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A HOLOCOENOTIC ANALYSIS OF ENVIRONMENT-PLANT RELATIONSHIPS

With Special Emphasis Being Given to the Calculation of Net Photosynthesis, Transpiration, and Sensible Heat Exchange

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1. INTRODUCTION

For the product of any analysis of environment-plant relationships to have a meaningful interpretation, there are, in the opinion of the author, two important principles that must form the basis of the approach employed. These are, first, that as far as possible the leaf, as the basic unit of net photosynthesis, transpiration, and sensible heat exchange, must be the focal point of one's attention; and second, that all environmental parameters must be considered in terms of their relationships with one another, with their effects upon the plant being expressed through effects they exert upon factors that have *direct meaning* for the plant.

The first of these principles is easily understood; we obtain the results we seek for all of the different types of leaves composing the plants we are studying and then compute a weighted average for the aggregation of leaves comprising the entire crop. The second of the principles implies that we determine what factors *directly influence* the phenomena we are studying, and that we then consider all of the many factor-factor and factor-plant relationships of the dynamic plant-environment system to arrive at specifications of these basic factors which will then determine the rates of the processes in question.

In the following pages there will be developed a method for the study of environment-plant relationships which is based upon these two principles. In particular, it will be a method for the calculation of net crop photosynthesis, which will, as a result of the calculations involved, also give the rates of latent and sensible heat transfer from the crop. The first step of this analysis will be to determine the factors having direct meaning for the processes of net photosynthate production, transpiration, and sensible heat exchange. Then the mechanics of specifying values of these factors in light of all the interrelationships among the many environmental parameters will be presented. Finally, the calculated values of these factors will be used to determine the rates of the processes in question, namely, net photosynthesis, transpiration, and sensible heat exchange.

2. THE HIERARCHY OF ENVIRONMENTAL PARAMETERS

It is the conclusion of mere armchair reflection that not all environmental parameters bear equivalent relationships to the internal affairs of a plant. Take, for instance, the parameter of wind speed, a factor of major importance in many plant processes, and consider its effects upon one of these: photosynthesis. It is common knowledge in the realms of the plant sciences that wind can affect the photosynthesis rate through its influence upon the canopy level concentration of carbon dioxide in the air. This is due to the role wind speed plays in the turbulent exchange of CO_2 between the fairly constant concentration of the free atmosphere and the fluctuating concentration of the effective canopy exchange surface. It is also becoming fairly well known (see, for example, Gates, 1965; Idso, Baker, and Gates, 1966; Idso and Baker, 1967a; and Idso and Baker, 1968c) that wind can influence net photosynthesis through its role in sensible and latent heat exchange from the plant, whereby leaf temperature is altered and respiration either increased or decreased. It is also evident that wind plays a role in the apparent photosynthetic efficiency of light utilization by plants, through its influence on the orientation of the canopy leaves.

It is fairly obvious from these considerations that although wind can influence net photosynthesis in a variety of ways, it does so _indirectly_ in all instances. In the first case mentioned it operates through the canopy level concentration of carbon dioxide, in the second through the parameter leaf temperature, and in the third through the effects of light intensity, all of which do directly influence net photosynthesis. The most direct effect of wind conceivable would probably be the uprooting of a plant or the breaking of its stems or branches; and even this would not have a direct effect on photosynthesis. Its only effect would be to remove the possibility of supplying water and nutrients to the leaves from the soil. Thus, a hierarchy of environmental parameters begins to present itself to the mind, wherein wind must occupy a secondary position with respect to leaf temperature, light intensity, and the carbon dioxide concentration of the canopy level air.

Now there are a few other factors that must be mentioned as having a direct effect upon photosynthesis too. These are the level of essential nutrients in the soil and the moisture regimes of both soil and atmosphere. All other factors of the environment, however, (excepting landslides, fire, hail, destruction by man and animals, etc.) are either secondary or tertiary factors, making their influence felt through their operations upon one or more of the previously mentioned five basic factors.

As a means of reinforcing these ideas and introducing more of the secondary and tertiary factors of the environment, figure 1 is presented. In the center of this figure are represented the photosynthetic and respiratory processes of the plant, and pointing to these processes are arrows from four of the five basic factors which directly affect them.

(The fifth factor, level of essential nutrients in the soil, is not dealt with here in order to preserve the essentially climatic nature of the analysis.) As is indicated by the arrows, the effects of these four factors upon net photosynthesis must be obtained experimentally; thus they are known in the form of correlations and not mathematical expressions. Also, there is one arrow leaving the photosynthetic and respiratory processes and returning to the basic factor, CO_2 concentration. This represents an effect of the plant upon this factor. In particular, it is the lowering of the carbon dioxide concentration of the canopy level air as the plant utilizes CO_2 in photosynthesis.

Focusing our attention now upon those factors represented as influencing the four basic factors of light intensity, leaf temperature, leaf water availability, and CO_2 concentration, we are confronted with two general types of parameters. First there is the component primary factor. This is a factor, such as incoming direct short wave radiation, which is actually a part or fraction of one of the four basic factors, in this instance light intensity. Other factors of this type represented in figure 1 are the remainder of the short wave radiant energy fluxes and the three components of the leaf water availability factor.

The other type of parameter manifest here is the secondary factor, which is not a component of one of the basic factors but which instead plays a direct role in determining the value of one or more of them. The basic factor most involved in this relationship is leaf temperature, to which five arrows from secondary factors converge.

Tertiary factors, as could be surmised at this point, are those factors of the environment which operate upon secondary factors in an analogous manner to their operation upon the four basic factors. The letters A, B, C, and D of figure 1 represent some of this group. In particular, we may say

A = latitude, slope and aspect of ground, cloud cover, dust and atmospheric pollutants; reflectance of ground and nearby objects.

B = cloud cover, temperature of ground and nearby objects, water vapor, and low level atmospheric ozone.

C = precipitation, height of water table, soil moisture content, and thus soil physical properties such as structure, texture, etc.

D = soil chemical properties: clay minerals, base exchange properties, pH, anions, organic compounds, etc.

Not all environmental parameters are easily put into one of these categories, however. For instance, it is seen that relative humidity is a component primary factor with respect to leaf water availability and a tertiary factor with respect to leaf temperature. Even more complicated is the case of air temperature which acts upon leaf temperature both as a secondary factor and as a tertiary factor. It can also be seen that the basic factor leaf temperature simultaneously acts as a tertiary factor with respect to the leaf-air vapor pressure deficit.

Finally, it must be noted that figure 1 is not complete. For one thing, the effect of wind upon the photosynthetic efficiency of light utilization by plants is not indicated, due to the unusual causative mechanism involved. Another omission is that of the effect of soil moisture tension upon transpiration, which may or may not be important (Idso, 1967); and it must be admitted that there are probably other interactions and factors not conceived by anyone, which in the future may yet be discovered. However, figure 1 does provide a good skeletal framework upon which to build until some of the more elusive factors and interrelationships of the environment can be better understood.

Before leaving this section we should perhaps give some justification for our choice of the four basic factors used. Actually, however, there is no choice involved. For if one considers the natures of the photosynthetic and respiratory processes, he is fairly forced to concede the first-order effects of these four factors. Since net photosynthesis is in essence a photochemical reaction whereby carbon dioxide and water in the presence of visible radiation and in association with chlorophyll in green plants are combined to form organic compounds, the reaction must be directly governed by the supply of reactants (CO_2 and water), the amount and type of incident short wave radiation, and the temperature of the reaction site. Thus, no other factors, excepting the level of certain essential nutrients, have a direct or primary effect upon net photosynthesis. They must instead exert their influence through the hierarchy of environmental parameters decreed by the very nature of this photochemical process.

3. PHYSICAL PROCESSES AND PLANT PROPERTIES

Besides bringing some order to the relationships among various environmental parameters and the ways by which they influence net photosynthesis, figure 1 performs two other utilitarian functions. It indicates by word the actual physical processes by which some of these relationships are sustained, and it notes by number the places in the plant-environment system where properties of the plant act as coupling devices between the environment and the plant. The identification of these properties is given below:

1 = absorptance, reflectance, and transmittance of plant leaves to direct and diffuse solar radiation, leaf distribution (of inclinations) function, leaf area index, canopy density, plant height, and percent cover of ground.

2 = same as 1.

3 = same as 1 but plant spectral properties now have reference to long wave radiation.

4 = leaf convection coefficient: thus, leaf size, leaf shape, leaf hairs, etc.; also, crop density (affects wind speed).

5 = same as 4.

6 = total leaf diffusion resistance to transpiration: thus, diffusion resistances of cuticle, stomata, substomatal cavity, and cell wall.

7 = same as 6.

8 = resistances of various plant parts (surfaces of root hairs, cortex, endodermis, vessels and tracheids in xylem, leaf veins) to water flow.

9 = permeability of different plant cell membranes.

10 = plant height.

11 = correlation between the four basic factors and the photosynthetic and respiratory processes.

Implicit in the principle of considering the relationships among the many environmental parameters is the understanding that, whenever possible, the actual physical processes by which these parameters are linked should be described analytically. This procedure, coupled with those already set forth for the general analysis, serves to place the method soon to be developed in a position whereby we can expect to derive reasons for calculated plant responses being as they are, a benefit not always reaped from analyses based solely on correlations. Also, plant properties become much more meaningful in such a context, and a real understanding of climatically modified or elicited biological activities may be achieved.

4. SPECIFICATION OF THE FOUR BASIC FACTORS

With the preceding three sections serving to introduce the principles upon which the holocoenotic analysis of environment-plant relationships is based, we will proceed now to outline in some detail the mechanics of specifying the four basic factors necessary to determine net photosynthetic rates.

4.1. Calculation of Light Intensity

The chief problem in specifying the light intensities of the variously oriented leaves of a plant canopy lies in determining what fractions of the leaves receive direct sunlight at various angles of incidence. De Wit (1965) developed a method for calculating the cumulative frequency of light interception by a plant canopy as a function of angle of incidence (actually as a function of the *sine* of the angle of incidence). Since it is a relatively simple process to transform these values into the ones we seek, a detailed derivation and redevelopment of his method (more detailed than his own development, in fact, which is rather difficult to follow at times) will be presented.

4.1.1. Introduction of Leaf Distribution Functions

The basic postulate upon which de Wit begins to build is that the leaves of a canopy "have not a preferred azimuth direction." This postulate has been experimentally shown to be sound for several plants, both by de Wit and by Nichiporovich (1961). This being so, de Wit indicates that it is sufficient to characterize the orientations of the leaves of a canopy by the frequency distribution of their inclinations from the horizontal. In this connection he found it convenient to distinguish four types of canopies: planophile canopies, where horizontal leaves are most frequent; erectophile canopies, where vertical leaves are most frequent; plagiophile canopies, where leaves at some oblique inclination are most frequent; and extremophile canopies, where leaves are least frequent at oblique inclinations. Figure 2 shows the cumulative frequency of occurrence of leaf inclination as a function of leaf inclination for these four characteristic types of canopies. Also shown is a theoretical erectophile leaf distribution function obtained by supposing that the relative frequency of leaf inclinations is the same as the relative frequency of the inclinations of the surface elements of a sphere. Its virtue lies in the fact that results of light interception calculations made for this leaf distribution are independent of the inclination or altitude angle of the sun. According to Nichiporovich (1961) [de Wit, 1965], the leaves of grasses, small grains, and corn manifest this spherical distribution; but de Wit's measurements only partly confirm this affirmation, as is evidenced by his measured leaf distribution function for corn, also shown in figure 2.

4.1.2. Derivation of the Light Distribution Function

We shall now direct our attention to figure 3 and derive from relations in evidence there the equation for the calculation of de Wit's "light distribution function." Part A of figure 3 is precisely as drawn by de Wit; but part B is a mirror image of his reorientation of part A and has two dotted lines as additions. It is felt these changes make the following derivations more clear. As to the meanings of the figures themselves, part A represents a leaf plane of given orientation with respect to the soil surface, and the line TS a ray of the sun. Part B is the same figure seen from a different point of view. The angles IS, IL, DA, and LS are, respectively, the Inclination of the Sun, the Inclination of the Leaf, the Difference between the Azimuths of the Leaf and the Sun, and the angle between the Leaf and the rays of the Sun.

We begin the derivations by noting that

$TS_h = TS \cdot COS(IS)$,

$OS_h = TS_h \cdot SIN(DA)$,

and

$OR = OS_h \cdot SIN(IL)$,

thus making OR also equivalent to

$OR = TS \cdot (COS(IS) \cdot SIN(IL) \cdot SIN(DA))$.

We next note that

$SS_h = TS \cdot SIN(IS)$

and that

$PS = SS_h \cdot SIN(IQ)$,

thus making

$PS = TS \cdot (SIN(IS) \cdot SIN(IQ))$.

However, since it is evident that $SIN(IQ) = COS(IL)$, we may also write

$PS = TS \cdot (SIN(IS) \cdot COS(IL))$.

Finally, since OR = S_LP and $SS_L = S_LP + PS$, we have

$SS_L = TS\cdot(SIN(IS)\cdot COS(IL) + COS(IS)\cdot SIN(IL)\cdot SIN(DA))$.

A second way of expressing SS_L which is evident from figure 3 is

$SS_L = TS\cdot SIN(LS)$.

Combining this equation with the previous one for SS_L and solving for SIN(LS) we get

$$SIN(LS) = A + B\cdot SIN(DA) \qquad [1]$$

where

$A = SIN(IS)\cdot COS(IL)$

$B = COS(IS)\cdot SIN(IL)$.

Now the light distribution function S (I) for a given value of IS and IL is what de Wit calls the "probability that a light ray is intercepted by a leaf with a sine of its angle to the light equal to or smaller than SIN(LS)." Since the amount of light intercepted by the leaves in a small azimuth interval is proportional to the size d(DDA) of this interval and since this amount of intercepted light is also proportional to the projection of the leaf surface elements in the direction of the sun, that is with SIN(LS), the light distribution function S(I), for I = SIN(LS), is

$$S(I) = \left(-\int_{-\frac{\pi}{2}}^{DAO} SIN(LS)\cdot d(DDA) + \int_{DAO}^{DA} SIN(LS)\cdot d(DDA)\right)\cdot W \qquad [2]$$

where W is a proportionality constant.

The reason for doing this integration in two parts is to distinguish between light falling on the uppersides and on the undersides of the leaves. Since light is parallel to a leaf when SIN(LS) = 0, the boundary angle DAO is defined as DAO = ARCSIN(-A/B) for IS < IL. Since no light falls on the undersides of the leaves if IS $\geq$ IL, the boundary angle in this case is defined as DAO $= -\frac{\pi}{2}$.

To determine the value of W, we note that if the integration is carried out to the maximum value of DA, that is $\frac{\pi}{2}$, we must have S(I) = 1, or

$$1 = \left(-\int_{-\frac{\pi}{2}}^{DAO} SIN(LS)\cdot d(DDA) + \int_{DAO}^{\frac{\pi}{2}} SIN(LS)\cdot d(DDA)\right)\cdot W.$$

Evaluating the first of these integrals, we have

$$-\int_{-\frac{\pi}{2}}^{DAO} SIN(LS)\cdot d(DDA) = -\int_{-\frac{\pi}{2}}^{DAO} (A + B\cdot SIN(DDA))\cdot d(DDA)$$

$$= -\left(A\cdot DDA\Big|_{-\frac{\pi}{2}}^{DAO}\right) - \left(-B\cdot COS(DDA)\Big|_{-\frac{\pi}{2}}^{DAO}\right)$$

$$= -A\cdot DAO - A\cdot\frac{\pi}{2} + B\cdot COS(DAO) - B\cdot COS(\frac{\pi}{2})$$

$$= -A\cdot(DAO + \frac{\pi}{2}) + B\cdot COS(DAO);$$

and evaluating the second integral, we have

$$\int_{\mathrm{DAO}}^{\frac{\pi}{2}} \mathrm{SIN(LS)\cdot d(DDA)} = \int_{\mathrm{DAO}}^{\frac{\pi}{2}} \mathrm{(A + B\cdot SIN(DDA))\cdot d(DDA)}$$

$$= \mathrm{A\cdot DDA}\Big|_{\mathrm{DAO}}^{\frac{\pi}{2}} - \mathrm{B\cdot COS(DDA)}\Big|_{\mathrm{DAO}}^{\frac{\pi}{2}}$$

$$= \mathrm{A}\cdot(\tfrac{\pi}{2} - \mathrm{DAO}) - \mathrm{B}\cdot(\mathrm{COS}(\tfrac{\pi}{2}) - \mathrm{COS(DAO)})$$

$$= \mathrm{A}\cdot(\tfrac{\pi}{2} - \mathrm{DAO}) + \mathrm{B\cdot COS(DAO)}.$$

Our initial expression thus reduces to

$$1 = \mathrm{(-2\cdot A\cdot DAO + 2\cdot B\cdot COS(DAO))\cdot W}.$$

The proportionality constant W is then given by

$$\mathrm{W} = \mathrm{(2\cdot B\cdot COS(DAO) - 2\cdot A\cdot DAO)}^{-1} \qquad [3]$$

Now, for DA < DAO, the light distribution function S(I) will be given by the integral

$$\mathrm{S(I)} = \Big(-\int_{-\frac{\pi}{2}}^{\mathrm{DA}} \mathrm{(A + B\cdot SIN(DDA))\cdot d(DDA)}\Big)\cdot \mathrm{W}.$$

Evaluating this expression we get

$$\mathrm{S(I)} = \Big(-\mathrm{A\cdot DDA}\Big|_{-\frac{\pi}{2}}^{\mathrm{DA}} + \mathrm{B\cdot COS(DDA)}\Big|_{-\frac{\pi}{2}}^{\mathrm{DA}}\Big)\cdot \mathrm{W}$$

$$S(I) = (-A \cdot DA - A \cdot \frac{\pi}{2} + B \cdot COS(DA) - B \cdot COS(-\frac{\pi}{2})) \cdot W$$

$$S(I) = (B \cdot COS(DA) - A \cdot (\frac{\pi}{2} + DA)) \cdot W \qquad [4]$$

For DA $\geq$ DAO, the light distribution function must be evaluated from the sum of the two integrals

$$S(I) = (- \int_{-\frac{\pi}{2}}^{DAO} (A + B \cdot SIN(DDA)) \cdot d(DDA) + \int_{DAO}^{DA} (A + B \cdot SIN(DDA)) \cdot d(DDA)) \cdot W$$

The first of these integrals results in the same expression as was obtained for the previous integral, except now DA is replaced by DAO. The second integral results in the expression

$$(A \cdot DDA \Big|_{DAO}^{DA} - B \cdot COS(DDA) \Big|_{DAO}^{DA}) \cdot W$$

$$= (A \cdot DA - A \cdot DAO - B \cdot COS(DA) + B \cdot COS(DAO)) . W.$$

Combining these results together, we get for the light distribution function for DA $\geq$ DAO,

$$S(I) = (B \cdot COS(DAO) - A \cdot (\frac{\pi}{2} + DAO) - A \cdot (DAO - DA) - B \cdot COS(DA) + B \cdot COS(DAO)) \cdot W$$

or

$$S(I) = (B . (2 \cdot COS(DAO) - COS(DA)) - A \cdot (2 \cdot DAO + \frac{\pi}{2} - DA)) . W \qquad [5]$$

4.1.3. Calculation of Crop Light Distribution Functions

The first step in the calculation of the light distribution function for a crop of arbitrary leaf distribution function for a given set of sun inclinations entails calculating such distribution functions for all 81 possible combinations of sun and leaf inclinations in increments of 10 degrees, that is, 5, 15, ..., 85 degrees. (Dividing leaf and sun inclinations into 10 degree groups provides sufficient accuracy for most applications.) The calculating procedure is given in PROGRAM I of section 7. First, a single combination of one value of IS and one value of IL is read into the computer. From these values, after converting them to radians, the values of A and B as defined in section 4.1.2 are arrived at, as well as the argument of the ARCSIN function for determining the boundary angle DAO. A test of this argument is then performed. If it is found to be smaller than minus one, no light falls on the undersides of the leaves, and DAO is set equal to $-\frac{\pi}{2}$; otherwise, it assumes the value of the ARCSIN(-A/B). At statement number 4 the proportionality constant W is then calculated.

The next set of calculations, commencing at the succeeding line and ending at statement number 5, results in the determination of the light distribution function for this combination of IS and IL. At first a value of SIN(LS) is generated, and from it and the values of A and B is calculated a value of SIN(DA). This number is then examined and if found less than minus one, which of course is not allowable, S(I) is set equal to zero and the process repeated for a newly generated value of SIN(LS); if it is found to be greater than plus one, S(I) is set equal to one and the process similarly repeated. For any value of SIN(DA) between plus and minus one, however, the value of DA is determined, checked for size as compared with DAO, and then used in the appropriate formula to calculate S(I). The entire process repeats 19 times until values of S(I) have been obtained for I = SIN(LS) = -0.90, -0.80, ..., 0.00, ..., +0.80, + 0.90.

Since it has been shown that it is not feasible to distinguish between the upper and undersides of leaves (Moss, 1964; de Wit, 1965), the next three lines of the program eliminate this distinction by subtracting the cumulative frequency for SIN(LS) = -0.90 from that for SIN(LS) = +0.90 and entering the result on the ordinate of SIN(LS) = +0.90, etc. Finally, the results are ordered according to increasing values of SIN(LS), punched on cards, and printed out. Then the entire process of the whole program is repeated for a new combination of IS and IL, coming to a stop when all 81 combinations have finally been treated.

PROGRAM II of section 7 now carries out the calculation of the light distribution function for any arbitrary leaf distribution function for sun inclinations IS of 5, 15, ..., 85 degrees. Beginning at statement number 100, the nine light distribution functions for one inclination of the sun and nine leaf inclinations are read. At statement number 1 a tenth value is added to each of the functions to define them all the way out to SIN(LS) = 1.0. The DO LOOP terminating at statement number 2 next generates the 10 numbers 0.05, 0.15, ..., 0.95 used in calculating the mean areas of the projection of one unit leaf area of each leaf class in the direction of the sun, which latter calculation is carried out by the DO LOOP terminating at statement number 3.

Upon completion of these calculations, the leaf distribution function for the crop in question is read. From this information a weighted average of the mean area of the projection of one unit leaf area for the crop as a whole in the direction of the sun is obtained at statement number 6. Then a weighted average for the crop as a whole of the light distribution function is obtained from the DO LOOP terminating at statement number 7. This function is then punched on a card and printed out on paper. As a final step, not a part of this calculation but useful later and most easily determined at this stage, the mean area of the projection of one unit leaf area in the direction of the sun for the crop as a whole is obtained from the light distribution function for the crop as a whole. It too is punched on a card and printed.

This entire process can be carried out nine times by inserting the proper code cards between the different sets of data for the nine sun inclinations in 10-degree increments of 5, 15, ..., 85 degrees. A few examples of the results obtained by this process for a planophile canopy and a corn crop as described by the leaf distribution functions of figure 2 are shown in Fig. 4. The differences are quite significant and, at least qualitatively, easily understood.

4.1.4. Calculation of the Fractions of Fully Sunlit Leaves Receiving Light Within Various SIN(LS) Intervals

The calculations of the previous section result in a light distribution function which represents the cumulative frequency (fraction) of intercepted *light*. For our purposes, however, it is desirable to obtain, not the fraction of *light*, but the fractions of *leaves* which receive the light within the various SIN(LS) intervals. Thus, some operations have to be performed upon the light distribution function in order to extract this information from it.

