Development of a Photosynthesis Model with an Emphasis on Ecological Applications

V. Test of the Applicability of a Steady-State Model to Description of Net Photosynthesis of *Prunus armeniaca* Under Field Conditions

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Summary. A physiologically based steady-state model of whole leaf photosynthesis (WHOLEPHOT) is used to describe net photosynthesis daily time courses in *Prunus armeniaca*. Net photosynthesis rates are calculated in response to incident light intensity, leaf temperature, air carbon dioxide concentration, and leaf diffusion resistance measured at five minute intervals. The steady-state calculations closely approximate the observed net photosynthesis rates for a broad range of weather conditions and leaf stomatal behavior.

In a previous publication in this series (Tenhunen and Westrin, 1979), a model of the whole leaf net photosynthetic process (WHOLEPHOT) was presented which allowed calculation of net photosynthetic rate as a function of the four independent variables, incident light intensity (PhAR), leaf temperature, carbon dioxide concentration, [CO_2], and oxygen concentration, [O_2]. The model behaves in simulation of net photosynthetic responses to single and multiple environmental factors in a fashion similar to that known for C_3 plant leaves. It was concluded that the model provides an effective means of describing net photosynthesis as affected by these important ecological factors.

The model is suggested to be of particular use in ecological studies because all model parameters describing the photosynthetic process may be derived from data of net carbon dioxide exchange. Although all of these data have not been commonly measured, they may be obtained with further development of measurement techniques familiar to ecologists. The model parameters used to describe the photosynthetic process can be related to specific physiological subprocesses of leaf carbon metabolism. On the other hand, these parameters do not describe discrete processes but over-all functioning of whole leaves as effected by several physiological and/or biochemical events. Thus each parameter may be seen as a simplification of and be equated with groups of parameters identified in more detailed mathematical treatments of leaf photosynthetic processes that have been presented (Peisker, 1976; Hall, 1979; see also Tenhunen et al., 1979a). The simplified parameters of WHOLEPHOT, which we realize impose certain limitations, are a necessary compromise to allow a balanced consideration of modeling of leaf physiology and modeling of linkage with a variable environment.

While the previous work directed at development of a leaf photosynthesis model (Tenhunen et al., 1976a, b, 1977; Tenhunen and Westrin, 1979) demonstrated that the model and model parameters were relevant to steady-state laboratory photosynthesis, we demonstrate here that the model is relevant to ecological appli-cation by comparing model responses to input of environmental conditions with the measured photosynthetic response of *Prunus armeniaca* (C_3 type of carbon metabolism) under field conditions. An important assumption is tested; that net photosynthesis rates measured under fluctuating environmental conditions are governed by steady-state limitations on the photosynthetic process to such an extent that they may be described with a model based on steady-state considerations.

Methods

Measurements of Gas Exchange

Experiments were conducted on one to two year old grafts of apricot (*Prunus armeniaca* L. var. Ungarische Beste). Plants were grown in large pots set into the ground in the Botanical Garden, University of Würzburg. They were given optimal mineral fertilizer and were watered daily to field capacity (see Lange and Meyer, 1979). The CO_2 and H_2O exchange of twigs with three to six leaves was measured with four temperature and humidity controlled cuvettes operating in parallel as part of a mobile field laboratory previously described (Lange et al., 1969; Koch et al., 1971; Schulze et al., 1972).

The system maintains air temperature within the cuvette with Peltier heat transfer elements at temperature sensed in the external air and dew point within the cuvette at external air dew point by rapid trapping of transpired water in a closed loop by-pass. Carbon dioxide concentration fluctuates over a limited range depending on leaf photosynthetic or respiratory activity and on fluctuation in external air [CO_2]. External air CO_2 concentration was not measured continuously during photosynthesis measurements but characteristic daily patterns of [CO_2] were established for the Botanical Garden by extensive measurement in 1978 with an infra-red gas analyzer operating in absolute mode. The patterns are so consistent that we can see no problem in applying this daily time course of [CO_2] to the 1976 data. Photosynthetic uptake of CO_2 was determined with a second infra-red gas analyzer which measured carbon dioxide concentration difference between external and chamber air. Air temperature was sensed with platinum resistance thermometers and leaf temperature with copper/constantan thermocouples. Incident light intensity was sensed with silicon photocells initially calibrated in kilolux. These sensors were subsequently calibrated in PhAR with a quantum sensor from LiCor Inc., Lincoln, Nebraska. Incident light intensity (L) as input to the photosynthesis model in PhAR (μEinsteins cm^{-2} s^{-1}) was obtained with the following empirical calibration equation:

$$L = (21.5 \text{ KLUX} - 0.356)/10,000. \tag{1}$$

Flow of air through the chamber was at all times greater than 100 l/h. With this flow rate, rapid changes in photosynthesis rate are observed in response to changes in light intensity and temperature, whether imposed artificially or due to natural conditions such as variable cloudiness. On the other hand, it is impossible to remove all time lag from the system (for more detailed discussion see Koch et al., 1971).

Incident light intensity, leaf and air temperatures, dew points of the incoming, by-pass, and outgoing air streams, and carbon dioxide gas concentrations were recorded at 5 min intervals. Net photosynthesis rates, transpiration rates, and leaf diffusion resistance to water vapor were calculated as described by Lange et al. (1969). Carbon dioxide concentration within the leaf varies in response to changes in chamber air $[CO_2]$, leaf diffusion resistance, and net photosynthesis rate. It was calculated as described by Gaastra (1959) from:

$$P = \frac{C_A - C_w}{1.56 R_{WV}^{total}} \qquad (2)$$

where: P is the net photosynthesis rate ($nM\,cm^{-2}\,s^{-1}$).

