GEOPHYSICAL FACTORS AFFECTING PLANT PRODUCTIVITY

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Introduction

The climate near a plant affects the leaf temperatures, the transpiration rate, and the photosynthetic rate and productivity of the plant. Climate is described by the fluxes of radiation incident upon a plant, the air temperature, the wind speed, and the water vapor pressure or relative humidity of the air. Climate interacts with a plant by the flow of energy between the plant and the environment. If the energy input to the ~~plant is high~~ the plant temperature may be relatively high. If the energy input to the plant is low the plant temperature may be relatively low.

Some of the energy received by a plant is consumed with the evaporation of water from the plant. In fact, the rate of evaporation, or transpiration rate, is an intimate part of the plant energy budget and directly affects the plant temperature. Not only must energy be available for water to be transpired by the plant, but the water vapor must diffuse along a water vapor pressure gradient from within the leaf mesophyll to the free air beyond the boundary layer adhering to the leaf surface. In order for transpiration to occur both energy must be available and diffusion must occur.

If a plant is to photosynthesize it must take in carbon dioxide to the chloroplasts embedded in the cells of mesophyll. If water vapor diffuses outward from the mesophyll through the stomates then carbon dioxide may diffuse inward through the stomates to the mesophyll and the chloroplasts. The rate of diffusion of carbon dioxide into the mesophyll depends upon the existence of a vapor pressure gradient of carbon dioxide from the air to the chloroplasts within the leaf. However, the concentration of carbon dioxide at the chloroplasts depends upon the relative rates of photosynthesis and respiration by the chloroplasts. The rate of respiration is a function of leaf temperature and somewhat a function of the amount of light. The rate of photosynthesis is a function of leaf temperature and of light quality and quantity at the chloroplasts.

Productivity, or the assimilation of carbon dioxide by the plant which involves the fixation of carbon dioxide to glucose phosphate, depends upon the leaf temperature, upon the amount of light, and upon the diffusion of carbon dioxide into the leaf. Hence, the energy budget of the leaf and the gas diffusion of water vapor, carbon dioxide, and oxygen must all occur in a self consistent manner such that one process does not contradict another. It is the purpose here to describe the manner in which the environment or climate of a plant leaf affects the productivity of the plant through the exchange of energy and the diffusion of gases.

Energy Exchange

Energy is transferred to and from a plant leaf by radiation, convection, and transpiration. The processes of energy exchange for a plant leaf have been discussed in detail by Gates (1968). If a plant leaf is in energy equilibrium with its environment the leaf temperature T_ℓ is given by the solution to the following equation.

$$Q_{abs} = \varepsilon\sigma T_\ell{}^4 + k_1 \left(\frac{V}{D}\right)^{1/2} (T_\ell - T_a) + L\ (T_\ell) \frac{{}_sd_\ell(T_\ell) - r.h.\ {}_sd_a\ (T_a)}{{}_{H_2O}r_\ell + k_2 \dfrac{W^{0.20}\ D^{0.35}}{V^{0.55}}} \qquad (1)$$

where the term Q_{abs} = radiation absorbed by the leaf, ε = emissivity of leaf, σ = Stefan Boltzmann constant, ($\sigma = 8.132 \times 10^{-11}$ cal cm^{-2} min^{-1} $°K^{-4}$), V = wind speed in cm sec^{-1}, D = characteristic dimension in cm of the leaf in direction of air flow, T_a air temperature °C, L (T_ℓ) = latent heat of vaporization as a function of leaf temperature (L = 580 cal gm^{-1} at 30°C, ${}_sd_\ell$ (T_ℓ) = saturation density of water vapor inside the leaf substomatal cavity as a function of T_ℓ, ${}_sd_a$ (T_ℓ) = saturation density of water vapor of the air as a function of the air temperature T_a, r.h. = relative humidity of the air, ${}_{H_2O}r_\ell$ = internal resistance of the leaf to water vapor in min cm^{-1}, and W = characteristic leaf dimension in cm in direction transverse to the air flow.

Each term in Eqn. (1) is expressed in cal cm^{-2} min^{-1} and the coefficients are all defined such that each term comes out in these units. The following values were obtained for k_1 and k_2 from careful measurements of leaves in a wind tunnel.

If	$W>D$ or $W=D>5$ cm or $D>10$ cm	$k_1 = 10 \times 10^{-3}$	$k_2 = 35 \times 10^{-3}$
If	$W<D\leq 10$cm or $W=D\leq 5$ cm	$k_1 = 16.2 \times 10^{-3}$	$k_2 = 26 \times 10^{-3}$

The transpiration rate of a leaf is the rate at which water vapor diffuses out of the leaf into the free air beyond the boundary layer of air adhering to the leaf surface. The transpiration rate E in gm cm^{-2} min^{-1} is given by

$$E = \frac{{}_s d_\ell(T_\ell) - \text{r.h.}\ {}_s d_a(T_a)}{{}_{H_2O}r_\ell + k_2 \dfrac{W^{0.20}\ D^{0.35}}{V^{0.55}}} \tag{2}$$

The quantity $k_2 \frac{W^{0.20}\ D^{0.35}}{V^{0.55}}$ represents the resistance of the leaf boundary layer which is proportional to the dimensions of the leaf and inversely proportional to the air speed across the leaf. The characteristic dimensions of a leaf are discussed for leaves of various shapes by Parkhurst, Duncan, Gates, and Kreith (1968).

If the transpiration rate, as given by Eqn. (2), and the leaf temperature, as given by Eqn. (1), are evaluated as a function of

Q_{abs}, T_a, r.h., V, and $_{H_2O}r_\ell$ one can express the results in various graphical forms. One such form is to plot the dependent variables of transpiration rate and leaf temperature as a function of air temperature and leaf resistance as shown in Fig. 1 or as a function of wind speed and leaf resistance as shown in *Fig.* 2. Other relations could be shown and are discussed by Gates (1968).

Carbon Dioxide Diffusion

In order for a plant to photosynthesize carbon dioxide must diffuse from the air into the leaf mesophyll through the stomates. However, in addition to the pathway for water vapor from the substomatal cavity through the stomate and boundary layer of adhering air, carbon dioxide diffusing into the leaf to the chloroplasts must diffuse through the cell walls and cellular cytoplasm. Therefore there is additional resistance for the passage of carbon dioxide into the leaf than there is to water vapor passing out of the leaf. For the same pathway the ratio of resistance for carbon dioxide to resistance for water vapor is approximately inversely proportional to the ratio of the diffusion coefficients. The diffusion coefficient for water vapor in air is approximately 0.24 $cm^{-2}sec^{-1}$ and for carbon dioxide in air is approximately 0.14 cm^{-2} sec^{-1}. The ratio of these is 1.7. Hence,

$$_{CO_2}r_\ell = 1.7\ _{H_2O}r_\ell + {}_{CO_2}r_m \qquad (3)$$

where $_{CO_2}r_m$ is the mesophyll resistance to carbon dioxide diffusion.

The total resistance to carbon dioxide diffusion from the free air beyond the boundary layer to the chloroplast must include the boundary layer resistance. Hence,

$$_{CO_2}r = {}_{CO_2}r_\ell + {}_{CO_2}r_a = 1.7\,{}_{H_2O}r_\ell + {}_{CO_2}r_m + 1.7\,k_2\,\frac{W^{0.20}\,D^{0.35}}{V^{0.55}} \qquad (4)$$

The driving force for the diffusion of carbon dioxide into the leaf is the concentration difference between the density of carbon dioxide in the free air ${}_{CO_2}d_a$ and the density of carbon dioxide in the leaf at the chloroplast ${}_{CO_2}d_\ell$. Hence, the diffusion equation for carbon dioxide is written:

$$_{CO_2}F = \frac{{}_{CO_2}d_a - {}_{CO_2}d_\ell}{{}_{CO_2}r} = \frac{{}_{CO_2}d_a - {}_{CO_2}d_\ell}{{}_{CO_2}r_\ell + 1.7\,k_2\,\dfrac{W^{0.20}\,D^{0.35}}{V^{0.55}}} \qquad (5)$$

The rate of net photosynthesis of the leaf cannot exceed the rate at which carbon dioxide is supplied to the chloroplasts by diffusion. For a given concentration of carbon dioxide in the air the maximum rate of carbon dioxide diffusion is achieved when the carbon dioxide concentration at the chloroplast ${}_{CO_2}d_\ell$ is zero. If the normal concentration of carbon dioxide in the air of 1.25×10^{-8} moles cm^{-3} is assumed to be the concentration difference between air and chloroplast (which assumes that the concentration at the chloroplast is zero) one can calculate the maximum rate of diffusion of carbon dioxide into the leaf as a function of the total resistance to flow of carbon dioxide, of air speed at the leaf, and of leaf dimension as shown in Fig. 3. The intersection of the lines of constant wind speed and leaf dimension with the ordinate give the maximum photosynthetic rates possible, as limited by carbon dioxide diffusion, when the internal diffusion resistance ${CO_2}r_\ell = 0$ and the diffusion rate is limited only by the resistance of the boundary layer of adhering air at the leaf surface. All plants must function within these limiting rates of carbon dioxide diffusion. If there is some internal resistance to diffusion, as indeed there always is, then the maximum possible photosynthetic rates are even less than without internal resistance and the rates are seen directly from Fig. 3. The straight line which is approached as the wind speed increases is the limiting case of maximum carbon dioxide diffusion when there is no adhering boundary layer of air and hence no boundary layer resistance, a situation approximated only at maximum wind speed.

Observations of Photosynthesis

Many measurements now exist to show the relation between photosynthesis and temperature or between photosynthesis and light for whole plants or for single plants leaves. The examples shown in Fig. 4 are taken from El-Sharkawy and Hesketh (1964) and are typical of many similar curves which are published for other plants. Each species will have a different relation between photosynthetic rate and temperature and differences will occur within species which have had different environmental histories, see Mooney and West (1964). Clearly the photosynthetic systems of plants are regulated by a complex of enzymes which respond to temperature and light. Alpine plants have optimum photosynthetic rates at temperatures as low as 12°C and some tropical grasses may have optima at temperatures as high as 40°C. Some higher plants will cease photosynthesis at temperatures between 40 and 45°C while some will photosynthesize at temperatures up to 60°C. Brock (1967) indicates that there seems to be a definite upper limit to photosynthetic life at a temperature of about 75°C for procaryotic algae. Some bacteria continue to live at temperatures as high as 90°C, see Bott and Brock (1969). It is suggested that organisms do not evolve proteins which are much more stable than they need to be for the environmental conditions encountered by the organism. ~~In fact it~~ seems that an organism will have optimum photosynthesis at a temperature compatible for the upper limit for growth.

