The Exchange of Carbon Dioxide Between the Atmosphere and the Plant

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THE aerodynamic technique has been used to determine the vertical transfer of carbon dioxide between the plant community and the atmosphere. It has also been extended to the aerial environment within the plant canopy to study the vertical distribution of the photosynthetic fixation of CO_2. The method permits the study of carbon dioxide exchange under field conditions for agricultural crops. Measurements of windspeed, plant canopy characteristics and carbon dioxide concentration distributions are required. The results give the relative importance of the various zones of the plant community in the net photosynthetic fixation of CO_2 and the diurnal nature of photosynthesis under field conditions as well as immediate response data to environmental conditions. Such information is valuable for developing models of ideal plant morphology, improved planting patterns for efficient light interception and photosynthesis, and for input into simulation programs.

Introduction

This is a brief review of the application of the aerodynamic approach for determining the exchange of carbon dioxide between the atmosphere and the plant. The intent of the more detailed oral presentation was to bring together information that has been obtained over the past several years on this subject for this special session on the response of plants to CO_2 enriched environments. Because several papers treating the subject have already been published (6, 7, 8, 16)* this summary is to outline the scope of the investigations which have been conducted and to provide specific references to the published results. The procedures for quantifying the mechanisms accomplishing the transfer of molecular CO_2 between the bulk air and the plant surfaces are discussed along with some of the notable results of recent field investigations.

As photosynthesis proceeds, CO_2 molecules are continually extracted from the air surrounding plants and synthesized into photosynthetic products. As a result, CO_2 concentration decreases in the air near the plant surfaces. During photosynthesis the plant acts as a sink for CO_2 and the atmosphere as a source, while during respiration, the situation is reversed. Accordingly a concentration gradient develops and the rate of exchange (flux) of CO_2 along this gradient is a function of the aerodynamic transfer processes which are characterized by a transfer coefficient. The flux of CO_2 is in direct response to the photosynthetic demand for CO_2 by the plant. Therefore, if the transfer coefficient can be determined in some manner and the CO_2 gradient can be measured, the rate of photosynthesis can be studied under field conditions. The aerodynamic approach provides a means of determining the transfer coefficient and thus permits such studies.

The aerodynamic approach has been used to calculate the vertical flux of CO_2 between the atmosphere and the total plant community since the late 1950's (3, 4, 5, 9, 10). Although subject to several critical assumptions and demanding an intensive measurement program, the method has permitted the study of these processes under natural field conditions. More recently the flux of CO_2 layer by layer within a crop has been determined in an attempt to assess the vertical distribution of the photosynthetic fixation of CO_2 within the plant canopy (8, 15, 16). The results of such studies should help explain some of the observed response of plants to controlled environments. They are also useful in developing idealized models of plant morphology, efficient planting patterns and in developing simulation programs. There is currently some very intensive research on these subjects.

Procedures

A means of determining the aerodynamic exchange of CO_2 within the aerial environment of plants is provided by the following equation:

$$P_s = \rho_a K_c (dc/dz) \quad . \ . \ . \ . \ . \ . \ [1]$$

where P_s is the vertical flux of CO_2 (g per sq cm per sec), ρ_a is air density (g per cu cm), K_c is the transfer coefficient for CO_2 (sq cm per sec), c is the specific CO_2 concentration (g CO_2 per g of air), and z is height above ground (cm). For valid calculations using this equation, there must be sufficient uniform area so that horizontal uniformity exists (horizontal divergence of concentration is zero). The gradient (dc/dz) is obtained by calculating the point slope of the vertical distribution of CO_2 concentration (CO_2 profile). The transfer coefficient K_c can be determined from windspeed measurements using an aerodynamic approach.

The transfer coefficient K_c is similar to a molecular diffusion coefficient in that it relates the CO_2 flux to the CO_2 concentration gradient. Both molecular and turbulent diffusion are involved in the aerodynamic transfer along the gradient. Molecular diffusion predominates within the thin zones of still air close to the leaf surface, while turbulent mixing accounts for most of the transfer in the bulk air. Turbulence is a type of mass transfer that involves the movement of macroscopic parcels of air normal to the mean direction of air flow. Therefore the transfer of the molecular constituents is quantitatively related to the transfer of momentum and the transfer coefficients for momentum and CO_2 can be taken to be nearly equal for fully developed turbulence.