C_A is the concentration of CO_2 in the air outside the boundary layer ($nM\,cm^{-3}$).

C_w is the concentration of CO_2 at cell walls in the intercellular air space ($nM\,cm^{-3}$).

R_{WV}^{total} is the total resistance to water vapor flux out of the leaf determined from transpiration measurements ($s\,cm^{-1}$).

1.56 is the ratio of the diffusion coefficients for water vapor and CO_2.

The total resistance to CO_2 diffusion in the boundary layer, through the stomata and to the cell walls within the leaf was denoted with the symbol (R_1) by Lommen et al. (1971), will be used further in the following discussion, and is equal to $1.56 R_{WV}^{total}$.

Rates Calculated from the Model and Model Adaptation to Apricot

The method of calculating net photosynthetic rates with the model WHOLEPHOT has been discussed in detail (Tenhunen and Westrin, 1979) as used for simulation of characteristic net photosynthesis responses to combinations of the four independent variables, light intensity, leaf temperature, internal air space $[CO_2]$, and $[O_2]$. These characteristics are all retained in the apricot model. Here the daily time course of net photosynthesis is simulated for apricot with WHOLEPHOT in response to a sequence of measured light intensities, leaf temperatures, chamber air CO_2 concentrations (external to the leaf), and leaf diffusion resistances for water vapor (used to estimate CO_2 diffusion resistance and in calculating leaf internal $[CO_2]$). In the application discussed here, i.e. to obtain a function specifically for apricot, minor changes were made in only two parameter values from those described by Tenhunen and Westrin (1979, appendix). Otherwise the stepwise calculation of net photosynthesis rate, photorespiration rate, and CO_2 concentration at the fixation site proceeds in the same manner as described in the previous paper where parameter settings were primarily based on data from wheat. In the present application, $[O_2]$ does not vary and as input to the model is set constant; $[O_2]=0.21$ (volume fraction).

In previous publications in this series, net photosynthesis rate was considered as a function of internal air space $[CO_2]$. This is a necessary step in parameter determination from gas exchange data, since response curves are needed which demonstrate the characteristics of fixation kinetics and CO_2 transport limitations. Internal air space $[CO_2]$ was again used as the CO_2 input variable in comparing general model behavior with general types of observed laboratory responses of net photosynthesis ($[CO_2]$ was constant as light, temperature or $[O_2]$ was varied in simulation; Tenhunen and Westrin, 1979) thus ignoring the effect of changes in stomatal resistance. Responses of net photosynthesis measured under natural conditions may be strongly affected by changes in stomatal resistance which result in changes in steady-state CO_2 concentrations in the leaf. This effect is included in the specific equations intended to describe measured apricot net photosynthesis data in the following manner.

Diffusion relationships within leaf cells were described by Lommen et al. (1971, appendix C) with a triangular resistance network where the intercellular air space, CO_2 fixation site, and photorespiratory site were located at the corners of the triangle. Analysis of the resistance network according to Kirchhoff's Law (see Nobel, 1974) and inclusion of kinetic equations for the fixation and photorespiratory reactions resulted in an equation for net photosynthesis with kinetic parameters and two complex resistance terms, S_1 and S_2. The same resistance analysis was retained in the present model of photosynthesis in a formal sense but the side of the triangle representing diffusion resistance between fixation and photorespiratory sites (R_4) was considered to be small compared to the other two sides, $R_2 = R_3$ (see Tenhunen et al., 1977). The ratio of R_2 to R_4 was included as the parameter $M = 100$. When further information is available, other values of M can be considered. As discussed previously, the resistance terms of Lommen can be expressed in terms of M such that $S_1 = R_1 + R_2 \left[\dfrac{M+1}{2M+1}\right]$. The resistance R_1 is the total CO_2 diffusion resistance from outside the boundary layer to the cell walls within the leaf. As M increases, S_1 approaches $R_1 + R_2/2$ as a limit. The term $R_2/2$ is equal to a single transport resistance in the mesophyll cell (R_M) so that $S_1 = R_1 + R_M$. The term S_2 equals $\dfrac{S_1 - R_1}{(1+M)} = \dfrac{R_M}{(1+M)}$. As discussed previously, when R_1 is very small (considering photosynthesis as a function of internal air space $[CO_2]$), S_1 approaches R_M and S_2 approaches $R_M/(1+M)$. Thus to consider now the model with variable and substantial stomatal resistance, only the manner in which S_1 is expressed in the over-all net photosynthesis function must be changed. The necessary change in the equations presented in the appendix of Tenhunen and Westrin (1979) occurs in equation A.4. The modified equation is:

$$P = \frac{AA - [(AA)^2 - BB]^{\frac{1}{2}}}{2R^*} \qquad (3)$$

where: $AA = C_A + K_C\beta + R^*(P_M - W_P) - W_P\left(\dfrac{R_M}{1+M}\right)$

$BB = 4R^*\left[\left(C_A - W_P\dfrac{R_M}{1+M}\right)(P_M - W_P) - W_P K_C\beta\right]$

$\beta = \left(1 + \dfrac{[O_2]}{K_{O_2}}\right)$

$R^* = R_1 + R_M\,(s\,cm^{-1})$

$R_1 = 1.56 R_{WV}^{total}\,(\text{see Eq. 1})$

P_M is the rate of photosynthesis at a specific light intensity, saturating carbon dioxide, and a specific leaf temperature ($nM\,cm^{-2}\,s^{-1}$)

W_P is the rate of photorespiration based on CO_2 evolution ($nM\ cm^{-2} s^{-1}$)

K_C is a constant equal to the chloroplast concentration of carbon dioxide (photorespiration = 0) at which $P = P_M/2$

K_{O_2} is a constant equal to the oxygen concentration (chloroplast $[CO_2] = 0$) at which W_P equals one-half the maximal photorespiration rate at the specific leaf temperature and light intensity ($nM\ cm^{-2} s^{-1}$)

For further information on the derivation of Eq. 3 see Tenhunen et al. (1977). The CO_2 input variable to the calculations has now become C_A (air concentration outside the boundary layer) rather than C_w (concentration in the air space at the cell walls).

