MASTER

RECEIVED BY DTIE APR 1 1970

THIRD ANNUAL TECHNICAL PROGRESS REPORT

FOR

ENERGY EXCHANGE WITHIN ECOSYSTEMS

AT

MISSOURI BOTANICAL GARDEN

ST. LOUIS, MISSOURI

PRINCIPAL INVESTIGATOR: DAVID M. GATES

Date of Report: February 19, 1970

DISCLAIMER

This report was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency Thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

I. Introduction

The objective of the program as conceived in 1966 was to test experimentally the theoretical relationship between a plant leaf and its immediate environment from an energy budget standpoint. It was also expected that certain matters pertaining to competition among plants for various environmental factors would be studied. A significant part of this proposal was completed during the first two and one-half year period. This is reported on here. In addition, our ideas have advanced considerably during this period and because of this, we can see that further theoretical research was required in order to establish the proper guidelines for more experimental and observational research. The theoretical research has added very significantly to our understanding and is progressing strongly at the present time.

Adequate theory must go hand-in-glove with experiment (or else precede experiment) so that any observations which are undertaken are done so with full recognition of various complications and complexities. About a year ago, we suddenly had some new ideas concerning the mechanisms which relate plant productivity to climate and environmental conditions. We realized that in order to answer certain questions concerning plant productivity, competition among plants, succession in plant communities, ecological adaptation and matters relating to leaf morphology that we would need to greatly improve our understanding of the coupling between a plant and its environment. We

had established earlier that a plant is coupled to the climate

around it by means of energy flow. Energy flow adequately accounts

for the temperature of a plant and its transpiration rate. Experiments

to confirm this are explained in Section III of this report. However,

a plant, in order to function properly, must take in carbon dioxide

and release oxygen during the process of photosynthesis and must

release carbon dioxide during the processes of respiration. So we have

set out to develop a theoretical model which will describe properly

these important events which couple a plant to its environment. A

plant interacts with its environment by means of energy and gas ex-

change with the atmosphere, and by the transport of water and nutrients

from the soil. So far, we have concentrated our efforts on the aerial

parts of plants--the interactions between the leaves and the air. The

interaction of the soil with the plant is of great importance as well,

but so far we have had more than enough to do by attempting to under-

stand the energy and gas exchange between plant and air.

II. Theoretical Model

The exchange of energy between a plant leaf and the micro-
climate nearby is fully accounted for by the following formulation.
The quantities and coefficients are all explained fully in some
of our publications, copies of which are attached, and need not
be written out again here.

Energy In = Energy Out

Radiation absorbed = reradiation + convection + transpiration

$$Q = \varepsilon \, \sigma \, T_{\ell}^{4} + k_1 \, V^{1/2} \, D^{-1/2} \, (T_{\ell} - T_a) + L \; \frac{{_s}d_{\ell} - (r.h.) \; {_s}d_a}{r_{\ell} + k_2 \, W^{0.20} \, D^{0.35} \, V^{-0.55}} \tag{1}$$

This equation assumes that the small amount of energy consumed by
photosynthesis is negligible in the general energy budget of the leaf.
However, it can very readily be included as a small consumptive term
entering the equality on the right hand side.

We then proceeded to write down the gas diffusion relation for
carbon dioxide which must diffuse from the air through the stomates
and cell walls into the chloroplasts buried in the mesophyll cells.
The resistance of the pathway to the diffusion of carbon dioxide is very nearly
equal to the resistance of the pathway to water vapor multiplied by the
ratio of the diffusion coefficients for the two gases, e.g. by 1.6,
plus the additional resistance of the pathway from the substomatal
cavity through the cell walls and cytoplasm to the chloroplast. Hence,

$$CO_2 r_\ell = 1.6 \, H_2O r_\ell + r_m \tag{2}$$

where r_m is the additional mesophyll resistance.

The diffusion of carbon dioxide from the atmosphere to the chloroplasts is written as follows:

$$P = \frac{CO_2{}^d a - CO_2{}^d \ell}{CO_2{}^r \ell + CO_2{}^r a} \tag{3}$$

where $CO_2 r_a$ is boundary layer resistance to CO_2 diffusion.

However, the rate of diffusion of CO_2 into the leaf must be in complete agreement with the rate of photosynthesis at the chloroplast. But the rate of assimilation by the chloroplast is dependent upon leaf temperature, light concentration, and carbon dioxide concentration.

That is, we have

$$P = fnc \, (T_\ell, \; L, \; CO_2{}^d{}_{ch\ell}) \tag{4}$$

Next it is necessary to define these functional dependencies as carefully as possible. We have used the Michaelis-Menton formulation in order to describe the relation of photosynthesis on light intensity and on carbon dioxide concentration. We use a more general relation to describe the dependence of reaction rate on leaf temperature. These are each described in more detail in the attached manuscript.

