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AN APPROACH FOR A PHOTOSYNTHESIS MODEL OF DESERT PLANTS

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INTRODUCTION

A number of approach efforts have been made to develop mathematical models to compute the net fixation of CO_2 by plants from meteorological parameters and to predict their productivity (e.g., DeWitt, 1965; Cunningham and Balding, 1972; Brittain, 1974; De Puit, 1973). One basic requirement for the realization of such models is a detailed knowledge of the functional relationships between the photosynthetic efficiency of a plant and the external conditions characteristic to its particular habitat. Special attention must be paid to the responses of the different morphological types, considering the variability of their physiological state and their capacity for regulative adaptations (Mooney and Shropshire, 1968; Bjorkman, 1968). With the more sophisticated models which have been proposed recently, large gaps in our knowledge about the influence of important internal and external factors on the CO_2 exchange of plants have become apparent (Lommen et al., 1971; Hall, 1971). Therefore, during our work on productivity of desert plants and the development of a model on net photosynthesis under desert conditions, we focused our interest on a functional analysis of the photosynthetic responses of the plants in their natural habitat.

The photosynthesis modeling committee of the Desert Biome recommended during its meeting (July 30, 1973), that emphasis should be given to an empirical model which is based on data which can be taken in the field and on data which are already present at this time. Consequently the following model follows the approach of Cunningham and Balding (1972) and Brittain (1974). The main stress was laid upon derivation of the input functions for the photosynthesis submodel from actual field data. Because of the short time period available for this work, *Hammada scoparia* was chosen as the test plant. We had access to a considerable amount of information on this species from previous work.* However, all programs were made so general that they can also be used for any other test plant.

THE MODEL

The model should calculate rates of net photosynthesis (NP) taking the meteorological factors, light (L), temperature (TEMP), water vapor concentration difference between leaf and air (WD), the water stress in the plant (WS), and the phenological stage of leaf development (DAY) into account as input variables. The changes in the photosynthetically active organs of the plants with time (aging, phenology) have to be defined separately by the phenology and translocation submodel. The water stress in the plant is handled as an independent input variable until it is possible to connect this value to the soil and atmospheric conditions. Whenever possible, water stress is handled as a time function connected to the phenological stage of the plant.

The general form of the model is:

$$NP = (NPMAX)*F(L, TEMP, WD, WS, DAY)$$

The maximal rate of net photosynthesis (NPMAX) is defined to be the rate of CO_2 uptake at light saturation, optimal temperature and humidity conditions but at the water stress and phenological condition typical for the time of the year.

The effect of the different environmental factors F (L,TEMP,WD,WS,DAY) is scaled from 0-1. In the first approach the different factors are connected multiplicatively. It is subject to further sensitivity analysis and empirical tests to show if other and different connections of these factors will be more useful for prediction of gas exchange under certain conditions.

The light factor (FL) determines the increase on NP with increasing light intensity from 0 to 120 Klux. This increase is due to stomatal opening as well as to increasing rate of biochemical CO_2 uptake.

The temperature factor (FT) describes the optimum curve of NP at light saturation and optimal air humidity. This temperature factor also includes a stomatal and a biochemical effect.

The effect of the water vapor difference between the leaf and the air on CO_2 uptake (FW) works through stomatal reaction.

The water stress factor (FS) reduces NP through stomatal closure and also through an effect on mesophyll resistance.

All these processes change with time, aging and phenology. Therefore, they are expressed as a function of DAY.

A general flow diagram of the photosynthesis model is drawn in Figure 1. The model should finally operate on two different possible levels of resolution: (1) the greatest

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*The field experiments were carried out in Avdat, Israel, 1971, by U. Buschbom, M. Evenari, L. Kappen, O. L. Lange, and E. D. Schultze. The methods used are described by Koch, Lange and Schultze (1971), Schultze, Lange and Lembke (1972) and Schultze (1972).
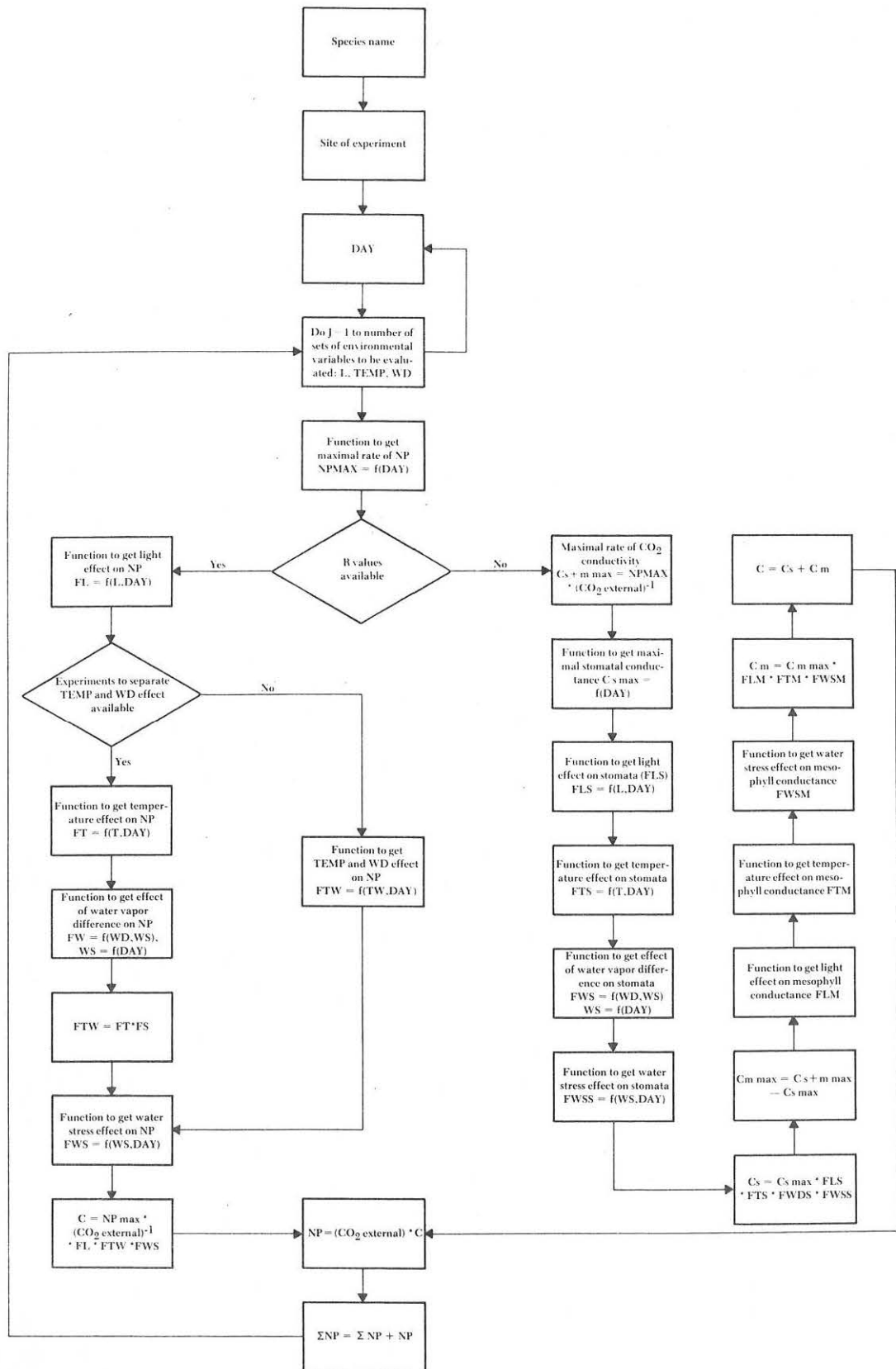
Figure 1. Flow diagram of the photosynthesis model.

refinement of the effect of environmental factors is obtained by separating the effects on stomatal and mesophyll resistance; (2) another level of refinement is obtained by calculating the influence of the environment on the gas exchange process as a whole. In the second case TEMP and WD can be handled separately or as a combined environmental stress factor. The decision as to which pathway is taken for a given species at a given site depends on the experimental data available. As long as mesophyll and stomatal resistance are not being measured separately, the accuracy of the predicted result is the same in both levels of resolution.

Since not all information on stomatal and mesophyll resistance can be worked up in the time available, most emphasis was placed on finding a mathematical resolution for the second level of refinement, taking TEMP and WD into account separately.

THE FUNCTION (FT) OF THE EFFECT OF TEMPERATURE ON NP

THE TEMPERATURE RESPONSE OF NET PHOTOSYNTHESIS

Input-Experiments measuring rates of CO_2 uptake at light saturation and at a high air humidity (WD almost 0) at varying temperatures during different times of the year.

Figure 2 shows a temperature response curve of net photosynthesis for *H. scoparia* in spring (March 28). Temperature optimum is at 28.6 C, the upper compensation point is at 46.3 C. The experimental data are not complete for a range of temperatures below the optimum of CO_2 uptake to the lower compensation point. This is because of the experimental difficulty of lowering temperatures in a cuvette in the field under desert conditions and in full sunlight to below the ambient air temperature. An important fact is that the temperature dependence of NP does not remain constant but changes throughout the year.
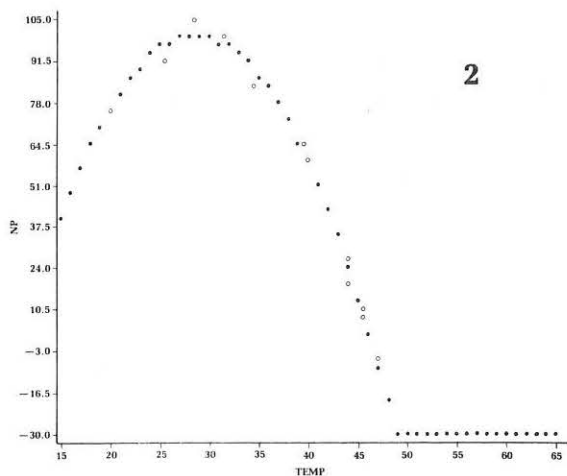
This is demonstrated in Figure 3. It shows the same kind of response curve for July 19. The temperature optimum shifted up 10.7 C to 39.3 C. At the same time the upper compensation point shifted up 12.1 C to 58.4 C. Later in the season the temperature dependence of NP shifted back again to a range of lower temperatures (Fig. 4, September 22). The temperature optimum is at 30.5 C and the upper compensation point is 50.8 C. Maximal shift in the temperature optimum during the year was 13.6 C, taking the lowest spring value as a basis.