Daily time courses of apricot leaf net photosynthesis were measured on 60 days. Preliminary analysis indicated that on 22 days for several groups of leaves, the photosynthetic capacity of leaves appeared to be much less than that observed in most cases. Thirty-eight days with high capacity photosynthesis were selected for applying the model. This provided a data set with approximately 7,600 observations at five minute intervals for each variable during the daytime (measurable light) hours. Days of observation were distributed from June 25, 1976 to September 30, 1976. Observed leaf temperatures varied from 9° C to 38° C at low light intensities (0–20 klx) and from 14° C to 45° C at high light intensities.

The initial version of the photosynthesis model WHOLE-PHOT, allowing calculation of net photosynthesis rate in response to four independent variables was for the most part based on data from wheat obtained by Jolliffe and Tregunna (1973). While a number of simplifying assumptions were made in the initial version due to lack of specific data, such as temperature independent constant mesophyll transport resistance, the model very closely reproduced observed wheat net photosynthesis responses, including a typical C_3 type temperature response curve whose optimum shifted to higher temperatures with increasing light intensity. Here we have attempted to adjust the model in a reasonable fashion in order to reproduce characteristics of net photosynthesis appropriate for the apricot data set described above. This was done by comparing an apricot temperature response curve, synthesized by sorting out net photosynthesis rates from the 7,600 individual observations at arbitrarily chosen values for light intensity and leaf diffusion resistance, with a temperature response curve simulated for the same conditions.

Immediately apparent upon comparison of calculated values from the original version of WHOLEPHOT with observed values of the specific temperature curve of apricot was that the absolute level of net photosynthesis calculated was slightly high and that while the calculated temperature response was generally correct, it was also too flat. As mentioned above, the wheat model included a constant value for mesophyll resistance (here defined as the reciprocal of the initial slope of the CO_2 response curve at 1% oxygen) which is most probably not the case. As discussed in the previous paper, there is evidence that mesophyll resistance decreases to a minimum around the temperature optimum for photosynthesis and then increases again with increasing temperature. Though critical experiments at 1% oxygen remain to be done to establish such a relationship for the C_3 apricot leaf, a parabolic temperature dependency was then included in the apricot model, based on the observations of mesophyll resistance in *Astrebla lappacea* as described by Doley and Yates (1976; their Fig. 8, short dashes).
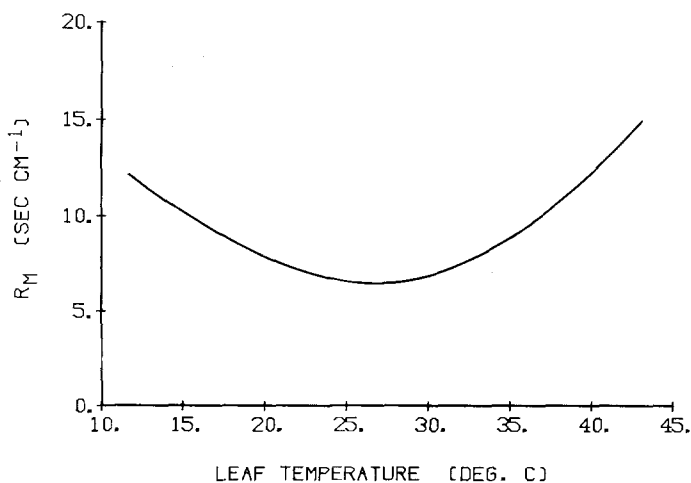

Fig. 1. Temperature dependency for mesophyll resistance included in the apricot version of WHOLEPHOT

The temperature response for apricot was then better reproduced in simulation when considered from the standpoint of curvature. The absolute level for calculated net photosynthesis was adjusted by moving the mesophyll resistance parabola obtained from the Doley and Yates data with respect to the temperature and mesophyll resistance axes (thus changing the magnitude of mesophyll resistance). In addition, the set value for P_{MLT}, the maximum capacity for photosynthesis at saturating CO_2, saturating light, and optimal leaf temperature, was decreased slightly. Further aspects of the work of Doley and Yates support the idea that mesophyll resistance as a function of temperature can be shifted depending on growth conditions and it is clear from work on various plants (Mooney and Harrison, 1970) that the minimum resistance level (lowest point of the parabola) is variable. It is possible that adjustment of the temperature dependencies for leaf affinities for CO_2 and O_2 (K_C and K_{O_2}; see Eq. 3) would provide a different and even better description of the apricot data to be presented. On the other hand, until more data has been gathered to re-evaluate the meaning of these controversial affinity parameters (Tenhunen et al., 1979b, c), alteration of the temperature dependencies built into WHOLEPHOT for K_C and K_{O_2} (Tenhunen and Westrin, 1979) would be even more speculative.

The final temperature dependency for mesophyll resistance used to simulate apricot net photosynthesis is shown in Fig. 1. The equation describing the curve is:

$$R_M = 0.028429\ T_x^2 - 1.7567\ T_x + 28.534 + 5.0 \tag{4}$$

where: R_M is in $s\ cm^{-1}$.
T_L is leaf temperature (°C).
T_x is ($T_L + 5.0$) and accounts for a shift of five degrees in the Doley and Yates parabola along the temperature axis (°C).