The photosynthetic curve for a bryophyte, Bryum Sandbergii, as a function of temperature is shown in Fig. 5. This moss has an optimum at about 30°C and would not photosynthesize at temperatures above about 45°C. In contrast to the higher plants the moss does not take in carbon dioxide through the stomates but rather through the cuticle and cell walls directly. The photosynthetic rate as a function of light is discussed by Hesketh and Moss (1963) but is not included as a part of the analysis presented here.

Kinetics of Photosynthesis

The relations observed for whole plants or whole leaves between photosynthetic rate and temperature or light are the products of all mechanisms by which carbon dioxide enters the leaf and by which assimilation takes place at the chloroplasts. In order to understand the specific influence of environmental or geophysical factors on photosynthesis or productivity it is necessary to separate the kinetics of photosynthesis from the dynamics of energy exchange and gas diffusion.

It is well known that many enzyme catalyzed chemical reactions proceed according to the Michaelis-Menton Equation which describes the rate of reaction as a function of substrate concentration. Hence, if P is the photosynthetic rate, P_m is the maximum photosynthetic rate possible, and $CO_2{}^d{}_\ell$ is the concentration of carbon dioxide at the chloroplasts, then:

$$P = \frac{P_m}{1 + \frac{K}{CO_2{}^d{}_\ell}} \tag{6}$$

where K is the Michaelis constant for the rate of reaction.

If the gas diffusion equation is written:

$$P = \frac{CO_2{}^d{}_a - CO_2{}^d{}_\ell}{CO_2{}^r} \tag{7}$$

Hence,

$$CO_2{}^r\ P = CO_2{}^d{}_a - CO_2{}^d{}_\ell \tag{8}$$

or

$$CO_2{}^d{}_\ell = CO_2{}^d{}_a - r\ P \tag{9}$$

Substituting this into Eqn. 6 one obtains

$$P = \frac{P_m}{1 + \frac{K}{CO_2{}^d{}_a - r\ P}} \tag{10}$$

This is now a quadratic in P with two roots.

One knows that as $CO_2{}^d{}_a \to \infty$ that $P \to P_m$. On this basis one finds after algebraic manipulation that the root with the minus sign is the only acceptable root to the problem. Hence the solution to the quadratic equation is:

$$P = \frac{(CO_2{}^r\, P_m + K + CO_2{}^d{}_a) - [(CO_2{}^r\, P_m + K + CO_2{}^d{}_a)^2 - 4\, CO_2{}^r\, CO_2{}^d{}_a\, P_m]^{1/2}}{2\, CO_2{}^r} \qquad (11)$$

It can be shown that

$$\lim_{CO_2{}^r \to \infty} P = \frac{CO_2{}^d{}_a}{CO_2{}^r} \text{ and } \lim_{CO_2{}^r \to o} P = \frac{P_m\, CO_2{}^d{}_a}{K + CO_2{}^r{}_a} \qquad (12)$$

The values of $CO_2{}^d{}_a$ and $CO_2{}^r$ are fairly easy to obtain. The normal density of carbon dioxide in the air is 300 to 310 ppm or 5.90×10^{-7} gm cm^{-3} to 6.28×10^{-7} gm cm^{-3} at standard temperature and pressure. The total resistance to carbon dioxide diffusion can take any value from a minimum near 0.017 min cm^{-1} or 1.0 sec cm^{-1} to infinity. The appropriate values of P_m and K must be evaluated for a particular plant. It is noticed from Eqn. (6) that K has the same units as $CO_2{}^d{}_a$ or $CO_2{}^d{}_\ell$, e.g. ppm or gm cm^{-3}. From data by Hesketh (1963) a determination was made of P_m and K for tobacco and maize. The values obtained are as follows: for maize, K = 800 ppm or 3.3×10^{-8} moles of CO_2 cm^{-3} and $P_m = 1.07 \times 10^{-8}$ moles of CO_2 cm^{-2} sec^{-1} and for tobacco, K = 5000 ppm or 21.0×10^{-8} moles of CO_2 cm^{-3} and $P_m = 3.1 \times 10^{-8}$ moles of CO_2 cm^{-2} sec^{-1}.

Temperature Functions

In order to proceed with our analysis of the photosynthesis of higher plants we need to know the maximum photosynthetic rate for the chloroplasts of higher plants as a function of their temperature when supplied with a saturated concentration of carbon dioxide when the flow of carbon dioxide is not limited by diffusion. Since the data we need are not available we must resort to an assumed temperature response for P_m. In order to estimate such a response we have reviewed the information available in the book by Johnson, Eyring, and Polissar (1954) concerning the chemical kinetics of enzyme systems and of organisms. Examples of the temperature dependence of moderately simple systems are shown in Fig. 6. Further consideration led us to believe that the temperature dependence of the photosynthetic rate of a bryophyte, without a gas diffusion pathway, might better approximate the situation for chloroplasts of higher plants. This is because a bryophyte has no stomates and the only resistance to carbon dioxide diffusion is resistance offered by the cell walls and cytoplasm. A photosynthetic temperature curve for Bryum Sandbergii taken from Rastofer and Higinbotham (1968), which has been shifted 12.5°C toward higher temperatures, is shown in Fig. 7. Normally its optimum temperature is at 30°C, but since we wish to apply a curve of this shape to the photosynthesis of sorghum, which has a high optimum temperature, we have shifted the optimum temperature to 42.5°C. In other words, we are using the photosynthetic curve for Bryum Sandbergii merely for shape and the curve shown in Fig. 6 is the model upon which we wish to base our calculations in order to demonstrate the procedure by which we are estimating the photosynthetic productivity of higher plants. If we were to estimate the photosynthetic rate of a plant with an optimum at lower temperatures, then a model curve for $P_m(T_\ell)$ would be selected with a low temperature optimum.

The temperature function for $P_m(T_\ell)$ is based on Fig. 7, but the photosynthetic rates, P, determined by the chemical kinetics and gas diffusion, are calculated from Eqn. 11. The shape of the curves obtained for P depend upon the specific values of P_m and K chosen for a particular species of plant as well as the resistance to CO_2 diffusion. For example, if $P_m = 5 \times 10^{-8}$ moles CO_2 cm^{-2} sec^{-1} and $K = 6 \times 10^{-8}$ moles CO_2 cm^{-3} then for a concentration of carbon dioxide in air of 1.25×10^{-8} moles CO_2 cm^{-3} one calculates from Eqn. 11 the photosynthetic rates P as a function of leaf temperature T_ℓ and total resistance $_{CO_2}r$ to carbon dioxide and obtains the curves shown in Fig. 8. It is interesting to note that for low values of total resistance the photosynthetic rates are quite sensitive to temperature, but at high resistances the rates are very insensitive to temperature.

Photosynthesis of Higher Plants

In order to select the proper values one must consider now a specific plant. Since there are measurements of the photosynthetic rate of *Sorghum* by El-Sharkawy and Hesketh(1964) we used the observed data in order to determine a set of values for P_m and K. A value of P at T_m was read from their photosynthetic curve. The value of P at optimum temperature $T_m = 42.5°C$ was 0.44×10^{-8} moles cm^{-2} sec^{-1}. At this stage it is assumed that the observed photosynthetic rate at maximum, e.g. 0.44×10^{-8} moles cm^{-2} sec^{-1}, is diffusion limited and that the concentration of carbon dioxide at the chloroplasts is zero. Reference to Fig. 3 shows that for $P = 0.44 \times 10^{-8}$ moles cm^{-2} $sec^{-1} = 1.9 \times 10^{-7}$ gm CO_2 cm^{-2} sec^{-1} the maximum resistance possible to carbon dioxide diffusion is about 3.0 sec cm^{-1}. This assumes a carbon dioxide concentration of zero at the chloroplasts. For kinetic reasons this is not realistic. If one assumes a more realistic concentration at chloroplast, e.g. half atmospheric concentration, then ${}_{CO_2}r = 1.5$ sec cm^{-1}. Equation 10 indicates that various specific pairs of K and P_m represent $P = 0.44 \times 10^{-8}$ moles cm^{-2} sec^{-1} for ${}_{CO_2}r = 1.5$ sec cm^{-1} and ${}_{CO_2}d_a = 1.25 \times 10^{-8}$ moles cm^{-2} sec^{-1}. The value of K for Sorghum must be estimated from the data available for maize since the appropriate information concerning photosynthesis as a function of carbon dioxide concentration is not available for Sorghum. K is determined from the observational data of Hesketh (1963) for maize plotted according to the Lineweaver - Burk method ($1/P$ versus $1/{}_{CO_2}d_a$). The value obtained for K is 1.0×10^{-8} moles CO_2 cm^{-3}. Then from Eqn. 10 the value for P_m is 1.19×10^{-8} moles CO_2 cm^{-2} sec^{-1}. Using this pair of values of P_m and K, derived from maize for application to Sorghum, and using the temperature dependence relation for $P_m(T_\ell)$ which was based on Fig. 8, one can calculate from Eqn. 11 for ${}_{CO_2}r = 1.5$ sec cm^{-1} a curve for photosynthesis P as a function of T_ℓ for Sorghum. The calculated curve is shown in Fig. 9 where it is compared with the observed photosynthetic rate for Sorghum as a function of the temperature. It is interesting to note that the rates of photosynthesis at optimum temperature and the shapes of the two curves agree rather well. The departure at very high temperatures, e.g. at $T_\ell > 50°C$, would be corrected if respiration was included in the calculations.

A similar procedure to that used for the calculation of the photosynthetic rate of Sorghum as a function of temperature was used for cotton for which $K = 1.0 \times 10^{-8}$ moles CO_2 cm^{-3} and $P_m = 1.186 \times 10^{-8}$ moles CO_2 cm^{-2} sec^{-1}. Estimating a total resistance to carbon dioxide diffusion for cotton one gets the calculated photosynthetic-temperature curve shown in Fig. 10. The shape of the calculated curve agrees well with the shape of the measured curve. The two curves would superimpose if the total resistance to carbon dioxide diffusion was reduced from 5.0 sec cm^{-1} to about 4.0 sec cm^{-1}.

Geophysical Factors Affecting Productivity

It is of interest to explore the dependence of photosynthesis and transpiration on the environmental conditions expressed by radiation, air temperature, wind speed, and relative humidity. By means of Eqns. 1 and 2 one can calculate the leaf temperature and transpiration rate for any set of Q_{abs}, T_a, V, and r.h. From Eqn. 11 one can calculate for a particular plant the photosynthetic rate as a result of the kinetics and gas diffusion for each particular leaf temperature. The results of these calculations are shown in Figs. 11 and 12. It is interesting to note the ratio of the number of carbon dioxide molecules assimilated to the number of water molecules transpired. At a relative humidity of 50% the ratio is between 1/100 and 1/300 as seen in Fig. 11. At high temperatures and low resistances an increase of wind speed produces an increase in the amount of water loss and of the photosynthetic rate, but the ratio 1/N decreases and the efficiency for productivity diminishes. Here N is the number of water molecules transpired for every carbon dioxide molecule assimilated. At low air temperatures throughout an increase of wind speed will reduce photosynthesis, reduce transpiration, and increase the ratio 1/N. At high air temperatures and high resistance an increase of wind will increase photosynthesis, decrease transpiration, and increase the ratio of 1/N.