Figures 2-4 show that it is probably necessary for a model of NP to take the shift of the temperature curve into account as an adaptive feature of the plant to its environment. If all the experimental data of the year are plotted together to obtain a general temperature response curve for this species (without taking the shift in the temperature optimum and the temperature compensation point into account) and if these data points are fitted by a polynomial equation, the resulting R^2 is .70. This further suggests that the data of temperature-dependent NP are distributed on the temperature axis with enough scatter so that the application of a general temperature function for that species and that year is not useful.
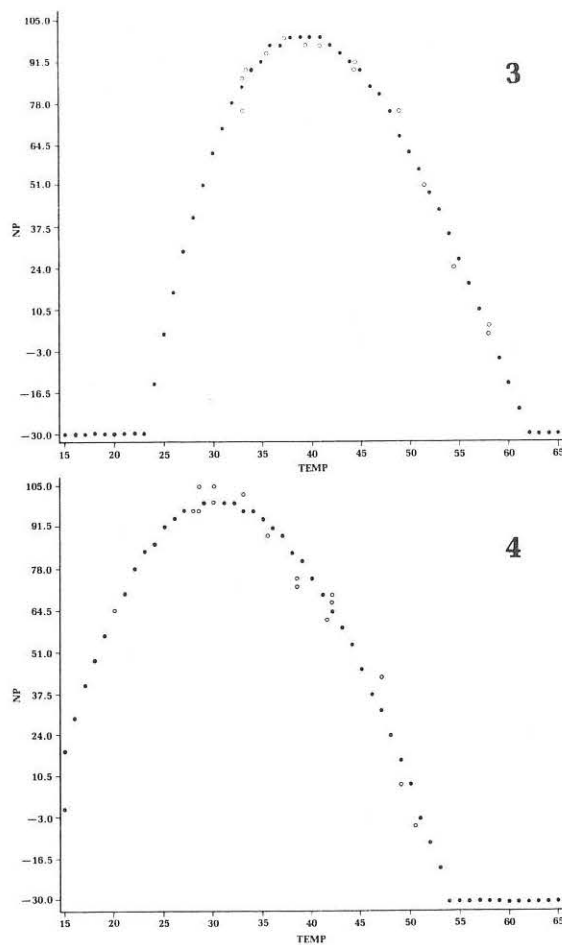
Figures 2, 3 and 4. Percent photosynthesis (NP) of *H. scoparia* (unwatered) as related to leaf temperature (TEMP) on March 28, 1971 (Fig. 2), July 19, 1971 (Fig. 3) and September 22, 1971 (Fig. 4). Fitted curve based on a polynomial equation (•); points of measurement (○). Optimum of the polynomial curve is 100%.

The Procedure to Calculate the Temperature Response of NP

It would be most desirable to apply a type of mathematical function which represents the process involved (Cunningham and Balding, 1972). The curve should show a variable optimum which originates from low temperatures assymptotically (dNP/dT, very small) and which drops to negative rates of gas exchange at high temperatures. Such a temperature function would provide the opportunity to extrapolate to a certain degree beyond the limits of experimental data, which would be advantageous for any predicting purpose. In this work we did not succeed in finding and applying a suitable non-polynomial function to the process of temperature-dependent net photosynthesis. Only polynomial equations were used, leaving this problem open for furt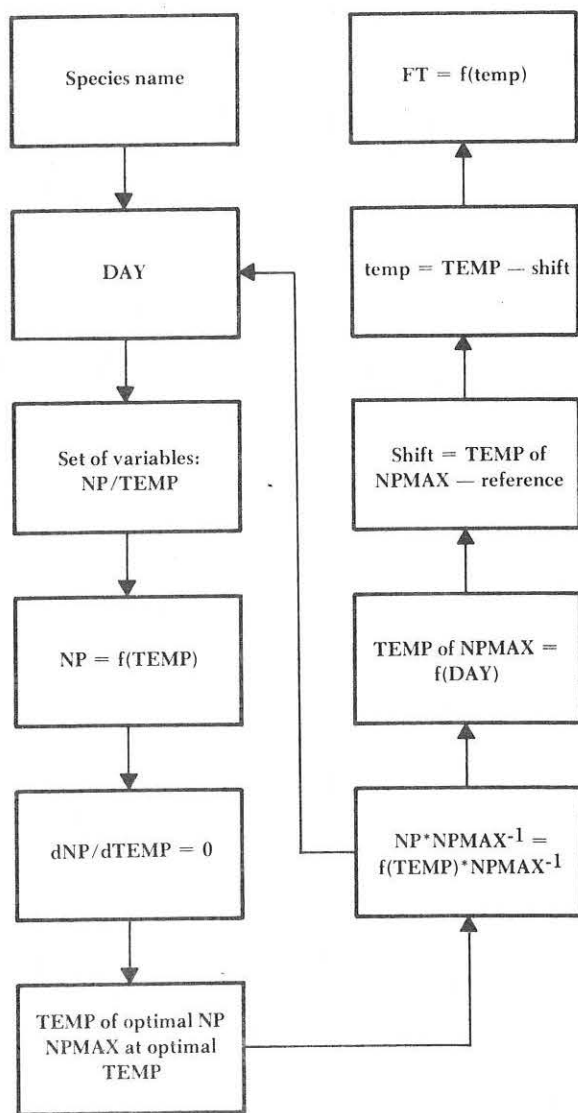her photosynthesis modeling work. In applying polynomial equations, it is essentially necessary to plot the function with the data points. This is because at a high R^2 the least square fit might not represent the biological process one wants to simulate and predict.

Figure 5 shows the flow diagram of the procedure to calculate the temperature response of NP used in the model:

1. Each set of data of one temperature experiment on a certain DAY is fitted with a third-degree polynomial (for 13 different temperature experiments, each having 8 to 16 measurements of temperature-dependent NP, the R^2 of the curve fit is .92 to .99).

2. The temperature optimum of each curve is the point at which the first derivative is zero. An iteration program determines the upper compensation point of NP.

3. Each parameter of the polynomial equations is divided by the maximal rate of NP at optimum temperature, so that the curves are scaled from 0 to 1.

4. The temperature of optimum NP versus time of year is fitted with a polynomial equation ($R^2 = .65$). This curve is shown in Figure 6.

5. Each value of temperature-dependent NP is shifted along the temperature axis to such a degree that all the optima of NP are the same and equal to the lowest temperature optimum as a reference (28.5).

6. One three-degree polynomial equation is fitted through all the shifted experimental data (for *H. scoparia*, R^2 of this equation is .86). Although this equation gives a high R^2, it was forced through some set-points to represent a biologically meaningful curve of predictive value. A four-degree polynomial equation should be considered instead. Figure 7 shows the measured values of the different temperature experiments being shifted to a common reference point and a polynomial equation fitted to these data. From the R^2 values of the curve fit, including the shift of the temperature curves compared to the R^2 before the shift, it is obvious that the shift of the temperature curves is significant. From Figure 7 it is obvious that the shape of the temperature response curve in the range from 10 C below the NP-optimum to the upper compensation point changes only to a small degree so that the temperature response is characterized with sufficient accuracy by a general equation and by the shift of the optimum. Major deviations from this general function will occur at temperatures of more than 15 C below the optimum, since the slope throughout this part of the curve will change with the value of the optimum. This deviation will be smallest if the temperature curves are not shifted to the lowest optimum as reference but to an average value of optimal temperature. For the purpose of this model, the range of temperature-dependent NP from 10 C below the optimum down to the lower compensation point was extrapolated linearly to a rate of NP of 0 at -5 C.
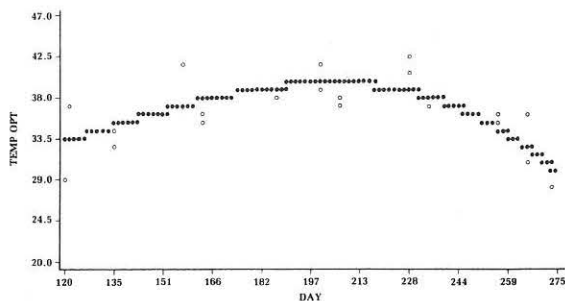

Figure 5. Flow diagram of the procedure to calculate the temperature effect on NP.

Figure 6. Change of the temperature optimum of net photosynthesis (TEMP OPT) with the time of year (DAY) for *H. scoparia* (unwatered).
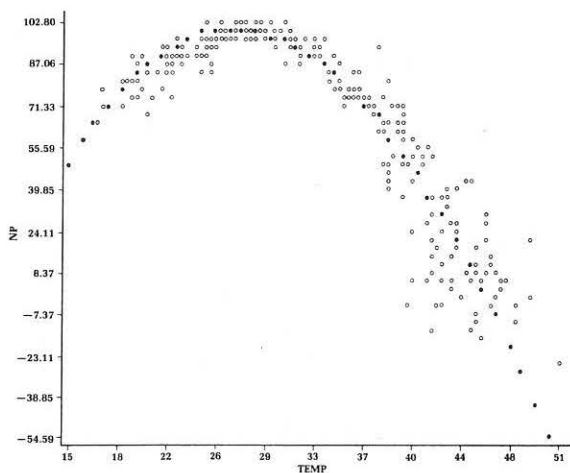

Figure 7. The measured values of percent net photosynthesis (NP) being shifted on the temperature axis to such a degree that all the optima of the single temperature curves of NP are the same and equal to the lowest temperature optimum as a reference as related to leaf temperature (TEMP) for *H. scoparia* (unwatered). Fitted curve based on a polynomial equation (●); points of measurement (○). Optimum of the polynomial curve is 100 %.

THE FUNCTION TO OBTAIN THE EFFECT OF TEMPERATURE ON NP (FT) IN THE MODEL

```
MOD1:
  PROC OPTIONS(MAIN);
  ON ENDFILE(SYSIN) STOP;
TOP:
  GET LIST(DAY,TEMP);
  TEMPOPT=34+22297*DAY*(-0.2169415*DAY*(0.002518485*DAY*0.000006494));
  PUT SKIP DATA(TEMPOPT);
  SHIFT=TEMPOPT - 27.34;
  TEMPIT=TEMP - SHIFT;
  IF TEMPIT > 19.0 THEN
    FACTOR=-161.6137*TEMPIT*(20.1694*TEMPIT*(-0.426328*TEMPIT*0.0014117));
  ELSE
    FACTOR=4.08*TEMPIT;
  TEMPFACTOR=FACTOR/100;
  PUT SKIP DATA(DAY,TEMP,TEMPFACTOR,SHIFT);
  GO TO TOP;
END MOD1;
```

The change of the temperature optimum during the seasons was observed not only on *H. scoparia* but also on several other plant species (Lange et al., in preparation). It

was observed on watered and non-watered plants of the same species. Figures 6 and 7 contain the values of watered and non-watered plants. It is obvious that there is no difference in temperature response due to water stress (for *H. scoparia* to a range of -86 bars). Furthermore, the watered plant was growing and producing new photosynthesizing organs throughout the year, which means that the change in the temperature optimum is not connected with a certain phenological stage. This response is probably an adaptive mechanism to the temperature, climate and the photoperiod of the habitat. This response, therefore, needs to be correlated to the EXOGEN submodel.