The equation is written with two constant terms. The first constant term is that appropriate for the Doley and Yates parabola. The second constant (5.0) accounts for the additional shift of the original parabola to higher resistance values. The final value for P_{MLT} for apricot is 3.7 $nM\ cm^{-2} s^{-1}$.
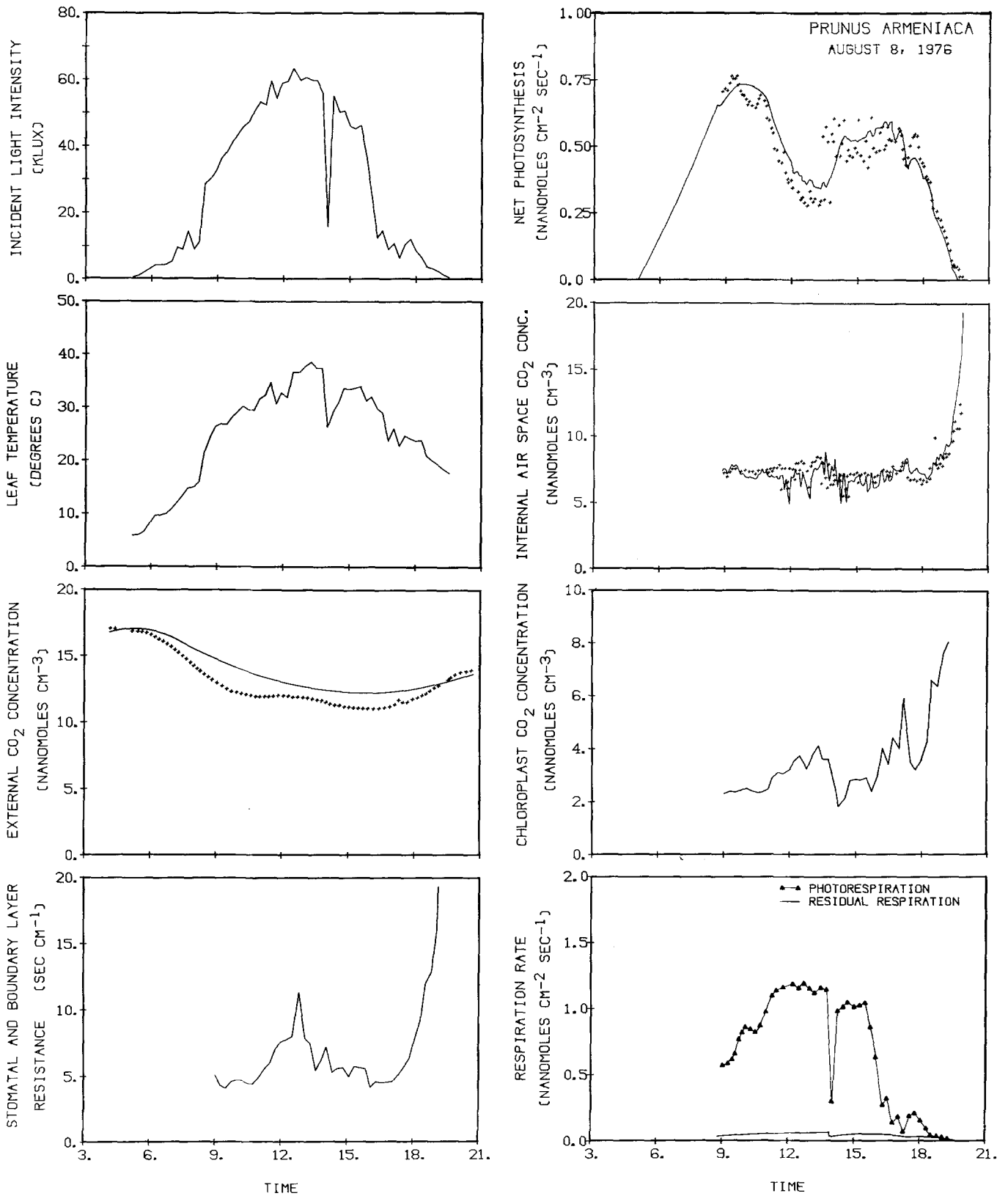
Fig. 2. Daily time courses of measured input data to the model *(left of figure)* and model response compared to observed leaf behavior *(right of figure)* for *Prunus armeniaca* on August 8, 1976. Solid line of external CO_2 concentration graph is concentration in external air; symbols are concentrations in air within the measurement cuvette. Solid lines in net photosynthesis and internal air space CO_2 concentration graphs are based on observed behavior of photosynthesis; symbols are steady-state calculated values from the model at 5 min intervals
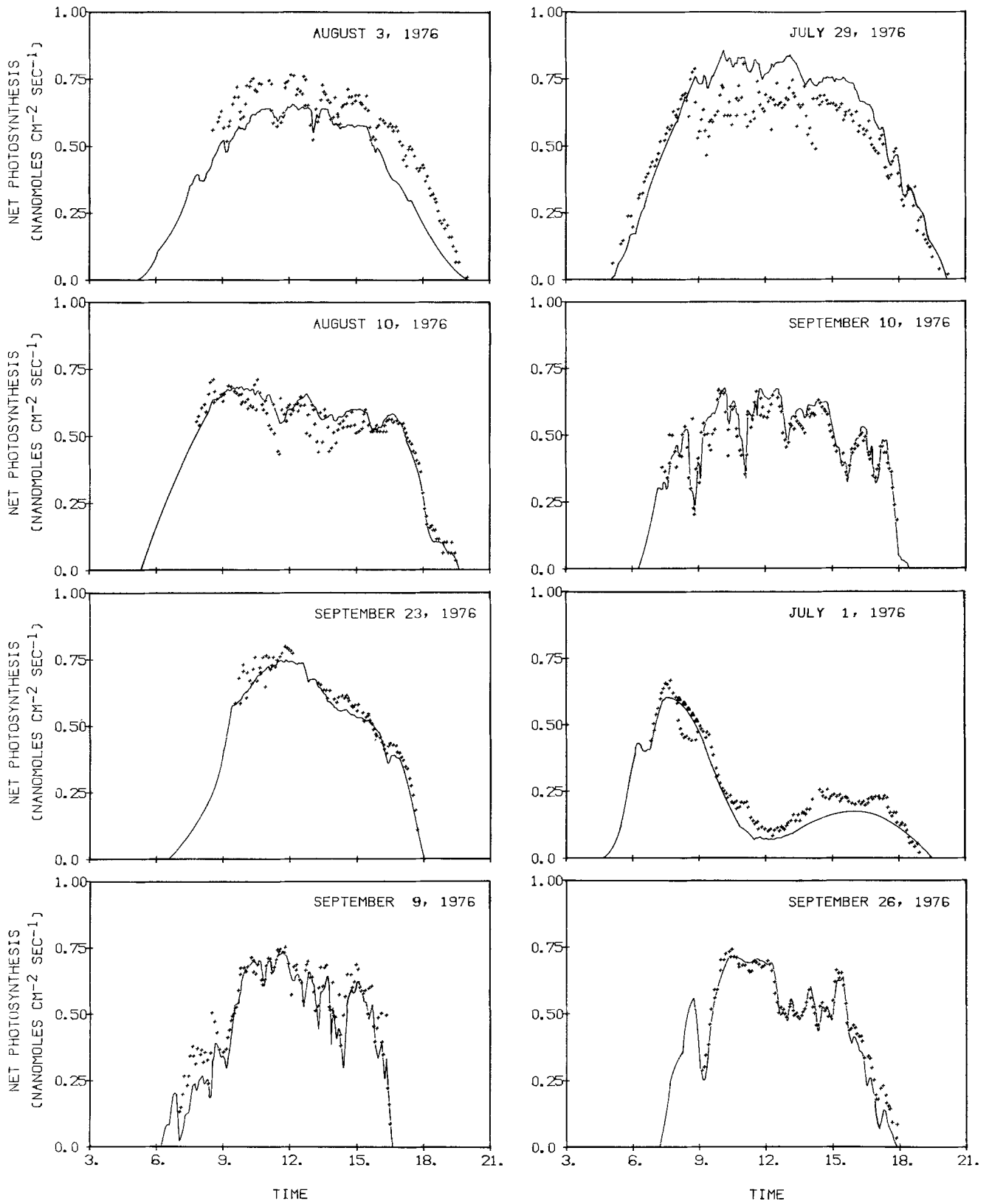
Fig. 3. Daily time courses of net photosynthesis observed in *Prunus armeniaca (solid lines)* compared to calculated net photosynthesis rates obtained with the model *(symbols)*