There are now serious complications which must be given careful consideration. Carbon dioxide is supplied to the chloroplasts not only

by diffusion from the air but also by diffusion from the sites

of respiration. There are at least two sources of respiratory CO_2,

1) the mitochondria which are scattered throughout the cytoplasm of

the mesophyll cells and 2) the sites of photorespiration which reside

in the cytoplasm and are likely to include the peroxisomes, small

organelles found in close association with the chloroplasts. Current

evidence indicates that mitochondrial respiration is suppressed at

all light intensities above dim light in chloroplast containing cells

and hence does not contribute significant amounts of CO_2 to photo-

synthesis. Photorespiration on the other hand may contribute signi-

ficantly in most plants. Its rate varies in a complex manner with

temperature, light intensity, and external CO_2 and O_2 concentration.

Photorespiration is greatly reduced or absent in a few plants, e.g.

certain grasses such as corn. In these plants the only significant

source of CO_2 for photosynthesis is the CO_2 in the air. Our second

model has worked with this situation only. In our very first model

we left out respiration knowing full well we could put it in at the

next level of approximation. When we do include respiration it is

necessary to develop a more complicated flow pattern and network within

the leaf mesophyll in order to describe the sources and sinks of CO_2

and the pathways which are possible. This we have now done.

When we put in the proper functional dependencies for

photosynthesis and the gas diffusion we get a fairly complicated quadratic

equation which includes all the appropriate plant properties, the

appropriate atmospheric properties, which relates to the energy exchange

as well. The point now is that the energy budget, the gas diffusion, and the photosynthetic and respiration rates must be self consistent and completely compatible. Our model insists on these conditions.

So far we have had good success with our ability to predict productivity or photosynthesis of certain specific examples for which measurements have been made. Our primary frustration stems from the lack of the fundamental input data which we require for our model. Now that we see clearly the kind of information which we need to have we are going to provide it for ourselves from our own laboratories. This will be the main task before us during the next year or two. A great deal depends upon our getting the complete mathematical model well established and confirmed by means of observations.

An important part of the problem outlined above is the matter of internal resistance to the flow of carbon dioxide and the question of sources and sinks of carbon dioxide within the leaf. Certainly the chloroplast is a sink of carbon dioxide and there are at least two sources of carbon dioxide through respiration. Of course, in addition, there is always an external source of carbon dioxide as well. Recently we have worked out a rather elaborate analysis of the circuitry within a leaf. We are currently preparing a manuscript of this for publication. It is not in finished form, but I enclose a copy to give evidence of the fact that we have progressed a long way with this analysis.

III. Energy Exchange

A very extensive series of measurements were conducted with single plants in a wind tunnel within a greenhouse in order to validate the whole matter of energy exchange and in particular to verify predicted transpiration rates. A wooden horizontal platform was built in the greenhouse through which a plant, mounted on scales beneath the platform, could extend and be ventilated by wind of a specific speed from a low velocity wind tunnel. The plant, growing in a pot, was resting on scales whose changing values would indicate the rates of water loss by the plant. The south facing roof of the greenhouse was modified by the insertion of a 4 by 8 foot plate of glass to avoid shadowing of plants by the laths of the normal roof.

The amount of sunlight directly incident upon the plant was monitored by an upward facing Eppley pyrheliometer and the quantity of reflected sunlight off of the horizontal board platform was monitored with an inverted Eppley pyrheliometer. The wind tunnel fan speed could be regulated to give the desired air flow rate at the plant as measured with a Hastings Raydist model RM-IX wind meter. Air temperatures as well as leaf temperatures were measured carefully with 40 gauge thermocouples whose signals were recorded on a Honeywell Electronik 15 multipoint recorder.

If we rewrite the energy budget relation for a plant leaf in the following simplified form we can discuss the procedure used here for checking the validity of the energy budget method.

$$\text{Radiation absorbed} = \text{Reradiation} + \text{Convection} + \text{Transpiration}$$

$$Q_{abs} = R + C + E \qquad (5)$$

The first scheme which we used for the determination of the transpiration rate of a plant was to compare a severed leaf in a potometer with an intact leaf on a plant. The two leaves had the same orientation and exposure to radiation and wind, each being side by side above the platform. The potometer measured the rate of water use by the severed leaf and by a comparison of the energy budgets of the two leaves the rate of water use by the intact leaf could be inferred. A measurement of the leaf temperatures allowed the radiation terms to be known accurately and a measurement of the wind speed allowed one to calculate the convection terms reasonably well. An assumption is made that the two leaves which are as nearly identical as possible, absorb the same amount of radiation. Hence,

$$Q_{abs} \text{ (Pot. Leaf)} = Q_{abs} = \text{(Intact Leaf)} \qquad (6)$$

Therefore,

$$(R_1 + C_1 + E_1) \text{ (Pot. Leaf)} = (R_2 + C_2 + E_2) \text{ (Intact Leaf)} \qquad (7)$$