THE FUNCTION OF THE EFFECT OF WATER VAPOR DIFFERENCE BETWEEN LEAF AND AIR ON NP (FW)

THE RESPONSE OF NP TO CHANGES IN WD

Input-Experiments measuring rates of CO_2 uptake at light saturation and at a constant temperature at varying WD during different times of the year.

In a number of plant species WD has a direct and reversible effect on the stomatal diffusion resistance (Lange et al., 1971; Schultze et al., 1972). Figure 8 shows a linear decrease of NP at increasing WD for *H. scoparia* in the spring (April 28) at good soil water conditions (maximal water potential of the plant in the morning, -13 bars; minimal ψ_p during the day, -31 bars). As the dry season proceeds this effect becomes more and more pronounced as shown in Figure 9 (June 2: ψ max of the plant in the morning, -41 bars; ψ_p min, -67 bars). An increasingly negative slope of the WD-dependent NP curve is obvious.

THE PROCEDURE TO CALCULATE THE WD RESPONSE OF NP

Figure 10 shows a flow diagram of the procedure to calculate the WD response of NP used in the model:

1. Each set of data of a humidity experiment on a certain DAY is fitted with a linear regression (for 13 different humidity experiments, each having 3-6 measurements of WD-dependent NP, the R^2 of the curve fit is .92 to .99).

2. The parameters of the equation are divided by the value of the y-axis intercept (NPMAX at WD=0), so that the regression lines are scaled from 0 to 1. It was tried to fit a time-dependent regression through the values of the slope of the WD-dependent NP (slope = f(DAY)). For any polynomial equation, R^2 remained very low (linear regression: R^2 = .02, second-degree polynomial regression: R^2 = .08, third-degree polynomial regression: R^2 = .11). This shows that there is no simple time function to calculate the seasonal change of the slope of the NP/WD experiments with sufficient accuracy.

3. From laboratory experiments it was obvious that the WD effect on the stomatal diffusion resistance is affected by water stress. Therefore, the slope of the NP/WD experiments is correlated to the minimal daily water potential of the plant during the day at that time of the year. Figure 11 shows this regression and the data points ($R^2 = .77$) for *H. scoparia*. The closing reaction of the stomata increases at increasing WD with decreasing water potential in the plant to a maximum value at about -65 bars. With a further decrease of water potential the reaction becomes smaller again, because of the overruling effect of internal water stress on the gas exchange process.

4. The change of the minimal daily water potential of the plants during the seasons is certainly dependent on the conditions in the atmosphere and in the soil. As a preliminary approach, a third-degree polynomial equation was fitted through the annual change of the daily minimal water potential of *H. scoparia* ($R^2 = .92$). Figure 12 shows a plot of this regression. It is obvious that the extremes are not covered by this regression (e.g., day 229), which certainly will cause an increased error in the overall photosynthesis model.

At large values of WD the stomata are expected to be closed, not allowing a positive uptake of CO_2. The experimental data do not show if the linear NP/WD relationship is valid under very dry air conditions (WD greater than 30 $mgH_2O/1$), and it is very possible that in this range of WD the rate of CO_2 uptake does not decrease with the same slope. This effect was not taken into account in the first model test. This means, that at large WD the reduction of NP is probably overestimated with the linear regression.

Figure 10. Flow diagram of the procedure to calculate the WD effect on NP.

Figures 8 and 9. Relative rate of net photosynthesis (NP) scaled from 0 - 1 as related to the water vapor concentration difference between leaf and air (WD) for *H. scoparia* (unwatered) at a low water stress of Ψ_p -31.5 bar(Fig. 8) and at a high water stress of Ψ_p -67 bar (Fig. 9).
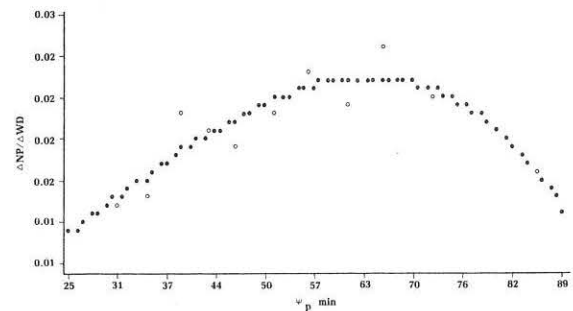
Figure 11. The change in net photosynthesis per 1 $mgH_2O/1$ increase of water vapor difference between leaf and air ($\Delta NP/ \Delta WD$) as related to the minimal pressure potential in *H. scoparia* (unwatered) during the day (Ψ_p min).

This overestimatation of the humidity effect became obvious during the first model tests. An example is given in Figure 13, where the observed values of NP show a one-peaked daily course of CO_2 uptake whereas the predicted NP has a pronounced depression during noon and afternoon. The difference is caused by the linearly extrapolated humidity effect.

For selected days the change of CO_2 uptake with WD at low air humidity was plotted from the daily course of NP and from the deviation between predicted and observed values (Fig. 14). In this case the decrease of NP with WD changes the slope at about 30 mg H_2O/l. Stomata did not close as rapidly as had been assumed from the first experiments. In this range of stomatal closure, plant internal control mechanisms (i.e. the mesophyll internal CO_2 concentration) counterbalance the humidity-induced closing response.
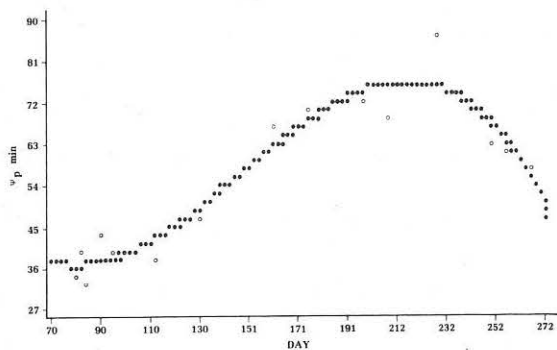
For the purpose of this model, the deviation between the linear regression and the observed change of NP with WD was corrected for the first part of the year until July 16 (DAY 197) with a correction function of the type $Y = A/X + B$, where A and B are time-dependent parameters. In future applications of the model this correction should be included into a single humidity function. For this purpose, however, humidity experiments need to be carried out at very dry air conditions.

The effect of the applied correction according to Figure 14 is shown in Figure 15 for the same day as was presented in Figure 13. In this figure the observed and predicted values of WD match perfectly.

Figure 14. Percent net photosynthesis of *H. scoparia* (unwatered) as related to WD (mgH_2O/l) plotted from the daily course of NP (half hourly means) for the time of light saturation of CO_2 uptake on June 8-12, 1971. Linear NP-WD relationship (- - - -); correction function (———).

Figure 12. Change of the minimal pressure potential in *H. scoparia* (unwatered) during the day ($\psi_p$min) versus the time of year (DAY).
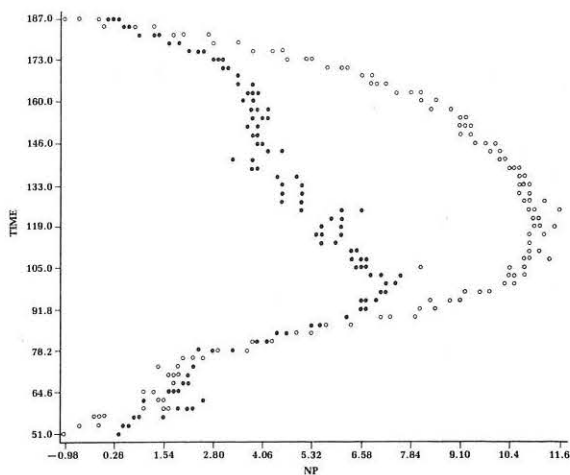

Figure 13. The daily course of net photosynthesis of *H. scoparia* (unwatered) on June 25, 1971. x-axis: rate of net photosynthesis per gram dry weight and hour (NP). y-axis: time of day in 1/10 of the hour (TIME). Predicted values (●); measured values (o).

Figure 15. The daily course of net photosynthesis of *H. scoparia* (unwatered) on June 25, 1971, but calculated with the additional WD correction. x-axis: rate of net photosynthesis per gram dry weight and hour (NP). y-axis: time of day in 1/10 of the hour (TIME). Predicted values (●); measured values (o).

THE FUNCTION (FW) TO OBTAIN THE EFFECT OF WD ON NP IN THE MODEL

Original Function Used-In the future, a similar function should be used after changing the equation of statement 8 to the non-linear relationship at high values of WD.

```
MOD2:
  PROC OPTIONS(MAIN);
  ON ENDFILE(SYSIN) STOP;
TOP:
  GET LIST(DAY,WD);
  WSMIN=94.80794*DAY*(-1.648292+DAY*(0.140833-DAY*0.00003169806));
  FACTOR=0.003882364*WSMIN*(0.000120063+WSMIN*(0.9728054E-05-WSMIN*
    0.1105827E-06));
  FACTOR=-FACTOR;
8-  FW=FACTOR * WD + 1;
  IF FW < 0.01 THEN
    FW=0.01;
  PUT SKIP DATA(DAY,WD,FW);
  GO TO TOP;
END MOD2;
```