For a given inclination of the sun we know the light distribution function for the crop in the form 0(1), 0(2), ..., 0(10), where 0(J) are the cumulative frequencies (fractions) of intercepted light at values of SIN(LS) = 0.1, 0.2, ..., 1.0. Thus, we know that leaves in class 1 (SIN(LS) between 0.0 and 0.1) intercept 0(1)/(0(10) - 0(9)) times as much light as those in class 10 (SIN(LS) between 0.9 and 1.0), and that leaves in class 2 intercept (0(2) - 0(1))/(0(10) - 0(9)) times as much light as those in class 10, etc.

Now each leaf in class 1 intercepts only 0.05/0.95 times as much light as one in class 10, and each leaf in class 2 intercepts only 0.15/0.95 times as much light as one in class 10, etc. Thus, the number of leaves in class 1 compared to those in class 10 is (9.95/0.95)·(0(1)/(0(10) - 0(9))), the number in class 2 compared to those in class 10 is

(0.95/0.15)·((0(2) - 0(1))/(0(10) - 0(9))), etc.

If we now replace the numbers 0.05, 0.15, ..., 0.95 by the symbols SN(1), SN(2), ..., SN(10), we can write the generalized formula for the fraction of the total number of leaves in class 1 as

$$FR(1) = \frac{\frac{SN(10)}{SN(1)} \cdot \frac{0(1)}{(0(10)-0(9))}}{\frac{SN(10)}{SN(1)} \cdot \frac{0(1)}{(0(10)-0(9))} + \frac{SN(10)}{SN(2)} \cdot \frac{(0(2)-0(1))}{(0(10)-0(9))} + \cdots + \frac{SN(10)}{SN(10)} \cdot \frac{(0(10)-0(9))}{(0(10)-0(9))}}$$

and the fraction of the total number of leaves in class 2 as

$$FR(2) = \frac{\frac{SN(10)}{SN(2)} \cdot \frac{(0(2)-0(1))}{(0(10)-0(9))}}{\frac{SN(10)}{SN(1)} \cdot \frac{0(1)}{(0(10)-0(9))} + \frac{SN(10)}{SN(2)} \cdot \frac{(0(2)-0(1))}{(0(10)-0(9))} + \cdots + \frac{SN(10)}{SN(10)} \cdot \frac{(0(10)-0(9))}{(0(10)-0(9))}}$$

etc.

Observing now that the factor SN(10)/(0(10)-0(9)) appears in every term of the numerator and denominator of these fractions, we can cancel it out. Then, defining

$$R(J) = (0(J) - 0(J-1))/SN(J)$$

and

$$SR = \sum_{J=1}^{10} R(J)$$

where 0(0) is set equal to zero, we can express the fraction of the total number of leaves in any class J by the general formula

$$FR(J) = R(J)/SR.$$

PROGRAM III of section 7 embodies these considerations. After defining the set of SN(J) values and reading in the light distribution functions for inclinations of the sun of 5, 15, ..., 85 degrees, the R(J) values for each of these sun inclinations are obtained at statement number 300. At statement number 400 the SR value for each inclination is calculated. Then the sought after fractions of leaves receiving direct light within various SIN(LS) intervals are determined, also for the 9 different sun inclinations. These results are both punched on cards and printed out on paper. Results for a planophile canopy and a corn crop are presented in table I.

4.1.5. Calculation of the Fraction of Leaves in Each Canopy Layer Receiving Diffuse Light Only and the Fractions Receiving Direct Light Within Various SIN(LS) Intervals

Up to this point we have been concerned with what in essence is the uppermost layer of leaves in the plant canopy. We must now, however, extend our analysis to include the interior canopy leaves too. Complications arise here because there are now interactions among the much more numerous leaves. These interactions are caused by the phenomena of absorption, transmission, and reflection of light by leaves, the most obvious expression of which is the extinction of short wave radiation within the canopy, or its converse, the penetration of light.

Besides being dependent upon the spectral properties of the leaves, the penetration of light into a canopy depends on canopy density (S), the leaf area index (LAI), and the leaf distribution function. Of these three factors, perhaps only canopy density may require further elucidation. This parameter was used by Monsi and Saeki (1953) in calculating the penetration of light into canopies consisting of layers of horizontal leaves which do not reflect or transmit light. As de Wit

(1965) recounts it:

> They supposed that the area of the leaves in each layer is $S (0 < S \leq 1)$ times the area of the soil. The fraction of light from the vertical direction penetrating through the first layer is then $(1-S)$ and the fraction of light penetrating through the Nth layer $(1-S)^N$. When the leaf area index is LAI the light that penetrates through the canopy is
>
> $$I = IO \cdot (1-S)^{LAI/S}$$
>
> in which IO is the amount of light arriving from the vertical direction at the canopy.

In the extreme situation when $S = 1$, the leaves are arranged in closed layers of $LAI = 1$, and no light penetrates to the second layer of leaves. At the other extreme, when $S = 0$, one has the case of infinitely small leaves distributed at random in the space above the soil. Apparently then S is characteristic of the extent to which the leaves are systematically arranged in this space.

In his own analysis, de Wit (1965) extended the ideas of Monsi and Saeki to include, not only canopies with horizontal leaves, but also canopies with *arbitrary* leaf distributions. He began his analysis of this problem as follows:

> At first the penetration of direct light at an inclination IS is considered. In any canopy the effect of a systematic distribution of the leaves in the space above the soil can be characterized

by a canopy density S between 0 and 1. Moreover, the interception of light by leaves is proportional to the projection of one unit leaf area in the direction of the light (OP(IS)), [OPG(K) of PROGRAM III], divided by the projection of one unit soil area in the same direction. The latter projection is of course equal to the sine of IS and the value of OP(IS) can be computed from the light distribution function at the inclination IS, as discussed in [the section on crop light distribution functions]. Hence the light that penetrates into the canopy [as a function of LAI/S] is

$$I = IO\cdot(1-S\cdot OP(IS)/SIN(IS))^{LAI/S} \qquad [6]$$

In PROGRAM IV we make some calculations based upon this equation. First, we calculate the set of numbers

$$X(K,I) = (1-S\cdot OP(IS)/SIN(IS))^{I} \qquad [7]$$

where I varies in integer steps from 1 to LAI/S = 3.5/0.1 = 35 (for a case to be considered later) and refers to the different canopy layers, and K varies from 1 to 9 as the inclination of the sun goes from 5 to 85 degrees. Since equation [6] describes the penetration of light into the canopy, these X(K,I) values thus represent the fractions of direct light <u>not intercepted</u> by each canopy layer I. This being so, it is readily seen that X(K, I-1) is the fraction of leaves in layer I receiving direct sunlight (plus skylight too, of course); for the fraction X(K, I-1) of light not intercepted by layer I-1 must impinge upon the fraction X(K, I-1) of the total area of layer I, and if it is assumed that the leaves are randomly distributed throughout the planar extent of their respective layers, the fraction X(K, I-1) of the leaves of layer I must be illuminated too.

The final calculations of this section are now quite easy; for the fraction of leaves in any layer I receiving diffuse light only is

$$DF(K,I) = 1 - X(K, I-1) \qquad [8]$$

and the fractions of leaves in each layer which in addition to diffuse light also receive direct light within specified SIN(LS) intervals are

$$DS(K,I,J) = FR(K,J) \cdot X(K, I-1), \qquad [9]$$

assuming a leaf distribution function invariant with depth in the plant canopy. The calculations of DF(K,I) are completed at statement number 1 of PROGRAM IV; and the calculations of DS(K,I,J) are completed at statement number 250. Both sets of numbers are punched on cards and printed out on paper. Due to the large number of answers involved (35 canopy layers x 11 leaf classes x 9 sun inclinations = 3,465 results), results of these calculations will not be shown. They can be found, however, in the Ph.D. thesis by Idso (1967).

4.1.6. Calculation of the Actual Intensities of Light Incident Upon the Eleven Leaf Classes Into Which Each Canopy Layer is Divided

At this point we have divided each canopy layer into 11 classes, one which receives diffuse light only and 10 others which, in addition, receive direct sunlight at values of SIN(LS) between 0.0 and 0.1, 0.1 and 0.2, ..., 0.9 and 1.0. We have also calculated the fractions of leaves in each of these classes for each layer for nine inclinations of the sun. Our goal now is to calculate the actual intensities of light incident upon each of these fractions as a function of time throughout the day.

4.1.6.1. Calculation of the Solar Time

Since we need some actual solar radiation data to achieve the objectives of this section, it is necessary that we know the times at which the sun inclinations IS = 5, 15, ..., 85 degrees occur in order to determine the correct solar radiation data to use. From the relation

$$\mathrm{SIN(IS)} = \mathrm{COS(L)}\cdot\mathrm{COS(H)}\cdot\mathrm{COS(D)} + \mathrm{SIN(L)}\cdot\mathrm{SIN(D)} \qquad [10]$$

where IS = inclination or altitude angle of the sun

L = latitude of position on earth

D = declination of sun for specified date

H = hour angle

as written by Threlkeld (1962), it is readily seen that we can calculate the solar time in hours before and after solar noon by the formula

$$\mathrm{T(K)} = \frac{1}{15}\left[\mathrm{ARCCOS}\left(\frac{\mathrm{SIN(IS)} - \mathrm{SIN(L)}\cdot\mathrm{SIN(D)}}{\mathrm{COS(L)}\cdot\mathrm{COS(D)}}\right)\right] \qquad [11]$$

PROGRAM V of section 7 carries out this calculation. Before it is used, however, equation [10] is solved for IS when H = 0. This gives the altitude angle of the sun at solar noon. From the result of this calculation one knows the upper limit of K to use in PROGRAM V.

For the illustrative case for which we will apply the holocoenotic method in this bulletin (a corn crop growing at Ithaca, New York, on

August 1, 1961), the value of IS at noon is just over 65 degrees. Thus, the upper limit of K is 7. The results of utilizing PROGRAM V under these conditions are the calculated hours before and after solar noon of 6.656, 5.738, 4.827, 3.922, 2.996, 1.987, 0.483 for the sun inclinations 5, 15, ..., 65 degrees.

4.1.6.2. Calculation of the Intensities of the Scattered Light Sources at Each Canopy Layer

Since light is both reflected and transmitted by the leaves of each canopy layer (scattered, in short), we must calculate the intensities of this light originating at each layer. The first step of this task is to calculate the incident diffuse light intercepted at each canopy layer. It is based upon the same general principles used in the calculation of the penetration of direct sunlight. The sky vault is divided into zones of 10 degrees width, centered at inclinations of 5, 15, ..., 85 degrees. Then, from table II (de Wit, 1965), which gives the relative contributions to the illuminance of a horizontal surface of 10-degree zones of a sky of uniform brightness, the penetration of diffuse light from these sections is determined as fractions of that incident upon a horizontal surface above the crop. These results are added together to give the penetration of diffuse light from the entire sky.

Making use now of the results of PROGRAM V, the actual intensities of diffuse light incident upon a horizontal surface above the crop at the times of the sun inclination 5, 15, ..., 65 degrees (for the August 1 situation at Ithaca) are fed into PROGRAM VI, which carries out the calculations at hand. These radiation data, as well as the direct solar radiation data soon to be used, were obtained from Lemon and Wright (1966b), Allen, Yocum, and Lemon (1964), and Threlkeld (1962). They are listed for reference in table III. Besides punching and printing out the final results of this program, which are the products of these diffuse intensities and the fractions of diffuse light penetrating to the various depths in the plant canopy, the fractions themselves (Z(I)) are also printed out, as they will be used a little later in another calculation.

The results of these calculations have two interpretations. First, they represent the actual total intensity of diffuse light arriving at the various canopy layers; and secondly, because of the diffuse nature of the light, they also represent the actual intensities of diffuse light incident upon the leaves of the various layers. The first of these interpretations will be used in the basic calculation of this section, and the second will be used later.

PROGRAM VII completes the calculation of the intensities of the scattered light sources at each canopy layer. At first the fractions of direct light passing through each layer as calculated by PROGRAM IV are read. These are then transformed into fractions of direct light <u>intercepted</u> by each layer and extended to cover the afternoon as well as the morning hours. The actual intensities of direct solar radiation incident upon a horizontal surface above the crop are next read, and this information used in conjunction with the previously calculated fractions to calculate the actual amounts of direct light intercepted by each layer. After this, the intensities of diffuse light incident upon each layer as computed from PROGRAM VI are read, and a similar set of values for diffuse light is calculated. Finally, the scattering coefficients (reflectance and transmittance) for direct and diffuse light plus twice the reflectance of the soil surface are read; and the actual intensities of the scattered light sources at each layer are at last obtained. (The reason for using twice the reflectance of the soil surface will be made clear in the following section.)

4.1.6.3. Calculation of the Contribution to the Total Illuminance of the Several Canopy Layers of the Light Scattered by Each Layer.

We consider now a canopy layer I. If ST(I) is the strength of the scattered light source at that layer and if Z(I) is the fraction of diffuse light incident upon a layer due to another layer I depths away (assumed equal to the Z(I) calculated in PROGRAM VI), we can draw the following conclusions. First of all, since the transmitted and reflected light are practically ideally scattered (Rabinowitch, 1951), half of the light scattered at a layer goes up and the other half down, thus making it possible to express the contribution of layer 1 to the illuminance of layer I as

(0.5)·ST(1)·Z(I-1).

Similarly, the contribution from layer 2 may be written as

(0.5)·ST(2)·Z(I-2)

the contribution from layer I-1 as

(0.5)·ST(I-1)·Z(1),

the contribution from layer I + 1 as

$(0.5)\cdot ST(I+1)\cdot Z(1)$,

the contribution from layer NMAX as

$(0.5)\cdot ST(NMAX)\cdot Z(NMAX-I)$,

and the contribution from layer NMAX + 1, the soil surface, as

$(0.5)\cdot ST(NMAX+1)\cdot Z(NMAX+1-I)$.

(The use of the factor 0.5 here is what necessitated our using <u>twice</u> the reflectance of the soil surface in calculating its scattering strength in the previous section.)

Writing these expressions in summation form, we may say that the total illuminance of a layer I due to scattered light from all other layers L is

$$S(I) = \sum_{L=1}^{I=1} (0.5)\cdot ST(L)\cdot Z(I-L) + \sum_{L=I+1}^{NMAX+1} (0.5)\cdot ST(L)\cdot Z(L-I) \qquad [12]$$

This equation serves as the basis for PROGRAM VIII. It is used first to calculate the illuminance of the several canopy layers due to scattered light originating from the scattered light sources determined by PROGRAM VII. Once this step is completed at statement number 5, secondary sources created by this scattered light are computed at statement number 6. The process is then repeated, with the illuminations due to these secondary sources being all obtained by statement number 9. Two of these cycles are sufficient to account for practically all of the scattered light, and thus their separate contributions are combined at statement number 10 and the results thereafter punched and printed out on paper.

4.1.6.4. Completion of the Light Calculations.

PROGRAM IX of section 7 finishes the specifications of the light regimes of the various leaf classes within the several crop layers. It essentially puts together the results of several preceding programs, giving the actual intensities of diffuse light incident upon those leaves which receive diffuse light only and the intensities of total short wave radiation incident upon the leaves receiving direct light also. Because of the increasing sizes of some of our fields, however, it is written in a somewhat different form from most of our earlier programs. Instead of making calculations at each step for each of the different sun inclinations, the data are now fed into the computer to be analyzed in their entirety for first one inclination, then a second, then a third, etc. This procedure is made possible by the large DO LOOP terminating at statement number 88.

Immediately after reading the number of canopy layers and commencing the large DO LOOP for each sun inclination, the intensities of incident diffuse light and scattered light received by the leaves of each layer are read. These diffuse components are added together at statement number 1 to give the total intensities of diffuse light received by the leaves of each layer. A value of direct sunlight as received at a horizontal surface above the crop for the time of the sun inclination in question is then read, followed by this latter inclination itself. The sun inclination in degrees is converted to radians and used to calculate the intensity of the direct solar beam as received on a surface perpendicular to the beam. This procedure finally allows the calculation of the intensities of direct light received by the leaves which receive this light within the various SIN(LS) intervals. At statement number 2 these values are determined and added to those representing the receipt of diffuse light to give the total intensities of light received by these leaves. The results are thereafter punched on cards and printed out on paper. Again, due to the large number of results obtained, their enumeration here is omitted, and anyone especially interested in them is referred to Idso (1967).

4.2. Calculation of Leaf Temperature

The calculation of the temperatures of the leaves within the various leaf classes, whose relative sizes were determined in section 4.1.5, is based upon an energy balance at the surfaces of these leaves. Thus, to carry out this calculation it is necessary to know the radiant heat loads on the leaves of the various classes. We in essence have the components of the heat loads due to short-wave radiation already determined, waiting only to be multiplied by the proper absorptances. However, the long-wave components have yet to be obtained, and we must deal now with this topic.

4.2.1. Calculation of Long-Wave Radiant Energy Regimes

All leaves of the several canopy layers are conceived of as receiving long-wave radiant energy from two major sources. These are, first, other leaves and the underlying soil surface, which emit thermal radiation fluxes of about equal magnitude, and, second, the atmosphere. Since all of these radiant energy fluxes are diffuse, it suffices to determine their contributions at a horizontal surface. Leaf inclination need not be considered directly, for the amount of sky which the upperside of an inclined leaf does not see will be precisely compensated for by the underside of the same leaf, and similarly with respect to the ground. This identical principle was tacitly assumed in the evaluation of the diffuse short-wave radiation contributions to the light intensity received by a leaf, and a pictorial elucidation of it is given here in figure 5.

The major problem of this section, then, is to determine the relative portions of the upper hemispheric view of a horizontal leaf occupied by other leaves and the sky. Here too our work is not as difficult as it first appears, for we in essence have already calculated these values when we determined the penetration of diffuse skylight (independent of scattering) into the plant canopy. The fraction of diffuse skylight passing through or incident upon the various canopy layers as given by the application of PROGRAM VI are exactly the fractions to be used for the amount of upper hemispheric long-wave radiation attributable to the atmosphere, with the remaining portions being due to other leaves. This, again, is a direct result of the diffuse natures and similar spatial origins of these two fluxes.

With these fractions at hand, the only remaining problem is to specify values for the thermal radiant energy fluxes from atmosphere and other leaves as received at a horizontal surface. In the case used to illustrate the method, the thermal radiation originating from the soil and from other leaves was approximated by calculating the black body radiation at the temperature of the air just above the crop and reducing these values by 3 percent to account for leaf and soil emittances of about 0.97. These values as calculated for times of the sun inclinations IS = 5, 15, ..., 65 degrees for the air temperature data of Ithaca, New York, on August 1, 1961, appear in table IV. Also given there are values for long-wave thermal radiation from the atmosphere for these same times. Since no data were available for this parameter, its values were calculated by performing an energy balance at an imaginary plane just above the crop. The concept used here is that atmospheric thermal radiation may be expressed as

$$R_A = R_N + R_G + rR_I - R_I \qquad [13]$$

where R_N = net radiation of all wavelengths

R_G = long-wave thermal radiation from the crop

R_I = incoming short-wave radiation

rR_I = reflected short-wave radiation.

Since all of these component energy fluxes were not available for the day and place in question either, values for a similar day and crop at the same place a year later as measured by Brown (1962) were used. Even so, the results as shown in table IV are thought to very closely approximate those of the day in question.

Since the mechanics of the final calculations of this section are combined with those of the following section, the description of the Fortran program which carries them out will be deferred until we have covered the preliminary groundwork of that section too. We thus move next to the...

4.2.2. Calculation of Radiant Heat Loads

At this stage we know the intensities of all the various radiant energy fluxes incident upon the 11 different leaf classes of each canopy layer (of which there are 35 for the case we are illustrating). To determine the heat loads arising from these fluxes, it is necessary to know the absorptances of the plant leaves for each of them. Since the total absorptance of a surface for a certain incident radiant energy flux is given by

$$\alpha = \frac{\int_0^\infty \alpha_\lambda H_\lambda d\lambda}{\int_0^\infty H_\lambda d_\lambda} \qquad [14]$$

where α = total absorptance of the absorbing surface

α_λ = spectral absorptance of the absorbing surface

H_λ = spectral distribution of incident radiation,

it is possible to compute these values if the spectral distributions of incident radiation and leaf absorptance are known. Pictorial representations of the first of these are given by Gates (1965) for a variety of natural environmental sources, and graphs of the second are given for corn by Yocum, Allen, and Lemon (1964). Using these data in a graphical solution of the integrations contained in [14], the values shown in table V are obtained. Similarly obtained values for the total reflectance and transmittance of a corn leaf are also listed there.

With this information we can now proceed with the description of PROGRAM X which carries out the actual calculations of the heat loads of the 385 leaf classes (35 layers x 11 classes) that we are concerned with for the 14 different times during the day when sun inclinations IS = 5, 15, ..., 65 degrees occur. First of all, it is noted that the large DO LOOP terminating at statement number 12 sets up the computer to make 14 sets of calculations for the 14 different times of day. After initiating this step, the absorptances of a corn leaf to diffuse short-wave radiation, direct short-wave radiation, and long-wave thermal radiation are read. After next reading the intensities of diffuse short-wave radiation incident on leaves of the several layers, the first of these absorptances is used at statement number 1 to calculate the heat load component due to this diffuse short-wave radiant energy flux. At statement number 2 the intensities of total short-wave radiation incident upon the various leaf classes are read; and at statement number 3, upon subtracting from them the corresponding diffuse components, the second of the absorptances is used to give the heat load components due to direct short-wave radiation. For those leaves that receive both of these types of short-wave radiation, their combined heat load effects are evaluated next at statement number 4.

Upon finishing with the short-wave radiation contributions, values of long-wave thermal radiation from other leaves and the atmosphere are read, along with the fractions of the upper hemispheric view of a horizontal leaf occupied by sky and not by other leaves.

These values are all used at statement number 5, together with the absorptance of corn leaves for long-wave thermal radiation, to obtain the contributions to the various leaf heat loads of these energy fluxes. The results are added to the diffuse short-wave contributions at statement number 6 to obtain the final heat loads of those leaves that receive only diffuse short-wave radiation, and at statement number 7 they are added to the total short-wave contributions to obtain the final heat loads of those leaves that receive direct short-wave radiation also. Following this, both sets of results are punched on cards and printed out on paper. The entire process then repeats until all 14 different times of the day have been similarly treated. Again, the results are too numerous to list.

4.2.3. Completion of Leaf Temperature Calculations

Having specified all the necessary leaf heat loads, it is now possible to complete the leaf temperature calculations. The method used is a relaxation technique commonly used in the solution of many heat transfer problems. It is applied here as follows:

First, for each leaf class an "unbalanced energy balance equation" is written:

$$A = HL - RR - SH - LH \qquad [15]$$

where HL = one-half of one of the previously calculated leaf heat loads

RR = average rate of energy dissipation from one leaf surface by reradiation

SH = average rate of energy dissipation from one leaf surface by convection

LH = average rate of energy dissipation from one leaf surface by transpiration

and where A is then seen to be a sort of residue, the result of the unbalance.

