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Photosynthesis Under Field Conditions. XA. Assessing Sources and Sinks of Carbon Dioxide in a Corn (*Zea mays* L.) Crop Using a Momentum Balance Approach[1]

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ABSTRACT

In a previous communication we described a meteorological method of assessing the vertical distribution of photosynthesis and respiration activity in a corn crop. The method, however, is tedious. Here we describe a much simpler method. Results indicate that all the leaves of a corn crop appear to follow the same near-linear light response curve, at least above the compensation point. Below the compensation point, all leaves evidently respire very little.

Additional key words: **Corn Canopy, Respiration, Light response, Photoefficiency.**

PREVIOUSLY, Wright and Lemon (1966a, 1966b) described an aerodynamic method for evaluating the source and sink distribution of carbon dioxide in plant communities. Data were presented for a corn crop, giving quantitative information about photosynthetic fixation and respiration release of carbon dioxide, layer by layer, within the crop.

With the method, the vertical distribution of CO_2 concentration and the windspeed of the bulk air were measured within and above the crop. The analysis of the windspeed measurements to calculate the necessary diffusivity coefficients required tedious analysis of windspeed fluctuations and the application of complicated statistical and mixing length theories. It is our purpose to present here a simpler method, which requires vertical profiles of mean windspeed, vertical profiles of mean carbon dioxide concentration and representative vertical profiles of the foliage surface area density of the plant community.

THEORY

Given the vertical flux intensity of CO_2 through two horizontal planes within a plant community, the difference between the two intensities gives the source strength (respiration) or sink strength (photosynthesis) of the layer of foliage between the two planes. The vertical flux intensity of CO_2 across each plane at height z above the ground is given by

$$P = K_c \, dC/dz \qquad [1]$$

where P is the flux intensity taken to be positive downwards in $g/cm^2/sec$, K_c is the CO_2 diffusivity coefficient in cm^2/sec, dC/dz is the CO_2 concentration gradient, C is the CO_2 density in the air in g/cm^3, and z is height in cm. The gradient dC/dz is the slope of a mean CO_2 concentration profile at the specified height z. The difference between the previously reported method and this simpler one, called a momentum balance approach, lies in the evaluation of K_c. The analysis of wind profiles by a momentum balance has been discussed by Uchijima and Wright (1964) and Wright (1965). With the reduction in horizontal windspeed at the plant surfaces, there is a transfer of momentum from the wind stream to the plant. Leaf-waving and stalk-bending are manifestations of the frictional drag of the wind on foliage surface. The vertical exchange of horizontal momentum across a windspeed gradient is given by a diffusion-type equation similar to the one for CO_2:

$$\tau = \rho \, K_m \, du/dz \qquad [2]$$

where τ is the mean flux intensity of vertical momentum exchange in $dynes/cm^2$ at some height z; ρ is the

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density of the air (0.00118 g/cm³ at 25 C and 1,013 mb); K_m is the diffusivity coefficient for momentum in cm²/sec; du/dz is the windspeed gradient or the slope of the mean windspeed profile at height z; and u is the mean horizontal wind velocity in cm/sec.

In the application of the momentum balance method it must be assumed that $K_m = K_c$. K_m can be found from Equation [2] by evaluating τ and du/dz at the appropriate level of z. This requires two measurements in the field; the distribution of foliage surface area of the plant community as a function of height and the mean 10- to 20-minute windspeed profile from the ground to well above the plant community. Fig. 1 schematically presents a generalized mean windspeed profile and a foliage area density profile. The figure also shows the method of evaluating τ_z at a specific level z. First, the momentum flux intensity at the top of the vegetation, τ_h, (which is the total downward flux intensity of momentum) is determined from an analysis of the log distribution of the wind velocity above the vegetation by