Function Used in This Model, Containing the Correction for the Effect of Large Values of WD on NP-

```
FW=FACTOR * WDI + 1.0
IF (FW .LE. 0) FW=0.01
FWCORR=FW
IF (FW .LT. 0.28) FWCORR=0.28
TEMP=A/FWCORR + B
IF (TEMP .GT. 1 .AND. DAY .LT. 197) FW=FWCORR * TEMP
```

where A and B are changing with DAY until July 16: A = .6177987E-04*DAY**2-.2787197E-01*DAY+.3445914E01
B = -.2558189E-03*DAY**2+.1056985E 00*DAY-.1643142E02
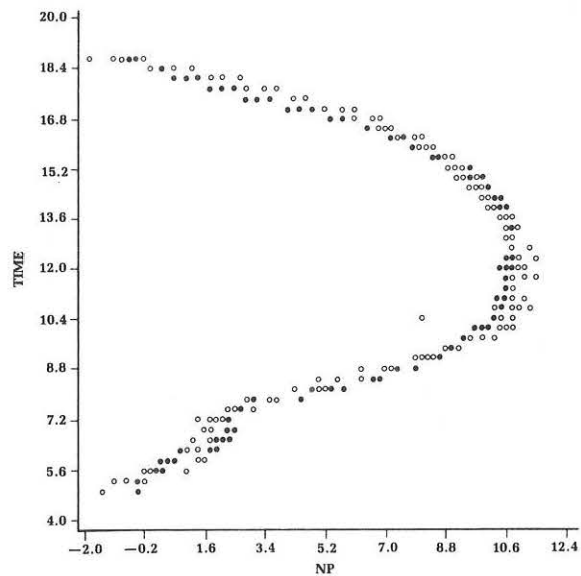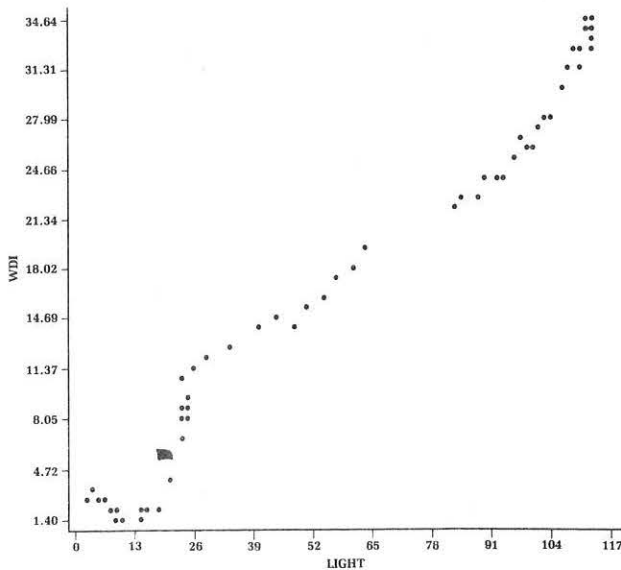

Figure 16. Change of the water vapor difference between the leaf and the air (WDI) throughout the day versus increasing light intensity (LIGHT) under natural conditions for *H. scoparia* (unwatered). (Avdat, July 28, 1971).

THE FUNCTION OF THE EFFECT OF LIGHT INTENSITY AND THE FUNCTION OF NPMAX

THE LIGHT RESPONSE OF NP

Input-Experiments measuring rates of CO_2 uptake during the course of a day from early morning until noon at varying light, temperature and humidity conditions.

Figures 16, 17 and 18 show the change of WD, temperature and NP with increasing light intensity during the course of a late summer morning until noon for *H. scoparia*. In the desert, as light intensity increases, the climate gets rapidly warmer and drier, which has a strong effect on NP at any time. The values of CO_2 uptake in the morning are measured when the air is moist but at temperatures far below the optimum. The values of NP at noon are measured at more favorable temperatures or at temperatures above optimum, but when the air is very dry. NP increases with light intensity to an optimum at 65-100 Klux. The rates decrease again at higher light intensities.
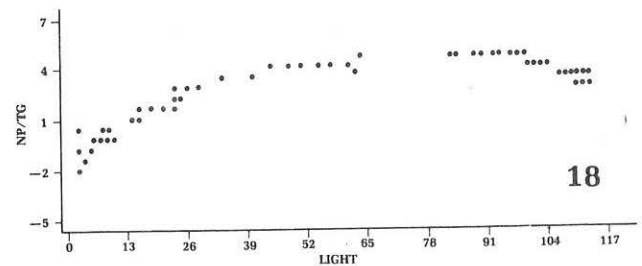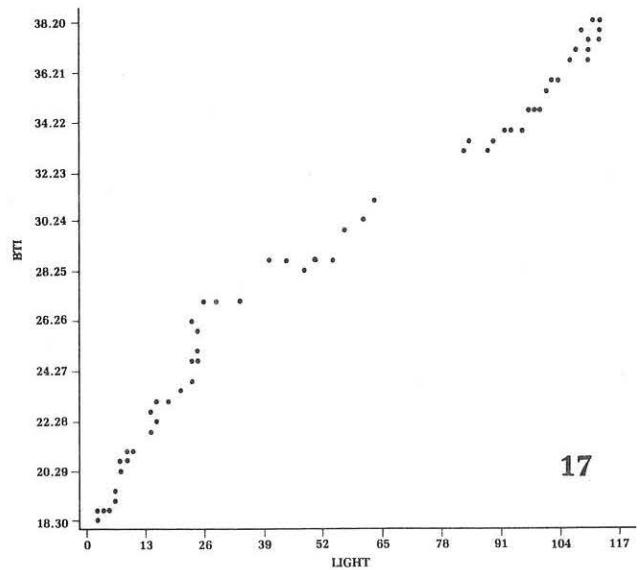
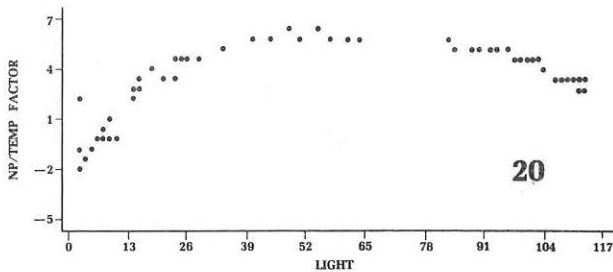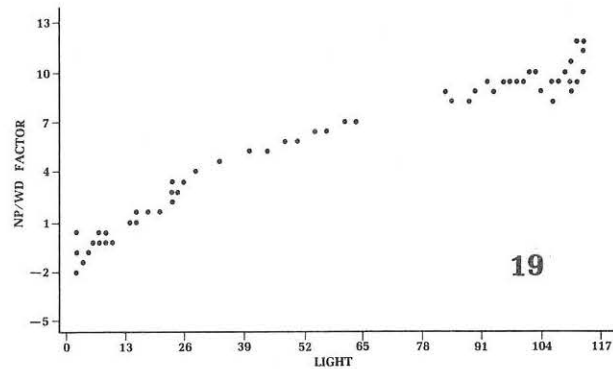Figures 17 and 18. Change of leaf temperature (BTI) (Fig. 17) and change of net photosynthesis per gram dry weight and hour (NP/TG) (Fig. 18) throughout the day versus increasing light intensity (LIGHT) under natural conditions for *H. scoparia* (unwatered). (Avdat, July 28, 1971).

To attain the physiological light response curve the environmental factors TEMP and WD need to be optimized using the functions FT and FW. In a first step, the rates of NP were corrected for the effect of WD only. Figure 19 shows the same data as in Figure 18 only corrected for the effect of WD. The rates at light saturation increased more than two-fold by this correction. If the data are corrected only for TEMP, the rates of NP increase at low light intensities, making the noon depression of NP even more pronounced (Fig. 20). The light response corrected for TEMP and WD is shown in Figure 21. There is no recognizable depression of the rates of NP at high light intensities. For this species the drop in water potential from early morning to noon (-39 bars to -68 bars) has no additional effect on stomatal aperture other than the increased sensitivity to air humidity (the data were calculated with WD=f [water stress - 68 bars]). For other species it is possible that with the correction of WD and TEMP the rates of NP at a high light intensity at noon do drop. This would indicate an additional effect of water stress, which has to be taken into account in the model separately.

The data of light-dependent NP, which were corrected for TEMP and WD, are fitted with an assymptotic function:

$$f(x,a,b,c,) = a(1-e^{-bx}) + c,$$

in which 'a+c' is the asymptote f(x) approaches with increasing x, and 'b' is a parameter determining the rate of rise by which the curve approaches 'a+c'; 'c' is the intercept

of the y-axis, which is negative and represents the respiration rate. This function was fitted with a non-linear regression program, which was especially adapted for this problem.

Figure 22 shows the flow diagram of the procedure to obtain the light response of NP from measurements of the daily course of gas exchange.

Figure 21. Change of net photosynthesis per gram dry weight and hour corrected for the effect of water vapor difference between leaf and air and corrected for the effect of leaf temperature (NPTW) versus increasing light intensity (LIGHT) under natural conditions. (●) calculated curve of the light equation; (○) points of measurement for *H. scoparia* (unwatered). (Avdat, July 28, 1971).

Figures 19 and 20. Change of net photosynthesis per gram dry weight and hour corrected for the effect of water vapor difference between leaf and air (NP/WD FACTOR) (Fig. 19) and for the effect of leaf temperature (NP/TEMP FACTOR) (Fig. 20) versus increasing light intensity (LIGHT) under natural conditions for *H. scoparia* (unwatered). (Avdat, July 28, 1971).
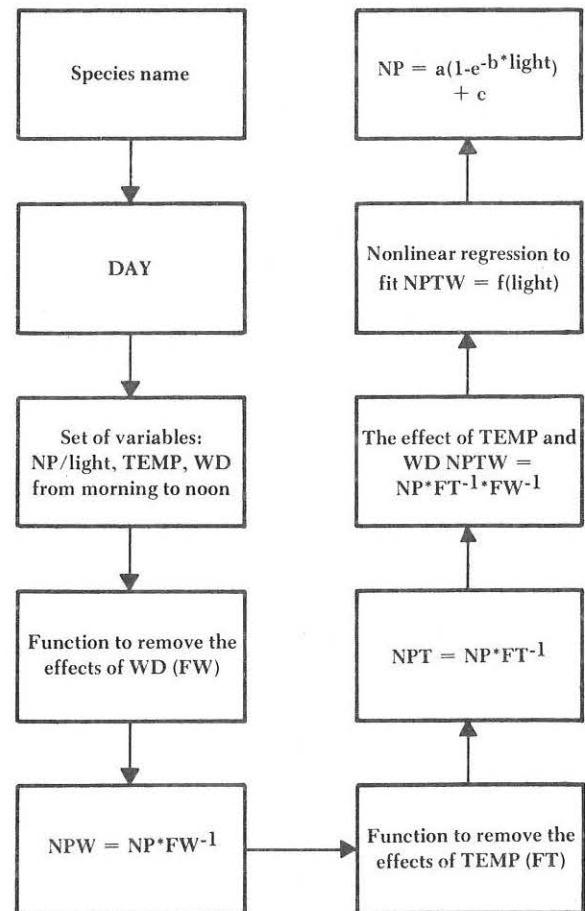

Figure 22. Flow diagram of the procedure to obtain the light response of NP.