Now the terms RR, SH, and LH all have a leaf temperature dependence which can be brought out by writing them more explicitly. Thus, it is useful to write

$$RR = \epsilon\sigma T_L^4 \qquad [16]$$

$$SH = 6.0 \times 10^{-3} \left(\frac{\Delta T}{L_1}\right)^{1/4} \Delta T \qquad [17a]$$

for free or natural convection and

$$SH = 5.7 \times 10^{-3} \left(\frac{V}{L_1}\right)^{1/2} \Delta T \qquad [17b]$$

for forced convection, and

$$LH = \frac{L_2}{R} \left({}_s\rho_{L,T_L} - \text{r.h.}\ {}_s\rho_{A,T_A}\right) \qquad [18]$$

where ϵ = emittance of leaf for long-wave thermal radiation, about 0.97

σ = Stefan-Boltzmann constant, 8.12×10^{-11} cal/cm^2/min/^{o}K^4

T_L = leaf temperature, ^{o}K

ΔT = temperature difference between the plant leaf and the ambient air ($T_L - T_A$), ^{o}C or ^{o}K

L_1 = characteristic dimension of leaf, cm

V = wind speed, cm/sec

$s\rho_{L,T_L}$ = saturation water vapor density of the air next to the mesophyll cell walls at the temperature of the leaf, gm/cm^3

$s\rho_{A,T_A}$ = saturation water vapor density of the free air at the temperature of the air, gm/cm^3

r.h. = relative humidity of the free air, expressed as a fraction

L_2 = latent heat of vaporization, 597 cal/gm at 0°C and 572 cal/gm at 50°C

R = total transpiration resistance of the diffusion pathway, min/cm.

Equation [16] is the familiar Stefan-Boltzmann radiation law, equations [17a, 17b] are the equations for sensible heat loss by convection from flat plates as written by Gates (1965), and equation [18] is the relation describing latent heat loss by transpiration as written by Lee and Gates (1964). Although [17a, 17b] are written for flat plates, an analysis by Idso (1967) indicates that they can be used to good approximation for all of the variously inclined leaves we are considering. Our incomplete knowledge about the effects of leaf groupings on branches and the effects of fluttering prohibits us at present from making any more detailed descriptions of the processes than these.

In light of these relationships, use of the relaxation technique begins by assuming a certain leaf temperature with respect to air temperature, continues by calculating rates of energy dissipation from equations [16, 17, 18], and terminates a first cycle by then calculating a residue "A" from equation [15]. A test is made of this residue for both size and sign. If too large positively, the leaf temperature is increased by a specified increment and a new residue is calculated. If too large negatively, the leaf temperature is decreased by a specified increment. When, after the necessary number of such cycles, the residue falls within a certain allowable small size range, the process is terminated. The leaf temperature responsible for this acceptable residue is then regarded as the final answer.

Before we can use this procedure to solve for the desired leaf temperatures, however, we need some more information. In particular, we need a specification of the vertical profiles in the plant canopy of the environmental parameters air temperature, wind speed, and relative humidity for the 14 different times of day we are considering. We also need a similar specification of the plant's transpiration resistance, and we need to know an array of saturated water vapor densities for all 500 possible air temperatures between 0 and 50°C in increments of 0.1°C.

Since the only available air temperature data for the illustrative case of August 1, 1961, at Ithaca, New York, were those immediately above the crop, the variations within the plant canopy were constructed, using these values as bases, from temperature profiles measured by Brown (1962) on a similar day the following year. In the case of relative humidity, no data at all were available, and the actual profiles of this parameter as measured by Brown were applied directly without alteration. Wind speed profiles, however, had been very carefully determined by Wright and Lemon (1966a); therefore, these much more difficultly obtained profiles were determined quite accurately.

Transpiration resistance profiles were obtained from a combination of two sources. Spatial and time variations calculated by Impens, et al. (1967) (admitted by them to be too large in absolute magnitude) were reduced to characteristically observed values for corn, exemplified by the measurements of El-Sharkawy and Hesketh (1965). These values and those for the three environmental parameters just dealt with can be found in their entirety for all 14 periods of the day and for all 35 canopy layers in the Ph.D. thesis by Idso (1967).

Finally, the 500 saturated water vapor densities required were obtained from a table in List (1958).

With this groundwork completed, we can now go directly to the description of PROGRAM XI which carries out the leaf temperature calculations. After reading the number of canopy layers, the entire 500 values in the saturated water vapor density array are read at statement number 1. Immediately following this step is the beginning of a large DO LOOP terminating at statement number 789. This loop sets up the computer to perform the leaf temperature calculations for the 14 different times of the day when sun inclinations of 5, 15, ..., 65 degrees occur. Following this, the air temperatures at the several canopy layers are read; and the first inner DO LOOP within the larger one just mentioned then generates two indices from each of these layer air temperatures and uses them to call forth from the array of saturated water vapor densities the values needed to specify this parameter throughout the vertical extent of the canopy. These values are then printed out for reference.

Next we read all of our remaining environmental parameters, plant properties, and previously calculated heat loads. At statement number 3 the heat loads of those leaves that do not receive any direct solar radiation are incorporated into the array of heat loads of those leaves that do, as the last column of that matrix.

We now encounter a large DO LOOP, terminating at statement number 30, which represents the heart of the leaf temperature calculation. Within this loop the first thing that is done is to test the magnitude of the wind speed. If it is less than 10 cm/sec, the sensible heat transfer from the leaf is best calculated by the formula for free convection [17a]; if it is greater than 10 cm/sec, it is best calculated by that for forced convection [17b]. From this point on, then, either one of two pathways is followed. That commencing at statement number 13 results in the calculations being carried out with equation [17a], and that commencing at statement number 14 results in the calculations being carried out with equation [17b].

The procedures followed along both of these routes are identical. First, a leaf temperature arbitrarily set at 5°K above air temperature is generated. Then a DO LOOP that makes calculations for the 11 leaf classes of each canopy layer is entered. The leaf temperature just generated is here used to calculate values of energy dissipation by reradiation, convection, and transpiration, which in turn are used together with the leaf heat loads to compute a residue in the energy balance equation as evaluated at this leaf temperature. (Again, indices are generated from the leaf temperatures to call forth the saturated water vapor densities needed to calculate the latent heat loss.)

The residue arrived at from this procedure is now tested for size and sign. If it falls within the interval -0.01 cal/cm^2/min $< A <$ $+0.01$ cal/cm^2/min, the first leaf temperature generated at either statement number 13 or 14 balances the energy balance equation with sufficient accuracy to accept it as being correct. Usually, however, this is not the case, and the leaf temperature is either adjusted upwards or downwards and the procedure of attempting to balance the energy balance equation is repeated. Eventually (and quickly on the computer), the correct leaf temperature is arrived at. When this happens a new leaf heat load is introduced for the calculation of a new leaf temperature. In this way the eleven leaf temperatures for each canopy layer are finally determined, punched on cards, and printed out on paper. Also punched and printed out at this time are the final values of sensible and latent heat losses. When this process has been repeated for each layer and for the 14 times of the specified sun inclinations, the program executes a stop. Again, the results at this stage are still too numerous to warrant their inclusion in this bulletin.

4.3. Calculation of Leaf Water Availability

The calculation of leaf water availability per se is a fairly simple procedure, involving nothing more (at least for our purposes) than the measurement of soil moisture tension and relative humidity profiles in the plant canopy. What is a good deal more elusive and rather controversial is the effect of leaf water availability upon photosynthesis. This subject will be dealt with next in some detail, immediately after the following comments on the ...

4.4. Calculation of the Carbon Dioxide Concentration of the Canopy Level Air

The chief factor in determining the CO_2 status of the canopy level air is the photosynthetic rate of the canopy itself. This sink for carbon dioxide creates a gradient between the CO_2 concentration of about 300 ppm at 30 meters and the usually lower value at the effective canopy exchange surface, defined by Rider (1954) and Monteith (in Evans, 1963), where all leaves of the canopy are considered to be in an atmosphere of CO_2 concentration equivalent to that at this surface.

The result of this gradient is a vertical flux of CO_2 directed downward and controlled both by the CO_2 gradient and the conditions of the atmosphere. Under turbulent conditions the bulk of this vertical flux is accounted for by turbulent mixing of the moving air stream, and thus molecular diffusion can be neglected. The result is that the vertical flux of CO_2 can be described by an equation (de Wit, 1965) of the form

$$FC = C(300 - XO)/RA \qquad [19]$$

where C = constant

XO = CO_2 concentration at the effective canopy exchange surface

RA = transfer resistance between the air at the exchange surface and at 30 meters.

Here the effects of the CO_2 gradient are immediately apparent, but the effects of the atmospheric turbulence are still hidden in the exchange resistance. To give de Wit due regard for the exposition of the atmospheric properties affecting this resistance, we quote below his analysis of this problem:

> The wind speed at a height Z above a canopy is under neutral conditions proportional to logarithm of (Z-ZD)/ZO, in which ZO and ZD are the roughness length and the zero plane displacement, respectively (Van Wijk, 1963 and other handbooks on this topic). Extrapolation of the wind profile inside the canopy gives an apparent wind speed equal to zero at the height ZO + ZD. Experience shows that ZO + ZD is somewhat smaller than the height of the canopy. It is remarked here that the actual wind speed is not yet zero at this height, and that turbulent exchange takes place much deeper into the canopy.

Now it is assumed by Monteith (in Evans, 1963) that the effective canopy surface is at the height ZO + ZD. This is obviously a sweeping generalization. However, he demonstrates that in this way reasonable values are obtained for transpiration, assimilation and stomatal resistance, so this simplification may very well do in the present case.

On the basis of the above assumption it can be shown that (Monteith, op. cit.)

$$RA = (\log_e((Z-ZO)/ZO))^2/(U \cdot K^2) \qquad [20]$$

in which K is the dimensionless Von Karmen constant (usually taken as 0.4) and U the wind speed at height Z.

Under non-neutral conditions the exchange is also governed by buoyancy. With Tanner (Evans, 1963) the contribution of buoyancy is neglected above closed canopies, sufficiently supplied with water and at wind velocities of more than 1.5 m/sec at a height of 30 meters.

According to Tanner and Pelton (1960) the roughness length may be estimated from the height of the canopy by

$$ZO = H/7.6 \qquad [21]$$

With Z at about 30 meters, the value of RA is not affected to a large extent by the zero plane displacement. Hence it suffices to estimate ZD with

$$ZD = 0.9H - ZO \quad [22]$$

With these relations it can be seen that once the plant height is specified, a relation between RA and U is at hand; for equation [21] gives ZO, whereupon equation [22] gives ZD, thus making all terms of equation [19] known except RA and U. We then have

$$FC = C(300 - XO)f(U) \quad [23]$$

where 1/RA has now been expressed as a function of U, the wind speed at 30 meters.

We now, to a first approximation, say that the product of leaf area index and the photosynthetic rate at the effective canopy exchange surface as determined by the crop's response to the three factors--light intensity, leaf temperature, and leaf water availability--is equivalent to FC, the vertical flux of CO_2. Knowing this value and the wind speed at 30 meters, we can thus solve equation [23] for XO, the CO_2 concentration at the effective canopy exchange surface. Then, knowing the photosynthetic response of corn to CO_2 from experimental analyses, we can adjust our original rate by the amount indicated. The new value for net photosynthesis can then be used again in equation [23] and a second value of XO can be calculated. This process quickly converges to give correct values for both XO and FC at the effective canopy exchange surface. This value of XO can then be used to correct the values of photosynthetic rates at all other crop levels too, as it has been shown by Idso (1967) that CO_2 concentrations elsewhere in the canopy will not be too different from XO at the effective canopy exchange surface.

Since the Fortran program which carries out the calculations here described is not used until the effects of light intensity, leaf temperature, and leaf water availability have been determined, its description will be deferred until these intermediate topics have first been covered.

5. CALCULATION OF NET PHOTOSYNTHESIS AND SENSIBLE AND LATENT HEAT EXCHANGE

Having reached the point now where we have either already specified or are capable of specifying simultaneous values of all four of the basic factors determined earlier as having direct effects upon net photosynthesis, we are ready to apply them and calculate the rate of this process and also those of sensible and latent heat exchange. To do so, however, we must know how each of these factors operates in unison with the others upon these processes, and upon net photosynthesis in particular.

5.1. The Response of Net Photosynthesis to Light Intensity and Leaf Temperature

Since the component processes of net photosynthesis are essentially chemical in nature, their combined expression, net photosynthesis, is a rate process which has an optimum temperature at which it proceeds maximumly. Being also a biological process, net photosynthesis has upper and lower temperature extremes beyond which the photosynthesizing tissue cannot remain alive. The implication of these two facts is that all plant species must exhibit a well-defined temperature dependence in addition to the obvious light dependence of their photosynthetic rates.

Two examples of the natures of these joint dependencies are shown in figure 6. The curve on the left was constructed by Gates (1965) from data due to Lundegardh (1931) and Waggoner, Moss, and Hesketh (1963); and the curve on the right was constructed by Idso (1966) from data due to El-Sharkawy and Hesketh (1964), Hesketh and Moss (1963), and Moss (1963). Idso (1967) has also collected evidence for similar responses in Russian sunflower, cotton, several races of the *Mimulus cardinalis-lewisii* species complex, and six different alpine species. Though differing among each other, all species exhibit the same general trends in evidence in figure 6.

5.2. The Light Intensity - Leaf Temperature Dependency of Net Photosynthesis as Affected by Leaf Water Availability

In this section we are concerned with the phenomenon usually referred to as "water stress." This is a somewhat ambiguous term, however; for in the opinion of the author there are actually *two* water stresses which operate in a plant, one acting at times to restrict transpiration and one doing likewise with photosynthesis. Furthermore, these two stresses are by nature nearly independent of each other, thus at times allowing wilted leaves to photosynthesize near maximum capacity and at others restricting fully turgid leaves to little or no fixation of CO_2.

A simple analysis of the processes of transpiration and photosynthesis is sufficient to illuminate the basis for such statements as these. Transpiration is the *physical movement* of water through the plant, whereas photosynthesis is the *chemical binding* of water in organic compounds. Thus, transpiration is controlled by a free energy or negative pressure *gradient* while photosynthesis is controlled by an energy *level*. Since a property gradient is something entirely different from a property level, with no necessary relation between the two, there is no basis whatever for expecting the two processes of transpiration and photosynthesis to necessarily be affected together by a single "water stress."

A somewhat more detailed look at the free energy profile of water in the soil-plant-atmosphere continuum (SPAC) will serve to make semi-quantitative these qualitative pronouncements. Thus, we include here figure 7 as drawn by Philip (1957) which emphasizes just this feature. It should perhaps be indicated that this figure is schematic. That is, the distance intervals along the horizontal axis are not to scale, and the straight lines of the DPD curve through the plant are not intended to imply that the permeability of all the plant parts is the same, nor that it is independent of turgor. However, the graph truly relates some extremely interesting characteristics of the system that will soon be found to be of great importance to us.

5.2.1. The Water Stress on Transpiration

In discussing the implications of figure 7, Philip (1957) noted that although the change of DPD across the mesophyll cells was indeed the greatest change encountered in the plant, it was still relatively insignificant compared to that between the outer surface of the mesophyll cells and the free atmosphere. Thus, he concluded that although the free energy status of the water on the plant-side of the mesophyll resistance may vary greatly, even to the point of permanent wilting, transpiration itself need not be affected in the slightest.

This analysis theoretically puts transpiration in the position of being almost completely controlled by the conditions of the atmosphere. Rutter and Sands (1958), however, point out that in reality this conclusion may not always hold true. To give "equal time" to their views, we reprint their remarks here:

> Following Edlefsen's (1941) thermodynamic treatment of the movement of water through the system soil-plant-atmosphere, it is sometimes stated that since the change in free energy of the soil moisture between field capacity and permanent wilting percentage is small compared with the free energy difference between the soil moisture and the atmospheric moisture, the rise in soil moisture tension over this range provides no *a priori* reason for a diminution of transpiration. But, as Edlefsen also pointed out, the rate at which water moves through the plant depends on the resistance to flow of the different parts concerned with conduction. The evidence of Loftfield (1921) and of Yemm and Willis (1954), which is confirmed by the present paper, shows that stomatal opening is sensitive to changes in soil moisture tension or to the related leaf water deficit. The variation of resistance by stomatal movement seems to provide a satisfactory

> explanation for the progressive restriction of transpiration as the soil dried, which has been shown for *P. Sylvestris*. Theoretical arguments are then of little use in forecasting the relation between transpiration and soil moisture above the permanent wilting percentage, since the response of the transpiration of a particular species to drying of the soil will depend on the nature of its stomatal response to leaf water deficit or cell suction, on the relative importance of cuticular and stomatal transpiration, and on possible effects of incipient drying on other resistances to water movement.

In spite of these side effects of incipient drying, however, the fact nevertheless remains that *theoretically* the change in free energy of the soil moisture between field capacity and the permanent wilting percentage provides no *a priori* reason for a diminution of transpiration; and, in fact, this phenomenon actually has been observed experimentally. In studying the effects of the availability of soil moisture upon vegetative growth and water use in corn, Haynes (1948) concluded that "water loss per unit of plant dry matter is independent of the degree of availability of water within the range of soil moisture from near saturation to near the permanent wilting percentage." This, then, is the prediction from specific free energy considerations of the effects of water stress on transpiration, whereby it is seen that to a very great degree transpiration is chiefly dependent upon the conditions of the atmosphere, being almost completely decoupled from the status of the soil moisture.

5.2.2. The Water Stress on Photosynthesis

The difficulty of most thought connected with this problem lies in supposing that the same stress that operates to restrict transpiration operates to restrict photosynthesis too. Neither theory nor experiment necessarily supports this view, as is made evident from the following free energy considerations.

If we use the equation $\Psi = 3.16 \times 10^6 \log_{10} (\frac{P}{P_s})$, relating the relative humidity with negative pressure, and the atmospheric value of Ψ from figure 7 to solve for the ratio $(\frac{P}{P_s})$, we find that the atmospheric water vapor free energy of figure 7 corresponds to a case of about 40 percent relative humidity. Thus, it represents the average minimum atmospheric water vapor free energy of most temperate climes and the corresponding average maximum atmospheric stress. Now, regardless of atmospheric conditions, the DPD difference between points B and F must remain essentially constant, just the same as it must also do for changing soil moisture free energies, as this slope is a property (or more truly a quasi-property) of the plant and not of the soil or atmosphere. This being so, the lowermost line, 1, of figure 7 becomes the controlling factor in determining by what order of magnitude the three curves may be lowered by an increase in the atmospheric water vapor free energy (a decrease in the atmospheric stress). They at most can be lowered by no more than about two atmospheres, no matter how high the atmospheric water vapor free energy rises (up to a relative humidity of about 98 percent), for a decrease of this magnitude would completely destroy the free energy gradient between the soil and the root, thus causing a situation in which soil at field capacity could not supply water to the plant. As the heights of curves 2 and 3 above 1 are determined by the soil moisture status, these curves could also be lowered by no more than two atmospheres.

Now, let us suppose that the specific free energy of the water at the plant side of the mesophyll cells for the condition described by curve 1 represents the level of no leaf water availability stress upon photosynthesis. Then, applying the postulate of photosynthesis being directly affected by the specific free energy level of the water at the site of the chloroplasts, let us assume that the specific free energy of the water at the plant side of the mesophyll cells for the condition described by curve 3 represents the level of specific free energy where photosynthesis is completely suppressed. This gives us a range of about 23 atmospheres over which photosynthesis ranges from its maximum potential to zero. As this range can be completely traversed by changing the free energy of the soil moisture while only a range of 2 atmospheres can be traversed by changing the relative humidity from 98 percent to 40 percent (minimal stress to average maximum temperate climate stress), it can be seen that the photosynthetic response of plants to leaf water availability is theoretically about 90 percent ($\frac{23-2}{23}$ x 100% = 91.3% ≈ 90%) accounted for by the condition of the soil moisture. Thus, whereas transpiration is almost completely controlled by conditions of the atmosphere, photosynthesis is almost completely controlled by conditions of the soil.

5.2.2.1. The Nature of the Photosynthetic Response to Soil Moisture Stress.

Having presented our ideas on the relative importance of soil and atmospheric moisture stresses to leaf water availability and thus the photosynthetic process, we are now prepared to present the natures of the responses to these two factors, beginning with the most important of the two, soil moisture stress. Since we have reasoned that the processes involved in photosynthesis are governed in respect to their rates by the free energy level of the water at the plant side of the mesophyll resistance, which in turn is chiefly determined by the soil moisture status, we shall assume that the photosynthetic response of a plant to decreasing soil moisture tension is a constant percentage decrease of the photosynthetic response to light intensity and leaf temperature under optimum water availability conditions. To clarify this statement we propose that for a plant such as maize there are a series of graphs such as figure 6, each one of which pertains to a different soil moisture tension, and that as the soil moisture tension increases, a different graph with all lines lowered by a constant percentage (determined by the soil moisture tension) will describe the plant's photosynthetic response to light intensity and leaf temperature.

The data of Baker and Musgrave (1964) shown in figure 8 enable us to determine some characteristic values of soil moisture tension at which various reductions in the scale of figure 6 for maize may occur. Taking the high-tension halves of their curves for the case of 0.2 inch Hg VPD (since this is the closest approximation to the minimum atmospheric moisture stress) and drawing tangents to their midpoints, we determine the soil moisture tensions at which complete suppression of net photosynthesis occurs to be 1.5, 2.0, 2.2, and 2.6 atmospheres. Although there is a fair amount of variability among these cessation points and a few more replications would be extremely desirable, this is the extent of Baker and Musgrave's data; thus, the average of these values, 2.1 atmospheres, is, for the present, the best evaluation we can make of the point at which soil moisture stress completely suppresses net photosynthesis.

On the other end of the soil moisture range, the tension at which photosynthesis is a maximum is seen to be 0.1 atmosphere for their first setup and 0.6 atmosphere for the second. Thus, the average is 0.35 atmosphere, resulting in an average range of 1.75 atmospheres over which the net photosynthetic response of corn to light intensity and leaf temperature will vary from 100 percent to 0 percent of that shown in figure 6. Actually, the optimum soil moisture tension for photosynthesis in maize may very well vary among different soil textures within the limits Baker and Musgrave observed (0.1 for coarse-textured soils to 0.6 for fine-textured soils). We merely use their average here as a convenience.

By drawing families of curves reduced to 80 percent, 60 percent, 40 percent, and 20 percent of those shown in figure 6, we get the sets of graphs shown in figure 9 as complements to the complete spectrum of soil moisture stress headed by figure 6. These sets of graphs, then, constitute the joint photosynthetic response of corn to light intensity, leaf temperature, and, to within about 90 percent, leaf water availability. Again, they are for the "average" case of maximum net photosynthesis occurring at 0.35 atmosphere soil moisture tension, for which complete suppression occurs at 2.1 atmospheres. For the two texturally determined extremes of 0.1 and 0.6 atmosphere optimum soil moisture tension, these suppressions could occur at 1.85 and 2.35 atmospheres, respectively.

5.2.2.2. The Nature of the Photosynthetic Response to Atmospheric Moisture Stress.

To evaluate completely the effects of leaf water availability upon photosynthesis, we must also account for the control exercised by atmospheric conditions. Since we have theoretically concluded that at 40 percent relative humidity there is a decrease in photosynthetic rate of about 10 percent of the maximum potential for any given set of leaf temperature and light intensity values, the assumption of no effect at 100 percent relative humidity with a linear interpolation between these two points gives the result that for each 6 percent decrease in relative humidity below 100 percent, the photosynthetic rate arrived at from the preceding set of graphs (figures 6 and 9) will be correspondingly decreased by 1 percent of the rate determined for the given set of leaf temperature and light intensity values under conditions of optimum soil moisture tension (figure 6). This, then, constitutes the final photosynthetic response of corn to light intensity, leaf temperature, and leaf water availability.

