A Model for Net Photosynthesis of Rose Leaves as a Function of Photosynthetically Active Radiation, Leaf Temperature, and Leaf Age

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Abstract. A mathematical description for the relationship between the rate of rose (Rosa hybrida L.) leaf net photosynthesis and photosynthetically active radiation, leaf temperature, and leaf age is developed. The model provides a tool for the prediction of these rates for leaves growing in a rose crop canopy.

Mathematical crop models are valuable tools for optimizing production practices for many agronomic crops (Whisler et al., 1986). Such models predict crop growth and development in response to environmental factors such as irradiance, temperature, and CO₂ concentration. One of the most feasible approaches in developing crop simulation models is to use modules (Reynolds et al., 1988) where each module focuses exclusively on one physiological phenomenon. Typically, there are modules for photosynthesis, respiration, assimilate partitioning, and various other processes that may be of specific interest, such as fruit or leaf abscission. This paper describes the development of one such module for a rose crop model: a net leaf photosynthesis model responsive to photosynthetically active radiation (PAR), leaf temperature, and leaf age.

Aikin and Hanan (1975) and Bozarth et al. (1982) measured the photosynthetic response of roses to irradiance. Both observed a pattern of saturation with increasing light levels. We (Pasian and Lieth, 1989) found a non-rectangular hyperbola to be a suitable mathematical description of the PAR response of rose leaves. We investigated the suitability of this model at various combinations of four temperatures and leaf ages and indicated that additional data over a wider range of leaf temperatures and ages were needed to incorporate these variables into the model.

Additional environmental variables can be incorporated into such a photosynthesis PAR response model by letting the saturated net photosynthetic rate (Pₘ), usually a parameter in such a model, vary with these variables. This approach is possible for leaf temperature because its effect on net photosynthesis is manifest mainly through its effect on Pₘ (Johnson and Thornley, 1984). Leaf age has also been shown to have an impact on Pₘ (Catsky and Ticha, 1980; Constable and Rawson, 1980; Field and Mooney, 1983) so that it can be dealt with in the same way. The objectives of this study were to: 1) supplement our earlier data (Pasian and Lieth, 1989); 2) formulate a mathematical model for net photosynthesis incorporating PAR, leaf temperature, and leaf age; and 3) calibrate this model.

Materials and Methods

All net ‘Cara Mia’ rose leaf photosynthesis rates were collected using a LI-COR 6000 photosynthesis meter (LI-COR, Lincoln, Neb.) (Pasian and Lieth, 1989). Plants were grown in containers in a greenhouse and moved to the site where measurements were to take place (usually a growth chamber). Measurements were made under a 1000-W metal-halide lamp suspended in a structure consisting of a metal tube framework.

Temperature response. Net CO₂ exchange rates of 20-day-old leaves at light saturation were collected with leaves at temperatures >37°C and <10°C. Growth chambers were used to provide conditions resulting in leaf temperatures up to 37°C. Leaf temperatures >37°C were attained by placing the frame and lamp, covered with black cloth, in direct sunlight outdoors on hot, sunny days during Aug. 1986 in Davis, Calif. While no sunlight penetrated to the leaves, the combination of high air temperature, long-wave radiation absorbed by the black cloth reradiating to the plant, radiation of heat from the lamp, and reduced air circulation resulted in controllable leaf temperatures ranging from 35 to 50°C. The interior of the structure was sprayed with deionized water every 5 min with a spray bottle so that the relative humidity (measured by the LI-COR 6000) was at least 30% for
Fig. 1. (A) Leaf net photosynthesis rates for temperatures <40°C measured in a growth chamber (circles) and for temperatures >35°C observed outdoors (squares), as described in text. (B) Graphs of \( g_1(T) \) (with \( b_1 = 2.33 \) and \( b_2 = 0.185 \)) and \( g_2(T) \) (with \( b_3 = 0.204 \)) and their product.