PROCEDURE TO OBTAIN THE LIGHT RESPONSE OF NP:

```
PLOTTER:
  PROC OPTIONS(MAIN);
  DCL I FLOAT,
      BB FIXED,
      (NPT,NPW,NPTW)(300) FLOAT,
      (A,X,C,D,E,FW,FT,FF,GG,XX)(300) FLOAT,
      STRINGS CHAR(25),
      B(2) FLOAT;
  ON ENDFILE(SYSIN)
     GO TO PART2;
  GET FILE(PARMS) LIST(DAY);
  STRINGS='DAY = '||DAY;
TOP:
  GET EDIT(AA,BB,CC,EE,DD)
     (COL(7),F(6,2),4F(6,2));
  IF AA = 0 | BB = 0 | CC = 0 | DD = 0 | EE = 0 THEN
     GO TO TOP;
  COUNT=COUNT + 1;
  A(COUNT)=AA;
  X(COUNT)=BB;
  C(COUNT)=CC;
  D(COUNT)=DD;
  E(COUNT)=EE;
  GO TO TOP;
PART2:
  CALL PLOT(COUNT,'*',X,A);
  CALL GRAPH(0,1,3,0,0,'LIGHT','TIME',STRINGS);
  CALL PLOT(COUNT,'*',X,C);
  CALL GRAPH(0,1,3,0,0,'LIGHT','BTI ',STRINGS);
  CALL PLOT(COUNT,'*',X,D);
  CALL GRAPH(0,1,3,0,0,'LIGHT','WDI ',STRINGS);
  CALL PLOT(COUNT,'*',X,E);
  CALL GRAPH(0,1,3,-5,8,'LIGHT','NP/TG',STRINGS);
  AMAT=94.80794*DAY*('1-6*8292+DAY*(0.0140833*DAY*0.3169806E-04));
  FACTOR=0.003832364*AMAT*(0.00012006J9*AMAT*(0.9720054E-05*AMAT*
      0.1105827E-06));
  FACTOR=FACTOR;
  PUT PAGE;
  DO I=1 TO COUNT;
     FW(I)=FACTOR * D(I) + 1.0;
     IF FW(I) < 0.01 THEN
        FW(I)=0.01;
     PUT SKIP DATA(DAY,D(I),FW(I));
     IF E(I) > 0 THEN
        NPW(I)=E(I)/FW(I);
     ELSE
        NPW(I)=E(I);
  END;
  CALL PLOT(COUNT,'*',X,NPW);
  CALL GRAPH(0,1,3,-5,8,'LIGHT','NP/WD FACTOR',STRINGS);
  XMAX=34.22297*DAY*('0.2169415*DAY*(0.002518485*DAY*0.000006694));
  XMAX=XMAX  -  27.34;
  DO I=1 TO COUNT;
     TEMPIT=C(I) = XMAX;
     COUNT1=COUNT1 + 1;
     IF TEMPIT < 7 THEN DO;
        FT(I)=1;
        GO TO ENDER;
     END;
     IF TEMPIT > 20 THEN
        FT(I)=161.6137*TEMPIT*(20.1694*TEMPIT*('0.426328*TEMPIT*
           0.014117));
     ELSE
        FT(I)=16.6 + 3.36*TEMPIT;
     FT(I)=FT(I)/100;
ENDER:
     PUT SKIP DATA(DAY,C(I),FT(I));
     IF E(I) > 0 THEN DO;
        NPT(I)=E(I)/FT(I);
        NPTW(I)=E(I)/FW(I)/FT(I);
     END;
     ELSE DO;
        NPT(I)=E(I);
        NPTW(I)=E(I);
     END;
  END;
  CALL PLOT(COUNT1,'*',X,NPT);
  CALL GRAPH(0,1,3,-5,8,'LIGHT','NP/TEMP FACTOR',STRINGS);
  CALL PLOT(COUNT1,'*',X,NPTW);
  CALL GRAPH(0,1,3,-5,8,'LIGHT','NPTW',STRINGS);
  DO I=1 TO COUNT1;
     PUT FILE(OUTPUT) EDIT(X(I),NPTW(I))
        (COL(1),2 (F(10,2),X(2)));
  END;
  CLOSE FILE(OUTPUT) OPTIONS(LOCK);
END PLOTTER;

EXPA:
  PROC OPTIONS(MAIN);
  DCL (XX,YY,X,Y)(300) FLOAT;
  GET FILE(OUTPUT) LIST(A,B,C);
  DO I=1 TO 130;
     XX(I)=I;
     YY(I)=A * (1.0 - EXP('B*I)) + C;
  END;
  ON ENDFILE(OUTPUT) GO TO PART2;
TOP:
  GET FILE(OUTPUT) EDIT(D,E)
     (COL(1),2 F10.2);
  COUNT=COUNT + 1;
  X(COUNT)=D;
  Y(COUNT)=E;
  GO TO TOP;
PART2:
  CALL PLOT(I = 1,'*',XX,YY);
  CALL PLOT(COUNT,'0',X,Y);
  CALL GRAPH(0,1,3,-5,8,'LIGHT','NPTW',' ');
  PUT SKIP DATA(YY(120),YY(130));
END EXPA;
```

For this plant species, the above mentioned FW-correction was applied for calculating the light response of NP. This special procedure is included in the following FORTRAN program:

```
      REAL LI(240),NPA(240),NPW(240),NPT(240),NPTW(240),NP,LI
      DIMENSION B(4)
      COMMON AA(807),XMIN,XMAX,YMIN,YMAX,FLG
      DATA FA1/94.80794/,A2/-1.64829E/,FA3/.0140833/,FA4/-.3169806E-04/
     1 ,F01/.003832364/,Fa2/.120063JE-0J/,F03/.9720054E-05/
     2 ,F04/-.1100027E-06/,X1/6.802J7/,X2/-.2109415/,X3/.002518485/
     3 ,X4/-0.649AE-05/,A1/3.445914/,A2/-0.027dJ179/,A3/.0177987E-04/
     4 ,B1/-10.43147,b2/.105998J/,BJ/-0.255o19VE-0J/,F1/-161.0137/
     5 ,F2/0.1694/,F3/-0.426328/,F4/.014117/
      DO 3 I=1,88/
    3 AA(I)=' '
      IDAY=101
      IDAY=JULIAN(IDAY) = 1
      READ(5,100) MUN,LI,BTI,NP,WDI
    1 IMON=MON
      ICNT=0
      DAY=JULIAN(MON) - IDAY
      WRITE(6,300)
      FACTOR=A1 + DAY * (FA2 + DAY * (FA3 + DAY * FA4))
      FACTOR=B1 + FACTOR * (FB2 + FACTOR * (FB3 + FACTOR * FB4))
      FACTOR=FACTOR
      XMAA=X1 + DAY * (X2 + DAY * (X3 + DAY * X4))
      A=A1 + DAY * (A2 + DAY * A3)
      BB=B1 + DAY * (B2 + DAY * B3)
    2 ICNT=ICNT + 1
      LI(ICNT)=LI
      NPA(ICNT)=NP
      FW=FACTOR * WDI + 1
      IF (FW .LE. 0) FW=.01
      TEMP=X/W + BB
      NPW(ICNT)=NP
      IF (TEMP .GT. 1) FW=FW * TEMP
      IF (NP .GT. 0) NPW(ICNT)=NP/FW
      TEMP=BTI - XMAX
      IF (TEMP .GT. 1V) GO TO 8
      FT=1.16 * TEMP + 16.8
      GO TO 9
    8 FT=F1 + TEMP * (F2 + TEMP * (F3 + TEMP * F4))
    9 FT=FT * .01
      WRITE(6,200) MUN,DAY,LI,BTI,NP,WDI,FW,FT
      IF (NP .LE. 0) GO TO 4
      NPT(ICNT)=NP/FT
      NPTW(ICNT)=NP/FW/FT
      GO TO 10
    4 NPT(ICNT)=NP
      NPTW(ICNT)=NP
   10 READ(5,100,END=5) MON,LI,BTI,NP,WDI
      IF (MON .EQ. IMON) GO TO 2
    5 SYM='0'
      XMIN=0
      XMAX=130
      YMIN=5.0
      YMAX=5
      CALL GRAPH(ICNT,SYM,LIA,NPA)
      WRITE(6,302)
      CALL GRAPH(ICNT,SYM,LIA,NPW)
      WRITE(6,301)
      CALL GRAPH(ICNT,SYM,LIA,NPT)
      CALL FNUN(LIA,NPTW,ICNT,B)
      DO 6 I=1,13
      NPA(I)=I
    6 NPW(I)=B(1) * (1.0 - EXP(B(2)*I)) + B(3)
      WRITE(6,304)
      DO 7 I=1,ICNT
      TEMP=B(1) * (1.0 - EXP(B(2) * LIA(I))) + B(3)
      FACTOR=NPT(I) - TEMP
    7 WRITE(6,202) LIA(I),NPT(I),TEMP,FACTOR
      WRITE(6,306)
      FLG=1
      CALL GRAPH(ICNT,SYM,LIA,NPTW)
      SYM='*'
      FLG=0
      ICNT=130
      CALL GRAPH(ICNT,SYM,NPA,NPW)
      WRITE(6,203) B
      IF (MON .NE. IMON) GO TO 1
      STOP
  100 FORMAT(4X,I4,4X,F3.0,1X,3F6.2)
  200 FORMAT(2I5,4F8.2,2F8.4)
  202 FORMAT(' ',4FB.2)
  203 FORMAT('0 CUEFFIENTS :',3G15.6,'   RSQUARE :',F10.5)
  300 FORMAT('1MMUD DAY    LI     BTI    NP/TP    WDI      FW
     1 'FT' / ' ',12('-----'))
  301 FORMAT('1            LI VERSUS NP/IP ')
  302 FORMAT('1            LI VERSUS NP/WD ')
  303 FORMAT('1            LI VERSUS NP/TEMP ')
  304 FORMAT('1       LI   NP/TG ENP/TG   DEV.' / ' ',9('====='))
  306 FORMAT('1            LIA VERSUS NP(3) AND ENP (*) ')
      END
```

THE FUNCTION OF NPMAX

From the light curve of NP which is corrected for the effect of TEMP and WD, the maximal rate of NP (NPMAX) is defined as the rate of NP at high light intensity (120 Klux).

The asymptote of the exponential light function was not taken as NPMAX, since many desert plants reach light saturation only at a high light intensity (Schulze, Lange and Koch, 1972). In such cases there is danger that the calculated light curve does not reach an asymptote within the given range of data, but could increase to very high values of the parameter 'a'. This parameter, therefore, does not represent a physiological capability in all cases.

The seasonal change of NPMAX is fitted with a third-degree polynomial equation: NPMAX = f (DAY). This curve is shown in Figure 23 (R^2 = .89).

THE FUNCTION (FL) OF THE EFFECT OF LIGHT INTENSITY

From the seasonal change of the light curves of NP it is obvious that the parameter 'a' of the exponential function has a high degree of variance. For this reason the seasonal change of the light curve is calculated from the function of NPMAX=f(DAY) and from the change of the parameter 'b'. The parameter 'c' is taken to be constant (average over the season) because of its low variability.

