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ANALYSIS OF LEAF PHOTOSYNTHESIS IN CONNECTION WITH CROP PRODUCTION

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INTRODUCTION

It is nowadays a common point of view that a better understanding of crop production could be obtained by the analysis of crop photosynthesis. Such analyses include studies of leaves as CO_2 sinks. These studies are often undertaken in the laboratory and there are usually difficulties in applying laboratory results to the field. The author (CHARTIER 1966) attempted to define a theoretical model of gross leaf photosynthesis. The measurement of parameters instead of using light-photosynthesis curves to characterise leaf photosynthetic ability is one conclusion of this study. These parameters include resistance of CO_2 diffusion in the air, stomatal resistance, light absorption coefficient of leaf and maximum efficiency of light energy conversion. Some other parameters e.g. mesophyll resistance and carboxylation resistance are now defined and methods for their measurement proposed. Technical features and experiments with bean are discussed in the present paper.

THEORETICAL STUDY

Theoretical features of this study are only summarized in the present paper, for details see (CHARTIER 1966). Photosynthesis of a unit leaf area can be divided into the diffusion process (GAASTRA 1959), photochemical and biochemical processes (RABINOVITCH 1951).

Diffusion process can be studied by means of the following expression (GAASTRA 1959):

$$(1)\quad P = \frac{C - C_1}{Ra + Rs + Rm}$$

P is photosynthesis intensity of unit leaf area or CO_2 flux from the air to chloroplast.

C, CO_2 concentration of the air around the leaf.

C_1, CO_2 concentration around chloroplasts.

Ra, diffusion resistance of CO_2 in the air.

Rs, stomatal resistance for CO_2.

Rm, mesophyll resistance for CO_2, from the substomatal cavity to chloroplasts.

From RABINOVITCH (1951) biochemical reactions may be summarized in the following way:

$$CO_2 + A \longrightarrow ACO_2$$
$$ACO_2 + H \longrightarrow \Pi + A$$

A is chemical acceptor for CO_2

ACO_2, carboxylated acceptor,

H, reductor from photochemical process,

Π, products of photosynthesis.

Reaction velocities are written:

(3) $P=V_1=K_1C_1 \quad [A]$

(4) $P=V_2=K_2 \quad [ACO_2]\,[H]$

K_1, K_2, are the constant of reaction velocities

$[A]$, $[ACO_2]$, $[H]$, the concentrations in A, ACO_2 and H.

RABINOVITCH added:

(5) $[ACO_2]+[A]=Ao$

(6) $[H]=K_3 \quad aII$

I, is the incident light energy (visible spectrum),

a, absorption coefficient of the leaf,

K_3, a constant of proportionality.

From equations 3 to 6, one gets:

(7) $$P=\frac{\alpha aI}{1+\frac{Ra\alpha}{C_1}aI}$$

α is the maximum efficiency of light energy conversion,

$\alpha = AoK_2K_3$

Rc is chemical or carboxylation resistance,

$$Rc=\frac{1}{AoK_1}$$

Rc is expressed in the same unit as the three diffusion resistances ($m^{-1}s.$) and is the biological resistance to the photosynthetic process which may be affected by temperature, mineral nutrition, physiological state, &c. Elimination of C_1 from equations (1) and (7) gives

$$(Ra+Rs+Rm)\,P^2+(Ra+Rs+Rm+Rc) \quad aIP+CP\text{-}C \quad aI=O$$

The graph of intensity of photosynthesis, P, against incident light energy, I, is a hyperbola similar to numerous experimental results.

Measuring Ra, Rs, Rm, Rc, a, , appears to be a better method for characterizing leaf photosynthesis ability.

11. *Material and Methods.*

Experiments were undertaken with phaseolus vulgaris, variety "Mistral" (VILMORIN), 12 days after sowing. Climatological conditions for growing were:

Light: 5000,-7,000 lux

Temperature: day 26° C

night 21° C

Relative Humidity: 85 %

Pots with sand and nutritive solution (formula from station de Physiologie Vegetale—INRA—Versailles) were used.

Simultaneous measurements of CO_2 and water vapour exchange were made by nsing an assimilation chamber, (figure 1). The entire plant was used. Artificial ventilation was given by means of micromotor introduced inside the chamber. Five thermocouples inside the leaf gave leaf temperature. Light was supplied by high pressure mercnry lamps in which distance from the experimental plant could be adjusted.

Difference of CO_2 concentration of the air before and after passage through the chamber was measured by means of IR analyser, in which the full scale deflection is 200 VP (controle de Chauffe—France). Saturation of the intake air with water vapour was achieved by bubbling through the water at the dew point temperature required. Dew point temperature of the outlet air was measured by means of a dew point analyser (Acqmel—France). The air streams passed over a mirror, with temperature regulated at the limit of condensation.