Results of Daily Time Course Simulations

Daily time courses of net photosynthesis were calculated for 38 days of observation with the specific apricot version of WHOLE-PHOT described. The example in Fig. 2 for calculations on August 8, 1976 shows typical time courses for input variables (left column of the figure) and variables calculated with the model (right column of the figure). The input variable values shown were used for the calculations in the following manner (see Methods and Appendix of Tenhunen and Westrin, 1979). Incident light intensity in kilolux is converted to µEinsteins cm^{-2} s^{-1} with Eq. 1 and enters as the variable L. Measured leaf temperature (°C) is converted to absolute leaf temperature ($T_L + 273$.) and enters as the variable T_K (see further Tenhunen et al., 1976 b). Early and late in the day, cuvette CO_2 concentration (symbols in external CO_2 graph) rises above outside air concentration (solid line) due to respiration. With positive net photosynthesis, the concentration is lowered below outside concentration dependent on the photosynthesis rate. The change is not more than 25 ppm. The [CO_2] indicated by the symbols enters the calculations as the variable C_A. The stomatal and boundary layer resistance for water vapor diffusion enters as the variable R_{WV}^{total}. The boundary layer component was not measured separately. Wind speed is constant at approximately 150 cm s^{-1}. The oxygen concentration input variable [O_2] is set constant at 0.21.

Shown in the second column of the figure are the model output values and the comparison of these values to the observed net photosynthesis and calculated internal air space CO_2 concentration. In these comparisons (top two graphs on right), the solid line is in each case the observed net photosynthesis rate or calculated internal CO_2 concentration based on observation, while the symbols are calculated estimates for the steady-state obtained as model output. The rationale for this presentation is that the measured values are integrated responses dependent on the time constant of the chamber and leaf and on continuous change in light and leaf temperature. The calculated values on the other hand result in response to point measurements. We expect and also observe for the steady-state calculations a much greater scatter, which when averaged closely approximates the observed response.

Since internal air space CO_2 concentration is estimated from either observed or calculated net photosynthesis rates and from measured leaf diffusion resistance in both cases, the two estimates will agree when net photosynthesis rate is accurately predicted as seen in Fig. 2. The model also predicts a time course for photorespiration and residual respiration rate and for [CO_2] at the chloroplast fixation site (see Tenhunen and Westrin, 1979). These are greatly affected by the assumptions of the model concerning diffusion or transport relationships between cytoplasm sites within leaf cells (Tenhunen et al., 1979 b). Thus, they should only be considered as hypothetical suggested values at the present time. Simulated photorespiration as described by this model appears to be most influenced by changes in incident light intensity and leaf temperature under natural conditions.