The procedure to calculate the effect of light (L) on NP(FL):

1. The seasonal change of the parameter 'b' is fitted with a third-degree polynomial equation: b=f(DAY). This curve is shown in Figure 24 (R^2 = .59, the F-values show that all regression coefficients are highly significant).

2. The change of NPMAX with time is known from NPMAX=f(DAY).

3. The parameter 'a' is calculated from the exponential light functions: $a = (NPMAX-c)^*(1-e^{-b^*120})^{-1}$.

4. The light curve of NP for any DAY is:

$$NP = a^*(1-e^{-b^*L})+c$$

5. The effect of light intensity is scaled from 0 to 1 by division of NP by NPMAX:

$$FL = NP^*NPMAX^{-1} = (a^*(1-e^{-b^*L})+c)^*NPMAX^{-1}.$$
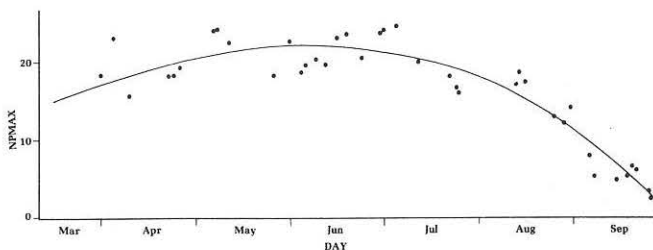

Figure 23. Change of the maximal rate of net photosynthesis (NPMAX) of *H. scoparia* (unwatered) versus the time of year (DAY).
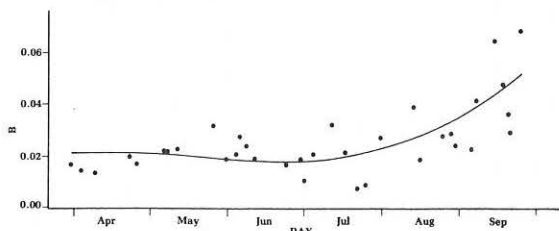

Figure 24. Change of the parameter "b" of the light equation (B) versus the time of year (DAY) for *H. scoparia* (unwatered).

THE FUNCTION (FL) TO OBTAIN THE EFFECT OF LIGHT INTENSITY ON NP IN THE MODEL

```
M003:
  PROC OPTIONS(MAIN);
  ON ENDFILE(SYSIN) STOP;
TOP:
  GET LIST(DAY,LIGHT);
  XNPMAX=7.934179*DAY*(0.745475*DAY*(0.7280825E*03*DAY**0.4022865E-05)));
  BFACT=-0.02174303*DAY*(0.001041343*DAY*(-0.7986124E-05*DAY*
    0.1909426E-07)));
  AFACT=(XNPMAX - 0.141463)/(1.0 + EXP(-BFACT * 120));
  XL=AFACT*(1.0 + EXP(-BFACT*LIGHT)) + 0.24436;
  FL=XL/XNPMAX;
  PUT SKIP DATA(DAY,LIGHT,FL);
  GO TO TOP;
END M003;
```

THE WATER STRESS FACTOR (FS)

An increase in plant water stress during the day is expected to reduce the TEMP and WD corrected rates of NP, especially at a high light intensity at noon. In this case the correction for the effect of TEMP and WD would not compensate for the noon depression. The decrease of the corrected NP values with increasing light would be a measure of the stress effect.

For *H. scoparia* the curves of light-dependent NP either level off or show an increasing rate of CO_2 uptake until high light intensity. Therefore, in this case, the development of a separate stress function was not possible. This, however, might be necessary for other desert species.

THE MODEL TO CALCULATE NP FROM THE TIME OF YEAR (DAY) AND FROM THE CLIMATIC DATA: LIGHT, TEMPERATURE AND DEWPOINT

Input-The climatic data (light, temperature and dewpoint) are obtained from the METEOR common block which contains the output of the EXOGEN program. The WD value is calculated from the temperature and the dewpoint data. For each species the following parameters must be determined:

1. parameters for the correction of the effect of TEMP (TEMPC1-TEMPC8)
2. parameters for the correction of the effect of WD (WDC1-WDC8)
3. parameters for the correction of the effect of L including the calculation of NPMAX (XLIC1-XLIC8)
4. constant for conversion of the output from $mgCO_2{}^*gdw^{-1}{}^*time^{-1}$ to $mgC^*gC^{-1}{}^*time\ span^{-1}$ (Const).

The model calculates NPMAX = f(DAY) and corrects this value for the effect of L, TEMP, WD multiplicatively (see Fig. 1). An effect of water stress still needs to be included if necessary.

The output of the model is mg $C^* gC^{-1}{}^*time span^{-1}$

The FORTRAN program interfaces with the Desert Biome "General-purpose" Model. It is as follows:

```
      SUBROUTINE PHOTOS

      COMMON /PARM/
     1 TEMPC1(15),TEMPC2(15),TEMPC3(15),TEMPC4(15),TEMPC5(15),TEMPC6(15)
     2,TEMPC7(15),TEMPC8(15),HDC1(15),HDC2(15),HDC3(15),HDC4(15),
     3 HDC5(15),HDC6(15),HDC7(15),HDC8(15),XLIC1(15),XLIC2(15),
     4 XLIC3(15),XLIC4(15),XLIC5(15),XLIC6(15),XLIC7(15),XLIC8(15),
     5 ,CONST(15)

      COMMON/INC/HV/I,IL,IR

      COMMON/STAT/CVEG(15,10,6)

      COMMON /CHANGE/CVEGQQ(15,10,6)

      COMMON/METEOR/EVAP,TDAY,THIGHT,DATHVP,DRINAV,DRINMX,DAPHOT,
     1 DAYRAD,DUST,DUSCOM(6),RAINLO(6),ERODL,DAYRUN,DRUNMI(6),DRUNUM(6)
     2 ,DRLNLT(5,U),DASNOW,DAHAIN,HTEMP(24),HLIGHT(24),HRELHU(24)
     3 HDEPT(24),HWIND(24),HEVAP(24)

      COMMON/SPEC/DUM(30),IYRDAY,U1(20),NDEBUG,U2(XA),NUNIT

      COMMON/TOTALS/U4(237),AVEG(15,10)

      NUNIT=NUNIT/1000
      DO 11 K=1,NUNIT
      DAY=IYDAY+K=1
      DO 11 J=1,24
      IF (HLIGHT(J).LT.2.)GO TO 11

C     CORRECTION FOR TIME EFFECT OF TEMPERATURE

      TEMPCP =TEMPC1(I)*DAY**3+TEMPC2(I)*DAY*DAY+TEMPC3(I)*DAY+TEMPC4(I)
      SHIFT=TEMPCP -27.34
      TEMPIT=HTEMP(J)-SHIFT
      IF (TEMPIT.LT.7.)GO TO 20
      IF (TEMPIT.GT.20.)
     *TF=TEMPC5(I)*TEMPIT**3+TEMPC6(I)*TEMPIT**2+TEMPC7(I)*TEMPIT
     1 +TEMPC8(I)/100
      IF (TEMPIT.LT.20.) TF=(3.36*TEMPIT+16.8)/100
      GO TO 30
20    TF=1
30    CONTINUE

C     CORRECTION FOR THE EFFECT OF WATER VAPOUR DIFFERENCE BETWEEN LEAF AND AIR

      HSMIN=HDC1(I)*DAY**3+HDC2(I)*DAY**2+HDC3(I)*DAY+HDC4(I)
      HDF=-(HDC5(I)*HSMIN**3+HDC6(I)*HDC7(I)*HSMIN+HDC8(I)
     1 *((.257827E-5*HTEMP(J)**4+.152/1VE-3*HTEMP(J)**3
     2 -(.10330/E-1*HTEMP(J)**2+.333707*HTEMP(J)+4.84756)
     3 -(.257827E-5*HDEPT(J)**4+.152/.9E-3*HDEPT(J)**3
     4 -.10330E-1*HDEPT(J)**2+.333707*HDEPT(J)+4.84756))+1
      IF (HDF.LT..01)HDF=.01
      FS=1

C     CALCULATION OF MAXIMAL RATE OF NET PHOTOSYNTHESIS

      XNPMAX=XLIC1(I)*DAY**3+XLIC2(I)*DAY**2+XLIC3(I)*DAY+XLIC4(I)

C     CORRECTION FOR THE EFFECT OF LIGHT

      BFACT=XLIC5(I)*DAY**3+XLIC6(I)*DAY**2+XLIC7(I)*DAY+XLIC8(I)
      AFACT=(XNPMAX*.141463)/(1+EXP(-BFACT*120))
      FL=AFACT*(1-EXP(-BFACT*HLIGHT(J)))-.141463
      FL=FL/XNPMAX

C     CALCULATION OF ACTUAL RATE OF NP

      XNP=XNPMAX*FL*HDF    *TF*FS
10    TOTNP=TOTNP+XNP
11    CONTINUE
      TOTNP=TOTNP*CONST(I)
      PSATE=TOTNP*AVEG(I,IL)
      CVEGQQ(I,IL,IR)=CVEGQQ(I,IL,IR)+PSATE
      RETURN
      ENTRY INPHOS
      DO 15 J=1,I
15    READ(5,/)TEMPC1(J),TEMPC2(J),TEMPC3(J),TEMPC4(J),TEMPC5(J),
     1 TEMPC6(J),TEMPC7(J),TEMPC8(J),HDC1(J),HDC2(J),HDC3(J),HDC4(J),
     2 HDC5(J),HDC6(J),HDC7(J),HDC8(J),XLIC1(J),XLIC2(J),XLIC3(J)
     3 XLIC4(J),XLIC5(J),XLIC6(J),XLIC7(J),XLIC8(J),CONST(J)
      RETURN
      END
```