$$\tau_h = \rho \left[\frac{ku}{\ln (z - D)/z_0} \right]^2 \qquad [3]$$

where k is the von Karman constant (0.4) D is a height displacement parameter (in cm) for the plant community and z_0 is the roughness coefficient in cm. Second, τ_z is evaluated by "partitioning" the momentum extraction with depth into the plant community above the specific level z by

$$\tau_z - \tau_0 = \tau_h - \rho \int_z^h C_D F u^2 \, dz \qquad [4]$$

where C_D is the drag coefficient (dimensionless); F is the leaf or foliage area density, and h is the height of the plant community. The drag at the soil surface, τ_0, is considered to be negligible in dense plant communities, thus in the analysis of data it is assumed that $\tau_0 = 0$.

Finally, the diffusivity coefficient is determined from τ_z by taking the slope du/dz of the mean windspeed profile at the specific height z and solving for K_m by Equation [2].

We shall take up the mechanics of evaluating the drag coefficient C_D, in Equation [4], as well as the other parameters after discussing the field measurements.

PROCEDURE

The necessary field measurements were made on a clear day, September 11, 1963, in an 8-ha (20-acre) cornfield at Ellis Hollow (Ithaca), New York. The site was that of the previous study (Wright and Lemon, 1966a and 1966b). The corn (M-3) was planted in 74-cm (29-inch) north-south rows at a density of 26,000 plants per acre. The crop was luxuriant, having been well fertilized and amply watered by favorable rains. All leaves were still green and evidently very active photosynthetically despite the late date.

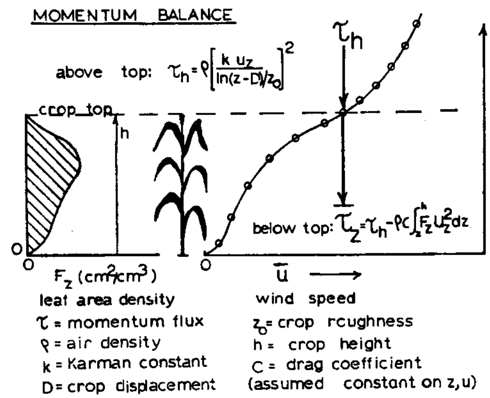


Fig. 1. Schematic representation of momentum balance analysis for a plant community. Profiles of foliage surface density (F) and mean wind velocity $(\bar{u})$ are illustrated. Total drag at the top of the community is indicated by (τ_h) and drag of the canopy layer from z to h is indicated by (τ_z) at level z. The drag coefficient is defined as (C). Other symbols are as found in the text.

test periods with cup anemometers (Thornthwaite Assoc.[3]) placed above the crop 465, 385, 345 and 325 cm above the ground. Crop height, h, was 285. Mean windspeed within the crop was determined by averaging 1-second readings for the 10-minute test period from the continuous recorder traces obtained with the heated thermocouple anemometers (Hastings-Raydist) placed 325, 275, 225, 175, 125, and 75 cm above the ground.

2. *Sampling procedure for CO_2.* Many improvements have been made over the sampling and analytical methods reported earlier for calculating carbon dioxide exchange rates. In the earliest work (Lemon, 1960) carbon dioxide profiles were obtained above the crop by simultaneously sampling the air above the plants at several levels using single hose openings as point sinks at each level. No attempt was made to obtain horizontal, spatially integrated samples, though the samples were time integrated. In more recent work concerning CO_2 profiles within the vegetated canopy of a corn crop (Wright and Lemon, 1966b), a spatially integrating sampling procedure was used; however, air samples were taken in time sequence at the several levels above the ground rather than simultaneously. Thus the profiles could have been nonrepresentative as a result of time fluctuations in carbon dioxide concentration. This error was minimized, nonetheless, because the sampling time was (a) relatively long (10 min) compared to the usual 1/3 to 1/2-cycle-per-minute CO_2 concentration fluctuations commonly experienced in our cornfield, and (b) relatively short compared to the diurnal fluctuations in CO_2 concentrations. In order to avoid the previous possible sampling errors due to time and space fluctuations in CO_2, the following improved sampling procedure was developed.