Fig. 2. Averages and SE bars for rose leaf net photosynthesis rates for leaf temperatures between 18 and 22°C at photosynthetically active radiation levels between 600 and 750 µmol·s\(^{-1}\)·m\(^{-2}\). The curve is \( f_2(a) \) with \( b_2 = 0.0357 \).

Table 1. Nonlinear least-squares summary statistics from fitting the model for \( P_m \) (mg·s\(^{-1}\)·m\(^{-2}\)) to the data. In this fitting, \( T_d \) and \( c_2 \) were fixed at 48.6°C and 0 mg·s\(^{-1}\)·m\(^{-2}\)·day\(^{-1}\), respectively.

| Source              | df  | Sum of squares |
|---------------------|-----|---------------|
| Regression          | 9   | 129.41        |
| Residual            | 601 | 4.68          |
| Uncorrected total   | 610 | 134.10        |

Parameter estimates

| Parameter | Estimate | Asymptotic SE | Asymptotic 95% CI |
|-----------|----------|---------------|-------------------|
| \( \alpha \) | 0.00341 | 0.00040       | 0.00263           |
| \( P_{m,T,a} \) | 1.03  | 0.07          | 0.90              |
| \( \theta \)  | 0.479  | 0.166         | 0.153             |
| \( b_1 \)    | 2.33   | 0.22          | 1.90              |
| \( b_2 \)    | 0.185  | 0.019         | 0.148             |
| \( b_3 \)    | 0.204  | 0.041         | 0.123             |
| \( c_2 \)    | 0.0357 | 0.0007        | 0.0343            |
| \( c_1 \)    | 0.00351| 0.00073       | 0.00208           |

Leaf age effect. \( P_m \) values at 20°C were measured on 12 leaves of ages 1, 3, 5, 15, 30, 50, 70, 89, 103, 110, and 142 days to supplement the existing data for ages 10, 20, 30, and 40 days. Leaf age was determined as the number of days since the date on which the leaflet unfolded. Six to eight photosynthetic measurements at PPFD of between 600 and 750 µmol·s\(^{-1}\)·m\(^{-2}\) were made for each selected leaf.

Results

Model development. The equation of the non-rectangular hyperbola (Thornley, 1976; Marshall and Biscoe, 1980), found to be suitable for rose leaf net CO\(_2\) exchange by Pasian and Lieth (1989), is:

\[
P_n = \frac{\alpha I + P_m - \sqrt{(\alpha I + P_m)^2 - 4\alpha I P_m \theta}}{2 \theta} - R_d\]  \([1]\)

where \( \alpha \) is photosynthetic efficiency, \( I \) is PPFD, \( P_m \) is PAR saturated rate of net photosynthesis, \( \theta \) is a parameter, and \( R_d \) is leaf dark respiration. Leaf temperature and age can be incorporated by replacing \( P_m \) with a function of leaf temperature \( (T) \) and leaf age \( (a) \). Assuming that these two effects are separate, this function takes the form:

\[
P_{m(T,a)} = P_{m,T,a} \cdot f_1(T) \cdot f_2(a)\]  \([2]\)

\( P_{m,T,a} \) is defined as the maximum net photosynthetic rate per unit leaf area over all PPFD levels, temperature, and ages. \( f_1(T) \) is a mathematical function describing the reduction from this absolute maximum due to leaf temperature. Similarly, \( f_2(a) \) is a function describing such a pattern for leaf age \( (a) \). The terms \( f_1(T) \) and \( f_2(a) \) must be selected to take on values between 0 and 1 so that \( P_{m(T,a)} \) will vary between 0 and \( P_{m,T,a} \). \( f_1(T) \) and \( f_2(a) \) can be constructed by considering \( P_n \) data at high PAR for a fixed level of \( a \) and \( T \), respectively.

