DIFFERENCES in photosynthesis of single leaves in intense light and 300 ppm CO₂ have been observed among species (3). Three causes of such differences have been proposed (3): (a) the existence of some kind of respiratory CO₂ leakage into the intercellular air spaces and/or out of the leaf in intense light and during active photosynthesis; (b) stomatal diffusion resistances associated with lack of stomata in the top surface of some leaves; and (c) a difference between warm-climate and cool-climate species which is thought to be associated with some internal characteristic of the leaf. Each of the three causal factors depressed photosynthesis by 15 to 20 mg. CO₂ dm⁻² hr⁻¹. Many tropical grasses with none of the limitations listed above have photosynthetic rates (P) of 60 to 70 mg. CO₂ dm⁻² hr⁻¹; deciduous tree species of the temperate zone have all three limitations and leaf P values of 10 to 20 mg. CO₂ dm⁻² hr⁻¹. In seeking more information about the three factors listed above, studies of internal anatomy of the leaf and CO₂ diffusion resistances were undertaken using species with various combinations of the three factors. Results of these experiments are reported here.

TECHNIQUE AND THEORY

The standard leaf chamber technique of studying photosynthesis was used and adapted to allow simultaneous measurements of water vapor and CO₂ in the air stream through the chamber. A Beckman Model IR 15A CO₂ analyzer was used to determine CO₂; H₂O was determined with a hygrometer. Air was bubbled through water of constant temperature to maintain a constant vapor concentration in the air stream.

Pieces of leaves were killed and fixed with a formalin-acetic acid-alcohol mixture, Johansen (6, p. 41). The plant tissue was then dehydrated with tertiary butyl alcohol and embedded in paraffin. Sections 8 to 10 microns in thickness were made with a microtome. Camera lucida drawings were made of leaf sections from 2 planes for the dicotyledonous species and from 3 planes for the monocotyledonous species. Drawings were then enlarged with an opaque projector. Lengths of curved cell walls were measured with a Keuffel and Esser chartometer. Irregular areas of cells and air spaces were cut from the enlarged drawings and weighed on a balance; areas were calculated from the weight-to-area ratio of the paper.

Calculations of characteristics of leaf anatomy were made according to equations of Turrell (10) for dicotyledonous species. The same characteristics were estimated for monocotyledonous species in a similar manner.

Details of the above techniques are given in the Ph.D. thesis of the senior author (Factors limiting photosynthetic rates of different plant species. 1965. University of Arizona, Tucson). Camera lucida drawings of the 15 species analyzed are included in the same thesis and also in a report (Camera lucida drawings of the internal anatomy of 15 species. Dept. Plant Breeding).


Theoretical equations for determining resistance into the leaf have been derived by Gastra (7):

\[ P = \frac{[(CO₂)_a - (CO₂)_{ch}] / (f_a + f_s + f_m)}{[(H₂O)_{cell surface} - (H₂O)_a] / (f_s + f_m)} \]

and Evaporation = \[ [(H₂O)_{cell surface} - (H₂O)_a] / f_s \]

Where \( (f_a)H₂O \) and \( (f_s)H₂O \) can be calculated from [7] assuming the air to be saturated with water vapor interfaces inside the leaf or at the evaporating surface of the leaf chamber at the respective leaf or water surface temperatures.

Where \( (f_a)CO₂ = (D_{CO₂}/D_{H₂O}) \) then:

\[ \text{If one assigns } (CO₂)_{ch} \text{ by assuming } (CO₂)_{ch} = 0 \text{ or } (CO₂)_{ch} \text{, then one can calculate } f_m \text{ for } CO₂. \]

These calculations are discussed (see 2, 9). Definition of the terms used here is given at the end of this section.

From Rabinowitch (8), the photosynthetic reaction can be simplified as follows (7):

\[ \frac{1}{f_1} \xrightarrow{r_1} \frac{1}{f_1'} \xrightarrow{r_1'} \frac{k_1}{(CO₂)_{ch} \xrightarrow{A} ACO₂} \]

If step [6] is considered to be irreversible and that \( A_0 = A + ACO₂ \), then

\[ P = k_s n[H] ACO₂, \]

and when photosynthesis is constant (steady state conditions are satisfied)

\[ \frac{d(ACO₂)}{dt} = k_s (A = A_0 - ACO₂) - k_s (ACO₂) - k_s (ACO₂) n[H]. \]

From [8],

\[ ACO₂ = k_s A_0 (CO₂)_{ch} / (k_s + k_s n[H]) + k_s n[H] \]

When comparing [10] with [1], \( (CO₂)_{ch} \) can be assumed to zero as assumed for calculations of resistances. No information has been obtained since 1956 about the photosynthetic reaction rates [4] through [6] which suggests that reaction [3] is irreversible with a large negative change in free energy or is reversible. If this is the case, then \( (CO₂)_{ch} \) will be zero. However, from the most recent information about reaction (1), the exact details of each step and consequently the values of \( (CO₂)_{ch} \) are still unknown.

Equation [10] is also a rectangular hyperbola of \( P \) on \( (CO₂)_{ch} / n[H] \) or light intensity (1) and is a reflection of the dark reactions made. The values of \( P \) and \( f_m \) depend upon the rate of the dark reactions [4] through [6], assuming that the rate of photosynthesis is constant and the leaf is in length in light and during active respiration.

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