A series of perforated sampling hoses were suspended horizontally and connected to the suction side of individual air pumps. This provided the means of spatially sampling the air at the various desired heights within and above the crop canopy. Continuous and simultaneous subsampling from the exhaust side of each pump into 24-liter PVC beach balls gave a composite sample, providing a time integration over the 10-min sampling periods.

Common PVC garden hose of 2 cm ID was used both for sampling and lead-in hoses. A 7.5-m section of hose with 0.1-cm-diameter holes drilled every 15 cm served as the horizontal spatial sampler at each given level. Each was connected to a 30-m lead-in hose running along the ground downwind to an instrument trailer housing the pumps and analytical equipment. The 7.5-m sampling hoses were suspended on a wire frame at right angles to the corn rows and the prevailing wind. Spatial canopy with the topmost smaller leaves and corn tassels extending another 50-60 cm above. The lead-in hoses were connected to suction pumps, each having a capacity of 28 liters per minute. This permitted uncontaminated sample air delivery with little delay.

Experience has shown that our relatively high lead-in air-flow rate is important when using plastic tubing because some CO_2 diffuses through the tubing walls when the lead-in is permitted to lie on the ground. Also, the inevitable slow evolution of organic gases out of the hose walls seriously contaminates the sample air if flow rates are too low and/or lead-in is too long. Fortunately, if used properly PVC garden hose is convenient, inexpensive, relatively impervious to CO_2, and of sufficient diameter to easily incorporate an internal heater wire. Internal heater wires are required to prevent water vapor condensation. (We have found, however, that mice chew heated PVC hose during the cool seasons.)

Two reasons are emphasized for preventing water vapor condensation in sample and lead-in hoses with internal heater wires: (*1*) condensed water absorbs and evolves CO_2, imparting historical effects on any given sample, and (*2*) differential evaporation or condensation of water in the sampling hoses creates wide differences in water vapor content in the air samples. This causes serious analytical problems with infrared analysis for CO_2. It is impossible for most of the commonly used commercial infrared CO_2 analyzers to completely discriminate between water vapor and CO_2. Water vapor can give an erroneously high measurement for CO_2. For studies where small CO_2 gradients are measured, water vapor errors have to be eliminated. Either the water vapor must be removed from the sample air before analysis or the measurements must be corrected by knowing both instrument discrimination characteristics and water vapor content of the sample. In these studies the water vapor was removed with magnesium perchlorate before the sample air passed into the storage balloons. Magnesium perchlorate is a preferred absorber. (The same cannot be said for silica gel because it imparts historical effects through absorption and evolution of CO_2 to a given sample of air.) (See Tamm, E. and Krzysch, G., 1959.)

3. *Analytical procedure for CO_2.* Since there were only six pumps available and nine sampling levels, cyclic sampling and analytical procedures were used. That is, six levels at 35, 95, 135, 165, 190, and 225 cm were first sampled simultaneously. The air was stored in six balloons then subsequently analyzed. During the analysis of these first six samples, a second series of six levels, i.e. 165, 190, 225, 250, 280, and 310 cm were sampled, filling a second series of six balloons for subsequent analysis. It was convenient to make simultaneous wind and carbon dioxide runs of 10-min duration twice each hour. Thus each of the two series of six levels was sampled once each hour.

After filling a given series of six balloons, analyses immediately began. This consisted of attaching two balloons to individual aquarium pumps which were matched to give equal flow rates into each of the two cells of the infrared analyzer. Flow rates were adjusted to 1 liter/min and monitored continuously. The outlets of the two cells of the analyzer were to ambient atmospheric pressure. The air from the 225-cm level was used as the reference. The air from this balloon provided reference air to the "reference" cell, and each of the other five sampling balloons of a given series was analyzed in turn by connection to the "sample" cell. During the analysis of each of the five samples against reference, the lead hose connections to the analyzer were reversed at least twice. This in effect mechanically reversed sample and reference cells of the analyzer, providing a check on each analysis and indicating any possible shift in instrument zero.