In Fig. 12 one sees the influence of relative humidity on the photosynthetic rate and transpiration rate. At any given temperature a decrease of humidity increases the inefficiency of productivity, in other words it decreases the ratio 1/N. Also an increase of temperature always produces a reduction in the efficiency of productivity. It is also of interest to note that under certain conditions of high humidity, an increase of air temperature produces first an increase of photosynthesis and then a decrease since the leaf temperature is exceeding the optimum temperature. However, at low humidity an increase of air temperature almost always produces an increase of photosynthetic rate except at very high resistances. The number of water molecules transpired to each carbon dioxide molecule assimilated may vary from 100 to 500 for plants of high resistance when going from very humid to very dry air. At low temperatures an increase of resistance results in a slight increase of photosynthetic efficiency, while at high temperatures an increase of resistance results in a decrease of photosynthetic efficiency. The ratio of the number of water molecules transpired to the number of carbon dioxide molecules assimilated is given as a function of air temperature and leaf resistance in Figs. 13 and 14 for wind speeds of 10 and 50 cm sec^{-1} respectively. At the higher wind speeds the photosynthetic efficiency increases with an increase of resistance for most air temperatures normally encountered.

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Fig. 1. Transpiration rate and leaf temperature as a function of the air temperature and the leaf resistance for the conditions indicated.

Fig. 2. Transpiration rate and leaf temperature as a function of the wind speed and the leaf resistance for the conditions indicated.

Fig. 3. Flux of carbon dioxide into a leaf of shape W = D as a function of total resistance to carbon dioxide for a wind of 10 cm sec^{-1} and 100 cm sec^{-1} for D = 1, 5, 10, and 20 cm.

Fig. 4. Observed net photosynthesis as a function of the leaf temperature for Sorghum, sunflower, and cotton.

Fig. 5. Relative rate of net photosynthesis for the bryophyte *Bryum Sandbergii* as a function of its temperature.

Fig. 6. Relative luminescence of bacteria and multiplication of *Echeri coli* as a function of temperature.

Fig. 7. Relative photosynthetic curve as a function of temperature with an optimum temperature of 42.5°C but with the shape of the curve based on Fig. 5 for *Bryum Sandbergii*.

Fig. 8. Calculated net photosynthesis as a function of leaf temperature and diffusion resistance to carbon dioxide for an air concentration of 1.25×10^{-8} moles of CO_2 cm^{-3}, a maximum photosynthetic rate of 5×10^{-8} moles of CO_2 cm^{-2} sec^{-1}, and a Michaelis-Menton coefficient of 6×10^{-8} moles CO_2 cm^{-3}.

Fig. 9. Comparison of calculated and observed net photosynthetic rate for Sorghum as a function of the leaf temperature.

Fig. 10. Comparison of calculated and observed net photosynthetic rate for cotton as a function of the leaf temperature.

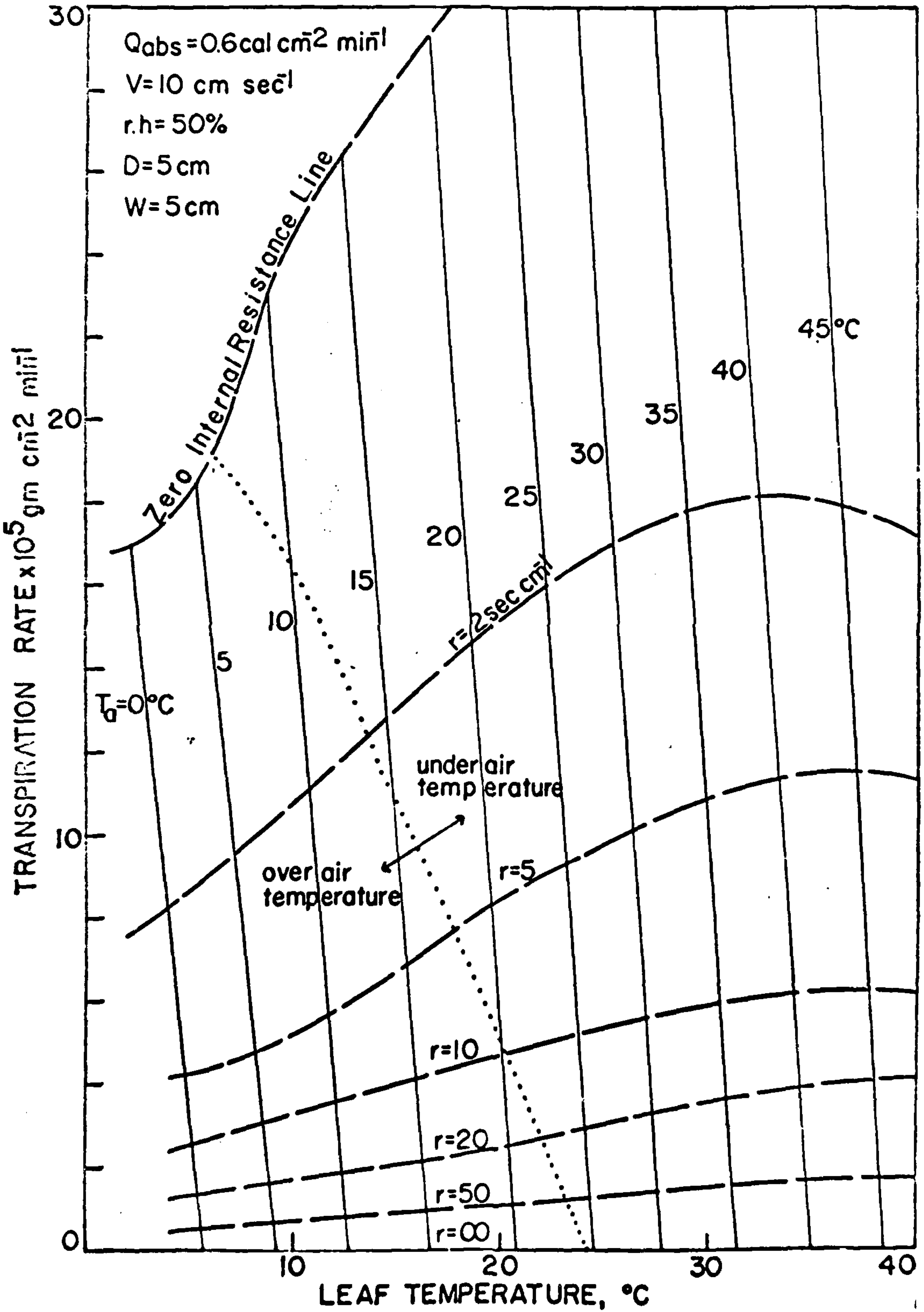
Fig. 11. Calculated net photosynthetic rate and transpiration rate as a function of the air temperature, the leaf resistance, and the wind speed for the conditions shown.

Fig. 12. Calculated net photosynthetic rate and transpiration rate as a function of the air temperature, the leaf resistance, and the relative humidity for the conditions shown.

Fig. 13. Ratio of transpiration rate to net photosynthetic rate as a function of the air temperature and the diffusion resistance for the conditions shown. A low value of E/P represents a high photosynthetic efficiency in terms of low water use per CO_2 molecule assimilated.

Fig. 14. Ratio of transpiration rate to net photosynthetic rate as a function of the air temperature and the diffusion resistance for the conditions shown. A low value of E/P represents a high photosynthetic efficiency in terms of low water use per CO_2 molecule assimilated.

Figure 1



Qabs=0.6 cal cm-2 min-1
V=10 cm sec-1
r.h=50%
D=5 cm
W=5 cm
Zero Internal Resistance Line
45°C
40
35
30
25
20
15
10
5
Ta=0°C
r=2 sec cm-1
r=5
r=10
r=20
r=50
r=∞
under air temperature
over air temperature
TRANSPIRATION RATE x10^5 gm cm-2 min-1
30
20
10
0
10
20
30
40
LEAF TEMPERATURE, °C

Figure 2

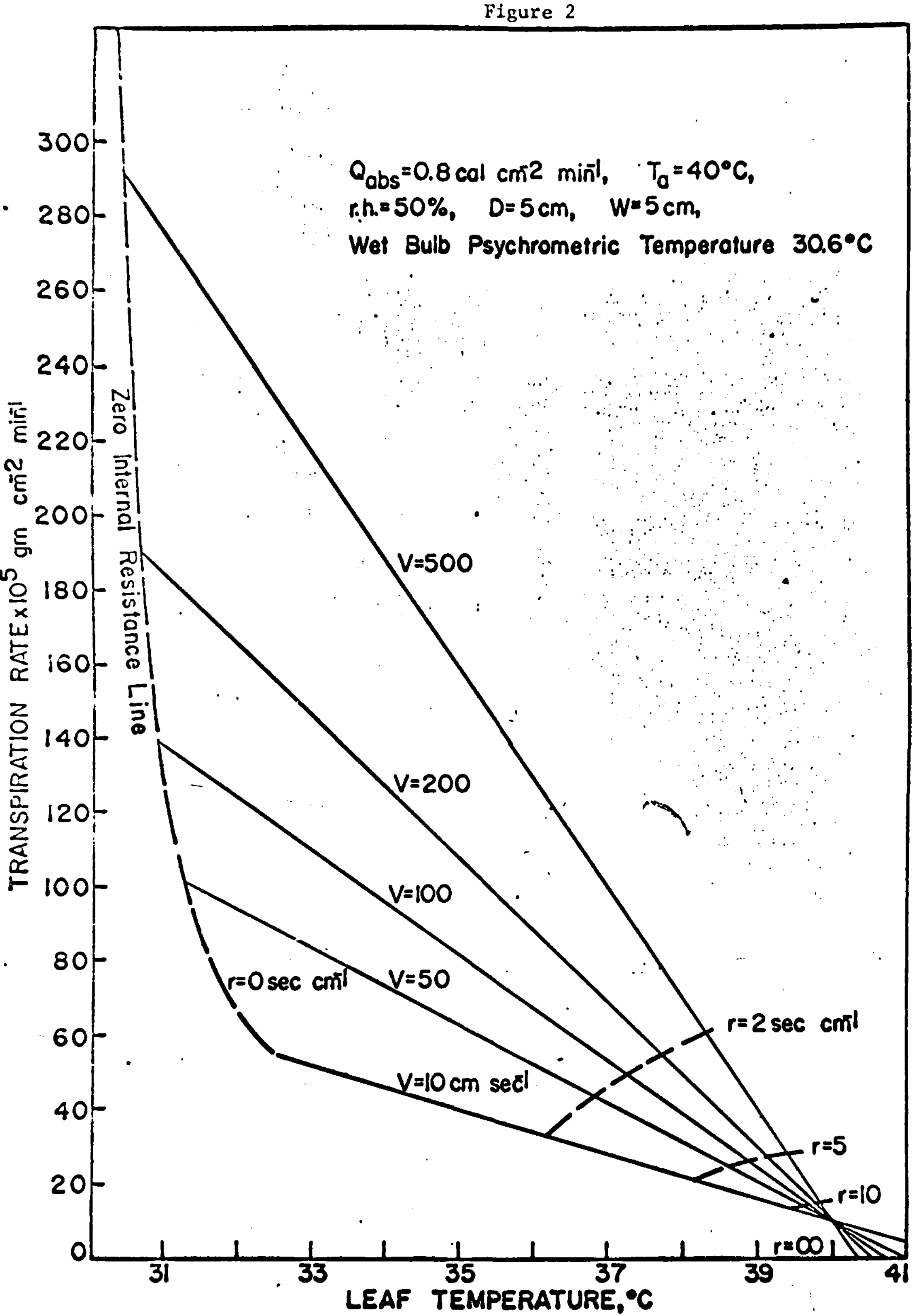

Q_{abs}=0.8 cal cm^{-2} min^{-1}, T_a=40°C,
r.h.=50%, D=5 cm, W=5 cm,
Wet Bulb Psychrometric Temperature 30.6°C
Zero Internal Resistance Line
V=500
V=200
V=100
V=50
V=10 cm sec^{-1}
r=0 sec cm^{-1}
r=2 sec cm^{-1}
r=5
r=10
r=∞
TRANSPIRATION RATE x 10^5 gm cm^{-2} min^{-1}
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
300
31
33
35
37
39
41
LEAF TEMPERATURE, °C