5.3. The Response of Net Photosynthesis to CO_2 Concentration

It has been decisively demonstrated that the carbon dioxide concentration of the air surrounding a leaf has a direct effect upon its photosynthetic rate. One example of this effect is shown for corn in figure 10. Thus, the chief question with respect to this effect nowadays is not whether it exists, but whether the response to CO_2 concentration will be the same under different conditions of light intensity, leaf temperature, and leaf water availability.

In the same paper from which figure 10 is taken, Moss, Musgrave, and Lemon investigate some effects of all four of these factors upon photosynthesis. They give no indications that the photosynthetic response to CO_2 concentration is conditioned by temperature or water availability; but they do feel, and present evidence to attempt to prove, that the response to CO_2 concentration is affected by the light intensity level. The evidence they present is that shown in figure 11, where at a high light intensity CO_2 variations have a substantial effect upon assimilation, in sharp contrast with the negligible effects at a low light intensity. Thus, the authors would perhaps feel that account would also have to be taken of light intensity when evaluating the effects of CO_2 concentration upon photosynthesis, and this could be done. However, in almost <u>all</u> instances this is probably <u>not</u> necessary. To see why, we examine the data of Moss, Musgrave, and Lemon a little more closely.

Though nothing is said of how the data of figure 11 were obtained, they indicate that each point of figure 10 was determined by a one-hour observation. Thus, figure 10 is considered to be very reliable. If one now replots the data of figure 10 in a form similar to that of figure 11, the results as shown in figure 12, are quite different from those of figure 11; and the feasibility of having one slope between 150 and 350 ppm CO_2 concentration representative of all light intensities is evident.

To get a final working relation between change in CO_2 concentration vs. change in photosynthetic rate, we obtain an average slope of all curves shown in figure 12 between 150 and 350 ppm. This is done by drawing tangents to them midway between these two concentrations and averaging their six slopes. The final result is 2 mg $CO_2/dm^2/hr/100$ ppm CO_2. This effect of CO_2 concentration upon photosynthetic rate is then considered to be superimposed upon the photosynthetic rate determined from the previously elucidated effects of light intensity, leaf temperature, and leaf water availability.

5.4. Calculation of Raw Net Photosynthetic Rates for the Eleven Leaf Classes of Each Canopy Layer

Having established the natures of characteristic plant photosynthetic responses to the four basic factors of light intensity, leaf temperature, leaf water availability, and CO_2 concentration, we can begin now the actual calculations of net crop photosynthesis by applying the results of our preliminary calculations which have specified simultaneous values of the first three of these factors and have indicated how to arrive at values for the last one. This first set of calculations determines the net photosynthetic rates of the 11 leaf classes of each canopy layer under conditions of optimum soil moisture tension and no atmospheric moisture stress (100 percent relative humidity). They are carried out by PROGRAM XII.

At statement number 100, 50 cards corresponding to the temperatures 1 to 50°C are read into the computer. The cards contain the photosynthetic rates of maize at these temperatures for 14 different light intensities, ranging from 0.1 to 1.4 $cal/cm^2/min$ in 0.1 $cal/cm^2/min$ size increments, as they are specified by the set of curves for maize in figure 6. Then, once these values have been stored in the computer, the previously computed light intensities and leaf temperatures for the 11 leaf classes of each canopy layer are read between statements 1 and 2. Indices are next generated from them which allow the retrieval from the memory system of the computer of the photosynthetic rates to which they correspond. If the light intensity is less than 0.1 cal/ cm^2/min, the photosynthetic rate is set equal to zero at statement number 11; and if it is greater than 1.4 cal/cm^2/min, it is set equal to the rate at that latter value (the light saturation level) at statement number 13. The final results are called from the memory system of the computer at statement number 5 and then punched on cards and printed out on paper. In this form they are still too numerous to include here for reference; however, they can be found in their entirety in Idso (1967) for the illustrative situation we have been considering.

5.5. Calculation of Unadjusted Mean Canopy Layer Photosynthetic Rates and Sensible and Latent Heat Profiles

The several sets of calculations involved in this section are all carried out by PROGRAM XIII. They begin with the reading of the fractions of leaves in each layer receiving diffuse light only and the fractions receiving, in addition, direct sunlight at values of SIN(LS) between 0.0 and 0.1, 0.1 and 0.2, ..., 0.9 and 1.0. Next, at statements 2, 3, and 4, respectively, the net photosynthetic rates and the rates of heat loss by convection and transpiration are read for these same leaf classes of each layer. These arrays are then multiplied by the fractions of leaves comprising each class on a layer-by-layer basis; and the results are added together to give mean values for the rates of these three processes at each canopy layer. Very detailed vertical profiles of mean photosynthetic rate and sensible and latent heat exchange are thus obtained. These are punched on cards and printed out on paper immediately following statement number 7.

This completes the evaluation of sensible and latent heat exchange; and the final results of this calculation are shown here in figures 13 through 16. Further manipulations of the photosynthetic rates continue as follows, however. At statement number 8 is completed the calculation of photosynthetic profiles under conditions of soil moisture stress corresponding to those for which the families of curves in figure 9 are assumed to be valid. After these results have been punched and printed out, the direct effects of atmospheric moisture stress are arrived at. The DO LOOP terminating at statement number 9 determines the common reduction in photosynthetic rate to be applied to all of the previously calculated rates due to the direct effects of relative humidity as discussed in section 5.2.2.2. These reductions are made at statements 10, 11, 12, 13, and 14, with the results being immediately punched and printed out. Their exhibition here is deferred, however, in favor of the final results to be arrived at in the next section.

5.6. The Final Calculation of the Mean Net Photosynthetic Rates of the Several Canopy Layers

This final set of calculations made by PROGRAM XIV carries out the evaluation of the effects of the reduced CO_2 concentration at the plant canopy due to the crop's photosynthesizing. Since we do not know beforehand the CO_2 concentration at the canopy, we use an iteration technique whereby we are able to calculate both this concentration and its effect upon the crop's photosynthetic rate. The process has already been described in detail (section 4.4) and thus will not be dealt with further here. We note only that the program must be used five times for the five different soil moisture tensions we have been considering, and that the number of iterations provided for by the program is more than sufficient to insure proper convergence, as is indicated by the printouts following each cycle when the program is used.

The final net photosynthetic rates as determined for several of the canopy layers under various soil moisture stresses are shown in figures 17 through 21. All layers definitely show a midday slump in photosynthesis, or at least a truncation, with the effect being accentuated in the uppermost portion of the canopy. As is shown from the leaf temperature calculations (results found in Idso, 1967), these reductions are not caused by unduly high leaf temperatures, but rather by the actual lowering of leaf temperature during the midday hours, with a reinforcement from lower relative humidities at these times too. Thus, surprisingly, the method has indicated the possibility of a midday slump in photosynthesis on cool to temperate days--a phenomenon completely unsuspected in the prototype energy environment investigations of Gates (1965), Idso, Baker, and Gates

(1966), and Idso and Baker (1967a), and thus an important contribution to our understanding of photosynthesis under field conditions.

What makes these results especially interesting is that there are no immediate indications from the environmental data that leaf temperature should decrease during midday. The air temperature <u>increases</u> during this period, as do the radiant heat loads on the various leaves. The factor that overrides these trends, however, is the great transpiration rate experienced by many of the upper leaves at this time. The latent heat removed from the leaves by this mechanism more than compensates for these two effects.

Since the method as presently conceived implies an unlimited water supply, this phenomenon may not be as marked as is indicated here for times of severe or moderate water shortage. However, for recently irrigated or naturally watered fields it may be a fairly common occurrence. This possibility is strengthened by measurements of leaf temperatures of irrigated crops growing in the sunny, semi-arid southwestern United States by Van Bavel[1], who has repeatedly found leaf temperatures of such crops to be below air temperature throughout the greater portions of many days.

Finally, to get a more integrated look at the results for the canopy as a whole, the results for the 35 layers have been averaged to give a representative value for the entire crop. Figure 22 shows these average photosynthetic rates for the five different soil moisture

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[1] Van Bavel, C. H. M. 1967. Personal Communication.

regimes we have been considering. The midday truncation is still very apparent for all five situations. Also inserted here as Table VI, to be referred to later, are the CO_2 concentrations as calculated for the effective canopy exchange surface as a byproduct of our analysis.

6. EXPERIMENTAL VERIFICATION OF THE HOLOCOENOTIC METHOD

To this point we have accomplished three major objectives: 1) set forth a philosophy we believe must be followed in order to obtain meaningful results from analyses of environment-plant relationships, 2) proposed a theoretical framework for the photosynthetic response of plants to their environment, and 3) described the mechanics of a method based upon this philosophy and framework, useful for calculating net photosynthesis and sensible and latent heat exchange. The remaining task of this bulletin must thus be of a confirmatory nature. That is, we must now give some indication that all our work to this point is indeed a reflection of the real world, and that the predictions of the holocoenotic method in relation to our illustrative test case are reasonable.

6.1. The Nature of Experimental Verification

If we are to cite evidence for the justification of our work to this point, it is natural to inquire just what will constitute experimental verification. Some may feel that the final results must coincide with measurements in the field, and this is usually the case. In our situation, however, this is not so, at least at our present state of knowledge. The reason for this peculiarity is that our final net photosynthetic results are based upon sets of curves such as those shown in figures 6 and 9, and no one individual has yet carried out a comprehensive determination of such curves for a single plant. All such curves are rather piecemeal constructions from data separated in space and time and obtained by many different investigators. Thus, although one knows beyond any doubt that all plants must behave in such a typical fashion, no one knows for sure yet the natures of the curves in good detail for any one plant. Here, then, is an area where much important work has yet to be completed before a valid check of our final results with measured values can be accomplished.

This does not mean that we have removed the method from any possibility of experimental verification, but rather that we have required the verification to be made at a different level. It is obvious that if one has the correct set of curves describing a plant's photosynthetic response to light intensity, leaf temperature, leaf water availability, and carbon dioxide concentration, he will calculate correct values of net photosynthesis if he calculates correct values of these four basic factors, and it is thus at this level that the holocoenotic method is best tested.

A second good reason for testing the method on this level is that there is still no very exact way of measuring net photosynthesis in the field without altering the environment to such an extent that one no longer has the natural conditions for which calculations are made. More will be said about this later when we do (for those curious about it) compare our final results with some measurements made by a method which is supposed to overcome this handicap. We will proceed now, however, with a consideration of testing the method on the level of the four basic factors.

6.2. Verification of the Light Intensity Calculations

Even at this level of one of the four basic factors it is difficult to give experimental verification of the calculated results--the reason, of course, being due to the number of different light intensities calculated for each of the many crop layers. This need not deter us from making some judgment as to their accuracy, however, for there are other considerations which may carry even more weight than the only average type of verification which could be given by experimental means.

To begin with, it is a simple matter to obtain a correct measurement of direct and diffuse solar radiation on a horizontal surface above the crop; and a simple calculation then gives the intensity of the direct solar beam as received on a surface perpendicular to it, with no more error inherent in it than that contained in the original measurement. When one then considers the differently oriented leaves of a crop and carries out the calculation of a crop light distribution function, he again is proceeding on sound mathematical principles. Due to the vast number of leaves comprising an entire crop, even the mathematical integrations performed are on a solid basis. Thus, the results obtained <u>of necessity</u> must be equally as valid as the original measurement of direct sunlight on a horizontal surface.

Similar statements can also be made about the penetration of direct light into the canopy and the penetration of diffuse light when it is considered as direct light coming from different sky sections. In determining the intensities of diffuse and scattered light <u>received</u> by the leaves of each layer, however, there may be some small errors introduced by some of the assumptions made there, but when added to the results of the direct light, any error they may introduce would be almost impossible to detect by experimental means.

The only significant error that can be associated with the light intensity calculations, then, is that which may be introduced by an incorrect specification of the leaf distribution function. Here there are two possibilities to consider. First, there is the initial measurement of the function and its possible variation with depth in the canopy. A measurement method has been suggested by de Wit (1965), but by its very nature it may not be too accurate. Second, the effects of wind are bound to be significant in altering the leaf distribution function as it varies in mean intensity and gustiness during the day. We have already cited this problem and noted its consequences for the apparent photosynthetic efficiency of light use by plants.

Another thought to be interjected here is that as the wind blows and causes the plant leaves to flutter, the specific leaves of the lower canopy layers which are sunlit and shaded will vary. However, if the leaf distribution function remains unaffected during the entire time of the windy period (which seems quite likely), the statistical fractions of sunlit and shaded leaves will remain the same. Thus, the only effect this phenomenon could have upon our final calculation would be due to time lags in the photosynthetic response of plants to changing light intensity, another subject which could stand some further looking into.

Combining these latter considerations with those mentioned earlier, it is evident that at the present time there is no good way of experimentally determining the accuracy of the light calculations. We have shown, however, that a good knowledge of the leaf distribution function and the factors affecting it are sufficient to make calculations of light intensity as accurate as possible. Thus, a concentration on this aspect of the problem (with the knowledge that the end result will then take care of itself) will serve to clarify just what types of errors may be involved and how they can be eliminated.

6.3. Verification of the Leaf Temperature Calculations

The situation with respect to leaf temperature is much the same as that with respect to light intensity. Almost anywhere in the plant canopy there is the possibility of measuring a great variety of leaf temperatures due to various leaf orientations and shading effects. About all one can do in this situation in the field is to select leaves which closely approximate a certain orientation, such as the horizontal, and determine the temperatures of several similar leaves to obtain a mean temperature and a range. This was done by Idso (1966) and demonstrated that the measured temperature range nearly always contained within it the calculated leaf temperature. A more detailed report of these results can be found in Idso and Baker (1968).

A further complicating effect for field verification of these calculations is that the wind speed usually varies considerably over very short time intervals, as is evidenced by the wind speed data obtained by Wright and Lemon (1966a) and Idso (unpublished) with a heated thermocouple anemometer. Variations of this parameter are such that leaf temperature is nearly always in a state of flux, usually about some mean, however. Just as more attention must be given to the time lag of photosynthetic response to light intensity, more effort seems justified to learn more of the time lag undoubtedly in operation here too.

Although the above considerations indicate the futility of really testing the results of leaf temperature calculations in the field, one need not despair about this fact; for enough is known about the heat transfer processes involved in the energy balance at a leaf to insure that if all of the plant properties relevant to energy exchange can be accurately determined, the results of leaf temperature calculations based upon them will be correct. Happily, these plant properties are becoming better understood day by day. Leaf absorptances to various radiant energy fluxes can now be determined quite accurately, and leaf convection coefficients are becoming better characterized also (Knoerr and Gay, 1965). One property still has much mystery connected with it; this is the leaf diffusion resistance to transpiration. Recent investigations by Van Bavel, Nakayama, and Ehrler (1965), Impens, et al. (1967), and E. Kanamasu (unpublished, University of Wisconsin) are beginning to illuminate it also, however.

Of leaf temperature calculations, then, we must conclude that the method will give just as good answers as the plant properties it is supplied with, and these are now becoming quite well characterized.

6.4. Verification of Leaf Water Availability Effects

In our considerations of leaf water availability we indicated that no calculations were needed to specify values of the two component factors making up this third of the four basic factors directly affecting net photosynthesis; thus it would appear that we have nothing to verify with respect to this topic. This is only partly true, however, for although values of relative humidity are quite easily directly determined, a value of soil moisture tension for the crop is not so easy to derive. Significant variations in soil moisture tension often occur within the rooting zone of a crop, and these must be integrated to give some sort of result characteristic of the entire crop. For the problems involved here and the procedures for obtaining such a value, one is referred to the paper by Wadleigh and Gauch (1948).

The main question of veracity surrounding this topic, however, deals not with the specification of soil moisture stress, but with the substantiation of the effects of water stress on photosynthesis, as postulated earlier. The effects of soil moisture stress were postulated as accounting for about 90 percent of the control; thus they are the phenomena requiring some further supporting evidence. Since Kramer (1963) has summarized much of the work in this area, we quote below from him:

> It has been shown in several studies that a relatively low average soil moisture stress sometimes produces measurable reduction in growth. For instance, Van Bavel (1953)

> reported that an average moisture stress of only 1.5 atm. reduced the yield and lowered the quality of cigarette tobacco in North Carolina. In Israel it is reported that bananas are quite sensitive to low soil water stress (Shmueli, 1953). In England, Goode (1956) reported that a maximum soil water tension of less than one atmosphere reduced both vegetative growth and fruit growth of apple. Sands and Rutter (1959) found that a maximum soil water tension of 1.5 atm. reduced dry weight and stem elongation of Scotch pine seedlings and a tension of only 0.5 atm. reduced needle elongation.
>
> It is now generally agreed that water becomes progressively less available as the water content of the soil decreases, rather than remaining available until the water content falls almost to permanent wilting, then suddenly becoming unavailable.

For further evidence of the validity of the newly proposed water stress theory, one is referred to Idso (1967).

6.5. Verification of the CO_2 Calculations

The carbon dioxide concentration at the effective canopy exchange surface is about the only one of the four basic factors that we can readily compare with reliable experimental data. Wright and Lemon (1966b) measured hourly profiles of the parameter in the same corn crop at Ithaca, New York, for which we carried through our set of illustrative calculations. From noon to 5 p.m. the CO_2 concentration they measured at this height varied from just under 268 ppm to just over 272 ppm. Our calculations of these concentrations (and others too) are given in table VI. The reader is left to draw his own conclusions.

6.6. Comparison of Our Final Results with Those of the Aerodynamic Technique

In their attempt to measure net photosynthesis under field conditions without altering the natural conditions of the environment, Wright and Lemon (1966b) use an aerodynamic technique to calculate net CO_2 fixation by layer from carbon dioxide profiles and wind speed data. Writing the expression for the vertical flux of CO_2 as

$$P_s = \rho_a \cdot K_c \cdot dC/dz \qquad [24]$$

where P_s = vertical flux of CO_2, gm/cm^2/sec

ρ_a = air density at the prevailing temperature and pressure, gm/cm^3

K_c = CO_2 transfer coefficient, cm^2/sec

dC/dz = CO_2 concentration gradient, gm CO_2/gm air/cm,

they calculate the CO_2 fixation of a layer by the difference in the vertical flux of CO_2 at its upper and lower bounds. Their integrated results for the crop as a whole are superimposed upon our final results in figure 23, and in this connection it should be emphasized that their results are reduced by a factor of three.

The first thing to be noted about this comparison is, of course, the difference in absolute magnitude. It can be seen that for a soil moisture tension of 1.05 atmospheres, our absolute values are about one-third as great as those obtained by Wright and Lemon, and for a tension of 0.35 atmosphere they are one-half as great. Such a difference in absolute magnitude, however, is not too disturbing. If it is due to our family of curves describing the joint photosynthetic response of maize to light intensity and leaf temperature being in error by a constant factor, this is easily corrected, or if it is due to Wright's and Lemon's CO_2 transfer coefficient being off similarily, their method too is easily corrected.

The second thing to be noted about the comparison is that all of our calculated curves exhibit each and every variation of their semi-empirical result, which, of course, must be gratifying to both of us. Wright's and Lemon's results show these variations to be more pronounced than ours, however, and the question thus arises as to which are more correct. For two reasons the author believes that his results may be the more correct. First, the effects of CO_2 upon net photosynthesis as determined earlier are felt to be too small to account for such great changes in photosynthetic rate as are indicated by Wright and Lemon. Second, the use of wind speed data to determine a turbulent transfer coefficient for carbon dioxide is open to question, and as Wright and Lemon themselves say, "The accuracy of these results depends to a large extent upon the accuracy of the turbulent transfer coefficient determinations."

7. FORTRAN PROGRAMS

This section contains the Fortran programs necessary for the calculation of net photosynthesis and latent and sensible heat exchange by the holocoenotic method. They are written for use on an IBM 360 computer and have all been used with success thereon. The statements are general except for some dimension and format statements which vary according to the values of leaf area index and canopy density. For the programs as written here, these values were 3.5 and 0.1, respectively, resulting in 35 canopy layers.

PROGRAM I

```
C     THE CALCULATION OF LIGHT DISTRIBUTION FUNCTIONS (SS) FOR ALL 81
C     POSSIBLE COMBINATIONS OF THE INCLINATIONS OF THE SUN (IS) AND
C     THE LEAVES (IL), WHEN IS AND IL ASSUME THE VALUES 5, 15, ..., 85
C     DEGREES. INPUT DATA ARE ARRANGED IN NINE GROUPS OF NINE CARDS
C     EACH. EACH GROUP REPRESENTS COMBINATIONS OF NINE VALUES OF IL
C     AND ONE VALUE OF IS. THE CARDS ARE ORDERED ACCORDING TO INCREASING
C     VALUES OF BOTH IS AND IL. THE NINE COMPUTED POINTS OF EACH LIGHT
C     DISTRIBUTION FUNCTION CORRESPOND TO VALUES OF SIN(LS) = 0.1, 0.2,
C     ..., 0.9, WHERE LS IS THE ANGLE BETWEEN THE LEAF AND THE RAYS OF
C     THE SUN.

      DIMENSION S(19),SS(9)
   22 FORMAT(2I2)
   23 FORMAT(1X,9F6.3,22X,I2)
      DO 100 K=1,81
      READ(1,22)IS,IL
      PHI=3.1416
      FIS=IS
      FIL=IL
```

```
      FIS=FIS*PHI/180.
      FIL=FIL*PHI/180.
      A=SIN(FIS)*COS(FIL)
      B=COS(FIS)*SIN(FIL)
      X=-A/B
      IF(X+1.)2,2,3
    2 DAO=-PHI/2.
      GO TO 4
    3 DAO=ATAN(X/SQRT(1.-X**2))
    4 W=(2.*B*COS(DAO)-2.*A*DAO)**(-1)
      DO 5 I=1,19
      FI=I
      SNLS=-1.+0.1*FI
      SNDA=(SNLS-A)/B
      IF(SNDA+1.)6,6,7
    6 S(I)=0.
      GO TO 5
    7 IF(SNDA-1.)8,9,9
    9 S(I)=1.
      GO TO 5
    8 DA=ATAN(SNDA/SQRT(1.-SNDA**2))
      IF(DA-DAO)10,11,11
   10 S(I)=(B*COS(DA)-A*(PHI/2.+DA))*W
      GO TO 5
   11 S(I)=(B*(2.*COS(DAO)-COS(DA))-A*(2.*DAO+PHI/2.-DA))*W
    5 CONTINUE
      DO 12 I=1,9
      JJ=20-I
   12 S(I)=S(JJ)-S(I)
      DO 13 I=1,9
      II=10-I
   13 SS(I)=S(II)
      WRITE(2,23)(SS(I),I=1,9),K
```

```
      WRITE(3,23)(SS(I),I=1,9),K
  100 CONTINUE
      STOP
      END
```