The instrument used for the differential analysis is of special design, having a range of $\pm$ 12.5 ppm with a sensitivity of $\pm$ 0.2 ppm. Other details of the instrument are reported elsewhere (Wright and Lemon, 1966b). This instrument and another unit used to measure absolute concentrations of CO_2 were calibrated with commercially available standard gases. Experience has shown that both instruments become very stable after 2 or 3 weeks of continuous operation, requiring only an occasional check on calibration span and zero.

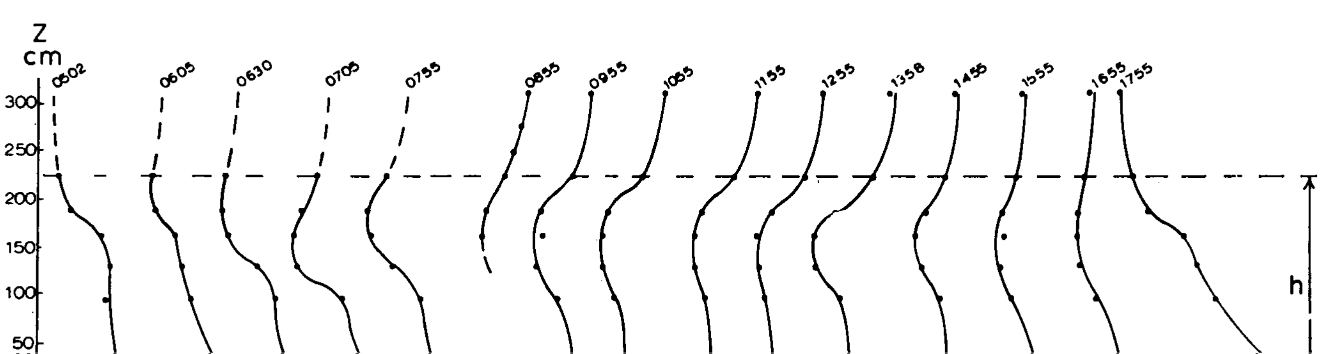
Air from the 225-cm level was continuously monitored for the absolute concentration of carbon dioxide. This permitted the expression of all profiles on an absolute basis.

Since the present study concerns the vertical distribution of activity within the canopy, emphasis is given to those series of samplings that provide complete profiles within the canopy. One profile above the canopy is presented in Fig. 2, however, for interest. Experimental points have been plotted at the 310-cm level for many of the "within canopy profiles." These 310-cm points are to be viewed with caution, however, since they were obtained 30 min after the "within canopy" profiles were taken. Invariably the "above canopy" 310-cm point fell to the right of the extrapolated profile line in the morning and to the left in the afternoon as one would predict. They are included here only as a guide and were not used in subsequent calculations.

4. *Foliage area density measurements.* The surface area of leaves and stalks in 50-cm height increments was measured on each of twenty representative individual plants giving a total of 20 area measurements for each of the five height increments. The surface area of stalk and tassel in the sixth or uppermost height increment was also estimated. The 20 plants chosen for area measurements were individually selected on the basis of height and stem diameter, being "mean" or "standard" plants chosen out of the large population. The leaf area was determined on a one-side basis by measuring length and width and multiplying by the factor 0.75, and estimating what part of each leaf fell within the specific 50-cm increments. Stalk area was estimated from stem diameters, treating them as cylinders.

From the average leaf area (one side) and average stem area per plant within each 50-cm increment, we plotted the accumulated surface area from the top of the crop downward. A smooth curve was then constructed through the points. From this cumulative curve and the population density, a representative foliage area density profile was constructed as shown in Fig. 3 and 4.

5. *Data analysis.* Experience has indicated (Wright, 1965) that more representative wind profiles can be obtained by combining numerous short-time profiles.