The shearing stress equation (where shearing stress and the vertical transfer of momentum are dimensionally equivalent) provides a method of determining the transfer coefficient:

$$\tau = \rho_a K_m (du/dz) \quad . \ . \ . \ . \ . \ . \ [2]$$

where τ is the shearing stress (dynes per sq cm) or the rate of the vertical transfer of momentum, K_m is the momentum transfer coefficient (sq cm per sec), and u is the the mean horizontal windspeed (cm per sec). Using this equation and assuming similarity of the transfer coefficients, the following expression for K_c is obtained:

$$K_c = K_m = (\tau/\rho_a)/(du/dz) \ . \ [3]$$

The windspeed gradient du/dz is calculated from profiles of windspeed. Aerodynamic techniques are usually required to determine the shearing stress as it is presently difficult to measure. The determination of K_m is sufficiently complex that it cannot be discussed here, but is discussed in detail elsewhere (5, 8, 14, 15). Suffice it to say that very careful windspeed measurements and extensive analysis of the data are required.

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Within the plant community the situation is even more complicated with the presence of the sources and sinks for momentum and CO_2 within the air stream where the aerodynamic transfer is occurring. However the determination of the transfer coefficient for the air layer within the plant canopy has been attempted to permit calculation of the rate of photosynthetic fixation of CO_2, layer by layer within the crop. Two different methods have been used to accomplish this. With the turbulent fluctuation approach, detailed measurements of the windspeed fluctuation at several heights within the crop are made and a statistical analysis of the fluctuation components is used to obtain the transfer coefficient distribution (15). With the momentum balance approach, mean windspeed profiles in and above the crop and the effective drag surface area of the plants are measured (8, 14). The calculation of the flux of CO_2 by equation [1] requires the careful measurement of CO_2 concentration profiles within and above the crop and the transfer coefficient distributions obtained by one of these methods. Very sensitive anemometers and CO_2 analyzers and meticulous measurements are required to accomplish this. The analysis of the data is also quite involved. (Measurement and data analysis procedures have been referred to in detail in the references already cited.)

Results and Conclusions

Studies of the aerodynamic transfer of CO_2 between the plant and the atmosphere have been conducted for corn (5, 8, 15, 16), sugarbeets (9, 10) and for some cereal crops (3, 4). The results agree well with some closed canopy studies conducted in the field (2, 11, 12).

The results of studies conducted within the crop give a very interesting picture of the pattern of photosynthesis and the relative importance of the various portions of the crop in the net fixation of CO_2 (6, 8, 15). There is some CO_2 evolution from the soil and respiration predominates in the lower portion of the crop so that there is a net upward flux of CO_2 from the lower to the upper portions of the crop. Photosynthesis predominates in the upper portion during favorable periods so that there is a net downward flux from the air above to this region. The height at which there is neither an increase or decrease in the upward or downward flux is the light compensation point of the canopy. The location of this point is important in evaluating the contribution of the various portions of the crop to the over all total production and efficiency of photosynthesis. Some of the results interestingly showed that the maximum level of respiration was near the ear level for a corn crop while the maximum level of photosynthesis was near the zone of maximum leaf area density.

For such crops as corn, the turbulent mixing processes seem to be very effective in transferring CO_2 from the air above to the air surrounding the leaves. Even during peak photosynthesis periods, the drawdown in CO_2 concentration was only about 5-10 ppm because even at low windspeeds the turbulent transfer coefficients were three orders of magnitude greater than the molecular diffusion coefficients. This is of importance to the management of controlled environments where air velocities are very low unless air circulation is increased by some means.

Results of studies of the fixation of CO_2 when combined with studies of the distribution of visible radiation within the crop (1, 8), permit the calculation of photoefficiency curves. Considering absorbed visible radiation, the maximum efficiency of the canopy for a crop of corn was found to be between 12 percent and 18 percent in the region of maximum leaf area density (13). Efficiency seemed to decrease both above and below this region. Further analysis along these lines indicated that apparently all leaves at any given hour followed the same light response curve in a well-fertilized and well-watered crop of corn regardless of the leaf position in the canopy, at least in the portion of the crop above the compensation point. The light response curves also appeared to be remarkably linear which agreed with the results of some closed canopy studies under field conditions (2). Results further indicated that the light compensation point was in some way directly related to the level of total photosynthetic activity of the canopy.

Even though some assumptions are required, studies of the aerodynamic transfer of CO_2 between the plant and atmosphere give sufficiently quantitative results to provide valuable information on the photosynthetic response of plants to available light and environmental conditions. Obtaining such information under natural field conditions seems essential if we are to effectively develop models of ideal plant morphology or to improve planting patterns for either more total production or more efficient production. It is anticipated that the results of these studies will also assist in the development of simulation programs.

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