PROGRAM II

```
C     THE CALCULATION OF THE LIGHT DISTRIBUTION FUNCTION (O(I)) FOR
C     INCLINATIONS OF THE SUN IS=5, 15, ..., 85 DEGREES AND FOR
C     ANY ARBITRARY LEAF DISTRIBUTION FUNCTION(F(J)).  ALSO, THE
C     CALCULATION OF THE MEAN AREA OF THE PROJECTION OF ONE UNIT
C     LEAF AREA FOR THE CROP AS A WHOLE IN THE DIRECTION OF THE
C     SUN (OPG).  S(J,I) ARE THE CUMULATIVE FREQUENCIES OF LIGHT
C     INTERCEPTION AT SIN(LS)=0.1, 0.2, ..., 0.9 FOR LEAF INCLINA-
C     TIONS OF 5, 15, ..., 85 DEGREES.  S(J,10) IS DEFINED IN THE
C     PROGRAM.  THE O(10) VALUES FOR EACH SUN INCLINATION CORRESPOND
C     TO VALUES OF SIN(LS)=0.1, 0.2, ..., 1.0.  EACH SET OF DATA FOR
C     A SUN INCLINATION IS PRECEEDED BY A CODE CARD WITH A POSITIVE
C     NUMBER ON IT.  THE LAST CARD OF THE DATA IS A BLANK.

      DIMENSION S(9,10),SN(10),OP(9),F(9),O(10)
   22 FORMAT(1X,9F6.3)
   23 FORMAT(11X,10F6.3)
   24 FORMAT(11X,F6.3)
   30 READ(1,22) CODE
      IF(CODE)40,40,50
   50 DO 100 J=1,9
  100 READ(1,22)(S(J,I),I=1,9)
      DO 1 J=1,9
    1 S(J,10)=1.
      DO 2 I=1,10
      FI=I
    2 SN(I)=-0.05+0.1*FI
      DO 3 J=1,9
      OP(J)=S(J,1)/SN(1)
      DO 4 I=2,10
    4 OP(J)=OP(J)+(S(J,I)-S(J,I-1))/SN(I)
    3 OP(J)=1./OP(J)
      READ(1,22)(F(J),J=1,9)
```

```
      Q=F(1)*OP(1)
      DO 6 J=2,9
    6 Q=Q+(F(J)-F(J-1))*OP(J)
      DO 7 I=1,10
      O(I)=F(1)*OP(1)*S(1,I)/Q
      DO 7 J=2,9
    7 O(I)=O(I)+(F(J)-F(J-1))*OP(J)*S(J,I)/Q
      WRITE(2,23)(O(I),I=1,10)
      WRITE(3,23)(O(I),I=1,10)
      OPG=O(1)/SN(1)
      DO 8 I=2,10
    8 OPG=OPG+(O(I)-O(I-1))/SN(I)
      OPG=1./OPG
      WRITE(2,24)OPG
      WRITE(3,24)OPG
      GO TO 30
   40 STOP
      END
```

PROGRAM III

```
C     THE CALCULATION OF THE FRACTIONS OF SUNLIT LEAVES (FR(K,J))
C     RECEIVING DIRECT LIGHT AT VALUES OF SIN(LS) BETWEEN 0.0 AND
C     0.1, 0.1 and 0.2, ..., 0.9 and 1.0 AT SUN INCLINATIONS IS=
C     5, 15, ..., 85 DEGREES.  O(K,J) ARE THE LIGHT DISTRIBUTION
C     FUNCTIONS FOR A CROP COMPUTED AT THESE SUN INCLINATIONS.

      DIMENSION SN(10),S(10),0(9,10),R(9,10),SR(9),FR(9,10)
   22 FORMAT(11X,10F6.3)
   23 FORMAT(1X,F6.3)
      SN(1)=0.05
      SN(2)=0.15
      SN(3)=0.25
      SN(4)=0.35
      SN(5)=0.45
      SN(6)=0.55
      SN(7)=0.65
      SN(8)=0.75
      SN(9)=0.85
      SN(10)=0.95
      DO 100 K=1,9
  100 READ(1,22)(0(K,J),J=1,10)
      DO 200 K=1,9
  200 R(K,1)=0(K,1)/SN(1)
      DO 300 K=1,9
      DO 300 J=2,10
  300 R(K,J)=(0(K,J)-0(K,J-1))/SN(J)
      DO 400 K=1,9
  400 SR(K)=R(K,1)+R(K,2)+R(K,3)+R(K,4)+R(K,5)+R(K,6)+R(K,7)
     1+R(K,8)+R(K,9)+R(K,10)
      DO 500 K=1,9
      DO 500 J=1,10
```

```
500 FR(K,J)=R(K,J)/SR(K)
    DO 600 K=1,9
    WRITE(2,22)(FR(K,J),J=1,10)
600 WRITE(3,23)(FR(K,J),J=1,10)
    STOP
    END
```

PROGRAM V

```
C     THE CALCULATION OF THE SOLAR TIME (T(K)) FOR THE SUN INCLINATIONS
C     IS=5,15, ..., 65 DEGREES. H IS THE HOUR ANGLE OF THE SUN, ED IS
C     THE DECLINATION OF THE SUN FOR THE DAY IN QUESTION, AND EL IS THE
C     LATITUDE, POSITIVE WHEN NORTH OF THE EQUATOR.
      DIMENSION EK(7),A(7),H(7),T(7)
   22 FORMAT(1X,2F7.4)
   23 FORMAT(1X,7F6.3)
      READ(1,22)EL,ED
      PHI=3.1416
      EEL=EL*PHI/180.
      EED=ED*PHI/180.
      EK(1)=5.*PHI/180.
      EK(2)=15.*PHI/180.
      EK(3)=25.*PHI/180.
      EK(4)=35.*PHI/180.
      EK(5)=45.*PHI/180.
      EK(6)=55.*PHI/180.
      EK(7)=65.*PHI/180.
      DO 6 K=1,7
      A(K)=(SIN(EK(K))-SIN(EEL)*SIN(EED))/(COS(EEL)*COS(EED))
      IF(A(K)),3,5,5
    3 H(K)=PHI-ATAN(SQRT(1.-A(K)**2)/(-A(K)))
      GO TO 6
    5 H(K)=ATAN(SQRT(1.-A(K)**2)/A(K))
    6 T(K)=H(K)*12./PHI
      WRITE(2,23)(T(K),K=1,7)
      WRITE(3,23)(T(K),K=1,7)
      STOP
      END
```

PROGRAM VI

```
C     THE CALCULATION OF THE FRACTIONS (Z(I)) OF DIFFUSE LIGHT INCIDENT
C     UPON THE VARIOUS CROP LAYERS COMPARED TO THAT INCIDENT ON A
C     HORIZONTAL SURFACE ABOVE THE CROP, AND THE CALCULATION OF THE
C     ACTUAL INTENSITIES OF DIFFUSE LIGHT (FDZ(K,I)) RECEIVED BY THE
C     LEAVES OF EACH CANOPY LAYER AND THE SOIL SURFACE AT TIMES T(K).
C     X(K,I) ARE THE FRACTIONS OF LEAVES IN EACH LAYER RECEIVING DIRECT
C     LIGHT AT TIMES OF THE SUN INCLINATIONS IS=5, 15, ..., 65 DEGREES.
C     B(K) ARE THE RELATIVE CONTRIBUTIONS TO THE ILLUMINANCE OF A HORI-
C     ZONTAL SURFACE OF 10 DEGREE ZONES CENTERED AT THESE INCLINATIONS
C     FROM A SKY WITH UNIFORM BRIGHTNESS.  FD(K) ARE THE ACTUAL INTENSITIES
C     OF DIFFUSE SKYLIGHT RECEIVED AT A HORIZONTAL SURFACE ABOVE THE CROP
C     AT TIMES T(K).

      DIMENSION X(9,35),B(9),A(9,36),Z(36),FD(14),FDZ(14,36)
   20 FORMAT(1X,I2)
   22 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   32 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,6F6.3)
   33 FORMAT(11X,10F6.3/11X,4F6.3)
      B(1)=0.030
      B(2)=0.087
      B(3)=0.133
      B(4)=0.163
      B(5)=0.174
      B(6)=0.163
      B(7)=0.133
      B(8)=0.087
      B(9)=0.030
      READ(1,20)NMAX
      DO 100 K=1,9
  100 READ(1,22)(X(K,I),I=1,NMAX)
      J=NMAX+1
      DO 11 K=1,9
```

```
   DO 11 I=2,J
11 A(K,I)=B(K)*X(K,I-1)
   Z(1)=1.
   DO 12 I=2,J
12 Z(I)=A(1,I)+A(2,I)+A(3,I)+A(4,I)+A(5,I)+A(6,I)+A(7,I)
  1+A(8,I)+A(9,I)
   WRITE(2,32)(Z(I),I=1,J)
   WRITE(3,32)(Z(I),I=1,J)
   READ(1,33)(FD(K),K=1,14)
   DO 50 K=1,14
   DO 50 I=1,J
50 FDZ(K,I)=FD(K)*Z(I)
   DO 15 K=1,14
   WRITE(2,32)(FDZ(K,I),I=1,J)
15 WRITE(3,32)(FDZ(K,I),I=1,J)
   STOP
   END
```

PROGRAM VII

```
C      THE CALCULATION OF THE ACTUAL INTENSITIES OF THE SCATTERED LIGHT
C      SOURCES (ST(K,I)) AT EACH CANOPY LAYER AND AT THE SOIL SURFACE
C      AT TIMES OF THE SUN INCLINATIONS IS=5, 15, ..., 65 DEGREES.
C      X(K,I-1) ARE THE FRACTIONS OF DIRECT LIGHT INCIDENT UPON EACH
C      LAYER I.  XX(K,I) ARE THE FRACTIONS OF DIRECT LIGHT INTERCEPTED
C      BY EACH LAYER, AS ARE THE XXX(K,I), WHICH MERELY EXPRESS EXPLI-
C      CITLY THE VARIATION THROUGHOUT THE ENTIRE DAY.  FS(K) ARE THE
C      ACTUAL INTENSITIES OF DIRECT SOLAR RADIATION INCIDENT UPON A
C      HORIZONTAL SURFACE ABOVE THE CROP, AND XXXX(K,I) ARE THE ACTUAL
C      INTENSITIES THUS INTERCEPTED AT THE SEVERAL CROP LAYERS.  FDZ(K,I)
C      ARE THE ACTUAL INTENSITIES OF DIFFUSE SKYLIGHT INTERCEPTED AT THE
C      LAYERS.  AGAIN, K IN ALL OF THESE CASES REFERS TO AN INCLINATION
C      OF THE SUN.  SCAT IS THE SCATTERING COEFFICIENT OF THE CROP LEAVES
C      FOR DIRECT SUNLIGHT, SSCAT IS THE SCATTERING COEFFICIENT FOR DIFFUSE
C      SKYLIGHT, AND SSSCAT IS TWICE THE REFLECTANCE OF THE SOIL SURFACE.

      DIMENSION X(9,35),XX(7,35),XXX(14,35),FS(14),XXXX(14,36),
     1FDZ(14,36),FDZZ(14,36),ST(14,36)
   22 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   25 FORMAT(1X,3F6.3)
   26 FORMAT(1X,I2)
   27 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,6F6.3)
   28 FORMAT(11X,10F6.3/11X,4F6.3)
      READ(1,26)NMAX
      DO 100 K=1,9
  100 READ(1,22)(X(K,I),I=1,NMAX)
      DO 2 K=1,7
      XX(K,1)=1.-X(K,1)
      DO 2 I=2,NMAX
    2 XX(K,I)=X(K,I-1)-X(K,I)
      DO 666 I=1,NMAX
```

```
      XXX(1,I)=XX(1,I)
      XXX(2,I)=XX(2,I)
      XXX(3,I)=XX(3,I)
      XXX(4,I)=XX(4,I)
      XXX(5,I)=XX(5,I)
      XXX(6,I)=XX(6,I)
      XXX(7,I)=XX(7,I)
      XXX(8,I)=XX(7,I)
      XXX(9,I)=XX(6,I)
      XXX(10,I)=XX(5,I)
      XXX(11,I)=XX(4,I)
      XXX(12,I)=XX(3,I)
      XXX(13,I)=XX(2,I)
  666 XXX(14,I)=XX(1,I)
      READ(1,28)(FS(K),K=1,14)
      DO 3 K=1,14
      DO 3 I=1,NMAX
    3 XXXX(K,I)=FS(K)*XXX(K,I)
      L=NMAX+1
      DO 4 K=1,14
    4 XXXX(K,L)=FS(K)*X(K,NMAX)
      DO 400 K=1,14
  400 READ(1,27)(FDZ(K,I),I=1,L)
      DO 6 K=1,14
      DO 6 I=1,NMAX
    6 FDZZ(K,I)=FDZ(K,I)-FDZ(K,I+1)
      DO 7 K=1,14
    7 FDZZ(K,NMAX+1)=FDZ(K,NMAX+1)
      READ(1,25)SCAT,SSCAT,SSSCAT
      DO 8 K=1,14
      DO 8 I=1,NMAX
    8 ST(K,I)=SCAT*XXXX(K,I)+SSCAT*FDZZ(K,I)
```

```
      DO 9 K=1,14
    9 ST(K,NMAX+1)=(XXXX(K,NMAX+1)+FDZZ(K,NMAX+1))*SSSCAT
      DO 700 K=1,14
      WRITE(2,27)(ST(K,I),I=1,L)
  700 WRITE(3,27)(ST(K,I),I=1,L)
      STOP
      END
```

PROGRAM VIII

```
C     THE CALCULATION OF THE INTENSITIES OF SCATTERED LIGHT (SSS(K,I))
C     INCIDENT UPON THE LEAVES OF EACH CANOPY LAYER AT TIMES OF THE
C     SUN INCLINATIONS K.  ST(K,I) ARE THE STRENGTHS OF THE SCATTERED
C     LIGHT SOURCES AT EACH LAYER AND Z(I) ARE THE FRACTIONS OF DIFFUSE
C     LIGHT INCIDENT UPON A LAYER DUE TO ANOTHER LAYER I DEPTHS AWAY.

      DIMENSION ST(14,36),Z(36),S(14,36),SST(14,36),SS(14,35),SSS(14,35)
   11 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   21 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,6F6.3)
   24 FORMAT(1X,F6.3)
   25 FORMAT(1X,I2)
      READ(1,25)NMAX
      M=NMAX+1
      DO 43 K=1,14
   43 READ(1,21)(ST(K,I),I=1,M)
      READ(1,21)(Z(I),I=1,M)
      DO 1 K=1,14
      S(K,1)=0.
      DO 1 I=2,M
    1 S(K,1)=S(K,1)+0.5*ST(K,I)*Z(I-1)
      DO 4 K=1,14
      DO 4 I=2,NMAX
      S(K,I)=0.
      N=I-1
      DO 3 L=1,N
      J=I-L
    3 S(K,I)=S(K,I)+0.5*ST(K,L)*Z(J)
      NN=I+1
      DO 65 L=NN,NMAX
      J=L-1
   65 S(K,I)=S(K,I)+0.5*ST(K,L)*Z(J)
    4 CONTINUE
```

```
      DO 5 K=1,14
      S(K,M)=0.
      DO 5 I=1,NMAX
      J=M-I
    5 S(K,M)=S(K,M)+0.5*ST(K,I)*Z(J)
      READ(1,24)XSCAT
      DO 6 K=1,14
      DO 6 I=1,M
    6 SST(K,I)=XSCAT*S(K,I)*(1.-Z(2))
      DO 7 K=1,14
      SS(K,1)=0.
      DO 7 I=2,M
    7 SS(K,1)=SS(K,1)+0.5*SST(K,I)*Z(I-1)
      DO 9 K=1,14
      DO 9 I=2,NMAX
      SS(K,I)=0.
      N=I-1
      DO 8 L=1,N
      J=I-L
    8 SS(K,I)=SS(K,I)+0.5*SST(K,L)*Z(J)
      NN=I+1
      DO 9 L=NN,NMAX
      J=L-I
    9 SS(K,I)=SS(K,I)+0.5*SST(K,L)*Z(J)
      DO 10 K=1,14
      DO 10 I=1,NMAX
   10 SSS(K,I)=S(K,I)+SS(K,I)
      DO 203 K=1,14
      WRITE(2,11)(SSS(K,I),I=1,NMAX)
  203 WRITE(3,11)(SSS(K,I),I=1,NMAX)
      STOP
      END
```

PROGRAM IX

```
C     THE CALCULATION OF THE INTENSITIES OF DIFFUSE AND SCATTERED LIGHT
C     (SSSS(I)) INCIDENT UPON THOSE LEAVES OF EACH LAYER THAT RECEIVE NO
C     DIRECT SUNLIGHT.  ALSO, THE CALCULATION OF THE INTENSITIES (SDSD(I))
C     OF LIGHT INCIDENT UPON THOSE LEAVES OF EACH LAYER WHICH RECEIVE
C     DIRECT SOLAR RADIATION AT VALUES OF SIN(LS) FROM 0.0 TO 0.1, 0.1 TO
C     0.2, ..., 0.9 TO 1.0.  FDZ(I) ARE THE INTENSITIES OF INCIDENT
C     DIFFUSE LIGHT RECEIVED BY THE LEAVES OF EACH LAYER AND SSS(I) ARE
C     THE INTENSITIES OF SCATTERED LIGHT RECEIVED BY THE SAME LEAVES.
C     FS(K) ARE THE INTENSITIES OF DIRECT SUNLIGHT RECEIVED AT A HORIZONTAL
C     SURFACE ABOVE THE CROP AT SUN INCLINATIONS IS=5, 15, ..., 65 DEGREES.
C     EK(K) ARE THE ANGLES 5, 15, ..., 65 DEGREES.  FFS(K) ARE THUS THE
C     INTENSITIES OF THE DIRECT BEAM AT THESE SUN INCLINATIONS AS RECEIVED
C     ON A SURFACE PERPENDICULAR TO THE BEAM.  SN(J) ARE THE VALUES OF
C     SIN(LS) OF 0.05, 0.15, ..., 0.95.
      DIMENSION FDZ(35),SSS(35),SSSS(35),SN(10),SDSD(35,10)
   21 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   22 FORMAT(11X,10F6.3)
   23 FORMAT(11X,F6.3)
   24 FORMAT(1X,I2)
      READ(1,24)NMAX
      DO 88 K=1,14
      READ(1,21)(FDZ(I),I=1,NMAX)
      READ(1,21)(SSS(I),I=1,NMAX)
      DO 1 I=1,NMAX
    1 SSSS(I)=FDZ(I)+SSS(I)
      WRITE(2,21)(SSSS(I),I=1,NMAX)
      WRITE(3,21)(SSSS(I),I=1,NMAX)
      READ(1,23)FS
      READ(1,23)EK
      EEK=EK*3.1416/180.
      FFS=FS/SIN(EEK)
```

```
   READ(1,22)(SN(J),J=1,10)
   DO 3 I=1,NMAX
   DO 2 J=1,10
 2 SDSD(I,J)=FFS*SN(J)+SSSS(I)
 3 CONTINUE
   DO 4 I=1,NMAX
   WRITE(2,22)(SDSD(I,J),J=1,10)
 4 WRITE(3,22)(SDSD(I,J),J=1,10)
88 CONTINUE
   STOP
   END
```

PROGRAM X

```
C     THE CALCULATION OF THE HEAT LOADS OF THE ELEVEN LEAF CLASSES OF
C     EACH CANOPY LAYER FOR SPECIFIED INCLINATIONS OF THE SUN (IS).
C     HLDO(I) ARE THE HEAT LOADS OF THE LEAVES RECEIVING DIFFUSE SHORT
C     WAVE RADIATION ONLY, AND HLTR(I,J) ARE THE HEAT LOADS OF LEAVES
C     RECEIVING DIRECT SOLAR RADIATION TOO.  ABSS, ABSD, AND ABLD ARE
C     THE ABSORPTANCES OF THE CROP LEAVES TO SCATTERED AND DIFFUSE
C     SHORT WAVE RADIATION, DIRECT SOLAR RADIATION, AND LONG WAVE
C     RADIATION, RESPECTIVELY.  SSSS(I) ARE THE INTENSITIES OF
C     SCATTERED AND DIFFUSE SHORT WAVE RADIATION WHICH IMPINGE UPON
C     LEAVES RECEIVING NO DIRECT SUNLIGHT, AND SDSD(I,J) ARE THE INTEN-
C     SITIES OF TOTAL SHORT WAVE RADIATION INCIDENT UPON LEAVES WHICH
C     RECEIVE DIRECT SOLAR RADIATION ALSO.  Z(I) ARE THE FRACTIONS OF
C     THE UPPER HEMISPHERIC VIEWS OF HORIZONTAL LEAVES IN THE SEVERAL
C     LAYERS OCCUPIED BY SKY AND NOT BY OTHER LEAVES.

      DIMENSION SSSS(35),ASSSS(35),SDSD(35,10),ADDDD(35,10),
     1ATSW(35,10),Z(35),SALW(35),HLDO(35),HLTR(35,10)
   21 FORMAT(IX,3F7.3)
   22 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   23 FORMAT(11X,10F6.3)
   24 FORMAT(1X,2F6.3)
      DO 12 K=1,14
      READ(1,21)ABSS,ABSD,ABLD
      READ(1,22)(SSSS(I),I=1,35)
      DO 1 I=1,35
    1 ASSSS(I)=ABSS*SSSS(I)
      DO 2 I=1,35
    2 READ(1,23)(SDSD(I,J),J=1,10)
      DO 3 I=1,35
      DO 3 J=1,10
    3 ADDDD(I,J)=(SDSD(I,J)-SSSS(I))*ABSD
      DO 4 I=1,35
      DO 4 J=1,10
```

```
 4 ATSW(I,J)=ADDDD(I,J)+ASSSS(I)
   READ(1,24)RG,RA
   READ(1,22)(Z(I),I=1,35)
   DO 5 I=1,35
 5 SALW(I)=(2.*RG+Z(I)*(RA-RG))*ABLD
   DO 6 I=1,35
 6 HLDO(I)=ASSSS(I)+SALW(I)
   DO 7 I=1,35
   DO 7 J=1,10
 7 HLTR(I,J)=ATSW(I,J)+SALW(I)
   WRITE(2,22)(HLDO(I),I=1,35)
   WRITE(3,22)(HLDO(I),I=1,35)
   DO 8 I=1,35
   WRITE(2,23)(HLTR)(I,J),J=1,10)
 8 WRITE(3,23)(HLTR)(I,J),J=1,10)
12 CONTINUE
   STOP
   END
```