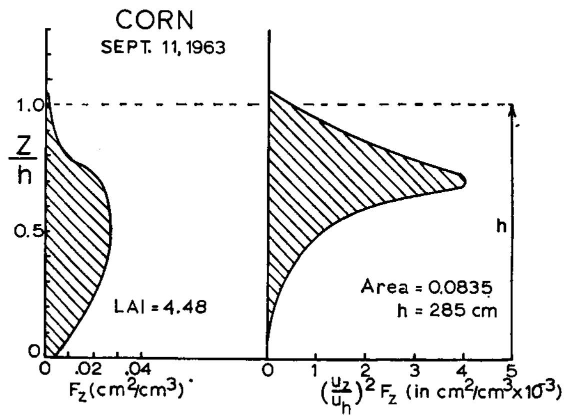


Fig. 3. Foliage area density profile (F_z) and drag distribution ($(u_z/u_h)^2$ F_z) in a cornfield. Ellis Hollow, N. Y.

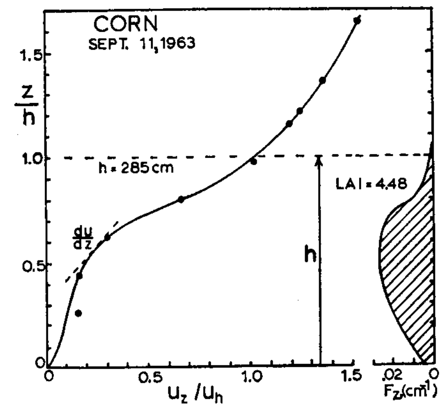


Fig. 4. Foliage area density profile (F_z) and relative mean wind velocity (u_z/u_h) profile in a cornfield. Wind velocity profile is normalized and represents a mean of all profiles taken during the day, September 11, 1963, Ellis Hollow, N. Y. The slope of the profile at a given level z is indicated by du/dz and dashed line.

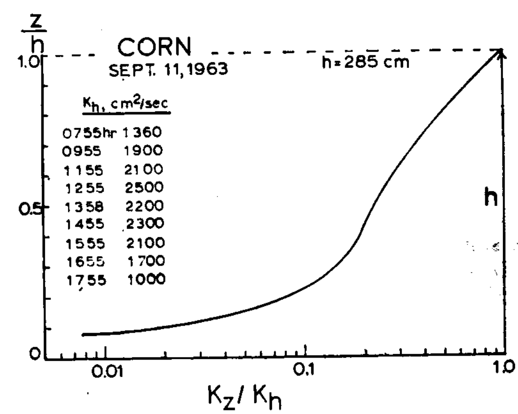


Fig. 5. Mean normalized profile of diffusivity coefficient (K_z/K_h) representing all profiles taken during the day in a cornfield, Ellis Hollow, N. Y.

Therefore, all the wind profiles for the day were individually normalized on the basis of the windspeed at a reference height and then averaged to give a mean normalized wind profile. This is presented in Fig. 4.

A systematic computer analysis of several hundred log wind profiles taken throughout the growing season in 1961, over a similar corn crop at the Ellis Hollow site, provided us with good representative values for the log profile wind parameters required in Equation [3]. The resulting parameter D was 140 cm and the roughness coefficient z_0 was 15 cm. Experience has indicated that Equation [3] does not have to be corrected for nonisothermal conditions when soil moisture is plentiful and thermal convection is therefore small.