Hence,

$$E = R_1 - R_2 + C_1 - C_2 + E_1 \qquad (8)$$

Obviously if the two leaves are nearly identical and if they have the same temperatures then $R_1 = R_2$, $C_1 = C_2$, and $E_1 = E_2$.

Usually their temperatures differ and one can determine E_2 by calculating each term in Eqn. 8. From the determination of transpiration rates E_2 one can solve the diffusion equation for the resistance as follows:

$$r = \frac{{}_s d_\ell(T_\ell) - r.h. \, {}_s d_a(T_a)}{E_2} \tag{9}$$

This was done with many experiments using cotton plants. The resistances obtained will be reported with the other information when the paper is submitted for publication.

As a part of the procedure to determine the accuracy of the energy budget determination for plants we evaluated the Q_{abs} by measuring the radiation fluxes incident upon the plant and the absorptivity of the plant. The absorptivities were determined by use of a Beckman spectrophotometer with integrating sphere attachment. For each series of measurements with each plant in the wind tunnel, exposed to sunlight, etc., we obtained a very satisfactory agreement between the Q_{abs} as evaluated from the amount of radiation and the absorptivity as compared with Q_{abs} given as the sum of R + C + E. The following results are typical of what we found by the two methods:

Experiment No.	Q_{abs} from Rad. x Abs.	Q_{abs} from R + C + E	
1	0.98	0.92	cal cm^{-2} min^{-1}
2	1.18	1.17	
3	1.27	1.21	
4	1.32	1.33	
5	1.33	1.39	

Experiments were done by which a single leaf was left on the stalk of a cotton plant when all other leaves were removed. The rate of water use per unit leaf area of the single leaf was always substantially greater than the rate of water use per unit leaf area averaged over all leaves of a plant. There are two reasons for this. First some of the leaves may be partly shaded and not receive the full illumination of the sun as did a single leaf. Second there seems to be a real competition among the leaves of a plant for the water which can be supplied by the roots and stem. We will report further on this when we write up all the results for publication.

Energy Budget and Water Loss Experiments
with Cryptogams

A series of experiments, believed to be the first of their kind, with cryptogams were undertaken to measure the energy budget and water loss rates of a foliose lichen, Parmelia, and with a liverwort, Reboulia hemispherica. These experiments were conducted in the same wind tunnel with solar irradiation as were the cotton plant experiments. For Reboulia we found a minimum diffusion resistance of 0.25 sec cm^{-1} in wind of 2.5 mph and that the plant took several hours to become very dry. For Parmelia we found a minimum resistance of 0.39 sec cm^{-1} in wind of 2.5 mph and that it dried out rapidly, generally about 18 or

20 minutes to be very dry. These resistances can be compared with
minimum values for cotton of the order of 1.4 to 2.0 sec cm^{-1}.

The results of the experiments with the cryptogams are being
written up for publication in the near future.

Senior Research staff working on this project in addition
to the Principal Investigator were: Dr. Hyrum Johnson 1967-8,
Dr. George Hoffman 1968-9, and Dr. Christa Swintzer 1969-present.

Technical Reports and Reprints

February 27, 1970

1. Gates, David M., Climate and Stability, Diversity and Stability
   in Ecological Systems, Brookhaven Symposia in Biology:
   No. 22 (1969).

2. Gates, David M., The Ecology of an Elfin Forest in Puerto Rico, 4.
   Transpiration Rates and Temperatures of Leaves in Cool Humid
   Environment, Journal of the Arnold Arboretum, 50 (1969).

3. Gates, David M., Hyrum B. Johnson, Conrad S. Yocum and Paul W. Lommen,
   Geophysical Factors Affecting Plant Productivity, Proc. Inter-
   national Symposium "Productivity of Photosynthetic Systems."
   Part II: Theoretical foundations of optimization of the
   photosynthetic productivity. Moscow, U. S. S. R. September,
   1969. (In Press).

4. Rough Draft, An Electric Analog Description of Photosynthesis.

5. Stock, Robert W., Saving the World the Ecologist's Way, The New
   York Times Magazine, October 5, (1969)