Daily variation in the time course of net photosynthesis in apricot depends on environmental factors directly affecting photosynthesis, such as degree of cloudiness as it determines light intensity and leaf temperature, but also on factors influencing stomatal behavior. The results shown in Fig. 3 demonstrate that the model predicts extremely well a variety of photosynthetic patterns under various actual weather conditions suggesting that for certain purposes at least, the description of interactions in the model is adequate. Due to leaf variability, the prediction of net photosynthesis is in some cases higher (August 3 in Fig. 3) and in other cases lower (July 29) than the measured values. But in all cases the characteristics for the day are well followed with simultaneous increments and decrements in the observed and predicted responses.

In apricot, the daily time course pattern is strongly determined by the response of stomata to vapor pressure deficits and to leaf temperature (Schulze et al., 1974). Increasing vapor pressure deficit tends to close stomates while increasing leaf temperature tends to open stomates. The resistance at any time results from a changing interplay of these factors. At low leaf temperatures and a low vapor pressure deficit, dome-shaped responses are observed where the maximum daily rate is rapidly attained in the morning and where photosynthesis drops in the afternoon in response to light intensity (August 10). This dome-shaped response can be greatly modified by fluctuating light due to variable cloudiness (September 10). As leaf temperatures and vapor pressure deficits increase, a tendency toward midday stomatal closure is observed in apricot. Under such conditions, photosynthesis rates may be reduced directly by temperature effects but also by restricted CO_2 supply. With only moderate increase in leaf temperature and in vapor pressure deficit, a photosynthetic response is observed with a pronounced shoulder in the late afternoon (September 23). At high leaf temperatures and large vapor pressure deficits, a pronounced midday stomatal closure occurs followed by re-opening of stomata as leaf temperature and vapor pressure deficit decrease in the afternoon. In this case a two peaked response curve is obtained for net photosynthesis (August 8 in Fig. 2). At extremely high leaf temperatures and vapor pressure deficits, extreme stomatal closure occurs, beginning in the late morning. Decreasing temperature and vapor pressure deficit in the afternoon may allow stomata to partially re-open. In this case, the observed net photosynthetic response reveals a morning peak in photosynthesis and a second extremely reduced afternoon peak (July 1). Finally, totally irregular patterns in photosynthetic response may be seen as fluctuating light intensity is superimposed on characteristic stomatal response patterns (September 9 and 26). In all cases, the model behaves in a fashion extremely similar to that of the leaves studied.

A frequent methodological problem seen in these data is the lack of good transpiration data in the early morning hours. Calculation of net photosynthesis rates with the model is only possible when reliable water exchange data and estimates of leaf diffusion resistance are obtained. The major causes of failure to obtain these data and of the consequent limitation on calculation of daily time course data with the model are condensation due to radiative cooling of the chambers during the night and problems associated with the dew point controlling systems as they adjust to condensation effects and renewed transpiration. Since CO_2 exchange data are easily obtained at all times, it should in the future be possible to use those data in conjunction with the photosynthesis model and environmental information to calculate the only values of resistance compatible with observation and thus from energy budget considerations to obtain the missing resistance values and transpiration rates.

A second methodological problem that can be corrected by applying the net photosynthesis model is shown in the time course data for July 1 in Fig. 3. Shadows may fall on the light sensor but not on the leaves or vice versa. In such situations, the model responds to the input of light sensor data whereas the leaves respond to actual conditions. An example of such a case where this error may be eliminated is shown on July 1 as indicated by the black triangle symbols. Here the light sensor was temporarily shaded, resulting in a sharp drop and recovery in the simulated photosynthetic response between 8 and 9 h. Such a decrease in
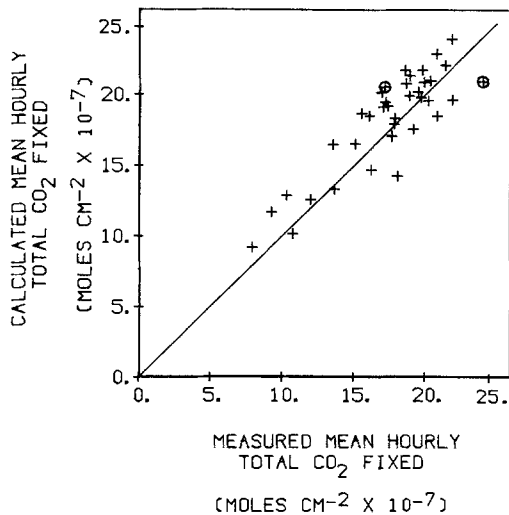
Fig. 4. Integrated net photosynthesis comparison based on observed and calculated rates for 38 days of observation with *Prunus armeniaca*. Integration is for those time periods in which water exchange data and calculated leaf diffusion resistance were reliable. Circled symbols are for August 3 and July 29 of Fig. 3 ($r^2 = 0.87$)

light intensity reaching the leaves would also have resulted in a decrease in observed net photosynthesis. When incident light intensity as input is corrected with data from another leaf chamber, the rates indicated with triangles are calculated.

In order to obtain an impression of the overall model performance for the 38 days of observation considered in the analysis, observed and calculated net photosynthesis rates were integrated for those time periods in which water exchange data and calculated leaf diffusion resistance were found to be reliable. Since the periods of integration were variable in length depending on controller function, the values were standardized as mean hourly values. The results are presented in Fig. 4. Each symbol represents a single day. The difference in magnitude of the mean hourly total CO_2 fixed is due to variation in environmental conditions. A one to one correspondence (solid line) between the model and observations (symbols) is closely approximated ($r^2 = 0.87$) for a considerable range in mean hourly total CO_2 fixed, i.e. for a considerable range in type of daily weather. Two plus symbols are further enclosed in a circle. These two symbols are those obtained on August 3 and July 29 (see Fig. 3). These days as presented are appropriate examples of the extremes of deviation of the model from measured data. Observations on other days are more closely approximated and the symbols fall closer to the solid line in Fig. 4.