We now need to return to the problem of determining the diffusivity coefficient K_m from the momentum balance. The momentum extracted from the wind stream is related primarily to the foliage area. The soil surface plays a negligible role in dense vegetation. Thus the total momentum flux or drag, τ_h, can be defined by:

$$\tau_h = \int_0^h \rho\, C_D\, F\, u^2\, dz. \qquad [5]$$

F and u are functions of height z for which we have field measurements. However, based on laboratory results concerning the drag coefficient C_D for fully developed turbulent flow, and in the absence of more detailed field measurements of C_D, we assumed C_D to be independent of height and windspeed. This permitted solving the equation for C_D:

$$C_D = (\tau_h/\rho) \Big/ \int_0^h F\, u^2\, dz \qquad [6]$$

Thus, if the total drag, τ_h, the foliage area density, F, distribution with height, and the main windspeed, u, distribution with height are known, C_D can be calculated. This gives a mean drag coefficient for the graphically by determining the area under the curve of the vertical distribution of the product F u^2 from z = 0 to z = h. Fig. 3 gives the results; it really presents the distribution of drag in the corn crop.

Having evaluated C_D, a vertical distribution of momentum flux intensities, τ_z, was determined by Equation [4]. Vertical profiles of the momentum diffusivity coefficient, K_m, were constructed from Equation [2].

$$K_m = \frac{\tau_z/\rho}{du/dz} = \frac{(\tau_h/\rho) - C_D \int_z^h F\, u^2\, dz}{du/dz} \qquad [7]$$

Fig. 5 presents the mean normalized profile of the diffusivity coefficient for the day. The absolute values at the top of the community ($K_z/K_h = 1.0$) are given for the specific hours of the day in tabular form in the depth into the canopy is almost linear to more than half way to the ground on a semi-log plot.

With the assumption that $K_m = K_c$, we are now ready to utilize gradients, dC/dz, from the CO_2 profiles in Fig. 2, to calculate CO_2 flux intensities, P, of several levels of z by Equation [1]. The results, presented in Fig. 6, show the quantative intensity of the net upward and downward diffusion streams of carbon dioxide. Positive values on the left-hand side of the figure indicate net downward diffusion. Negative values indicate net upward diffusion on the right of the zero axis. It can be noted here that there was very little CO_2 coming from the soil. Returning to Fig. 2, it can be seen that there was very little increase in CO_2 as the soil was approached. More sampling points very near the soil surface are needed, however, to clarify this point. In any event the increase in upward CO_2 flux into the canopy is evidence that the lower portion of the canopy was respiring. At the level where there was neither a decrease nor increase in upward flux, depending upon the hour of the day, the leaves were at the light compensation point at that position of the canopy. Above this level the upward flux progressively decreased, since photosynthesis was taking CO_2 out of the air, until a level was reached where the CO_2 was no longer diffusing upward but downward from the atmosphere. It is significant that the CO_2 evolved from the ground and the lower portions of a canopy may be reabsorbed in the upper photosynthesizing portions during the day. The 1755-hour profile suggests that reabsorption was not quite complete, since there was then an upward flux throughout the whole profile.

From the slopes of the profiles in Fig. 6, one can construct flux divergence profiles, or source and sink profiles, of carbon dioxide. Fig. 7 presents some representative profiles of this nature. The left-hand side of the axis presents the rate at which CO_2 is being absorbed in photosynthesis in a unit volume of canopy space. On the right of zero is the quantitative rate at which CO_2 is being generated through respiration in a unit volume of canopy space. The qualitative discussion of the curves in Fig. 6 is now elucidated on a quantitative basis in Fig. 7 insofar as defining the levels of photosynthesis and respiration are concerned. The light compensation point is the zero axis profile intercept in this figure. Maximum respiration apparently occurs near corn ear level, while maximum photosynthesis is near maximum foliage area density.