Rs value are got from:

$$Rs\,(H_2O) = (Ra\text{-}Rs)_{(H_2O)} - Ra_{(H_2O)}$$

and Milthorpe Penman 1967

$$Rs_{(CO_2)} = 1{,}54 Rs_{(H_2O)}$$

Rs depends on incident light energy (figure 1). It appears from this figure that light energy is needed for a large opening of stomata: $100 A.m^{-2}$ or about 15,000 lux in photometric unit.

In the presence of adequate light supply, Rs increases if the water conditions become unfavourable (soil dryness, low relative humidity of the air, large radiative energy). Effects of these factors on the variations of Rs are being studied carefully.

(c) *Determination of Mesophyll resistance Rm and Chemical Resistance Rc*

With light energy neither too low nor too high (below saturation) one can measure:

Ra, air resistance for CO_2

Rs, stomatal resistance for CO_2

, maximum efficiency of light energy conversion (initial slope of the photosynthesis—light energy curve),

a light absorption coefficient of the leaf,

P, photosynthesis intensity,

I, incident light energy,

C, CO_2 concentration of the air,

We have got a general expression of the photosynthesis which is:

$$-(Ra+Rs+Rm)P^2+(Ra+Rs+Rm+Rc)Ip+CP\text{-}CaI = O$$

Rm and Rs are the only unknowns in this expression, so for one experimental point, this expression can be expressed in this way:

$$Rc = aIRm + bI.$$

For other points, one gets:

$$Rc = a_2 Rm + bI.$$

$$Rc = a_3 Rm + b_3 \ \&c\ldots$$

The system of n equations for two unknown variables can be solved by means of the computer of less elaborate methods.

(a) *Determination of Diffusion Resistance of CO_2 in the air Ra*

Evaporation measurements from a piece of blotting paper similar to the leaf on shape and colour and placed in the same position allowed for determination of Ra (GAASTRA, 1959):

$$Ra\ (H_2O) = \frac{(H_2O\ \text{leaf}) - (H_2O)\ \text{air}}{\text{Evaporation}}$$

The air resistance for CO_2 can be calculated according to (Milthorpe, Penman, 1967)

$$Ra_{(CO_2)} = 1{,}36 Ra_{(H_2O)}$$

Without any artificial ventilation (fans stopped), a leaf having an area of 150cm^2 had a Ra value of about 400 m^{-1}s, with a rate of air flow equal to 200 I. H.$^{-1}$. This value was so great compared with other resistances that it could hide variations of Rs, Rm or Rc. Moreover this great value lowered the maximal intensity of photosynthesis observed in experiments.

Artificial ventilation was therefore, used in experiments.

(b) *Determination of Stomatal Resistance, Rs.*

From transpiration and leaf temperature measurements one can get (GAASTRA 1959):

$$(Ra+Rs)_{(H_2O)} = \frac{(H_2O\ \text{leaf} - (H_2O)\ \text{air}}{T}$$

(H_2O) leaf is the water vapor concentration of the air, saturated at the leaf temperature,

(H_2O) air is the actual water vapor concentration of the open air around the leaf,

T is the transpiration rate.

TABLE 1

Carbon Dioxide Resistances ($m^{-1}s$).

	Plant I	Plant II	Conditions
Ra	54	89	With ventilation
Rs	350	230	Light Saturation
Rm	328	405	
Rc	134	100	
Ra+Rs+Rm+Rc	866	824	Light saturation
$\frac{C}{P_{max}}$	850	700	Light saturation

From two series of experiments with two different plants we got:

$Rm = 328\ m^{-1}s$

$Rc = 134\ m^{-1}s$

$Rm = 405\ m^{-1}s$

$Rc = 100\ m^{-1}s$

Mesophyll resistance, Rm, varies from one leaf to the other depending on anatomical structure. For the same species, variations caused by climatological conditions during growth are important. Rm is the greatest resistance when stomata are opened (table 1), so that modifications of leaf structure by means of plant breeding is one possibility of improving leaf photosynthesis.

Chemical resistance, Rc, is an expression of resistance of a biological nature: temperature effects, leaf age, mineral nutrition, &c...Under good growing conditions Rc values are relatively low (Plate 1).

(d) *Determination of the maximum efficiency of Light Energy Conversion*

It is easier to obtain the product $a\alpha$ than α alone:

$$a\alpha = \frac{P}{I}$$

P, is photosynthesis of unit leaf area for low values of I,

I, is incident light energy,

a, coefficient of light absorption of the leaf.

A number of experiments with Phaseolus vulgaris "Minstral", 12 days old, gave values of α from 100 to 110 dg of CO_2 per Joule. Concentration of chlorophyll (a+b) per leaf unit area is about 3 mg dm^{-2}.

CONCLUSIONS

Definition of characteristic parameters of the anatomical or physiological components of a biological process can improve the study of effects of environmental factors on plant photosynthesis. A more analytical approach, for instance, can be developed for on the effect of water supply of photosynthesis, by means of measuring parameters such as Ra, Rs, Rm than by using intensity of photosynthesis directly.

This kind of analysis may lead to the discovery and characterization of the bottleneck in the process of photosynthesis. It may then be possible to remove this bottleneck by plant breeding.