Discussion and Conclusion

In previous studies of seasonal change in the photosynthetic response of apricot (Lange et al., 1974), measurements of the "potential maximum" of net photosynthesis at saturating light intensity, optimal temperature, and with high humidity to effect minimal stomatal resistances indicated that after an initial increase in capacity during early vegetative stages, very little change in photosynthetic capacity takes place. Constancy in the photosynthetic capacity is supported by the results presented, demonstrating

that a single equation (single maximum capacity P_{MLT}) can be applied from late June to late September. This apparent constancy of photosynthetic capacity in apricot suits it well for analysis with the photosynthesis model presented and has helped considerably in development of the model to its present stage. Analysis of the net photosynthesis response of other species in which previous study suggests continuous change in photosynthetic capacity, e. g. continuous rise in the "potential maximum" for net photosynthesis in newly sprouted shoots of *Hammada scoparia* (Lange et al., 1974), may be much more difficult.

The previous studies of apricot net photosynthesis mentioned above at the Avdat Farm in the Negev included determination of the net photosynthesis response to temperature at saturating light and 100% relative humidity (vapor pressure deficit leaf to air constant at zero). A marked shift in the temperature response curve (optimum temperature and upper compensation point) occurred over time even in additionally irrigated apricot grown under run-off farming conditions. In the present investigation, an attempt was made to sort out temperature response curves from daily time course data measured early in the season (June 25 to July 31) and late in the season (September) at otherwise constant values of water concentration deficit leaf to air and light intensity. It was hoped that it might in this way be possible to gain further insight into possible seasonal changes in the temperature response curve for wellwatered plants as reported previously. This attempt was, however, unsuccessful due to the extreme correlation of temperature and vapor pressure deficit leaf to air. At any value of vapor pressure deficit, only a limited range of leaf temperatures are experienced and it is not possible to synthesize a temperature response curve from these. Therefore, it is not known whether a shift in the temperature response of net photosynthesis of the type described previously occurred in the present study. We can only say that within existing error, the temperature characteristics built into the model are equally applicable early and late in the season.

The model of net photosynthesis used here has the advantage of providing a comprehensive description of net photosynthesis under natural conditions based on model parameters derived from gas exchange data. The model is assembled such that some of the gas exchange measurements must be carried out under extreme or "unnatural conditions" in order to determine values of parameters which have physiological meaning. These physiological parameters are then used to predict the behavior of net photosynthesis in response to a naturally limited range of CO_2 concentration at constant $[O_2]$ and with variable light intensity and leaf temperature.

The slope of the P response to internal CO_2 concentration has been called the carboxylation efficiency (Forrester et al., 1966; Tregunna et al., 1966), where it should be noted that carboxylation efficiency is oxygen dependent. Following further a tradition established by Gaastra (1959), the reciprocal of the carboxylation efficiency obtained at 21% oxygen has often been termed the mesophyll resistance to carbon fixation with the realization that part of this resistance is due to the biochemical step of fixation and part is due to photorespiratory production of CO_2.

In the analysis discussed here, mesophyll resistance to CO_2 transport (the parameter R_M) is defined slightly differently as the reciprocal of the initial slope of the CO_2 response curve of net photosynthesis to internal air space CO_2 concentration under nonphotorespiring conditions. It is a fundamental component of the "apparent" mesophyll resistance encountered with ambient gas concentrations (photorespiring conditions; see also Tenhunen et al., 1979a). We have attempted to establish a parameter at

present interpreted as affecting CO_2 transport to the fixation site, but a parameter free from photorespiratory influence. Changes in this paramter R_M with respect to light intensity and temperature are not well understood. It remains a parameter of extreme complexity containing both true transport components dependent on leaf and cell geometry and biochemical components as discussed by Yocum and Lommen (1975), Raven (1977), Sinclair et al. (1977), and Prioul et al. (1975). A continuing effort must be devoted to interpretation and re-interpretation of the biochemical meaning of R_M and of the other parameters that have been effectively used to describe net photosynthesis response, since it is desirable to interpret leaf gas exchange under field conditions in physiological and biochemical terms.

At the present stage of development, the model provides an extensive hypothesis concerning the response of apricot net photosynthesis. Experimentation under the "unnatural conditions" mentioned above has not been completed such that we can at present support the settings used for parameter values. These assumptions built into the model must be further tested. Further experimentation under controlled laboratory conditions and in the field may, however, allow a better understanding of the relationship of steady-state laboratory photosynthesis to simulated steady-state photosynthesis and thus to actual net photosynthesis under fluctuating conditions. Further elaborations and improvements will be made in the model as new information becomes available but we feel that we have demonstrated the soundness of our approach and have accomplished a first approximation of the linking of net photosynthetic mechanisms and environment in the context of necessary compromises and simplifications. The present predictive model can be used now to examine characteristics of leaf net photosynthetic behavior and how they relate to other ecologically important aspects of leaf function, e.g. water use efficiency. The model for photosynthesis provides also a baseline under optimal well watered conditions for examination of photosynthesis in response to drying or other types of stress. The goal of further endeavors will be to adapt the model to various plants in order to evaluate the physiological bases of species-specific differences in primary photosynthetic production.