Figure 3

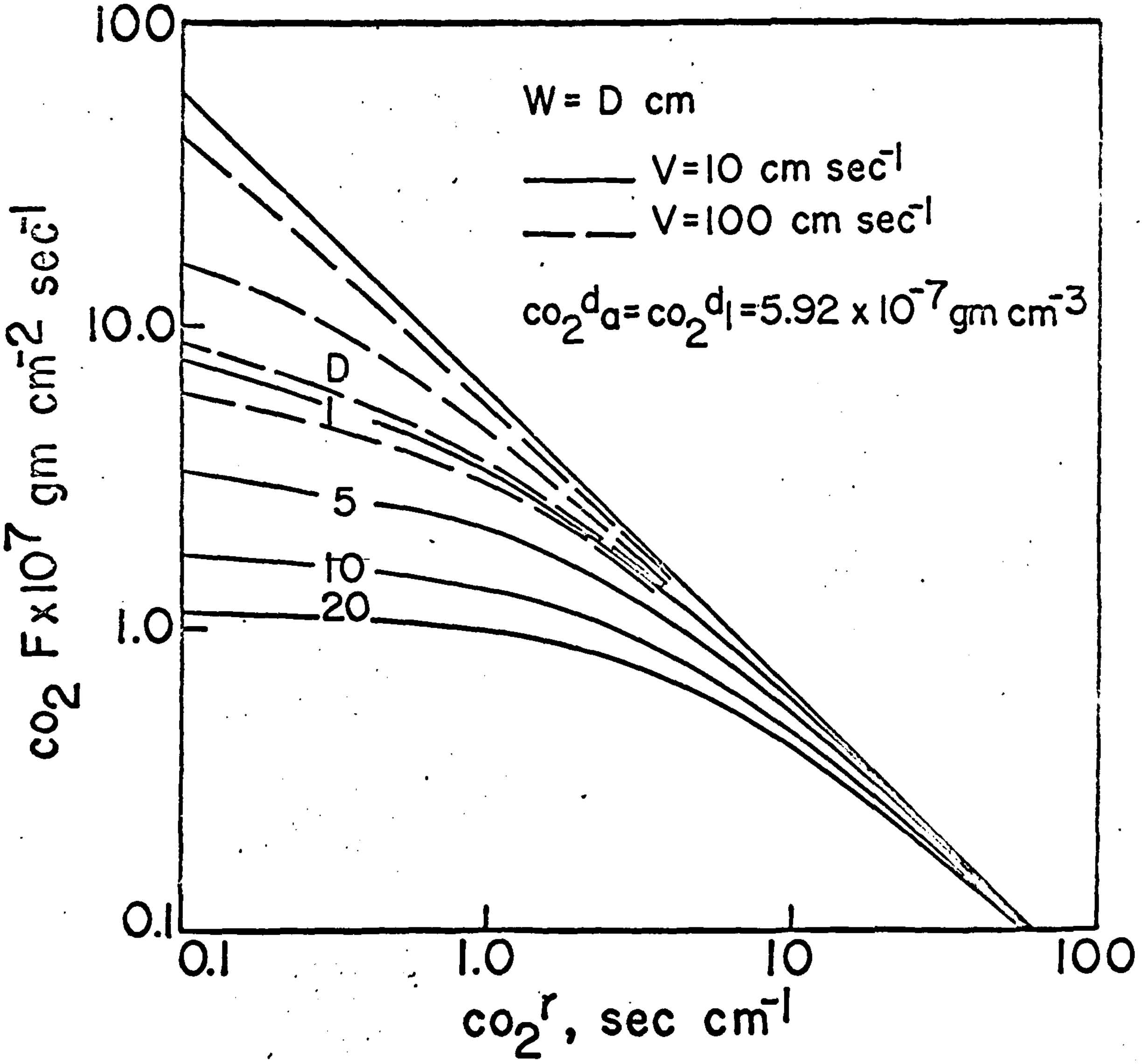
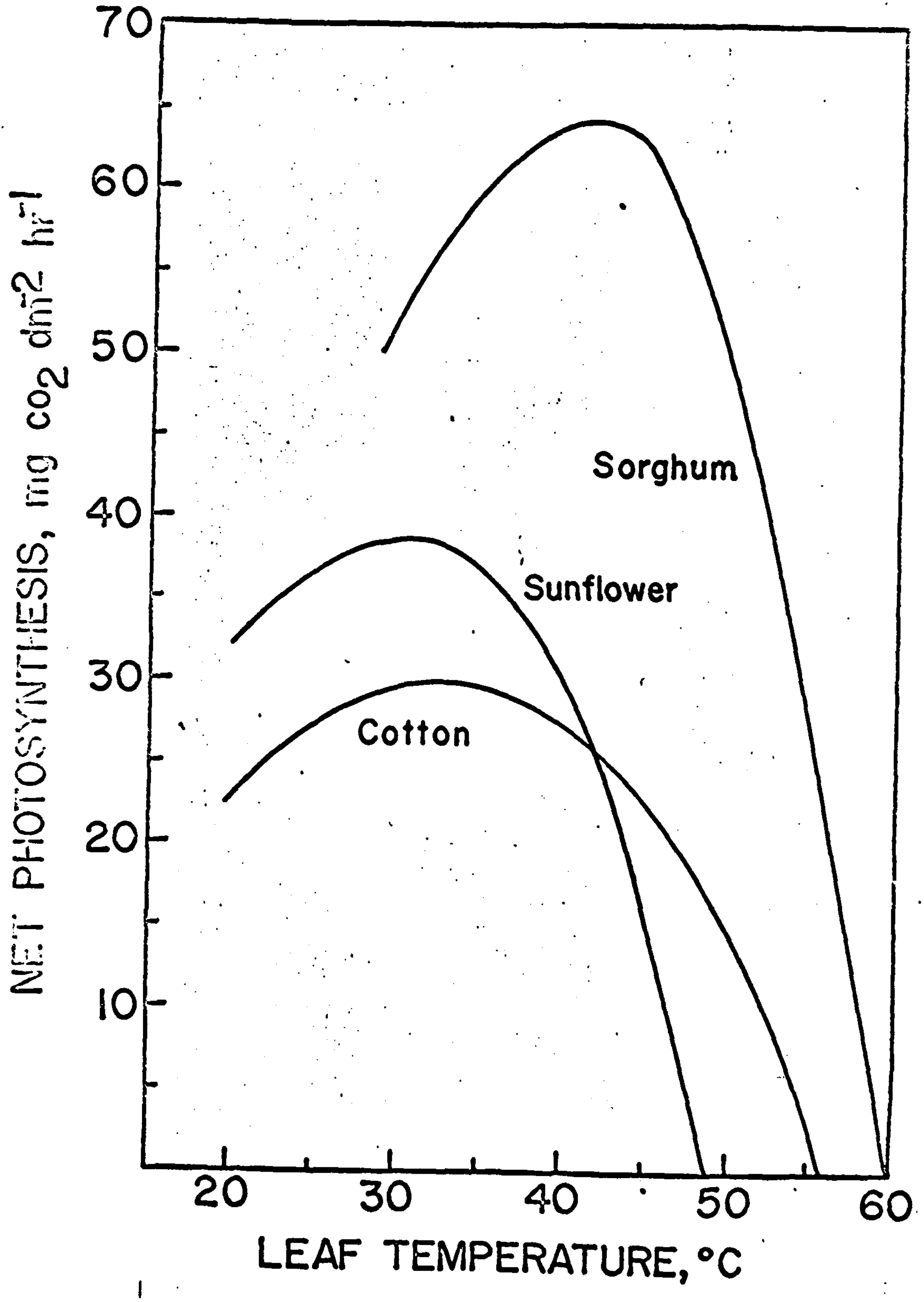

W= D cm
V=10 cm sec^{-1}
V=100 cm sec^{-1}
$co_2d_a = co_2d_l = 5.92 \times 10^{-7}$ gm cm^{-3}
D
1
5
10
20
100
10.0
1.0
0.1
0.1
1.0
10
100
$co_2F \times 10^7$ gm cm^{-2} sec^{-1}
co_2r, sec cm^{-1}

Figure 4



70
60
50
40
30
20
10
NET PHOTOSYNTHESIS, mg co$_2$ dm^{-2} hr^{-1}
Sorghum
Sunflower
Cotton
20
30
40
50
60
LEAF TEMPERATURE, °C