THE TEST OF THE MODEL

The model was tested against NP measurements which were taken under natural conditions in the field but were not incorporated during building of the model. For the period from April to September, 104 days were chosen. For these days, NP was predicted on a 6-min time step. The result was compared with the actual measured rates of gas exchange. The test program worked on a 6-min time step, with only one species, taking WD as an input variable. The test program is as follows (for this species, the NP-WD relationship was corrected for the non-linearity in the range of large values of WD):

```
FILE  4=FILE4,UNIT=READER,RECORD=14
FILE  5=FILE5,UNIT=DISKPACK,RECORD=14,BLOCKING=30
FILE  6=FILE6,UNIT=PRINTER,RECORD=22
FILE  7=FILE7,UNIT=PRINTER,RECORD=22
```

```
      REAL LI,HR,HRA(240),NP,NPA(240),NPMAX
      DIMENSION FNA(240),TA(240),FLA(240),ENPA(240),ABC(8),XC(8),FC(8)
     1 ,FACT(8),ENPB(240),FNO(240)
      COMMON AA(907),XMIN,XMAX,YMIN,YMAX,FLG
      DATA AA/8E7*' '/
      IDAY=101
      IDAY=JULIAN(IDAY) = 1
      READ(4,/) ABC,XC,FC,FACT
      CLOSE 4
      WRITE(6,201) ABC,XC,FC,FACT
      READ(5,100) MON,HR,LI,BTI,NP,HD1
1     IMON=MON
      ICNT=0
      DAY=JULIAN(MON) = IDAY
      FACTOR=FC(4) + DAY * (FC(3) + DAY * (FC(2) + DAY * FC(1)))
      FACTOR=FC(8) + FACTOR *(FC(7) + FACTOR *(FC(6) + FACTOR * FC(5)))
      FACTOR=FACTOR
      XMAX=XC(4) + DAY * (XC(3) + DAY * (XC(2) + XC(1)))
      A=ABC(4) + DAY * (ABC(3) + DAY * (ABC(2) + DAY * ABC(1)))
      B=ABC(8) + DAY * (ABC(7) + DAY * (ABC(6) + DAY * ABC(5)))
      NPMAX=FACT(4) + DAY * (FACT(3) + DAY * (FACT(2) + DAY * FACT(1)))
      BFACT=FACT(8) + DAY * (FACT(7) + DAY * (FACT(6) + DAY * FACT(5)))
      BFACT=-BFACT
      AFACT=(NPMAX * 2.24436)/(1.0 - EXP(BFACT * 120))
      WRITE(6,300)
      SNP=0
      SENP=0
      SENP1=0
2     ICNT=ICNT + 1
      HR=DIFIX(HR/100) + MOD(HR*100)/60.0
      HRA(ICNT)=HR
      NPA(ICNT)=NP
      TEMP=BTI - XMAX
      IF (TEMP.GT.19) GO TO 3
      FT=3.36 * TEMP + 16.8
      GO TO 4
3     FT=XC(8) + TEMP * (XC(7) + TEMP * (XC(6) + TEMP * XC(5)))
4     FT=FT * .01
      FL=AFACT * (1.0 - EXP(BFACT * LI)) - 2.24436
      FL=FL/NPMAX
      FN=FACTOR * HD1 + 1.0
      IF (FN .LE. 0) FN=.01
      FNOLD=FN
      FNCORR=FN
      ENPI=NPMAX * FL * FN * FT
      IF (FN .LT. 0.26) FNCORR=0.28
      TEMPHA=FNCORR + B
      IF (TEMP .GT. 1) FN=FNCORR * TEMP
      ENPA=NPMAX * FL * FN * FT
      IF (NP .EQ. 0) NP=.01
      QUOT=NP/NP
      WRITE(6,202) MON,DAY,HR,LI,BTI,HD1,FNOLD,FN,TEMP,FT,FL,ENP,ENP1,NP
     1 ,QUOT
      SNP=SNP + NP
      SENP=SENP + ENP
      SENP1=SENP1 + ENP1
      FNO(ICNT)=FNOLD
      FNA(ICNT)=FN
      FTA(ICNT)=FT
      FLA(ICNT)=FL
      ENPB(ICNT)=ENP1
      ENPA(ICNT)=ENP
      READ(5,100,END=6) MON,HR,LI,BTI,NP,HD1
      IF (MON .EQ. IMON) GO TO 2
6     WRITE(6,203) SENP,SENP1,SNP
      SNP=100.0/SNP
      SENP=SENP * SNP
      SENP1=SENP1 * SNP
      WRITE(6,204) SENP,SENP1
      WRITE(6,205) MON,DAY,FACTOR,XMAX,A,B,NPMAX,BFACT,AFACT
      SYM='*'
      XMIN=4
      XMAX=20
      YMIN=0
      YMAX=1
      WRITE(6,307)
      CALL GRAPH(ICNT,SYM,HRA,FNO)
      WRITE(6,301)
      CALL GRAPH(ICNT,SYM,HRA,FNA)
      WRITE(6,302)
      CALL GRAPH(ICNT,SYM,HRA,FTA)
      YMIN=0.2
      WRITE(6,303)
      CALL GRAPH(ICNT,SYM,HRA,FLA)
      WRITE(6,304)
      XMAX=16
      XMIN=-2
      YMAX=20
      YMIN=4
      FLG=1
      CALL GRAPH(ICNT,SYM,ENPA,HRA)
      FLG=0
      SYM='U'
      CALL GRAPH(ICNT,SYM,NPA,HRA)
      WRITE(6,306)
      FLG=1
      CALL GRAPH(ICNT,SYM,NPA,HRA)
      FLG=0
      SYM='*'
      CALL GRAPH(ICNT,SYM,ENPB,HRA)
      IF (IMON .NE. MON) GO TO 1
      STOP
100   FORMAT(4X,2I4,F4.0,3F6.2)
200   FORMAT(2I5,6.2,I5,11F8.2)
201   FORMAT(4(5X,E15.7))
202   FORMAT('0MMUD   DAY   FACTOR(HD)       SHIFT       A(HDCORR)'
     1 '     B(ACORR)     NPMAX       BFACT(FL)    AFACT(FL)'/
     2 1('=====') / 2I5,/G15.7)
203   FORMAT('0TOTALS',70X,3F8.2)
204   FORMAT(' PERCENTS',68X,2F6.2)
300   FORMAT('1MMUD  DAY  TIME   LI      BTI      HD1  FHOLD      FN  '
     1 ,'TEMP      FT      FL      XNP     XNP1    NP/IR   QUOT,'/' ',
     2 1('=====')
301   FORMAT('1         FN VERSUS TIME  ')
302   FORMAT('1         FT VERSUS TIME')
303   FORMAT('1         FL VERSUS TIME')
304   FORMAT('1         XNP (*) AND NP/IR (U) VERSUS TIME WITH FN ',
     1 'CORRECTION ')
306   FORMAT('1         XNP (*) AND NP/IR (U) VERSUS TIME WITHOUT ',
     1 'FN CORRECTION ')
307   FORMAT('1         FN WITHOUT CORRECTION VERSUS TIME')
      END
```

Figure 25 shows the test result in a drawing, in which the measured and predicted daily sums of CO_2 uptake are plotted as a function of DAY. The scatter of the observed values (o) is greater than that of the predicted (●) values. Extreme high and low observed values (i.e. DAY 129, 141 and 142) should be checked on the original recordings of the raw data. The average deviation of the predicted and the observed values of the daily sum of CO_2 uptake is -18 to +14 mg $CO_2{}^*gdw^{-1}{}^*DAY^{-1}$, which is on the total average, an error of -8%. It is important that the scatter of the predicted and observed values seems to be random. There is no systematic over- or under-estimation of the predicted NP at any time of the year.

A great number of daily courses of NP is predicted very closely. An example is given for a day in spring (April 22) in Figure 26; for a day in summer (June 17) in Figure 27; and for a day in late summer (September 17) in Figure 28. The predicted values (●) match the observed ones (o) for all conditions throughout the day.

The limitations of the model are obvious from days with extreme climatic conditions and from days where production is systematically over- or under-estimated. Figure 29 (July 28) shows an example, where the predicted values (●) are much higher than the observed values (o). The reason for such an over-estimation of production is mainly due to a wrong estimation of NPMAX at that point of the annual curve. For long-term prediction of CO_2 uptake, for instance the NP estimation of a whole growing season, such errors should equilibrate. For extreme climatic conditions, however, there is still a need to test whether the approach of handling the effect of various factors multiplicatively is correct. In some situations an average effect of the various factors, or the effect of the minimum factor only, might lead to a better result.
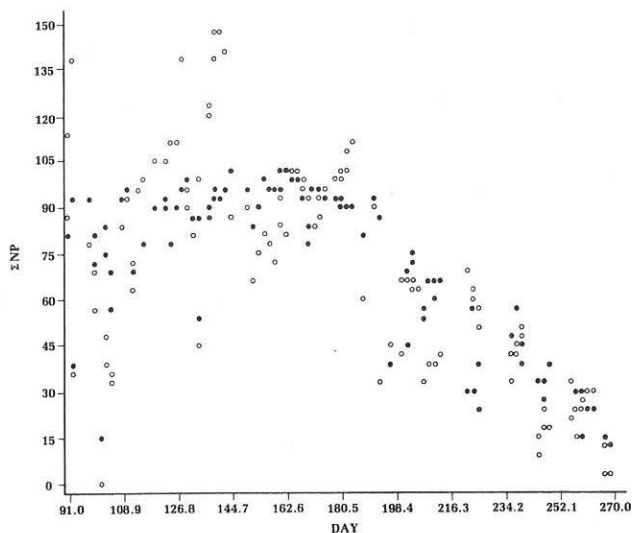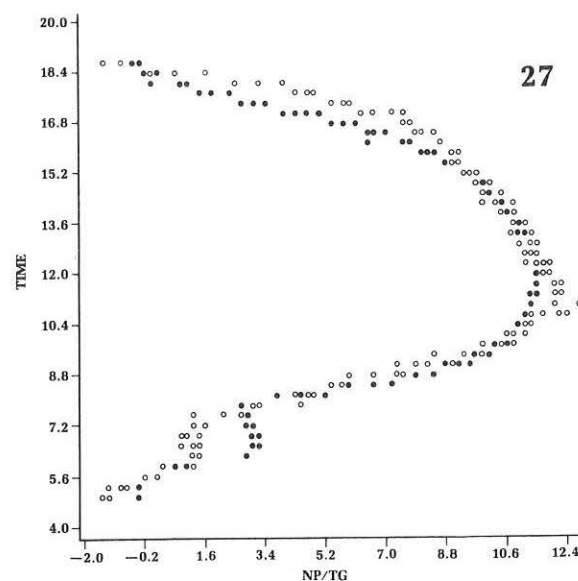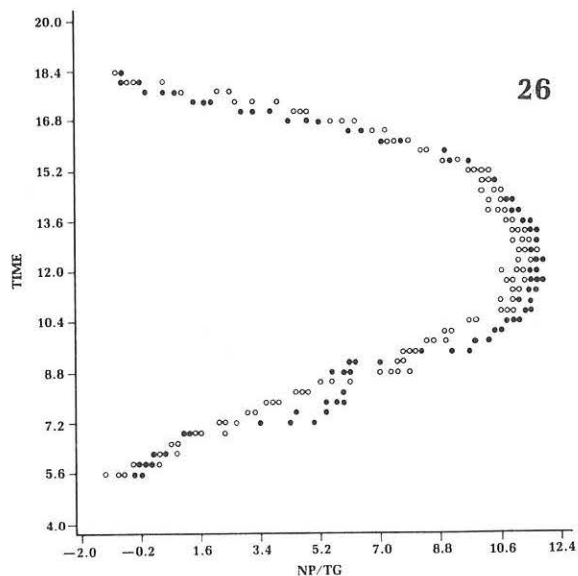
For the ecosystem model the sum of CO_2 uptake over the season is the most important result of the photosynthesis model. During the time from April 1 to September 30, for 104 test days from a total of 183 days, the total sum of CO_2 uptake is calculated. The predicted sum of CO_2 uptake is 7063.54 $mgCO_2{}^*gdw^{-1}$, whereas the measured rate is 7078.22 mg $CO_2{}^*gdw^{-1}$. The difference between the measured and the predicted result over this period of time is only -14.69 mg $CO_2{}^*gdw^{-1}$. Thus the final error of this model test is in this case less than -1%


Figure 25. Daily sum of CO_2 uptake (ΣNP) as related to the time of year (DAY) for *H. scoparia* (unwatered). Predicted values (●): measured values (o).