PROGRAM XI

```
C     THE CALCULATION OF LEAF TEMPERATURES, TL(J), OF THE ELEVEN
C     LEAF CLASSES OF EACH CANOPY LAYER, I, FOR SPECIFIED INCLINA-
C     TIONS OF THE SUN.  ALSO, THE CALCULATIONS OF THE SENSIBLE
C     AND LATENT HEAT LOSSES, SH(J) AND LH(J), BY THESE LEAVES.
C     SWVD(M,N) ARE THE SATURATED WATER VAPOR DENSITIES OF AIR (x10^6)
C     AT THE TEMPERATURES 274.0, 274.1, 274.2, ..., 323.7, 323.8,
C     323.9 DEGREES KELVIN.  INCREMENTS IN THE INDEX M CORRESPOND TO
C     INTERGER TEMPERATURE INCREMENTS AND THOSE IN THE INDEX N TO
C     TEMPERATURE INCREMENTS OF OF 0.1 DEGREES.  TA(I), V(I), RH(I),
C     AND DIFRES(I) ARE, RESPECTIVELY, THE AIR TEMPERATURE, WIND SPEED,
C     RELATIVE HUMIDITY, AND LEAF DIFFUSION RESISTANCE AT THE SEVERAL
C     CANOPY LAYERS.  HLDO(I) ARE THE HEAT LOADS OF THOSE LEAVES OF
C     EACH LAYER THAT RECEIVE DIFFUSE SHORT WAVE RADIATION EXCLUSIVE
C     OF DIRECT SUNLIGHT, WHILE HLTR(I,J) ARE THE HEAT LOADS OF THOSE
C     LEAVES THAT RECEIVE DIRECT SOLAR RADIATION TOO. EMIS, SIGMA,
C     CHARD, HTVAP ARE THE EMITTANCE OF A CROP LEAF, THE STAFAN-BOLTZ-
C     MANN CONSTANT, THE CHARACTERISTIC LEAF DIMENSION, AND HEAT OF
C     VAPORIZATION.

      DIMENSION SWVD(50,10),TA(35),SWVDTA(35),V(35),RH(35),DIFRES(35),
     1HLDO(35),HLTR(35,11),TL(11),SH(11),LH(11)
      REAL LH
   20 FORMAT(1X,I2)
   21 FORMAT(1X,10F7.3)
   22 FORMAT(1X,13F6.1/1X,13F6.1/1X,9F6.1)
   23 FORMAT(1X,F4.2,1X,F15.13,1X,F3.1,1X,F5.1)
   24 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   25 FORMAT(11X,10F6.3)
   26 FORMAT(11X,11F6.1)
   27 FORMAT(11X,F7.3)
   28 FORMAT(11X,11F6.3)
```

```
  READ(1,20)NMAX
  DO 1 M=1,50
1 READ(1,21)(SWVD(M,N),N=1,10)
  DO 789 K=1,14
  READ(1,22)(TA(I),I=1,NMAX)
  DO 2 I=1,NMAX
  M=TA(I)-273.0+0.03
  XM=M
  N=(TA(I)-273.0-XM+0.1)*10.+0.5
  SWVDTA(I)=SWVD(M,N)
2 WRITE(3,27)SWVDTA(I)
  READ(1,23)EMIS,SIGMA,CHARD,HTVAP
  READ(1,22)(V(I),I=1,NMAX)
  READ(1,22)(RH(I),I=1,NMAX)
  READ(1,24)(DIFRES(I),I=1,NMAX)
  READ(1,24)(HLDO(I),I=1,NMAX
  DO 3 I=1,NMAX
  READ(1,25)(HLTR(I,J),J=1,10)
3 HLTR(I,11)=HLDO(I)
  DO 30 I=1,NMAX
  LL=V(I)
  IF(LL-10)13,13,14
13 TLL=TA(I)+5.
  DO 31 J=1,11
  TL(J)=TLL
16 M=TL(J)-273.0+0.03
  XM=M
  N=(TL(J)-273.0-XM+0.1)*10.+0.5
  SH(J)=0.006*SQRT(SQRT(ABS(TL(J)-TA(I))/CHARD))*(TL(J)-TA(I))
  LH(J)=(HTVAP/DIFRES(I))*(SWVD(M,N)-RH(I)*SWVDTA(I)*0.01)*0.000001
  A=HLTR(I,J)/2.-EMIS*SIGMA*TL(J)**4-SH(J)-LH(J)
  IF(A-0.01)15,31,17
```

```
17 TL(J)=TL(J)+0.3
   GO TO 16
15 IF(A+0.01)18,31,31
18 TL(J)=TL(J)-0.3
   GO TO 16
31 CONTINUE
   WRITE(2,26)(TL(J),J=1,11)
   WRITE(3,26)(TL(J),J=1,11)
   WRITE(2,28)(SH(J),J=1,11)
   WRITE(3,28)(SH(J),J=1,11)
   WRITE(2,28)(LH(J),J=1,11)
   WRITE(3,28)(LH(J),J=1,11)
   GO TO 30
14 TLL=TA(I)+5.
   DO 32 J=1,11
   TL(J)=TLL
36 M=TL(J)-273.0+0.03
   XM=M
   N=(TL(J)-273.0-XM+0.1)*10.+0.5
   SH(J)=0.0057*SQRT(V(I)/CHARD)*(TL(J)-TA(I))
   LH(J)=(HTVAP/DIFRES(I))*(SWVD(M,N)-RH(I)*SWVDTA(I)*0.01)*0.000001
   A=HLTR(I,J)/2.-EMIS*SIGMA*TL(J)**4-SH(J)-LH(J)
   IF(A-0.010)35,32,37
37 TL(J)=TL(J)+0.3
   GO TO 36
35 IF(A+0.010)38,32,32
38 TL(J)=TL(J)-0.3
   GO TO 36
32 CONTINUE
   WRITE(2,26)(TL(J),J=1,11)
   WRITE(3,26)(TL(J),J=1,11)
   WRITE(2,28)(SH(J),J=1,11)
```

```
      WRITE(3,28)(SH(J),J=1,11)
      WRITE(2,28)(LH(J),J=1,11)
      WRITE(3,28)(LH(J),J=1,11)
   30 CONTINUE
  789 CONTINUE
      STOP
      END
```

PROGRAM XII

```
C     THE CALCULATION OF THE PHOTOSYNTHETIC RATES (PHOTO(I,J)) OF THE
C     ELEVEN LEAF CLASSES OF EACH CANOPY LAYER FOR THE SUN INCLINATIONS
C     IS=5, 15, ..., 65, 65, ..., 15, 5 DEGREES.  PHOSYN(M,N) ARE LEAF
C     PHOTOSYNTHETIC RATES AT THE TEMPERATURES INDEXED BY M AND THE
C     LIGHT INTENSITIES INDEXED BY N.  THE TEMPERATURES RANGE FROM 1 TO
C     50 DEGREES CENTIGRADE IN INTEGER INCREMENTS, AND THE LIGHT INTEN-
C     SITIES RANGE FROM 0.1 TO 1.4 CAL/CM2/MIN IN 0.1 INCREMENTS.  TL(I,J)
C     ARE THE LEAF TEMPERATURES OF EACH CLASS AND LAYER, SSSS(I) ARE THE
C     INTENSITIES OF DIFFUSE AND SCATTERED LIGHT INCIDENT UPON LEAVES OF
C     EACH LAYER, AND SDSD(I,J) ARE THE INTENSITIES OF DIRECT SUNLIGHT
C     INCIDENT UPON LEAVES OF EACH CLASS AND LAYER.

      DIMENSION PHOSYN(50,14),TL(35,11),SSSS(35),SDSD(35,11),
     1NTL(35,11),NSDSD(35,11),PHOTO(35,11)
   20 FORMAT(1X,I2)
   21 FORMAT(1X,14F5.1)
   22 FORMAT(11X,11F6.1)
   23 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   24 FORMAT(11X,10F6.3)
   25 FORMAT(11X,11F5.1)
      DO 100 M=1,50
  100 READ(1,21)(PHOSYN(M,N),N=1,14)
      READ(1,20)NMAX
      DO 66 K=1,14
      DO 1 I=1,NMAX
    1 READ(1,22)(TL(I,J),J=1,11)
      READ(1,23)(SSSS(I),I=1,NMAX)
      DO 2 I=1,NMAX
      READ(1,24)(SDSD(I,J),J=1,10)
    2 SDSD(I,11)=SSSS(I)
      DO 3 I=1,NMAX
      DO 3 J=1,11
```

```
 3 NTL(I,J)=TL(I,J)-273.0+0.03
   DO 4 I=1,NMAX
   DO 4 J=1,11
 4 NSDSD(I,J)=SDSD(I,J)*10.+0.03
   DO 5 I=1,NMAX
   DO 5 J=1,11
   N=NSDSD(I,J)
   IF(N)11,11,12
11 PHOTO(I,J)=0.
   CONTINUE
12 IF(N-14)31,31,13
13 N=14
31 M=NTL(I,J)
 5 PHOTO(I,J)=PHOSYN(M,N)
   DO 6 I=1,NMAX
   WRITE(2,25)(PHOTO(I,J),J=1,11)
 6 WRITE(3,25)(PHOTO(I,J),J=1,11)
66 CONTINUE
   STOP
   END
```

PROGRAM XIII

```
C     THE CALCULATION OF THE MEAN PHOTOSYNTHETIC RATES(PHOTOL(I)),
C     MEAN SENSIBLE HEAT LOSSES (SHL(I)), AND MEAN LATENT HEAT
C     LOSSES (LHL(I)) FOR THE SEVERAL CANOPY LAYERS AT THE TIMES OF
C     THE SUN INCLINATIONS IS=5, 15, ..., 65, 65, ..., 15, 5 DEGREES.
C     ALSO, THE CALCULATION OF MEAN PHOTOSYNTHETIC RATES PHOTOE(I),
C     PHOTOS(I), PHOTOF(I), AND PHOTOT(I) UNDER CONDITIONS OF SOIL
C     MOISTURE STRESSES OF 0.70, 1.05, 1.40, and 1.75 ATMOSPHERES, AS
C     OPPOSED TO A TENSION OF 0.35 ATMOSPHERE FOR PHOTOL(I). THEN,
C     THE CALCULATION OF THE MEAN PHOTOSYNTHETIC RATES ADPHOL(I),
C     ADPHOE(I), ADPHOS(I), ADPHOF(I), AND ADPHOT(I) ADJUSTED FOR THE
C     DIRECT EFFECTS OF RELATIVE HUMIDITY (RH(I)).  DF(I) ARE THE
C     FRACTIONS OF LEAVES IN EACH LAYER RECEIVING DIFFUSE SHORT WAVE
C     RADIATION ONLY, and DS(I,J) ARE THE FRACTIONS OF THE LEAVES OF
C     EACH LAYER RECEIVING DIRECT SOLAR RADIATION ALSO.  PHOTO(I,J)
C     ARE THE PHOTOSYNTHETIC RATES OF THE ELEVEN LEAF CLASSES OF EACH
C     LAYER, SH(I,J) ARE THE SENSIBLE HEAT LOSSES FROM THE ELEVEN LEAF
C     CLASSES OF EACH LAYER, AND LH(I,J) ARE THE LATENT HEAT LOSSES
C     FROM THESE LEAVES.
      DIMENSION DF(35),DS(35,11), PHOTO(35,11), SH(35,11),LH(35,11),
     1PHOTOL(35),SHL(35), LHL(35),PHOTOE(35),PHOTOS(35),PHOTOF(35),
     2PHOTOT(35),RH(35),PHNEG(35),ADPHOL(35),ADPHOE(35),ADPHOS(35),
     3ADPHOF(35),ADPHOT(35)
      REAL LH
      REAL LHL
   20 FORMAT(1X,I2)
   21 FORMAT(11X,10F6.3/11X,10F6.3/11X,10F6.3/11X,5F6.3)
   22 FORMAT(11X,10F6.3)
   23 FORMAT(11X,11F5.1)
   24 FORMAT(11X,11F6.3)
   25 FORMAT(11X,10F5.1/11X,10F5.1/11X,10F5.1/11X,5F5.1)
   27 FORMAT(1X,13F6.1/1X,13F6.1/1X,9F6.1)
```

```
  READ(1,20)NMAX
  DO 789 K=1,14
  READ(1,21)(DF(I),I=1,NMAX)
  DO 1 I=1,NMAX
  READ(1,22)(DS(I,J),J=1,10)
1 DS(I,11)=DF(I)
  DO 2 I=1,NMAX
2 READ(1,23)(PHOTO(I,J),J=1,11)
  DO 3 I=1,NMAX
3 READ(1,24)(SH(I,J),J=1,11)
  DO 4 I=1,NMAX
4 READ(1,24)(LH(I,J),J=1,11)
  DO 5 I=1,NMAX
  PHOTOL(I)=0.
  DO 5 J=1,11
5 PHOTOL(I)=PHOTOL(I)+PHOTO(I,J)*DS(I,J)
  DO 6 I=1,NMAX
  SHL(I)=0.
  DO 6 J=1,11
6 SHL(I)=SHL(I)+SH(I,J)*DS(I,J)
  DO 7 I=1,NMAX
  LHL(I)=0.
  DO 7 J=1,11
7 LHL(I)=LHL(I)+LH(I,J)*DS(I,J)
  WRITE(2,25)(PHOTOL(I),I=1,NMAX)
  WRITE(3,25)(PHOTOL(I),I=1,NMAX)
  WRITE(2,21)(SHL(I),I=1,NMAX)
  WRITE(3,21)(SHL(I),I=1,NMAX)
  WRITE(2,21)(LHL(I),I=1,NMAX)
  WRITE(3,21)(LHL(I),I=1,NMAX)
  DO 8 I=1,NMAX
  PHOTOE(I)=0.8*PHOTOL(I)
```

```
   PHOTOS(I)=0.6*PHOTOL(I)
   PHOTOF(I)=0.4*PHOTOL(I)
 8 PHOTOT(I)=0.2*PHOTOL(I)
   WRITE(2,25)(PHOTOE(I),I=1,NMAX)
   WRITE(3,25)(PHOTOE(I),I=1,NMAX)
   WRITE(2,25)(PHOTOS(I),I=1,NMAX)
   WRITE(3,25)(PHOTOS(I),I=1,NMAX)
   WRITE(2,25)(PHOTOF(I),I=1,NMAX)
   WRITE(3,25)(PHOTOF(I),I=1,NMAX)
   WRITE(2,25)(PHOTOT(I),I=1,NMAX)
   WRITE(3,25)(PHOTOT(I),I=1,NMAX)
   READ(1,27)(RH(I),I=1,NMAX)
   DO 9 I=1,NMAX
   FACT=0.01*(100.-RH(I))/6.
 9 PHNEG(I)=FACT*PHOTOL(I)
   WRITE(3,25)(PHNEG(I),I=1,NMAX)
   DO 10 I=1,NMAX
10 ADPHOL(I)=PHOTOL(I)-PHNEG(I)
   WRITE(2,25)(ADPHOL(I),I=1,NMAX)
   WRITE(3,25)(ADPHOL(I),I=1,NMAX)
   DO 11 I=1,NMAX
11 ADPHOE(I)=PHOTOE(I)-PHNEG(I)
   WRITE(2,25)(ADPHOE(I),I=1,NMAX)
   WRITE(3,25)(ADPHOE(I),I=1,NMAX)
   DO 12 I=1,NMAX
12 ADPHOS(I)=PHOTOS(I)-PHNEG(I)
   WRITE(2,25)(ADPHOS(I),I=1,NMAX)
   WRITE(3,25)(ADPHOS(I),I=1,NMAX)
   DO 13 I=1,NMAX
13 ADPHOF(I)=PHOTOF(I)-PHNEG(I)
   WRITE(2,25)(ADPHOF(I),I=1,NMAX)
   WRITE(3,25)(ADPHOF(I),I=1,NMAX)
```

```
      DO 14 I=1,NMAX
   14 ADPHOT(I)=PHOTOT(I)-PHNEG(I)
      WRITE(2,25)(ADPHOT(I),I=1,NMAX)
      WRITE(3,25)(ADPHOT(I),I=1,NMAX)
  789 CONTINUE
      STOP
      END
```

PROGRAM XIV

```
C     THE CALCULATION OF THE MEAN PHOTOSYNTHETIC RATES (READPH(I)) OF
C     THE SEVERAL CANOPY LAYERS AS ADJUSTED FOR THE CARBON DIOXIDE
C     CONCENTRATION OF THE AIR AT THE EFFECTIVE CANOPY EXCHANGE SURFACE.
C     ALSO, THE SIMULTANEOUS CALCULATION OF THIS CO2 CONCENTRATION.
C     THE CALCULATIONS ARE MADE FOR FIVE DIFFERENT SOIL MOISTURE CON-
C     DITIONS AND FOR TIMES OF SUN INCLINATIONS IS=5, 15, ..., 65, 65,
C     ..., 15, 5 DEGREES.  HEIGHT IS THE HEIGHT OF THE CROP IN METERS,
C     V IS THE WIND SPEED AT 30 METERS EXPRESSED IN CM/SEC, AND ADPHO(I)
C     ARE THE MEAN PHOTOSYNTHETIC RATES CALCULATED BY PROGRAM XIII WHICH
C     ARE THE RESULT OF LIGHT INTENSITY, LEAF TEMPERATURE, SOIL MOISTURE
C     TENSION, AND RELATIVE HUMIDITY CONSIDERATIONS.

      DIMENSION ADPHO(35),READPH(35)
   20 FORMAT(1X,I2)
   21 FORMAT(11X,10F5.1/11X,10F5.1/11X,10F5.1/11X,5F5.1)
   22 FORMAT(1X,F4.2)
   23 FORMAT(1X,F5.1)
   24 FORMAT(1X,F4.2,1X,F4.2,1X,F6.1,1X,F6.1,1X,I2,1X,F5.1)
   25 FORMAT(1X,F5.1,1X,F6.1)
   26 FORMAT(15X,10F5.1/15X,10F5.1/15X,10F5.1/15X,5F5.1)
      READ(1,20)NMAX
      READ(1,22)HEIGHT
      DO 789 K=1,14
      READ(1,23)V
      READ(1,21)(ADPHO(I),I=1,NMAX)
      ZO=HEIGHT/7.6
      ZD=0.9*HEIGHT-ZO
      XX=(30.-ZO)/ZO
      RA=((ALOG(XX))**2)/(V*0.16)
      SNMAX=NMAX
      M=0.1*SNMAX
      FC=ADPHO(M)
```

```
      WRITE(3,24)ZO,ZD,XX,RA,M,FC
      XO=300.-FC*RA/0.48
      FC=FC-2.*(300.-XO)/100.
      WRITE(3,25)XO,FC
      X00=300.-FC*RA/0.48
      FC=FC-2.*(XO-X00)100.
      WRITE(3,25)X00,FC
      X000=300.-FC*RA/0.48
      FC=FC-2.*(X00-X000)/100.
      WRITE(3,25)X000,FC
      X0000=300.-FC*RA/0.48
      FC=FC-2.*(X000-X0000)/100.
      WRITE(3,25)X0000,FC
      X00000=300.-FC*RA/0.48
      REDUC=2.*(300.-X00000)/100.
      DO 5 I=1,NMAX
    5 READPH(I)=ADPHO(I)-REDUC
      WRITE(3,26)(READPH(I),I=1,NMAX)
      WRITE(2,26)(READPH(I),I=1,NMAX)
  789 CONTINUE
      STOP
      END
```

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Table I. The fractions of sunlit leaves of a planophile canopy and a corn crop receiving direct light within various SIN(LS) intervals at nine different sun inclinations.

IS/SIN(LS)	0.0 to 0.1	0.1 to 0.2	0.2 to 0.3	0.3 to 0.4	0.4 to 0.5
5	0.288	0.328	0.086	0.093	0.072
15	0.097	0.212	0.226	0.195	0.109
25	0.059	0.088	0.075	0.233	0.297
35	0.043	0.054	0.043	0.086	0.071
45	0.026	0.038	0.033	0.051	0.040
55	0.014	0.034	0.020	0.035	0.029
65	0.016	0.016	0.016	0.029	0.023
75	0.000	0.017	0.013	0.024	0.020
85	0.000	0.011	0.007	0.024	0.030
			Planophile Canopy		
			Corn Crop		
5	0.145	0.164	0.108	0.116	0.123
15	0.111	0.142	0.129	0.130	0.122
25	0.101	0.120	0.096	0.129	0.147
35	0.081	0.105	0.085	0.106	0.094
45	0.066	0.096	0.073	0.092	0.078
55	0.060	0.076	0.057	0.082	0.069
65	0.038	0.064	0.051	0.071	0.061
75	0.027	0.049	0.040	0.074	0.067
85	0.027	0.041	0.030	0.070	0.071

Table I. The fractions of sunlit leaves of a planophile canopy and a corn crop receiving direct light within various SIN(LS) intervals at nine different sun inclinations.

IS/SIN(LS)	0.5 to 0.6	0.6 to 0.7	0.7 to 0.8	0.8 to 0.9	0.9 to 1.0
5	0.034	0.039	0.030	0.020	0.011
15	0.040	0.047	0.035	0.023	0.016
25	0.066	0.074	0.049	0.032	0.027
35	0.311	0.210	0.085	0.051	0.044
45	0.100	0.263	0.280	0.101	0.069
55	0.059	0.099	0.251	0.335	0.123
65	0.047	0.066	0.111	0.312	0.365
75	0.043	0.058	0.079	0.146	0.600
85	0.031	0.055	0.076	0.112	0.653
			Planophile Canopy		
			Corn Crop		
5	0.076	0.089	0.078	0.061	0.039
15	0.078	0.092	0.081	0.061	0.053
25	0.083	0.093	0.085	0.074	0.072
35	0.128	0.113	0.096	0.091	0.100
45	0.097	0.125	0.134	0.114	0.125
55	0.093	0.108	0.139	0.166	0.150
65	0.099	0.113	0.132	0.172	0.199
75	0.091	0.122	0.137	0.151	0.243
85	0.097	0.122	0.137	0.158	0.248

Table II. The relative contribution to the illuminance of a horizontal surface of 10 degree zones from a sky of uniform brightness. From de Wit (1965).

Inclination (degrees)	0	10	20	30	40	50	60	70	80	90
Rel. Contrib.	0.030	0.087	0.133	0.163	0.174	0.163	0.133	0.087	0.030	

Table III. Diffuse skylight and direct solar radiation, in cal/cm^2/min, as reconstructed for Aug. 1, 1961, at Ithaca, New York, from data due to Wright and Lemon (1966b), Allen, Yocum, and Lemon (1964), and Threlkeld (1962) at times of the sun inclinations IS=5, 15, ..., 65 degrees.

IS	5	15	25	35	45	55	65
Diffuse Skylight	0.000	0.027	0.056	0.082	0.109	0.122	0.150
Direct Solar Rad.	0.000	0.200	0.420	0.620	0.820	0.920	0.130

Table VI. The CO_2 concentrations at the effective canopy exchange surface in ppm at times of the sun inclinations IS=15, 25, ..., 65, 65, ..., 25, 15 degrees for cases of crop photosynthesis occurring at soil moisture tensions of 0.35, 0.70, 1.05, 1.40 and 1.75 atmospheres.

IS/TSMT	0.35	0.70	1.05	1.40	1.75
15	282.9	286.4	289.9	293.4	296.9
25	272.4	278.0	283.6	289.5	295.1
35	258.0	266.8	275.5	283.9	292.7
45	259.1	267.8	276.2	285.3	293.7
55	259.1	267.8	276.6	285.7	294.1
65	263.3	271.3	279.0	287.1	295.1
65	266.4	273.4	281.1	288.5	295.5
55	261.5	269.9	278.0	286.7	295.1
45	262.2	270.6	278.7	286.7	294.8
35	264.7	272.4	280.1	287.8	295.1
25	260.5	268.9	276.9	285.3	293.7
15	264.0	271.0	278.3	285.7	293.0

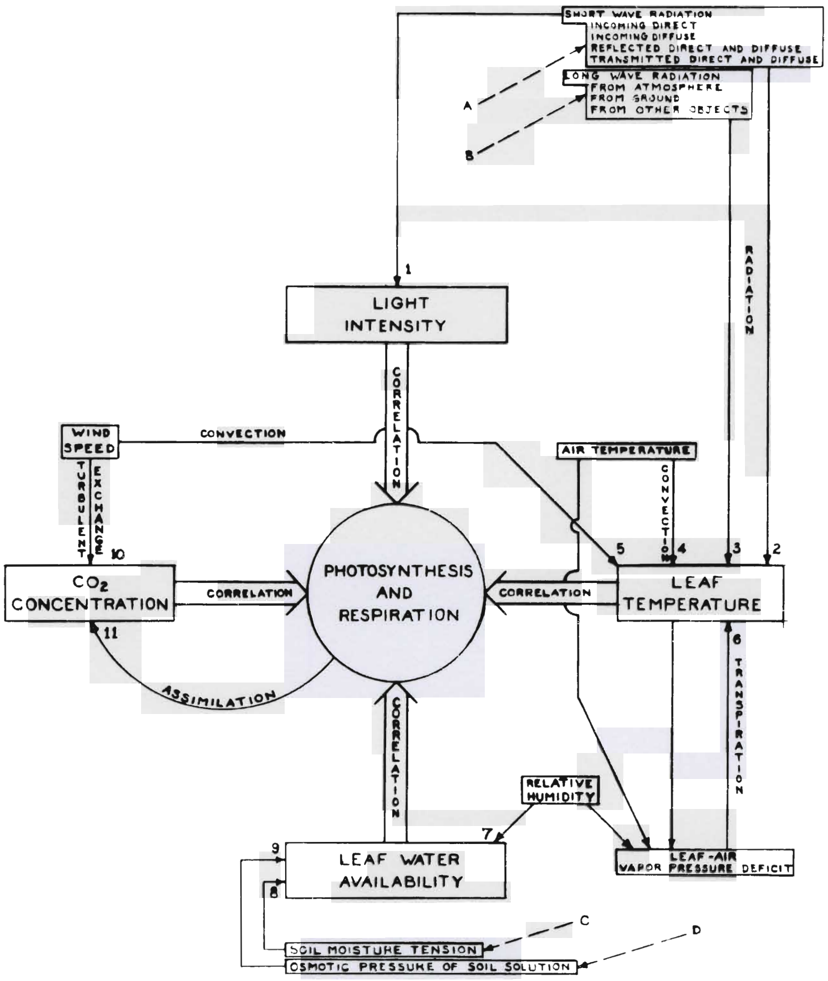

Figure 1. Diagramatic representation of the interrelationships among various environmental parameters and the channeling of their effects into the net photosynthetic process through the four basic factors; light intensity, leaf temperature, leaf water availability, and carbon dioxide concentration.