Figure 5

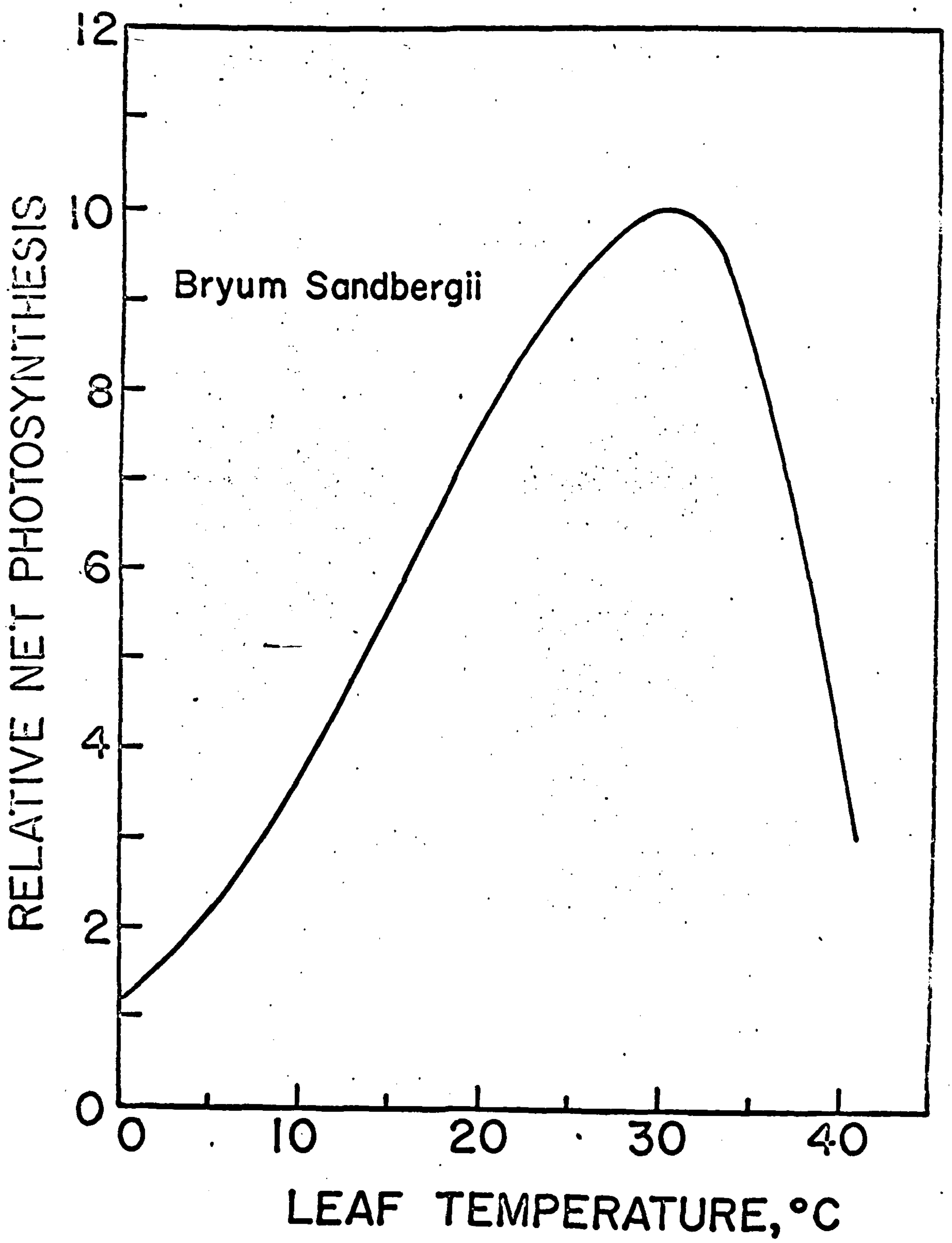
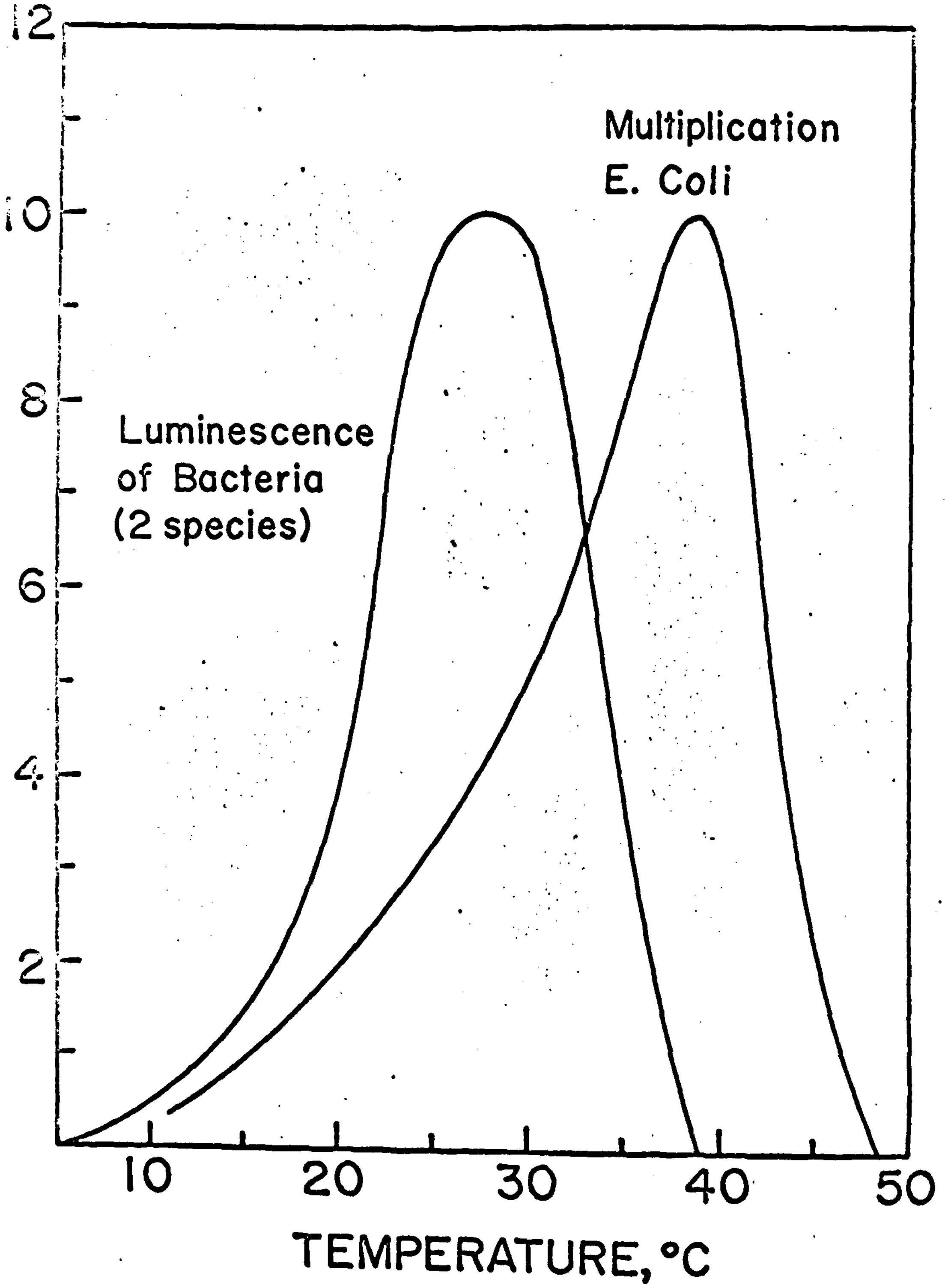

Bryum Sandbergii
RELATIVE NET PHOTOSYNTHESIS
0
2
4
6
8
10
12
0
10
20
30
40
LEAF TEMPERATURE, °C

Figure 6



12
10
8
6
4
2
Multiplication
E. Coli
Luminescence
of Bacteria
(2 species)
10
20
30
40
50
TEMPERATURE, °C