Figures 26 and 27. The daily course of net photosynthesis of *H. scoparia* (unwatered) on April 22, 1971 (Fig. 26) and June 17, 1971 (Fig. 27) with FW correction. x-axis: rate of net phosynthesis per gram dry weight and hour (NP/TG). y-axis: time of day in 1/10 of the hour (TIME). Predicted values (●); measured values (o).
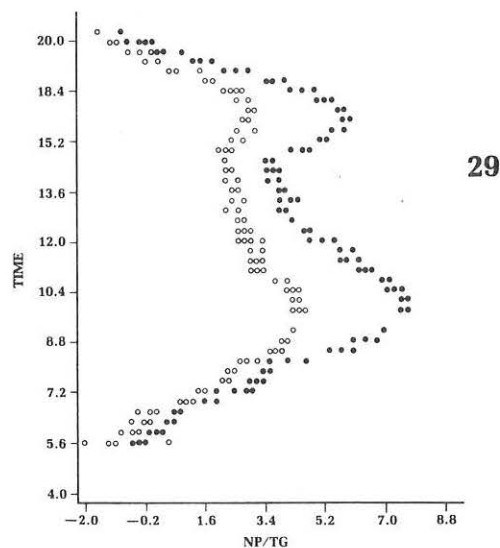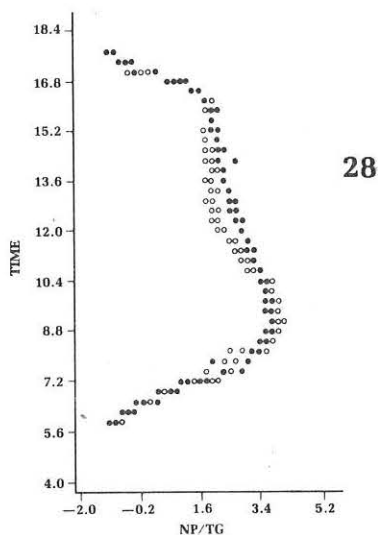
Figures 28 and 29. The daily course of net photosynthesis of *H. scoparia* (unwatered) on September 17, 1971 (Fig. 28) and July 28, 1971 (Fig. 29) without FW correction. x-axis: rate of net photosynthesis per gram dry weight and hour (NP/TG), y-axis: time of day in 1/10 of the hour (TIME). Predicted values (•); measured values (o).

CONCLUSIONS

When we began to build the model it was not known if this approach would lead to a reasonable result. Especially, it was not known whether the function of the effect of L, TEMP and WD would be sufficient to predict NP under natural conditions in the field. For *H. scoparia* this approach seems to be sufficient and correct. For other species, however, other mechanisms may be of more importance, and may be added in a similar approach to the existing model.

For the application of this approach to other species, all the parameters of the different equations have to be determined from field data. If no data are available, new experiments should be carried out. For species comparison, it would be most desirable if similar sets of experiments could be performed.

SENSITIVITY ANALYSIS OF THE MODEL
AND AN APPLICATION

A model gives the opportunity to test single factors in their effect on the system as a whole which usually cannot be accomplished by the original data set. Such an extrapolation is certainly possible only within a limited range given by the experiment.

In the following, an attempt is made to solve a specific problem taking the primary production of *H. scoparia* as an example. From the SST project the question has been asked, What effect has a certain change in climate on plant production? For 40°-60° latitude the following cases ought to be tested:

1. change in mean temperature °C: -3, -1.5, -.75, + .75
2. change in wind and precipitation: -10%, -5%, -2.5%, 0
3. change in radiation: -3.1%, -1.6%, -.8%, 0

These changes should occur over a three-year period.

In solving this problem the following restrictions have been made:

1. The model was run for 104 out of 180 days ranging from April 1 to September 30. This is the main growing season of *H. scoparia* in the Negev desert. The last heavy rains occurred in mid-April. There is no rain until the end of October. The percentage change of each case is calculated.

2. The mean change of any parameter was accomplished by subtracting this change from the original field data. This is certainly not correct, since a mean change has a certain statistical variation. A 3° change in mean temperature means that also a change of 10° and more is possible. Such episodial events have a drastic influence on plant distribution. They are not covered here.

3. The model does not account for any acclimation, which certainly will occur in a plant if conditions change over a period of time.

4. A change in climate might reach certain physiological threshold values (e.g., temperature induction of enzymes, influence of photoperiod, etc.) which again have a feedback on net photosynthesis and which are not covered by the model.

5. A change in climate will influence many other physiolog-
    ical processes besides photosynthesis and respiration,
    which in a feedback loop influence NP again. The
    model does not account for such indirect effects.

6. Long-term changes of climate will certainly influence
    the competition between plant species and induce a new
    succession. Also this problem cannot be solved by
    a photosynthesis model.

The model determines the relative importance of certain
factors for this special plant in its habitat. It also will show,
under certain changing conditons, if new factors and
functions have to be considered as important for the model.

H. scoparia shows the following responses in NP at the
proposed changes in external conditions:

1. Influence of a change in leaf temperature **without** taking
    a change in WD into account: a change in leaf tempera-
    ture will certainly affect NP differently during the cold
    temperatures in spring as compared to the hot summer.
    Figure 30 shows the result of a temperature change on
    the total rate of CO_2 uptake over the season.

Change in TEMP	Rel. rate of CO_2 gain
-5.0 C	85.77 %
-3.0 C	92.13 %
-1.5 C	96.43 %
0	100.00 %
+1.5 C	102.76 %
+3.0 C	104.47 %
+5.0 C	104.97 %

For a desert plant adapted to a hot desert climate, a
temperature drop of -3 C would decrease production by
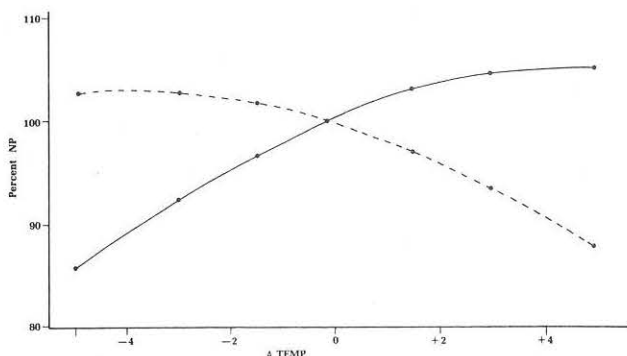7.9 %. This change will certainly be smaller if this

Figure 30. Relative change of the photosynthetic gain
(percent NP) for *H. scoparia* (unwatered) at a certain change
in mean temperature ($\triangle$ TEMP) **without** taking a change in
WD into account. Constant WD (———): changing WD with
TEMP (----).

temperature change occurs over a long period of time,
since *H. scoparia* shows a great adaptation in its temper-
ature response (see Fig. 6). It is a remarkable result that if
WD is not changed, production of *H. scoparia* will
increase 4-5 % with a temperature rise of 3-5 C.

2. Influence of a change in leaf temperature **with** taking a
    change in WD into account: a change in leaf tempera-
    ture has a large effect on WD if the dew point is constant
    especially at high temperatures typical for a desert day.
    Figure 30 shows also the result of a TEMP and WD
    change on the total rate of CO_2 uptake over a growing
    season.

Change in TEMP	Rel. rate of CO_2 gain
-5.0 C	102.56 %
-3.0 C	102.85 %
-1.5 C	101.99 %
0	100.00 %
+1.5 C	97.26 %
+3.0 C	93.23 %
+5.0 C	88.08 %

The result shows that in contrast to case (1), NP increases
2-3 % with decreasing temperature. This increase is
terminated at a temperature change of -3 to -5 C because
of the great effect of the unfavorable cool temperatures.
Although a pure temperature increase will increase pro-
duction, rising temperatures with a simultaneous
change in WD will decrease total production 12 % at +5
C by humidity-induced stomatal closure.

3. Influence of a change in rainfall: a change in rainfall in a
    desert area could have severe effects on plant growth.
    All the cumulative effects on phenology will mainly
    change the NPMAX curve. At decreasing rainfall the
    maximal rates of CO_2 uptake will be lower. However,
    since the effect of phenology on NPMAX is not modelled
    yet, the effect of decreasing rainfall cannot be
    handled properly by the model.

4. Influence of a change in radiation: the influence of
    light intensity on the gain of CO_2 uptake is expected to be
    small in the desert (Fig. 31). It might have an additional
    effect on a change in leaf temperature and WD which is
    not accounted for.

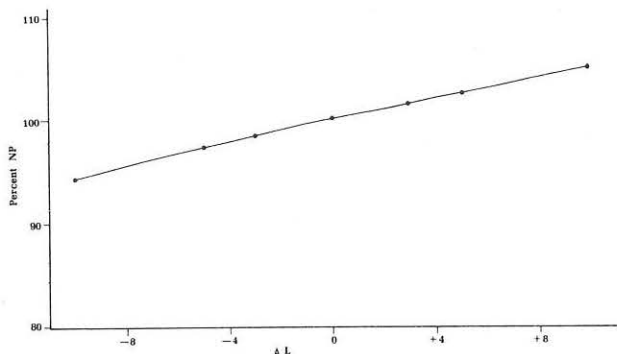| Change in light	Rel. rate of CO_2 gain
+10 %	105.00 %
+ 5 %	102.58 %
+ 3 %	101.57 %
0	100.00 %
- 3 %	98.37 %
- 5 %	97.25 %
-10 %	94.33 %

Figure 31. Relative change of the photosynthetic gain (percent NP) at a change in light intensity (Δ L) for *H. scoparia* (unwatered).

The results show the dominating effect of WD and TEMP on the rate of NP of *H. scoparia*. The effect of changing water stress still needs to be investigated. The changing light intensity will influence NP in the given range only insignificantly.

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