Dark respiration \( (R_d) \) has been observed to increase with temperature in various species (Penning de Vries et al., 1979; Gent and Enoch, 1983), including roses (Pasian and Lieth, 1989). Variations in \( R_d \) with age have been observed in coffee and
cotton (Yamaguchi and Friend, 1979; Constable and Rawson, 1980), but not conclusively for roses (Pasian and Lieth, 1989).

The replacement of $R_d$ in Eq. [1] with a function of $T$ and $a$, i.e., $R_d(T,a)$, was also explored in this study.

**Modeling the leaf temperature effect.** Between 35 and 40°C, the values of $P_m$ obtained indoors ranged between 0.6 and 0.8 mg·s$^{-1}$·m$^{-2}$ (circles, Fig 1A), while those collected outdoors ranged from 1.0 to 1.1 (squares, Fig. 1A). This disparity (of unknown cause) precluded pooling the data. The data collected outdoors allowed estimation of the high temperature compensation point and the rate of decline of $P_m$ with high temperatures.

Above 37°C, $P_m$ for the 20-day-old leaves decreased with a steep negative slope (Fig. 1B) to zero. As temperatures increased above 48°C, the leaf wilted and dried out rapidly resulting in permanent damage.

All net photosynthetic rates for PPFD above 600 µmol·s$^{-1}$·m$^{-2}$ below 37°C for 20-day-old leaves increased with temperature up to $\approx 18$C followed by a leveling between 18C and 35C (Fig. 1A). Above 35C the rate decreased. This pattern is consistent with the flat plateau observed by Bozarth et al. (1982).

Assuming the high-temperature denaturization process to be separate from the remaining temperature effects, $f_1(T)$ was expressed as the product:

$$f_1(T) = g_1(T) \cdot g_2(T)$$

where $g_1(T)$ represents the reduction in $P_{m,T,a}$ for moderate and low, non-optimal temperatures, while $g_2(T)$ represents the denaturalization effect. As with $f_1(T)$ and $f_2(a)$, $g_1(T)$ and $g_2(T)$ must be elected so that their ranges are between 0 and 1. The function $g_1(T)$ should have a flat plateau for $T$ between 20 and 35C and a steep slope for $T$ between 5 and 10C (Fig 1B). The equation

$$g_1(T) = 1/(1 + e^{b_1 - b_2 T})$$

which satisfies these conditions, was used.

As temperatures rose above 40C, the decline in net photosynthesis became very pronounced, so that above some high temperature ($T_d$), the photosynthetic process was completely interrupted. The expression $1.0 - e^{-b_3(T_d-T)}$ has this pattern in that it is less than, but almost equal to, 1.0 for moderate and low values of $T$ where no denaturalization occurs, while declining rapidly for $T$ approaching $T_d$. The rate of the onset of decline (degree of convexity) is determined by the parameter $b_3$. As-
Fig. 4. Cross sections through the (four-dimensional) rose leaf photosynthesis surface at leaf ages of 5, 10, 20, 30, 40, 60, 100, and 140 days. Each three-dimensional cross section consists of the response surface for net photosynthesis (mg·s\(^{-1}\)·m\(^{-2}\)) as a function of leaf temperature (°C) and photosynthetically active radiation (µmol·s\(^{-1}\)·m\(^{-2}\)).

assuming no enzymatic activity for T above T\(_d\) resulted in the brane composition (Fong and Heath, 1977; Novitskaya et al., 1977). The function:

\[
g_2(T) = \begin{cases} 
1 - e^{-b_3(T_d-T)} & \text{if } T < T_d \\
0 & \text{if } T \geq T_d
\end{cases}
\]  

so that \(f_1(T)\) has the desired shape (Fig. 1B).