Figure 7

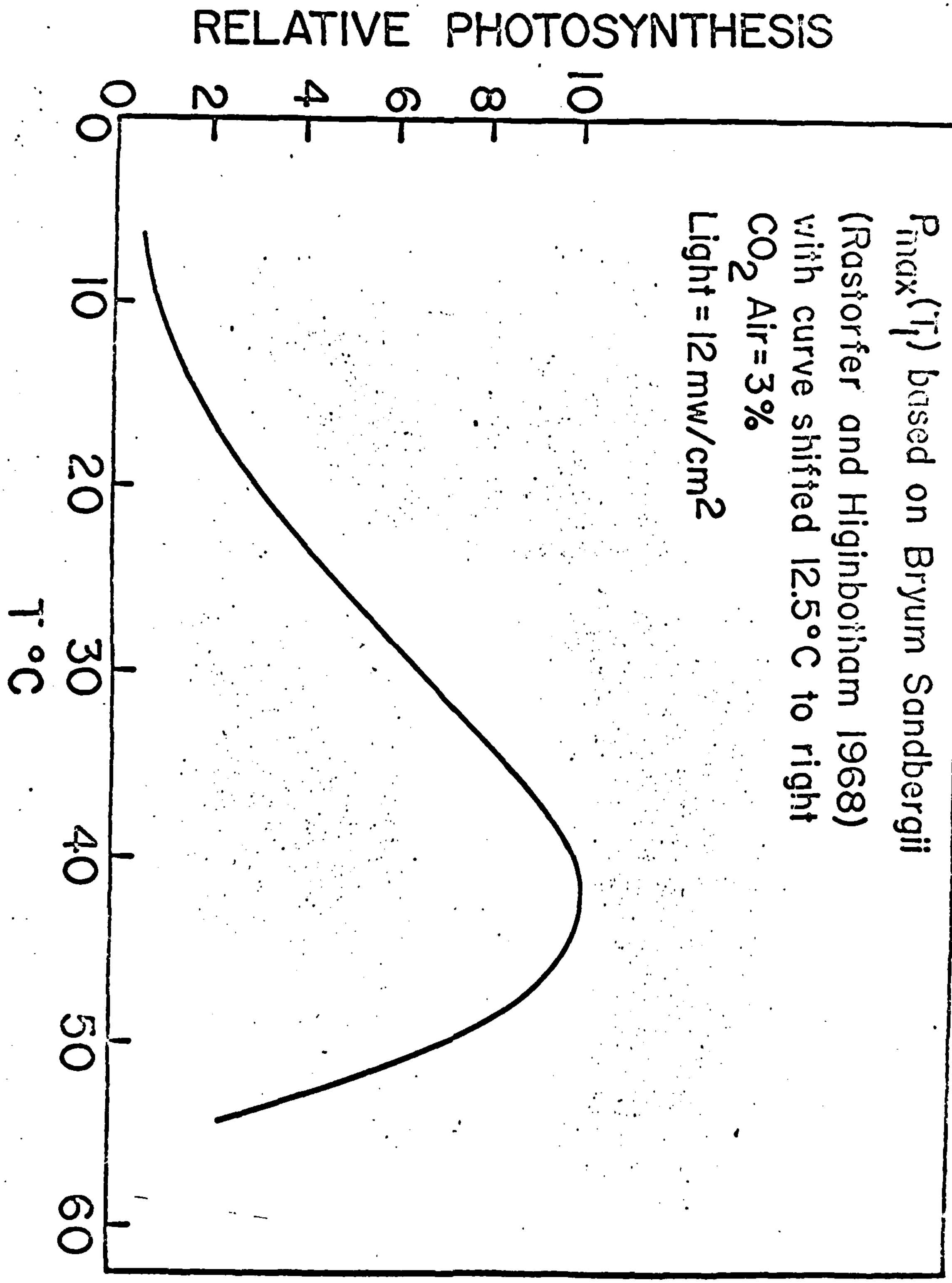
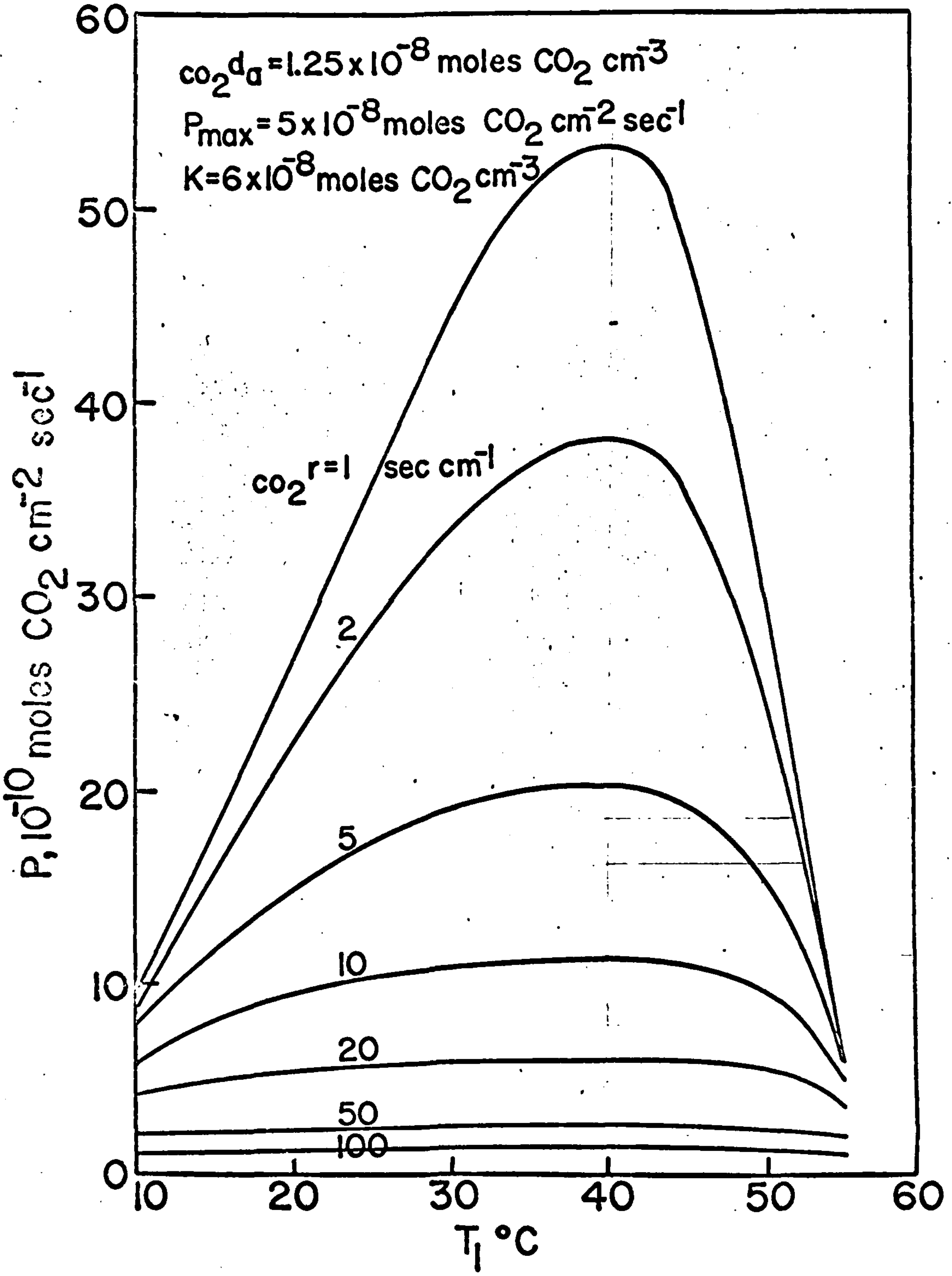
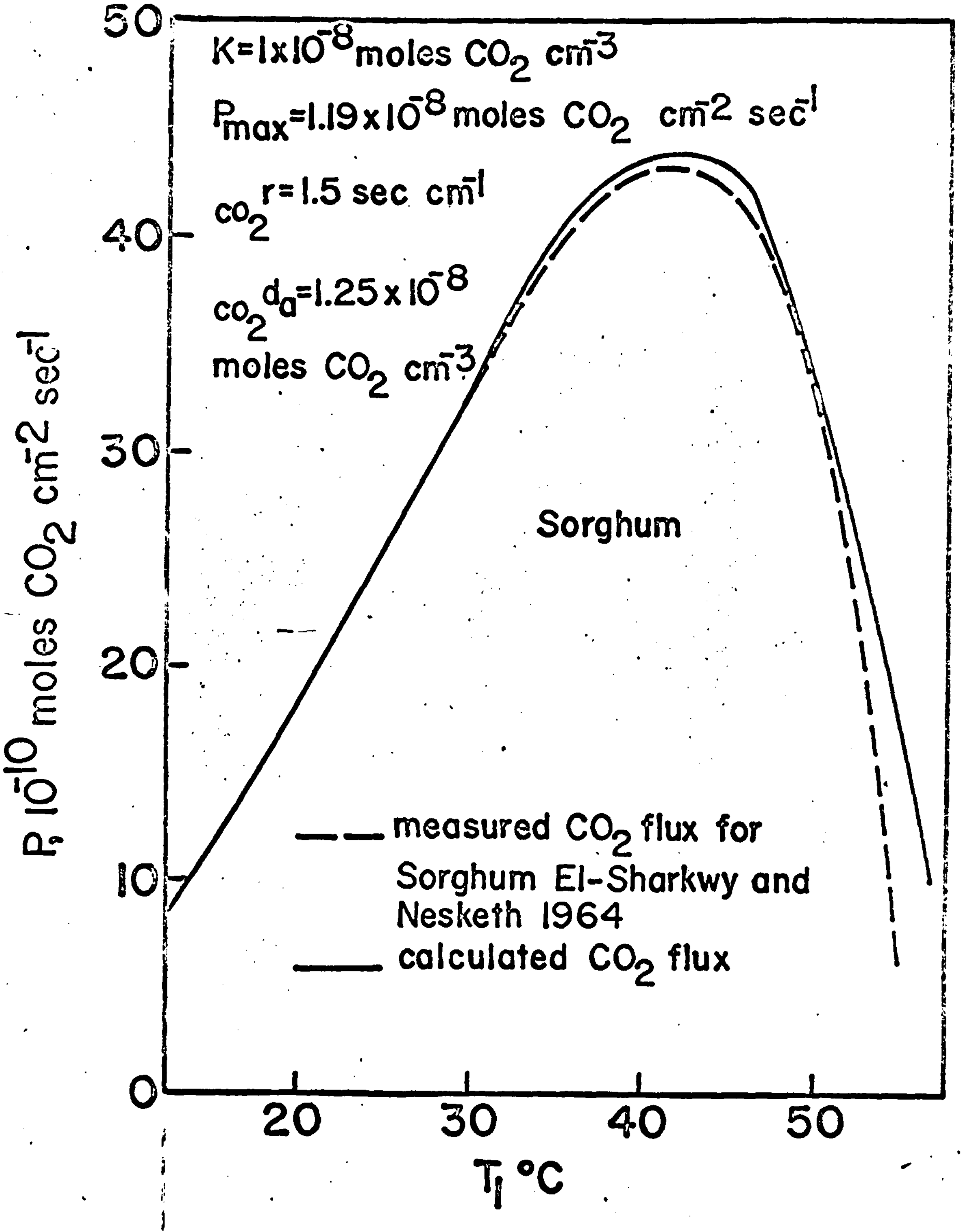

RELATIVE PHOTOSYNTHESIS
0
2
4
6
8
10
0
10
20
30
40
50
60
T °C
$P_{max}(T_l)$ based on Bryum Sandbergii
(Rastorfer and Higinbotham 1968)
with curve shifted 12.5°C to right
CO_2 Air = 3%
Light = 12 mw/cm2

Figure 8



$_{CO_2}d_a = 1.25 \times 10^{-8}$ moles CO_2 cm^{-3}
$P_{max} = 5 \times 10^{-8}$ moles CO_2 cm^{-2} sec^{-1}
$K = 6 \times 10^{-8}$ moles CO_2 cm^{-3}
$_{CO_2}r = 1$ sec cm^{-1}
2
5
10
20
50
100
$P, 10^{-10}$ moles CO_2 cm^{-2} sec^{-1}
0
10
20
30
40
50
60
T_l °C

Figure 9



K=1x10⁻⁸ moles CO₂ cm⁻³
Pmax=1.19x10⁻⁸ moles CO₂ cm⁻² sec⁻¹
co₂r=1.5 sec cm⁻¹
co₂da=1.25x10⁻⁸ moles CO₂ cm⁻³
Sorghum
measured CO₂ flux for Sorghum El-Sharkwy and Nesketh 1964
calculated CO₂ flux
P, 10⁻¹⁰ moles CO₂ cm⁻² sec⁻¹
0
10
20
30
40
50
20
30
40
50
Tl °C