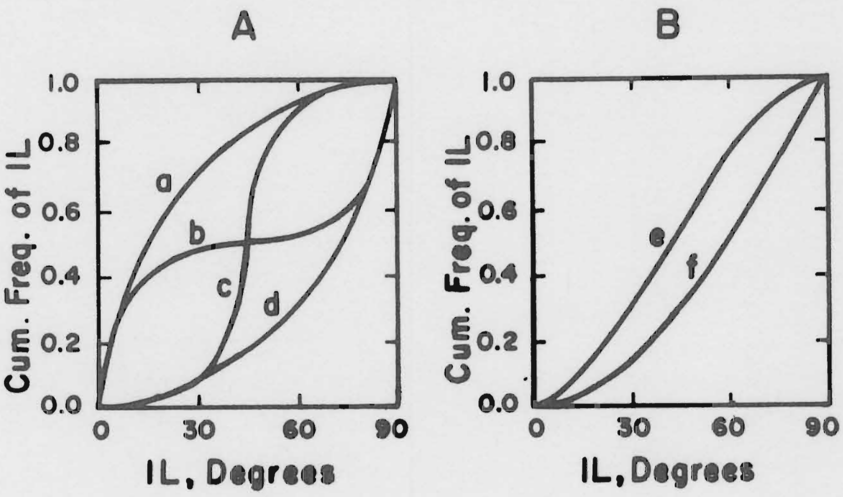

Figure 2. A. The four types of leaf distribution functions:

a. Planophile b. Extremeophile c. Plagiophile

d. Erectophile.

B. Two special leaf distribution functions:

e. Corn canopy (measured) f. Spherical.

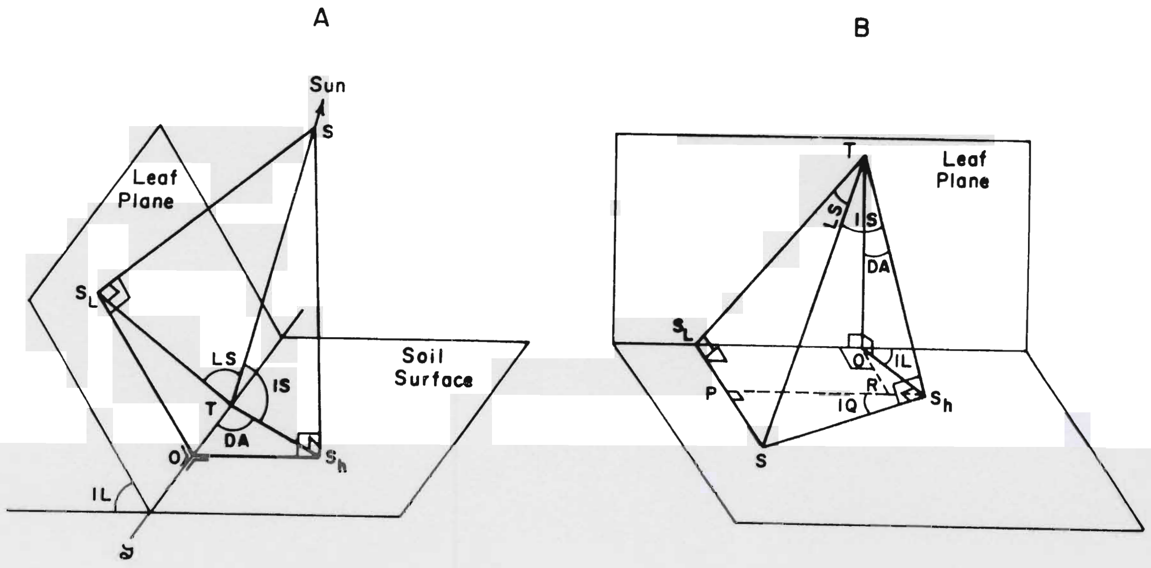

Figure 3. Geometrical representations of the relations between a leaf plane, the soil surface, and a ray of the sun. Part A from de Wit (1965).

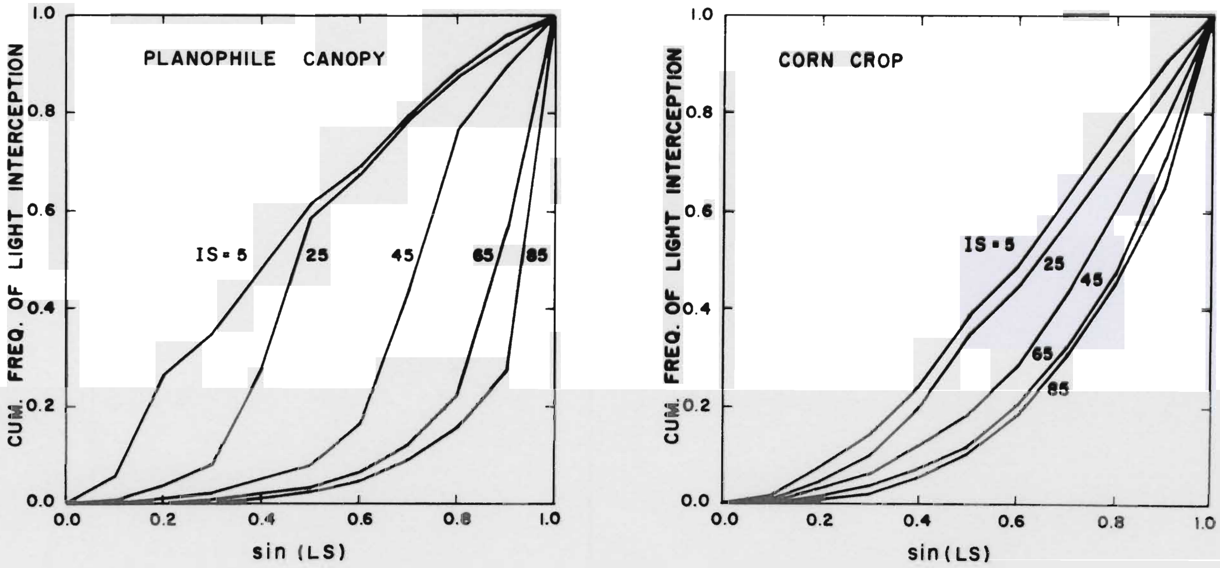

Figure 4. Crop light distribution functions for a planophile canopy and a corn crop for inclinations of the sun (IS) of 5, 25, 45, 65, 85 degrees.

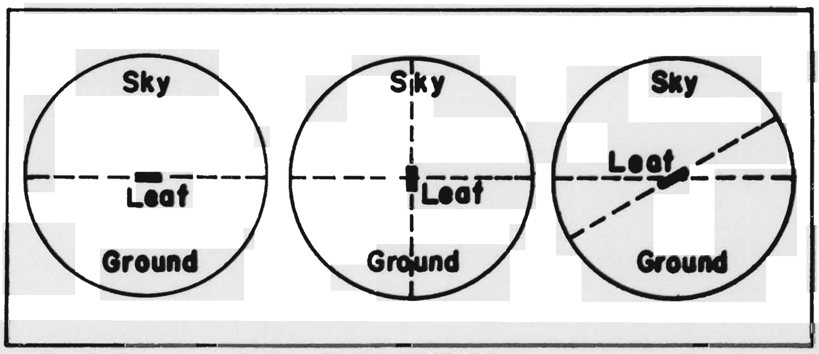

Figure 5. The upper and lower hemispheric views of a leaf at three different leaf inclinations.

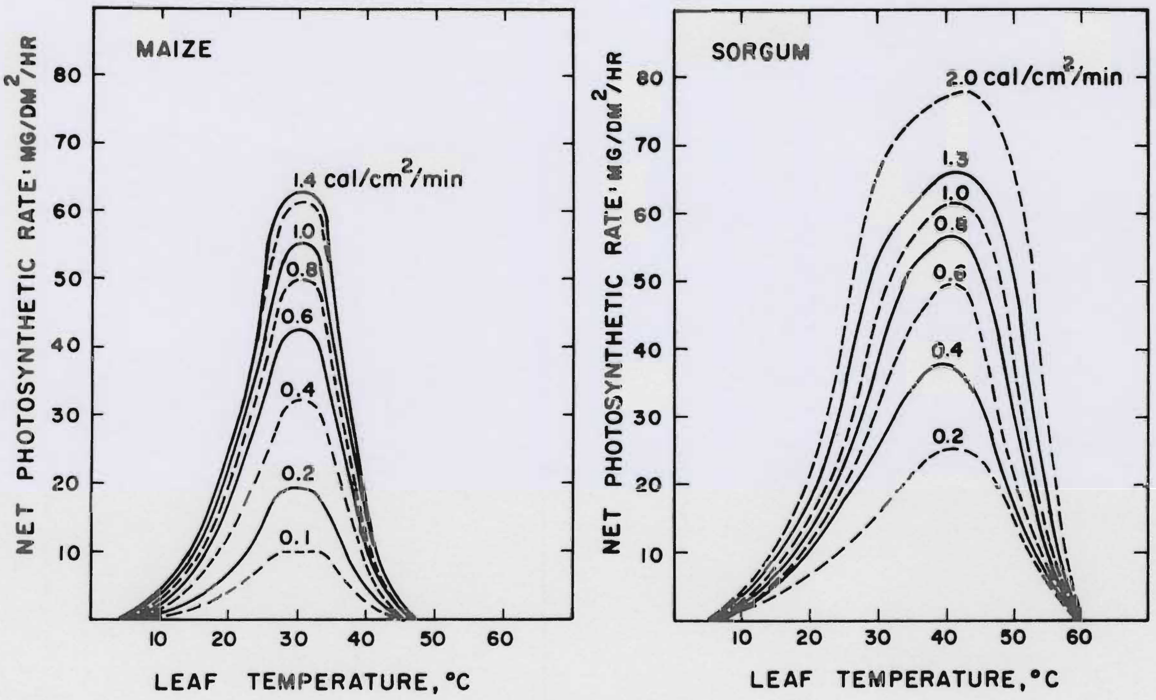

Figure 6. Net photosynthesis in maize and sorghum as a function of light intensity and leaf temperature. After Gates (1965) and Idso (1966).

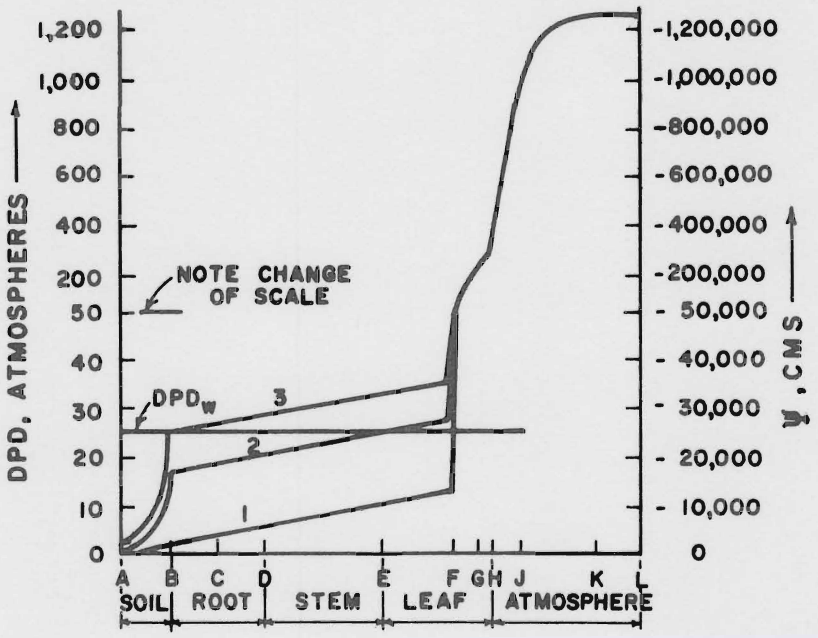

Figure 7. The soil-plant-atmosphere continuum (SPAC), showing energy profiles; (1) during normal transpiration; (2) during temporary wilting; (3) at permanent wilting. Points on the transpiration path: A. Soil (a definite distance from plant root); B. Surface of root hairs and of absorbing epidermal cells; C. Cortex; D. Endodermis; DE. Vessels and tracheids in xylem; E. Leaf veins; F. Mesophyll cells; FG. Intercellular space and substomatal cavity; GH. Stomatal pore; HJ. Laminar sub-layer; JK. Turbulent boundary layer; KL. Free atmosphere. After Philip (1957).

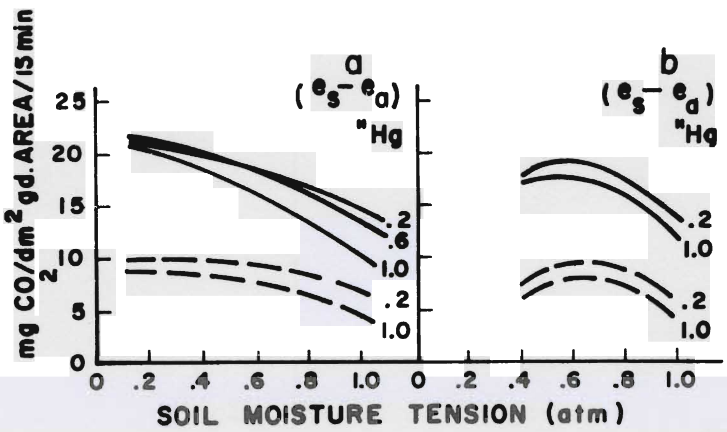

Figure 8. Apparent photosynthesis vs. soil moisture tension at several vapor pressure deficits and two light intensities. a = first setup; b = second setup. Solid lines, 20 ly/15 min; dashed lines, 8 ly/15 min. From Baker and Musgrave (1964).

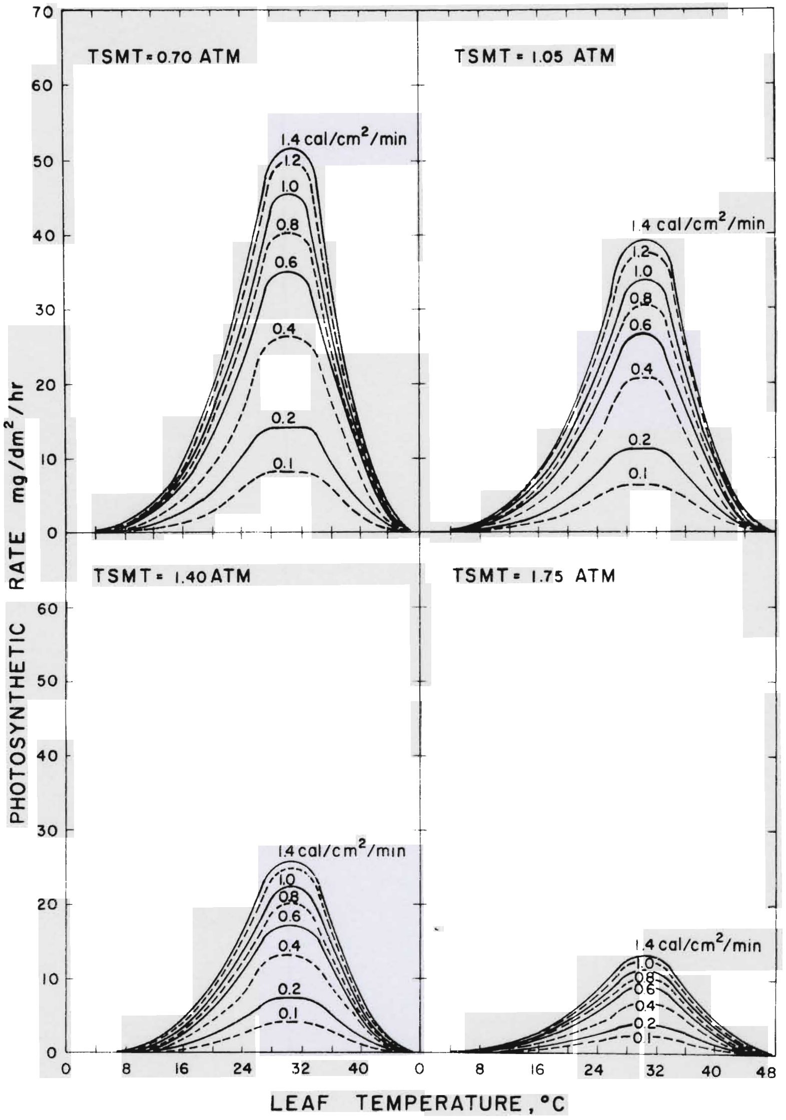

Figure 9. Photosynthesis in maize as a function of light intensity, leaf temperature, and total soil moisture tension (TSMT).

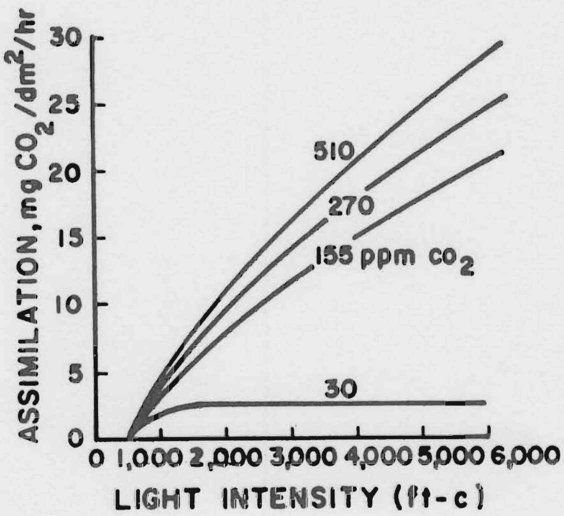

Figure 10. Apparent photosynthesis in corn plants as a function of light intensity of four CO_2 concentrations. From Moss, Musgrave, and Lemon (1961).

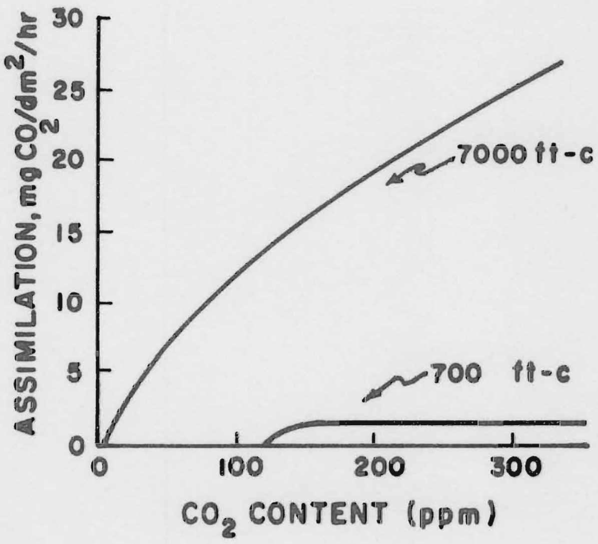

Figure 11. Apparent photosynthesis in corn plants as a function of CO$_2$ concentration at two light levels. From Moss, Musgrave, and Lemon (1961).

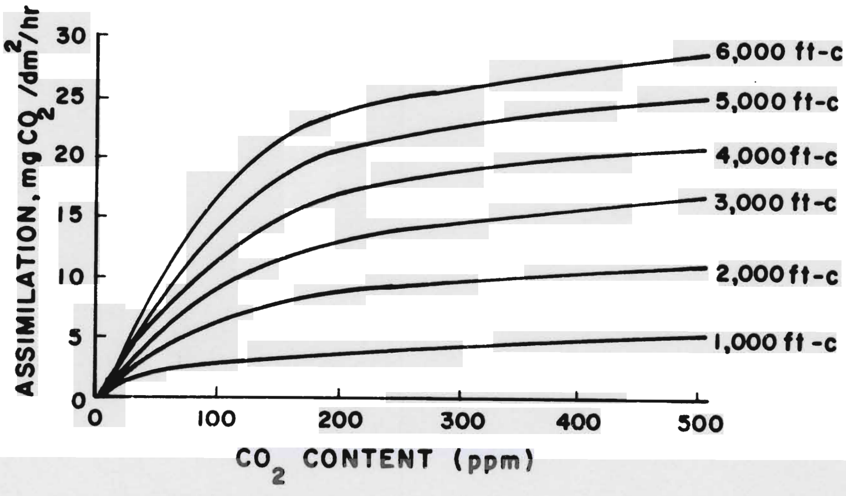

Figure 12. Apparent photosynthesis in corn plants as a function of CO_2 concentration at six light levels. Adapted from our Fig. 10 from Moss, Musgrave, and Lemon (1961).

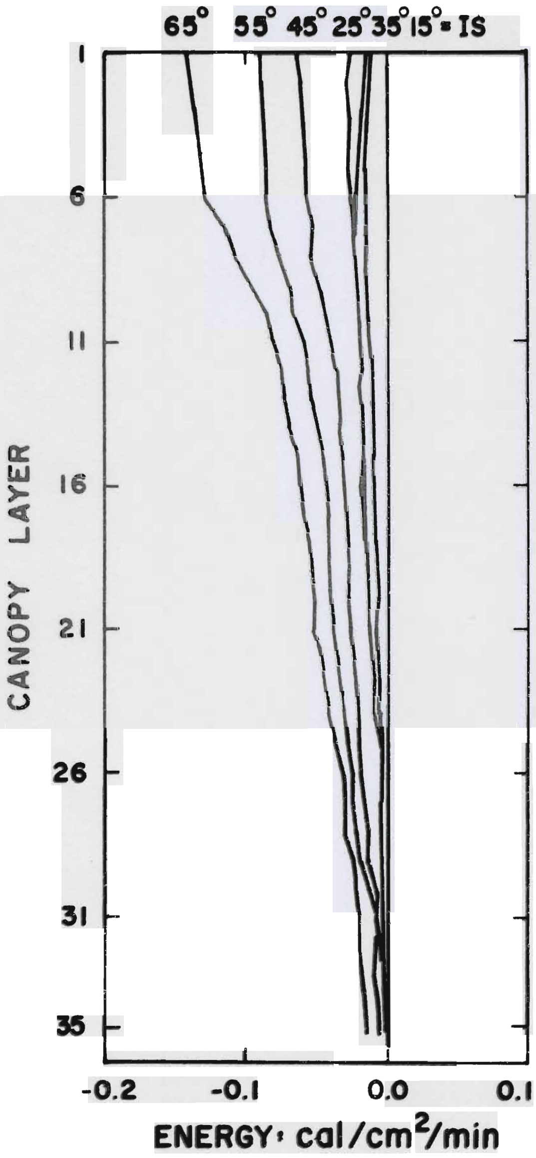

Figure 13. The forenoon canopy profiles of mean sensible heat transfer.