A much more detailed analysis of these last profiles is possible by referring to the radiation studies made simultaneously in the same field by Allen and Brown (1965). They made a careful study of the mean radiation distribution in the canopy in the 0.3 to 0.7μ wave length interval (visible or "photosynthetically active" radiation). From their work one is able to obtain both radiation flux intensities and flux divergence (absorbed light) distributions with height in the canopy. From the latter, photoefficiency curves

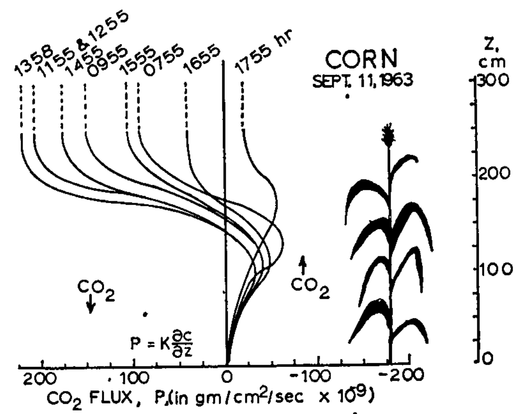


Fig. 6. CO_2 flux (P) profiles in a cornfield as indicated by hour (EST) at the top of each profile. Negative flux indicates net upward CO_2 movement and positive flux indicates net downward CO_2 movement. Ellis Hollow, N. Y.

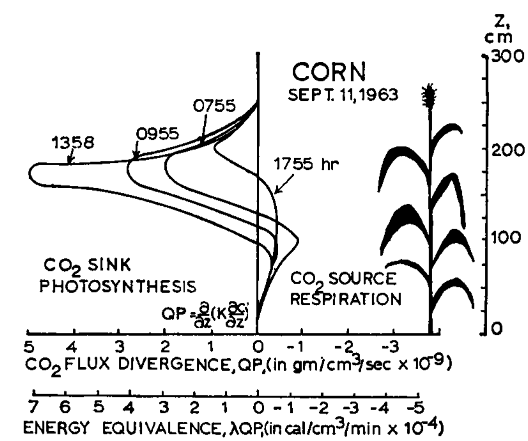


Fig. 7. Source and sink intensity distribution of CO_2 (QP) and photochemical energy (λQP) for indicated time in a corn crop. Negative values signify net respiration and positive values, net photosynthesis. Ellis Hollow, N. Y.

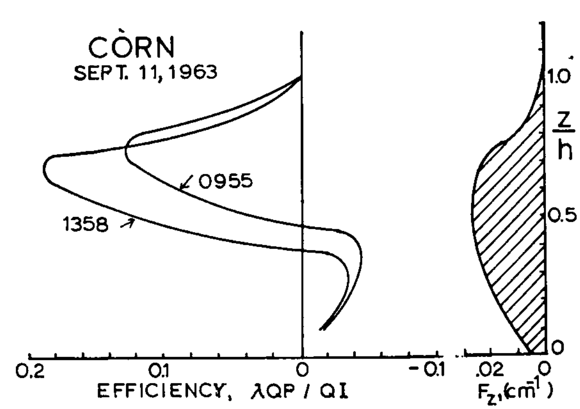


Fig. 8. Efficiency profiles (λQP/QI) of photochemical energy equivalence per unit of absorbed radiation (0.3-0.7μ wave length) in a cornfield at indicated hours. Foliage area density (F_z) profile presented for reference. Positive efficiency

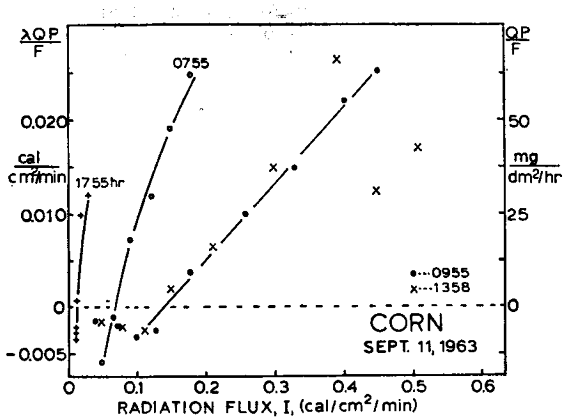


Fig. 9. Light response curves for corn plant community as indicated by hour. Radiation flux is incident intensity (0.3-0.7μ wave length). Photosynthesis and respiration expressed on a foliage area basis as CO_2 exchange or energy equivalence. Each point at a given hour represents a given leaf level in the canopy beginning with the top leaves at 225 cm at the highest radiation intensity and progressing downwards into the canopy in 25-cm increments with decreasing radiation. Not all 1755 and 0755 points near the bottom of the canopy are plotted. Each point is the "mean" response of all foliage at a given level. Ellis Hollow, N. Y.

tion of the 1358 curve compared to that of the 0955 curve.