Figure 10

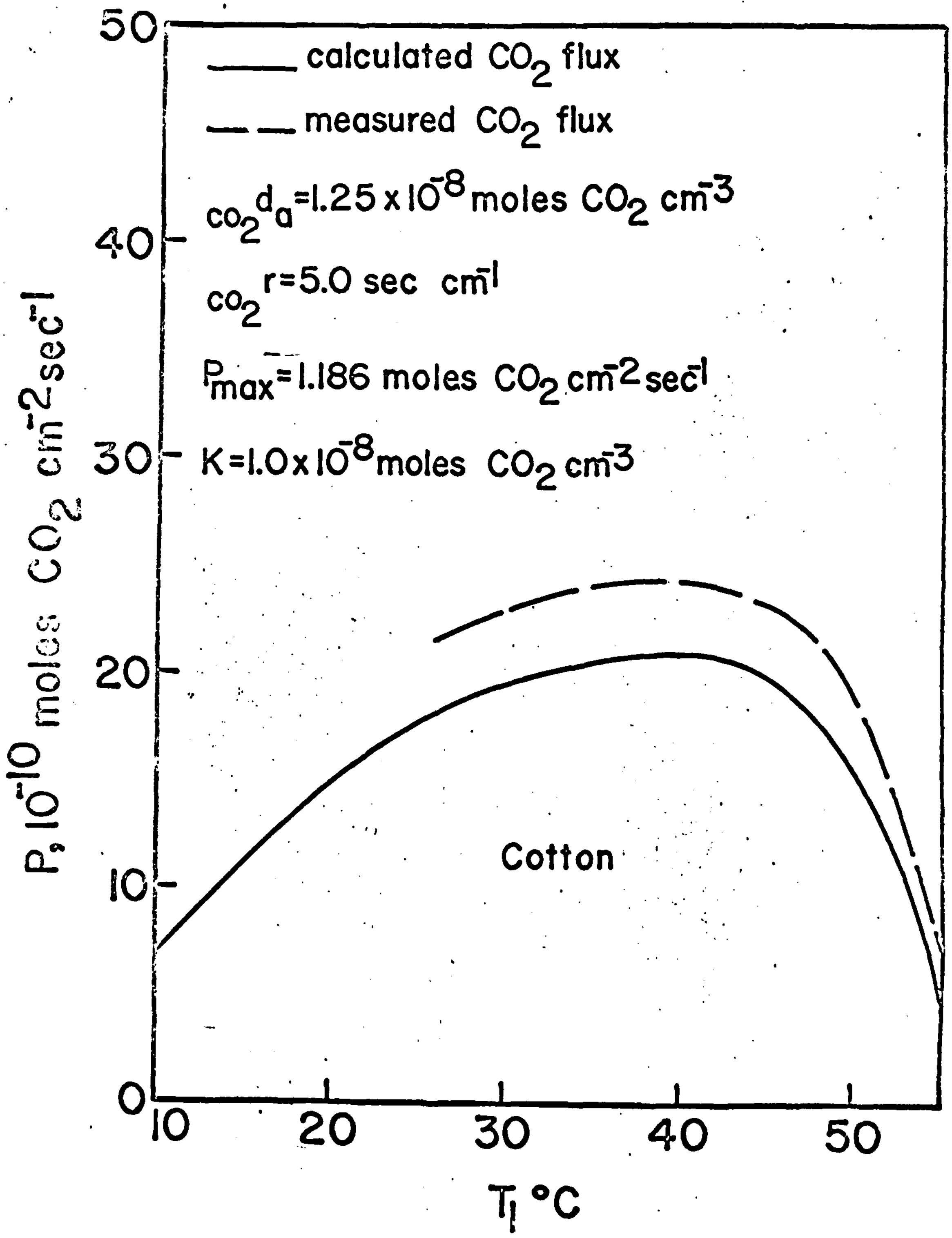
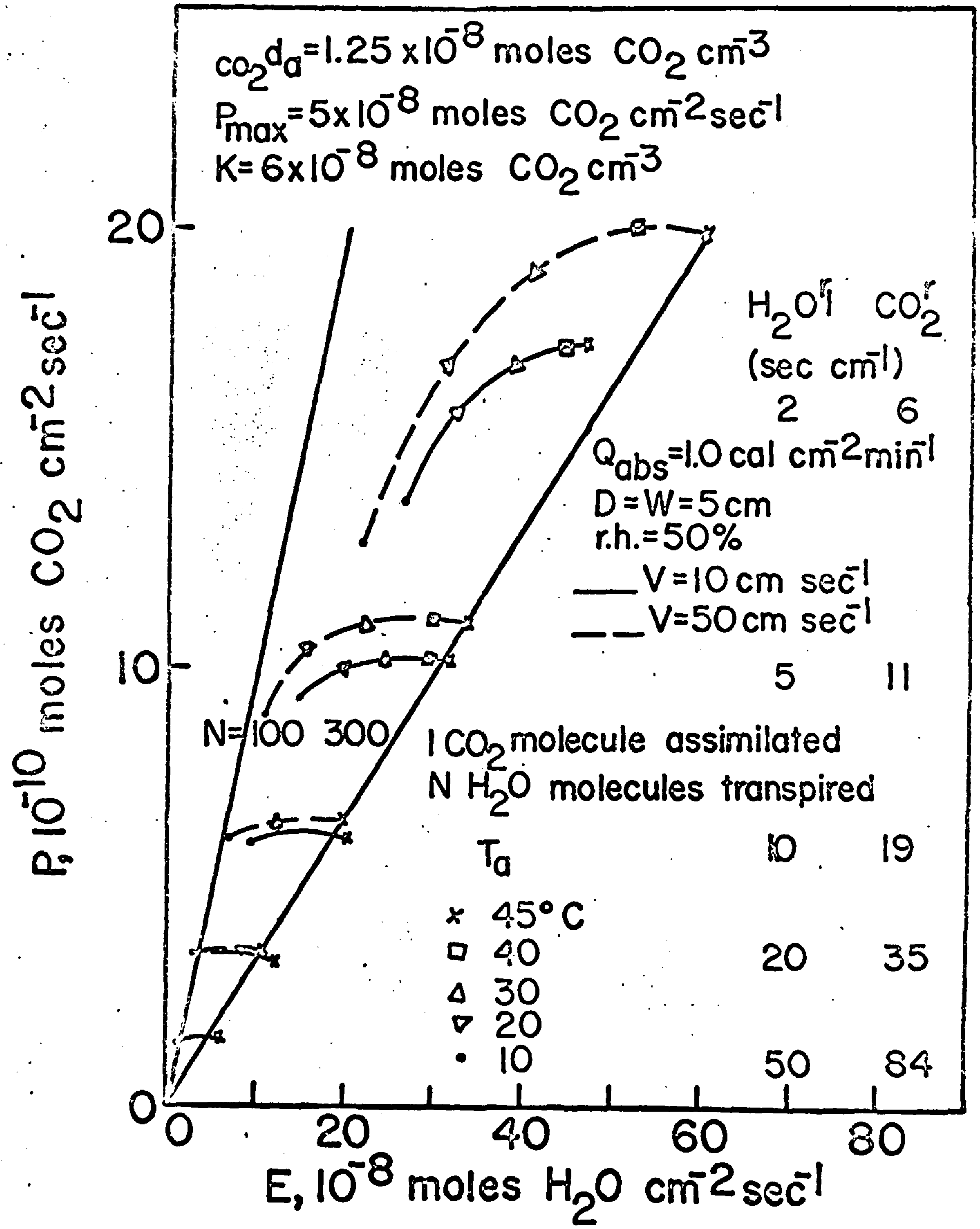
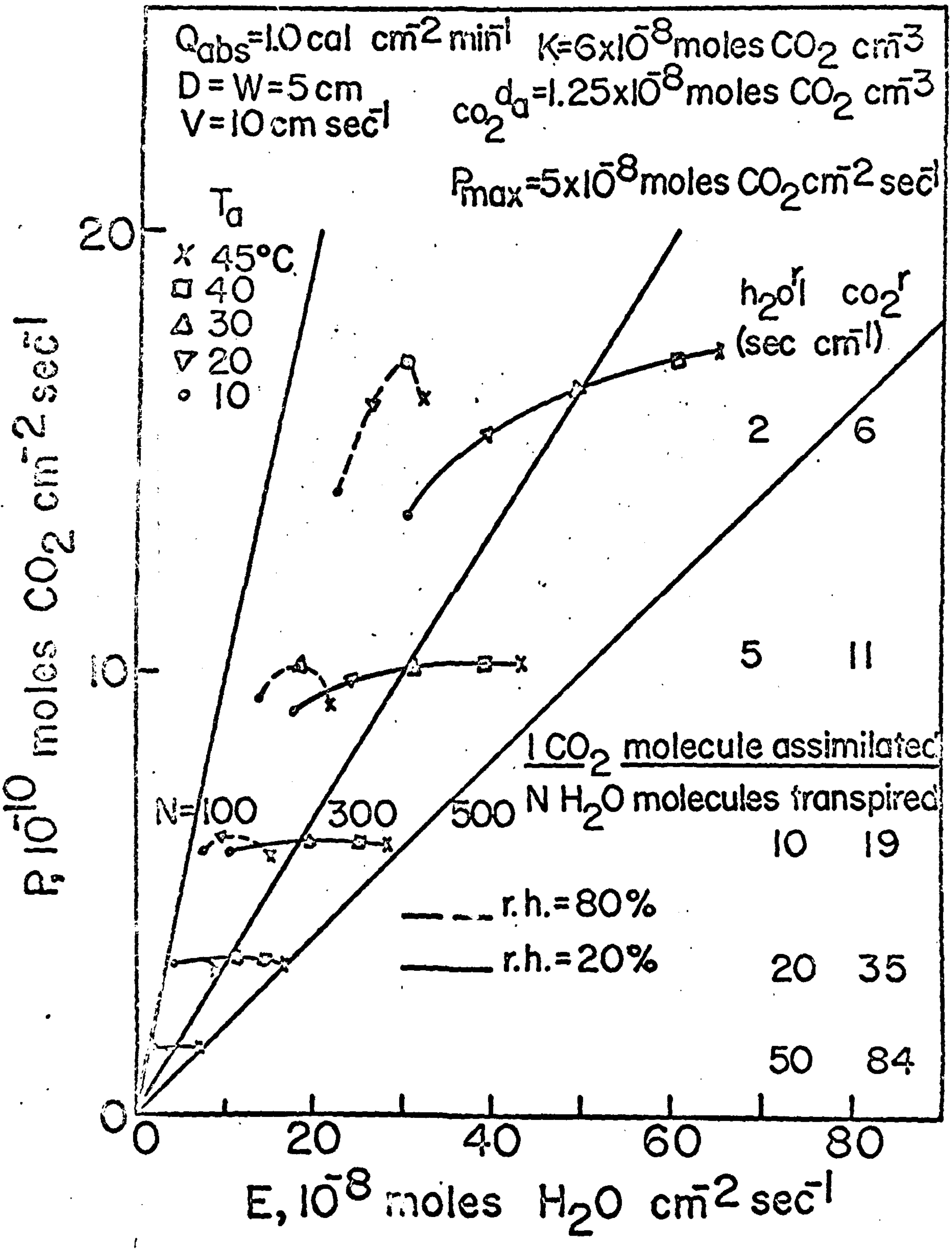

calculated CO_2 flux
measured CO_2 flux
$_{CO_2}d_a = 1.25 \times 10^{-8}$ moles CO_2 cm^{-3}
$_{CO_2}r = 5.0$ sec cm^{-1}
$\bar{P}_{max} = 1.186$ moles CO_2 cm^{-2} sec^{-1}
$K = 1.0 \times 10^{-8}$ moles CO_2 cm^{-3}
Cotton
P, 10^{-10} moles CO_2 cm^{-2} sec^{-1}
0
10
20
30
40
50
10
20
30
40
50
T_l °C

Figure 11



$co_2d_a = 1.25 \times 10^{-8}$ moles CO_2 cm^{-3}
$P_{max} = 5 \times 10^{-8}$ moles CO_2 $cm^{-2} sec^{-1}$
$K = 6 \times 10^{-8}$ moles CO_2 cm^{-3}
$H_2O^r l$ CO_2^r
(sec cm^{-1})
2 6
5 11
10 19
20 35
50 84
Q_{abs}=1.0 cal $cm^{-2} min^{-1}$
D=W=5cm
r.h.=50%
V=10 cm sec^{-1}
V=50 cm sec^{-1}
N=100 300
1 CO_2 molecule assimilated
N H_2O molecules transpired
T_a
× 45°C
□ 40
△ 30
▽ 20
• 10
P, 10^{-10} moles CO_2 $cm^{-2} sec^{-1}$
0
10
20
0
20
40
60
80
E, 10^{-8} moles H_2O $cm^{-2} sec^{-1}$

