within the natural environment. The accuracy of these results depends to a large extent upon the accuracy of the turbulent transfer coefficient determinations.

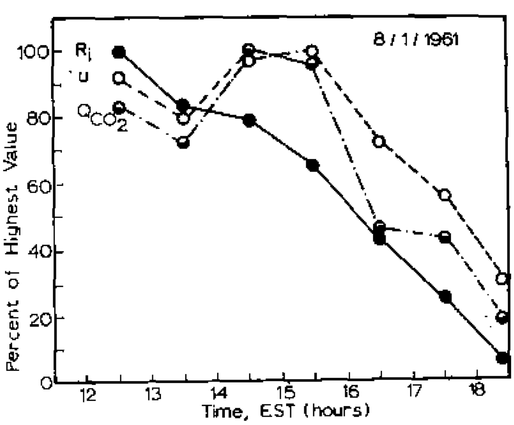

Fig. 4. An hourly comparison of the windspeed at 400 cm, total fixation of CO_2, and incident radiation; all expressed as percentages of the corresponding highest intensity for the afternoon hours (corn crop, Ellis Hollow).

[3] A further comparison for the same period has been made against exchange rates obtained simultaneously from a closed plastic chamber placed over a representative patch of corn in the same field. (Lemon, E. R., Micrometeorology and the Physiology of Plants in Their Natural Environment. *In* Plant Physiology Vol. IV A, (ed.) F. C. Steward, Academic Press 1965.) These data are from the unpublished work of R. B. Musgrave and his former student D. N. Baker. Their peak exchange rates approached 240×10^{-9} g CO_2 cm^{-2} sec^{-1} or 8.6 g m^{-2} hr^{-1}.

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