As for further elucidation of light relationships in the cornfield let us look at some light intensity response curves. In Fig. 9 are plotted the CO_2 exchange rates on a foliage area basis as a function of light intensity. The exchange rates now are expressed in conventional energy and mass units usually employed in the agronomic literature. Foliage area includes leaves and stalks. However, stalk area is an extremely small proportion of the total compared to leaf area. The light intensity is expressed as radiation flux intensity falling on a horizontal surface in the 0.3 to 0.7μ wave length interval. Each point plotted represents a different 25 cm layer of leaves in the cornfield for the hour specified, beginning with the top leaf level of 225 cm at the maximum radiation for that hour and proceeding downward in 25 cm increments with decreasing light intensity. Not all the lower points are plotted for the 0755 and 1755 hours.

Several significant observations can be made from Fig. 9:

(*1*) Apparently all leaves at any given hour follow the same light response curve in well-fertilized and well-watered full-grown corn regardless of the leaf position in the canopy, at least until the compensation point is reached.

(*2*) The light response curves are remarkably linear. This perhaps should be expected on two counts. In the first place the curves represent integrated responses of leaves at all angles in a dense random array with an LAI of 4.3. Baker and Musgrave (1964) using another technique, obtained near linear response for the whole canopy at an LAI of 3.4 to 4.3. In the second place

(*3*) The light compensation point is directly related in some way to the level of total photosynthetic activity of the canopy.

(*4*) The respiration rate is very low and curiously becomes rather constant once the compensation point is reached. Evidently lower leaves of corn are not very "parasitic." The respiration rates and compensation points seem rather insensitive to temperature since they varied: 14 C at 0755, 19 C at 0955, 23 C at 1358 and 19 C at 1755 hours.

Turning back to the differences noted in Fig. 8, it can be seen in Fig. 9 that the light response curves for both the 0955 and 1358 hours are alike except for the upper two or three leaf levels at the top of the canopy. As mentioned previously, the upper leaves might have been under water stress at 1358. Evidently the gross differences in the two curves in Fig. 8 can be fully explained on the basis of a greater radiation flux at 1358. The incident visible radiation flux intensity at the top of the crop was 0.51 cal/cm²/min at 1358 and 0.45 cal/cm²/min at 0955.

On the basis of visible light intensity, the slope of the 0955 and 1358 curves in Fig. 9 yields a photoefficiency of 7.3%. The other two yield efficiencies greater than 25% during periods of low radiation.

In summary, despite the assumptions required in the momentum balance analysis, the end results seem reasonable. This may be due to blind luck in choosing the test crop. Several reasons can be given as to why corn might be a lucky choice: (*1*) First, corn is a relatively open and uniform system. (Several subsequent points arise from these conditions.) (*2*) Open structure prevents development of large gradients in light, wind, temperature, water vapor and carbon dioxide. Thus corn leaves in different portions of the canopy are not exposed to as wide a variation in climate as leaves in a compact system such as clover. This prevents, for example, wide respiration differences due to wide temperature differences. This also prevents disease due to wide variation in humidity. (*3*) Good wind flow characteristics in corn may favor a high Reynolds number so that the assumption of constant drag coefficient is more realistic than in a compact system. (*4*) Forced convection in an open system makes more realistic the assumption that $K_m = K_c$ where "free" convection is probably not as important to diffusion as in a compact system.

Probably the energy balance method of determining the diffusivity coefficient is more correct in compact communities, and the momentum balance method is more applicable to open canopies under good wind conditions.

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