Figure 12



Q_{abs}=1.0 cal cm^{-2} min^{-1}
D = W = 5 cm
V = 10 cm sec^{-1}
K=6x10^{-8} moles CO$_2$ cm^{-3}
co$_2$d$_a$=1.25x10^{-8} moles CO$_2$ cm^{-3}
P$_{max}$=5x10^{-8} moles CO$_2$ cm^{-2} sec^{-1}
T$_a$
x 45°C
□ 40
△ 30
▽ 20
○ 10
h$_2$o^{r}l co$_2^r$
(sec cm^{-1})
2 6
5 11
10 19
20 35
50 84
1 CO$_2$ molecule assimilated
N H$_2$O molecules transpired
N=100
300
500
r.h.=80%
r.h.=20%
P, 10^{-10} moles CO$_2$ cm^{-2} sec^{-1}
0
10
20
E, 10^{-8} moles H$_2$O cm^{-2} sec^{-1}
0
20
40
60
80

Figure 13

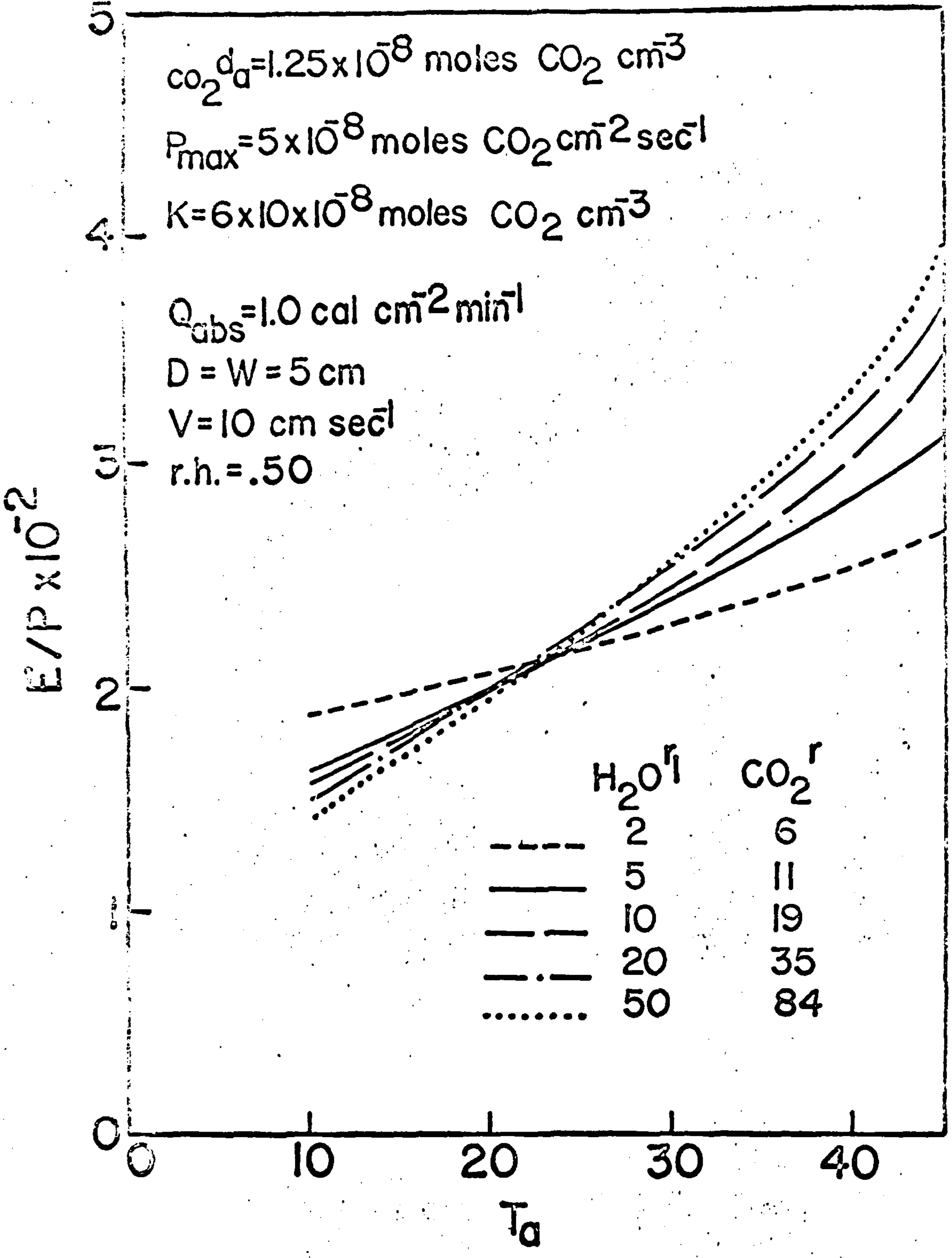
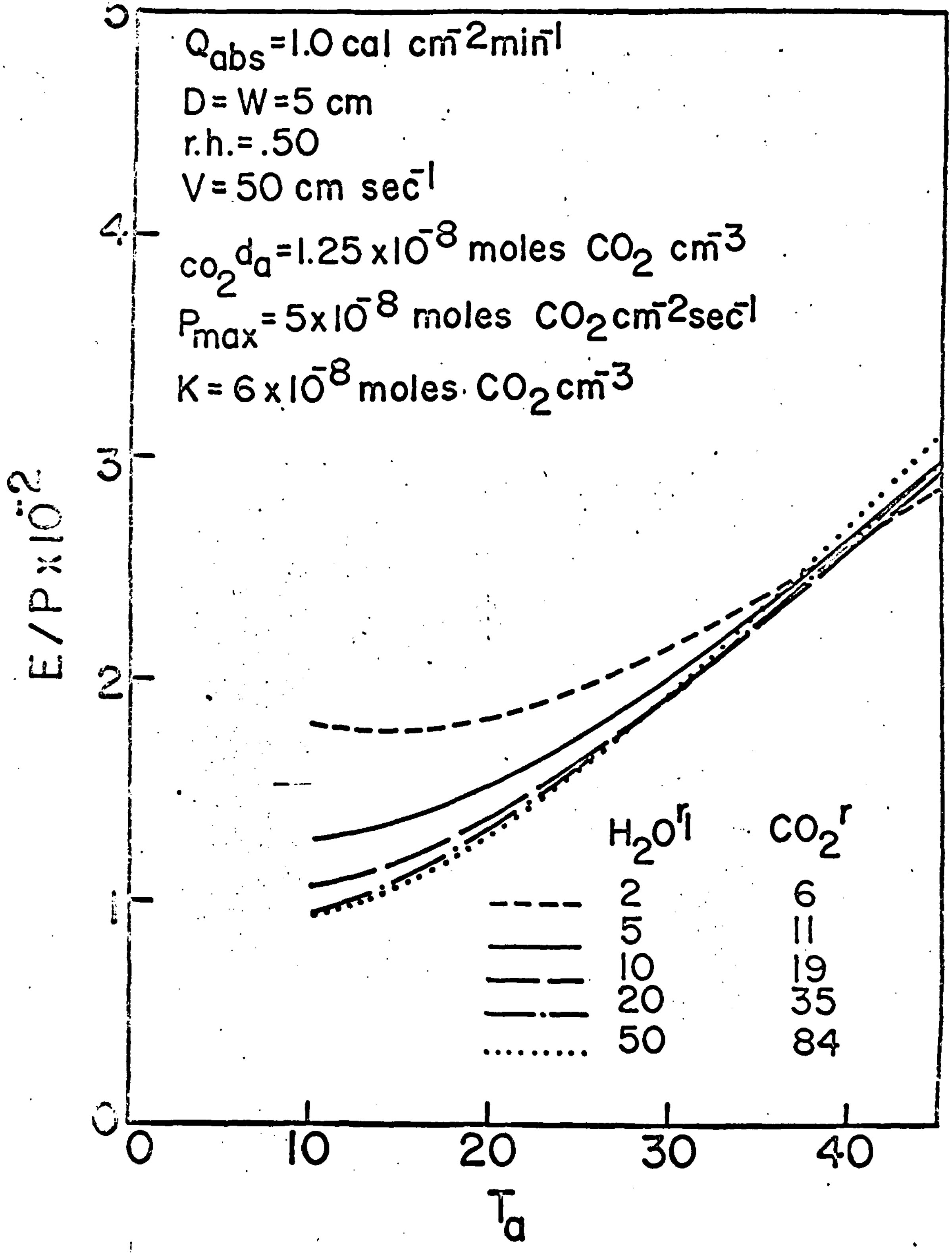

co_2d_a=1.25x10^{-8} moles CO_2 cm^{-3}
P_{max}=5x10^{-8} moles CO_2cm^{-2}sec^{-1}
K=6x10x10^{-8} moles CO_2 cm^{-3}
Q_{abs}=1.0 cal cm^{-2}min^{-1}
D = W = 5 cm
V=10 cm sec^{-1}
r.h.=.50
$H_2O^r l$
CO_2^r
2
6
5
11
10
19
20
35
50
84
5
4
3
2
1
0
E/P x10^{-2}
0
10
20
30
40
T_a

Figure 14



Q_{abs}=1.0 cal cm^{-2}min^{-1}
D=W=5 cm
r.h.=.50
V=50 cm sec^{-1}
co_2d_a=1.25×10^{-8} moles CO_2 cm^{-3}
P_{max}=5×10^{-8} moles CO_2cm^{-2}sec^{-1}
K=6×10^{-8} moles CO_2cm^{-3}
E/P×10^{-2}
0
1
2
3
4
5
0
10
20
30
40
T_a
H_2O^r1
CO_2^r
2
6
5
11
10
19
20
35
50
84

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13. ABSTRACT

A model for productivity is presented. It combines a model for photosynthesis with an energy budget approach to leaf energy balance. The photosynthesis model describes the rate of photosynthesis of a leaf as a function of leaf temperature, diffusive resistance to CO_2 and biochemical reaction rate (using the Michaelis-Menton equation). The energy budget approach describes the temperature of a leaf as determined by air temperature incident radiation, wind speed, relative humidity, diffusive resistance to water vapor, leaf size, leaf orientation, and leaf spectral characteristics.

When the photosynthesis and energy budget approaches are combined, photosynthetic rate and rate of water loss, transpiration, can be calculated as functions of any combination of the above variables (wind speed, air temperature,etc). Also the ratio photosynthesis ÷ transpiration can be calculated, giving a measure of the relative productive efficiency of the plant for the particular conditions used in the calculation. A number of graphs of this ratio as it varies with several important geophysical factors are given along with comments as to the significance of the relationships.

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