References

Doley, D., Yates, D.: Gas exchange of Mitchell grass [*Astrebla lappacea* (Lindl.) Domin] in relation to irradiance, carbon dioxide supply, leaf temperature and temperature history. Aust. J. Plant Physiol. **3**, 471–487 (1976)

Forrester, M., Krotkov, G., Nelson, C.: Effect of oxygen on photosynthesis, photorespiration and respiration in detached leaves. I. Soybean. Plant Physiol. **41**, 422–427 (1966)

Gaastra, P.: Photosynthesis of crop plants as influenced by light, carbon dioxide, temperature and stomatal diffusion resistance. Med. Land. Wageningen **59**, 1–68 (1959)

Hall, A.E.: A model of leaf photosynthesis and respiration for predicting carbon dioxide assimilation in different environments. Oecologia, (Berl.) **43**, 299–316 (1979)

Jolliffe, P., Tregunna, E.: Environmental regulation of the oxygen effect on apparent photosynthesis in wheat. Can. J. Bot. **51**, 841–853 (1973)

Koch, W., Lange, O.L., Schulze, E.-D.: Ecophysiological investigations on wild and cultivated plants in the Negev Desert. I. Methods: A mobile laboratory for measuring carbon dioxide fixation and water vapor exchange. Oecologia (Berl.) **8**, 296–309 (1971)

Lange, O.L., Meyer, A.: Mittäglicher Stomataschluß bei Aprikose (*Prunus armeniaca*) und Wein (*Vitis vinifera*) im Freiland trotz guter Bodenwasser-Versorgung. Flora **168**, 511–528 (1979)

Lange, O.L., Schulze, E.-D., Evenari, M., Kappen, L., Buschbom, U.: The temperature-related photosynthetic capacity of plants under desert conditions. I. Seasonal changes of the photosynthetic response to temperature. Oecologia (Berl.) **17**, 97–110 (1974)

Lange, O.L., Schulze, E.-D., Koch, W.: CO_2-Gaswechsel und Wasserhaushalt von Pflanzen in der Negev-Wüste am Ende der Trockenzeit. Ber. Dtsch. Bot. Ges. **82**, 39–61 (1969)

Lommen, P., Schwintzer, C., Yocum, D., Gates, D.M.: A model for describing photosynthesis in terms of gas diffusion and enzyme kinetics. Planta **98**, 195–220 (1971)

Mooney, H., Harrison, A.: The influence of conditioning temperature on subsequent temperature related photosynthetic capacity in higher plants. Prediction of photosynthetic productivity, pp. 411–418. Wageningen, The Netherlands: Pudoc 1970

Nobel, P.: Introduction to Biophysical Plant Physiology, W.H. Freeman, San Francisco, 1974

Peisker, M.: Ein Modell der Sauerstoffabhängigkeit des photosynthetischen CO_2-Gaswechsels von C_3-Pflanzen. Kulturpflanze **24**, 221–235 (1976)

Prioul, J., Chartier, P.: Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO_2 fixation: A critical analysis of the methods used. Ann. Bot. **41**, 789–800 (1977)

Raven, J.: Ribulose biphosphate carboxylase activity in terrestrial plants: Significance of O_2 and CO_2 diffusion. Current Advances in Plant Science **30**, 579–590 (1977)

Schulze, E.-D., Lange, O.L., Evenari, M., Kappen, L., Buschbom, U.: The role of air humidity and leaf temperature in controlling stomatal resistance of *Prunus armeniaca L.* under desert conditions. I. A simulation of the daily course of stomatal resistance. Oecologia (Berl.) **17**, 159–170 (1974)

Schulze, E.-D., Lange, O.L., Lembke, G.: A digital registration system for net photosynthesis and transpiration measurements in the field and an associated analysis of errors. Oecologia (Berl.) **10**, 151–166 (1972)

Sinclair, T., Goudriaan, J., de Wit, C.: Mesophyll resistance and CO_2 compensation concentration in leaf photosynthesis models. Photosynthetica **11**, 56–65 (1977)

Tenhunen, J., Hesketh, J., Gates, D.M.: Leaf photosynthesis models. Predicting photosynthate production and use for ecosystem models. West Palm Beach: CRC Press 1979a

Tenhunen, J., Hesketh, J., Harley, P.: Modeling C_3 leaf respiration in the light. Predicting photosynthate production and use for ecosystem models. West Palm Beach: CRC Press 1979b

Tenhunen, J., Weber, J., Filipek, L., Gates, D.M.: Development of a photosynthesis model with an emphasis on ecological applications. III. Carbon dioxide and oxygen dependencies. Oecologia (Berl.) **30**, 189–207 (1977)

Tenhunen, J., Weber, J., Yocum, C., Gates, D.M.: Development

of a photosynthesis model with an emphasis on ecological applications. II. Analysis of a data set describing the P_M surface. Oecologia (Berl.) **26**, 101–119 (1976b)

Tenhunen, J., Weber, J., Yocum, C., Gates, D.M.: Solubility of gases and the temperature dependency of whole leaf affinities for carbon dioxide and oxygen. An alternative perspective. Plant Physiol. **63**, 916–923 (1979c)

Tenhunen, J., Westrin, S.: Development of a photosynthesis model with an emphasis on ecological applications. IV. WHOLE-PHOT – Whole leaf photosynthesis in response to four independent variables. Oecologia (Berl.) **41**, 145–162 (1979)

Tenhunen, J., Yocum, C., Gates, D.M.: Development of a photosynthesis model with an emphasis on ecological applications. I. Theory. Oecologia (Berl.) **26**, 89–100 (1976a)

Tregunna, E., Krotkov, G., and Nelson, C.: Effect of oxygen on the rate of photorespiration in detached tobacco leaves. Physiol. Plant **19**, 723–733 (1966)

Yocum, C., Lommen, P.: Mesophyll resistances. Perspectives of biophysical ecology, Ecological Studies 12. pp. 45–54 Berlin-Heidelberg-New York: Springer 1975