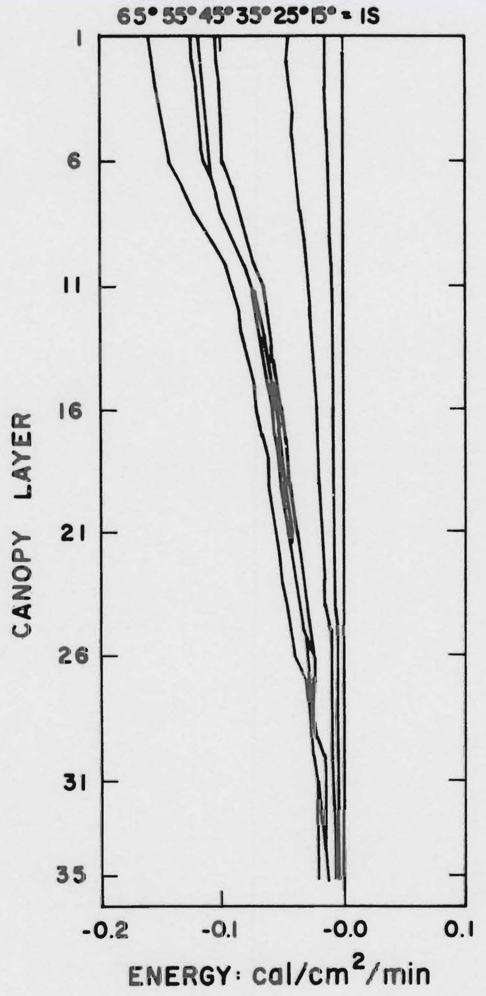

Figure 14. The afternoon canopy profiles of mean sensible heat transfer.

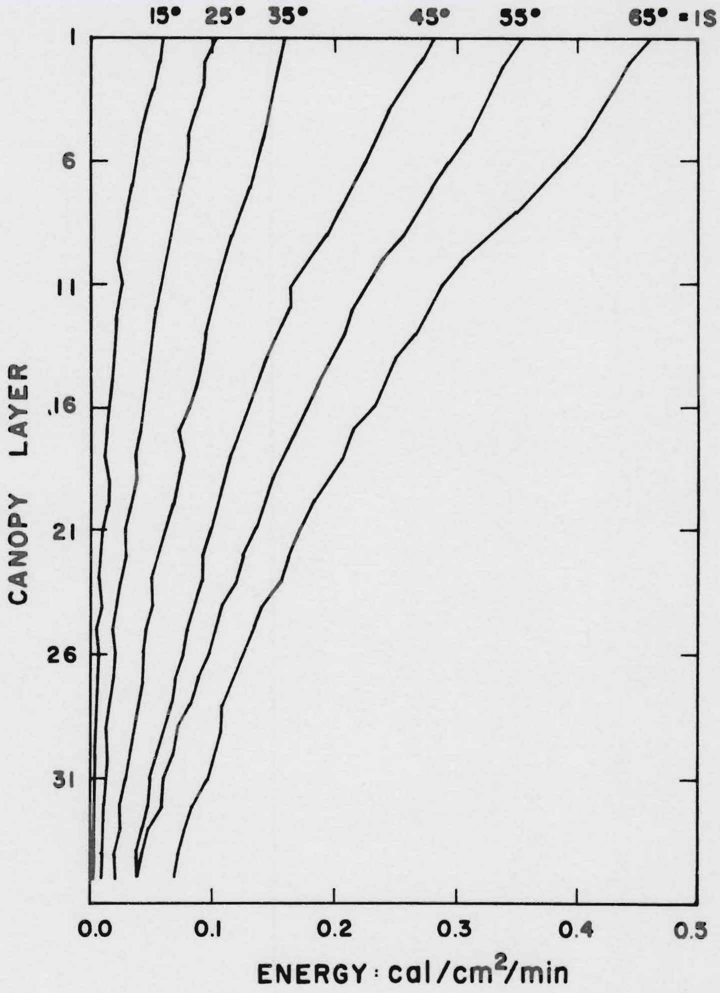

Figure 15. The forenoon canopy profiles of mean latent heat transfer.

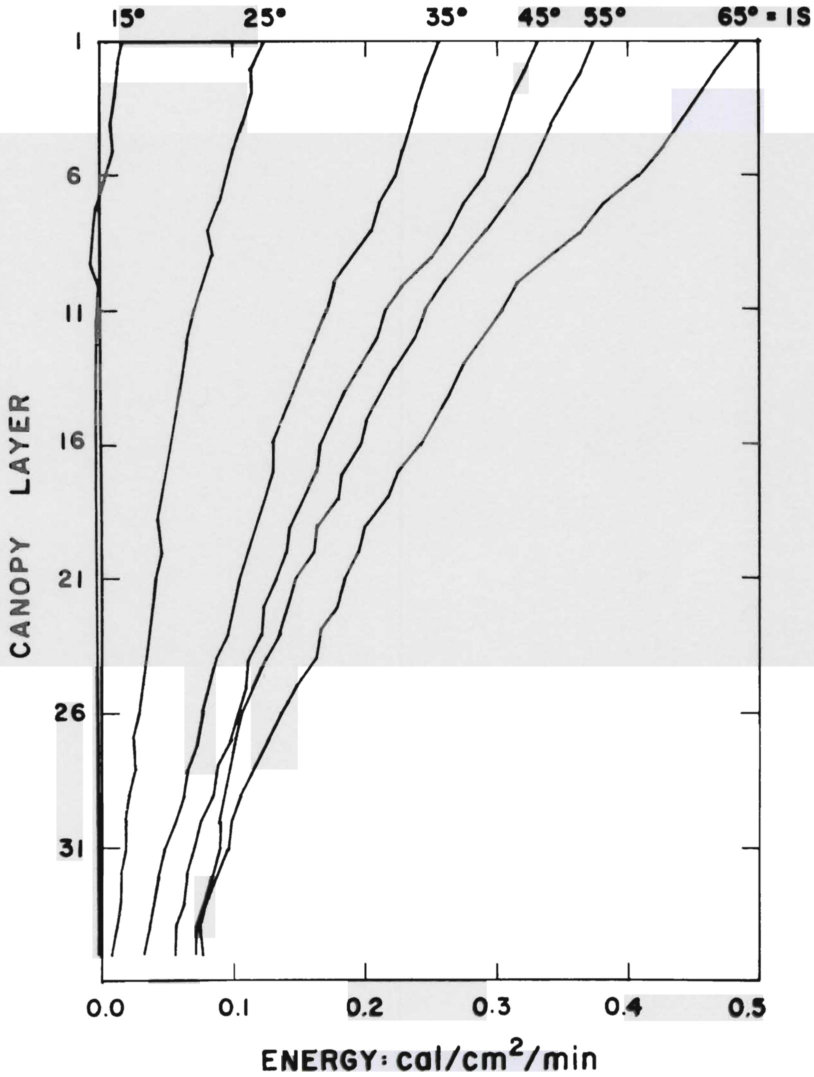

Figure 16. The afternoon canopy profiles of mean latent heat transfer.

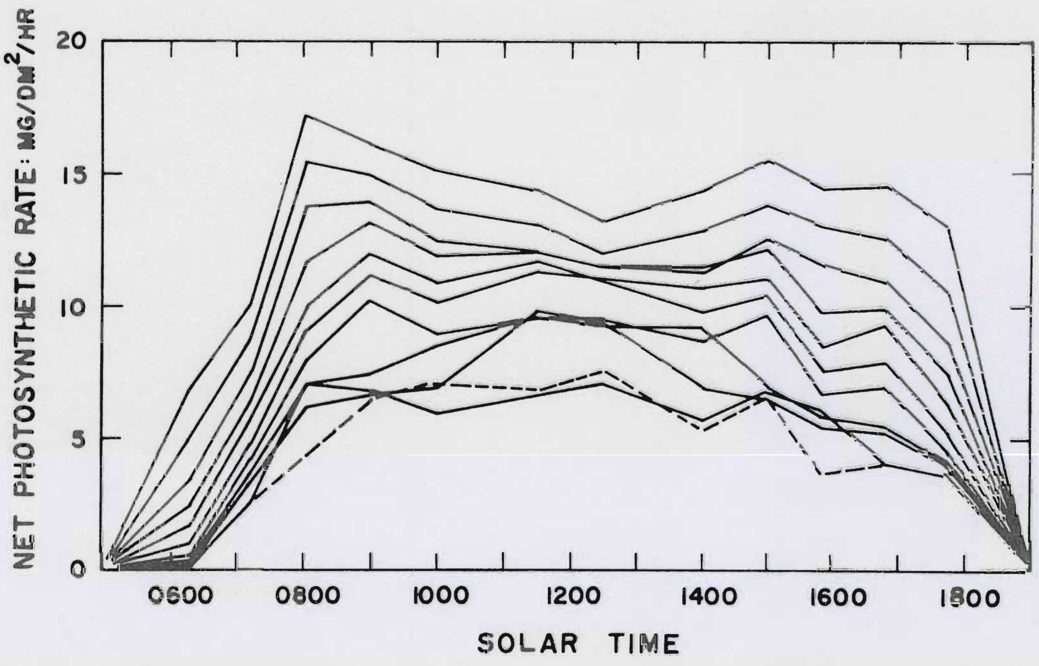

Figure 17. The net photosynthesis rates of canopy layers 1 (uppermost), 3, 5, 7, 9, 12, 15, 21, 25, 31, and 35 (slashed) for our illustrative corn crop growing under conditions of minimal soil moisture stress (0.35 atmosphere).

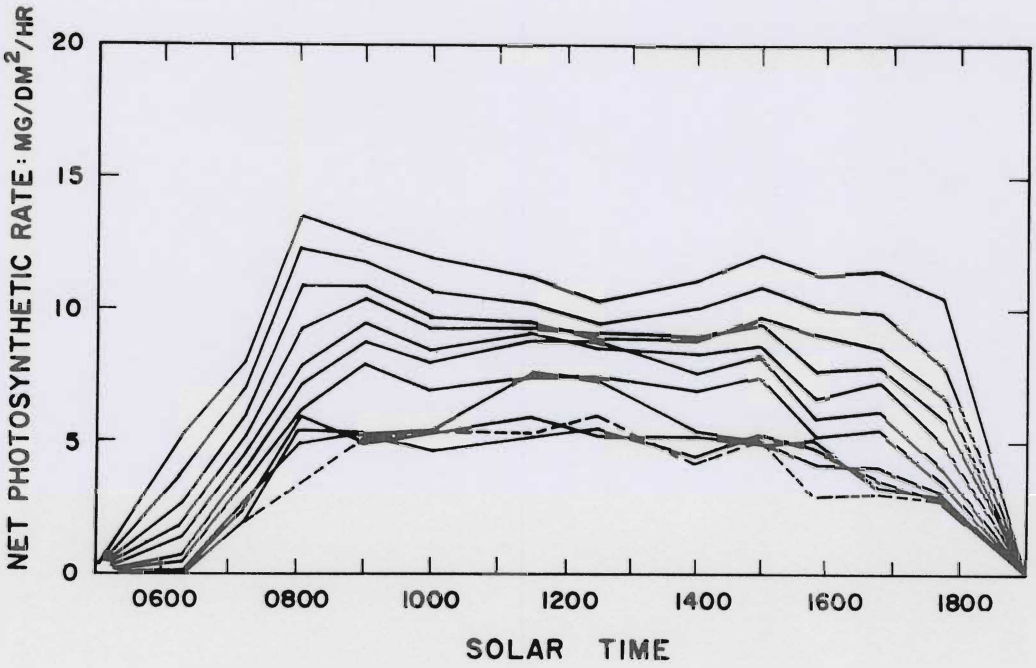

Figure 18. The net photosynthetic rates of canopy layers 1 (uppermost), 3, 5, 7, 9, 12, 15, 21, 25, 31, and 35 (slahsed) for our illustrative corn crop growing under a soil moisture stress of 0.70 atmosphere.

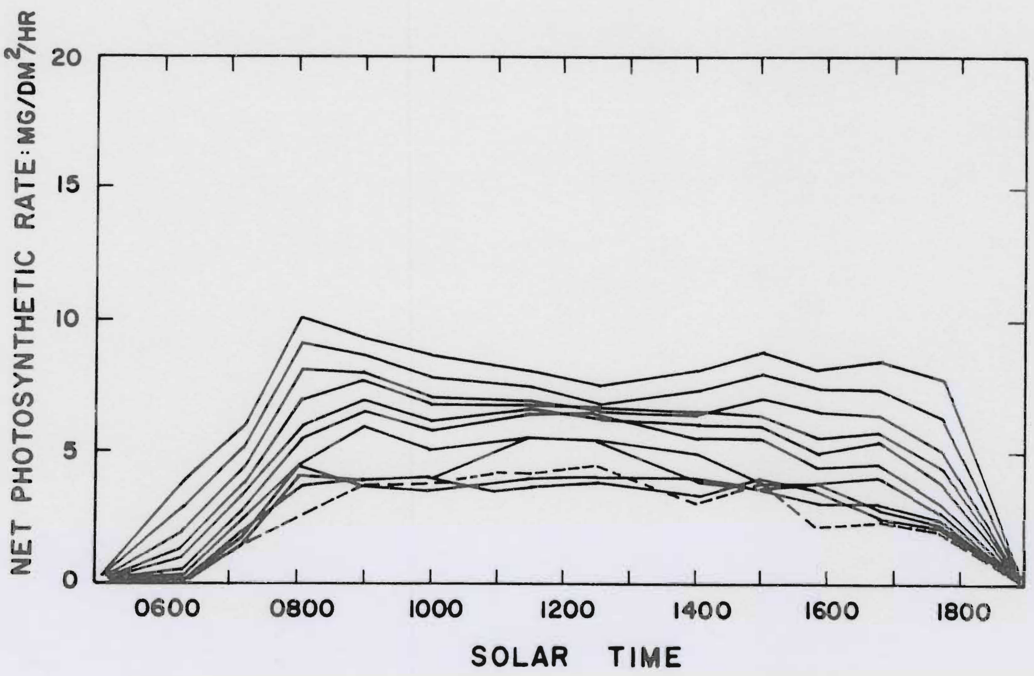

Figure 19. The net photosynthetic rates of canopy layers 1 (uppermost), 3, 5, 7, 9, 12, 15, 21, 25, 31, and 35 (slashed) for our illustrative corn crop growing under a soil moisture stress of 1.05 atmospheres.

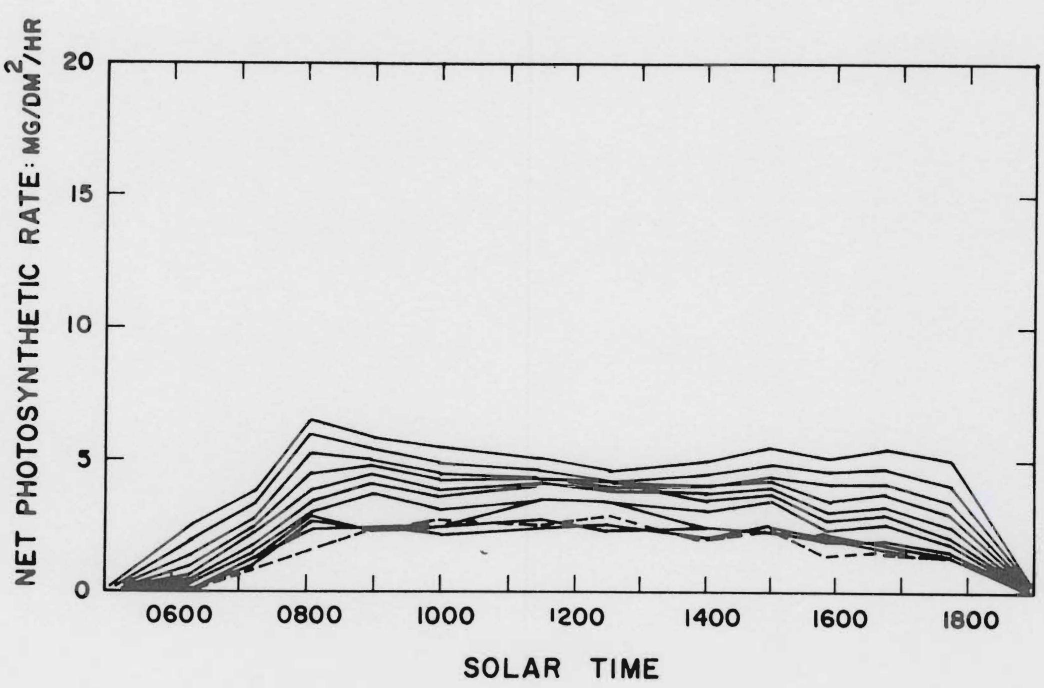

Figure 20. The net photosynthetic rates of canopy layers 1 (uppermost), 3, 5, 7, 9, 12, 15, 21, 25, 31, and 35 (slashed) for our illustrative corn crop growing under a soil moisture stress of 1.40 atmospheres.

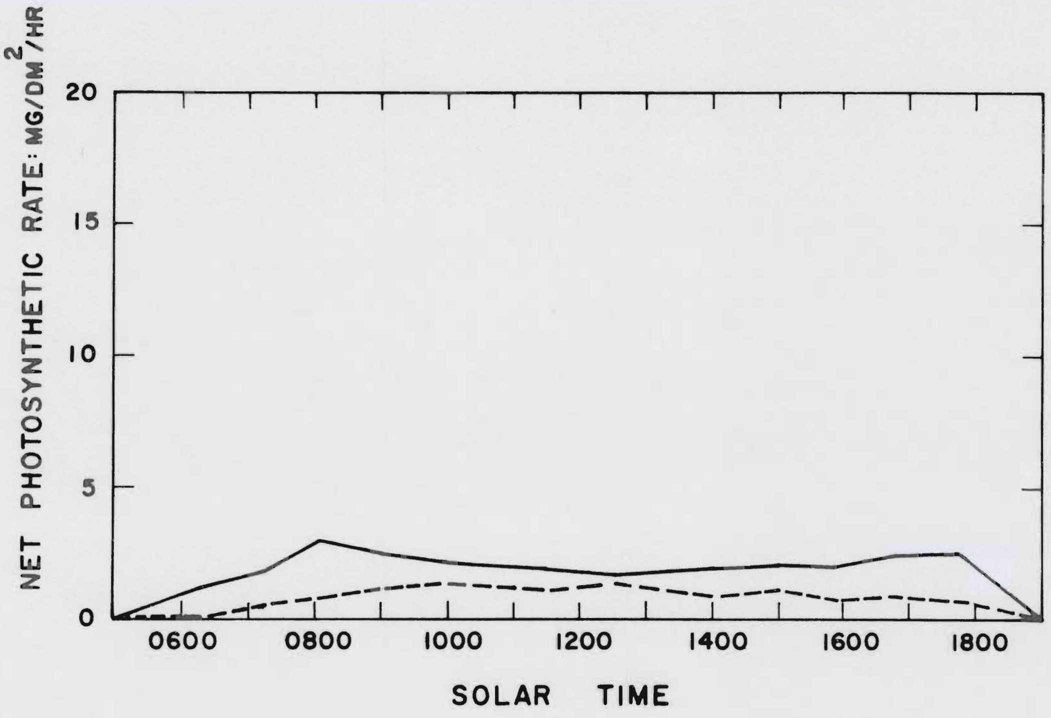

Figure 21. The net photosynthetic rates of canopy layers 1 (uppermost) and 35 (slashed) for our illustrative corn crop growing under a soil moisture stress of 1.75 atmospheres.

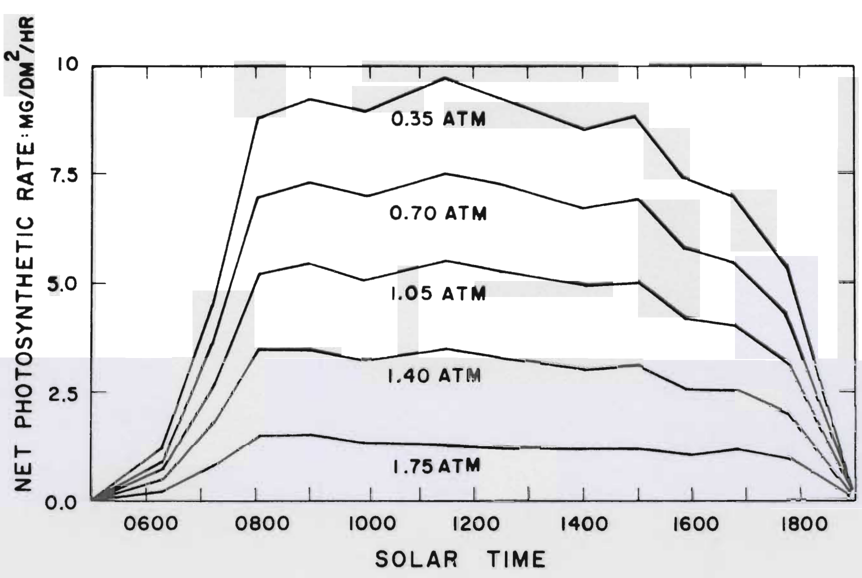

Figure 22. The mean net photosynthetic rates of the entire canopy under various conditions of soil moisture stress.

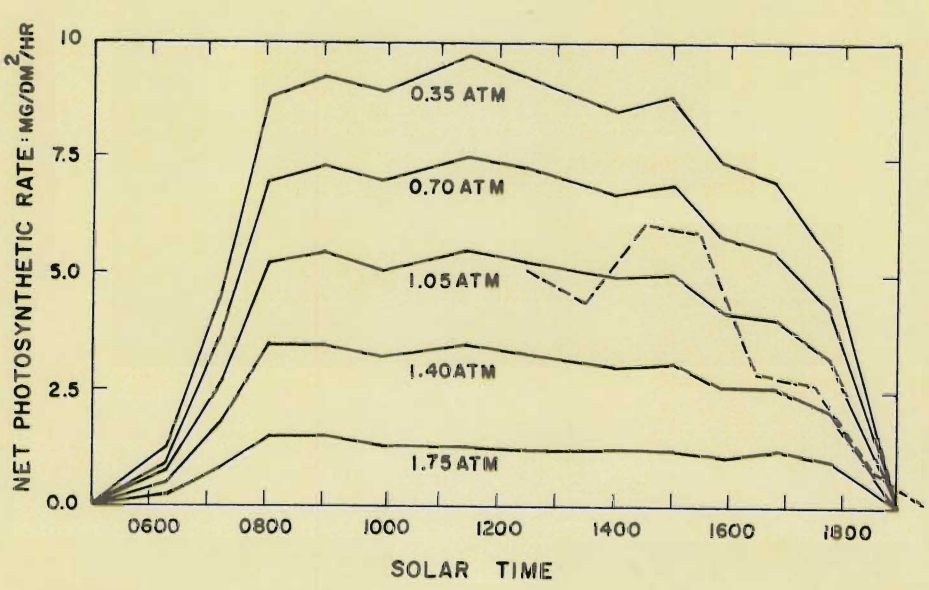

Figure 23. The mean net photosynthetic rates of the entire canopy under various conditions of soil moisture stress. The dotted line is the measured result of Wright and Lemon (1966b) reduced by a factor of 3.