Modeling the leaf age effect. \(P_{\text{net}}\) as approximated by \(P_n\), measurements at PPFD above 600 µmol·s\(^{-1}\)·m\(^{-2}\), was low for young, rapidly expanding leaves, maximal at some intermediate age, followed by a gradual decline as leaves aged (Fig. 2). The increase for young leaves can be attributed to biochemical changes in the production of fully developed chloroplasts, including synthesis of a variety of molecules and increases in the total number of chloroplasts (Possingham, 1980; Leech and Baker, 1983). Reductions in photosynthetic rates as leaves age have been attributed to reductions in the concentrations of enzymes involved in the various photosynthetic reactions (Sestak, 1969; Hall and Brady, 1977; Zima and Sestak, 1979) and chloroplast membrane composition (Fong and Heath, 1977; Novitskaya et al., 1977). The function:

\[
f_2(a) = b_4 a e^{1 - a b_4}
\]  

was used since it has the desired shape (rapid increase to a maximum, gradual decline thereafter) and ranges between 0 and 1.0 (curve, Fig. 2).

Leaf dark respiration. In roses, \(R_d\) has been shown to increase with temperature, while no conclusive pattern was observed with age (Pasian and Lieth, 1989). Respiration rates generally follow a convex pattern with temperature (Penning de Vries et al., 1979) that has been interpreted to be exponential (Gent and Enoch, 1983). Todaria (1986) observed linear increases with temperatures up to 45°C in leaf samples of various subtropical species followed by a rapid decline between 45°C and 55°C. Although a form more complex than a linear equation is likely to be appropriate for temperatures <50°C, it could not be justified with the current data. Also, for temperatures above \(T_d\), \(R_d\) was
Model predictions (curves) and observed (circles) net photosynthesis rates for 20-day-old leaves over a range of leaf temperatures at PPFD > 600 µmol·s⁻¹·m⁻².

![Graph showing net photosynthesis rates for different temperatures](image)

Assumed to be zero due to the destruction of leaf tissue observed above this temperature. Thus, $R_d$ was represented as:

$$R_d(T,a) = \begin{cases} 
  c_0 + c_1T + c_2a & \text{if } T \leq T_d \\
  0 & \text{if } T > T_d 
\end{cases} \quad [7]$$

**Leaf net photosynthesis model calibration.** The individual components of the model (Eqs. [4]-[7]) were fit to the corresponding subsets of the data set with the nonlinear regression procedure, PROC NLIN, of the Statistical Analysis System (SAS Institute, 1987) to obtain preliminary estimates of all parameters. Combining Eqs. [1] through [7] resulted in the desired rose leaf net photosynthesis model that was then fit to the data using PROC NLIN, of the Statistical Analysis System (SAS Institute, 1987) to obtain preliminary estimates of all parameters and functions for each variable. Data would, of course, have to be collected over a wide range of all the variables. Mathematical equations for these functions could be formulated fitting of the model, the value of $c_2$ was found to be $0.0 \pm 0.00028$ mg·s⁻¹·m⁻²·day⁻¹. Setting $c_2$ to zero (i.e., removing the leaf age effect from the $R_d$ function) and refitting resulted in the parameter values shown in Table 1. This fit is highly significant with 97% of the total uncorrected sum of squares being accounted for by the model. All remaining parameters are significantly different from zero as indicated by the 95% confidence intervals.

**Discussion**

Grouping the accumulated $P_D$ data by the four leaf ages: 10, 20, 30, and 40 days, and four temperatures: 10, 20, 30, and 37°C (± 2°C), allows comparison of the predicted and observed $P_D$ rates (Fig. 3). On the whole, the model predicts all observed PAR response data satisfactorily, although substantial overestimation occurs for 30-day-old leaves at 20 and 37°C, while underestimation occurs for one case 20-day-old leaves at 10°C. Such deviations are not unexpected because the model assumes uniform conditions and plant material, while the data includes variation attributable to inter-plant variability, slight fluctuations in calibration of the photosynthesis meter, and leaf area measurement errors.

A sequence of three-dimensional plots (Fig. 4) illustrates the changes in the photosynthetic response to temperature and irradiance with leaf age. At all ages, the temperature response is fairly flat between 20 and 35°C, while the PAR cross section is always the saturation response of Eq. [1]. Above 48.6°C the denaturation response is evident ($P_o = 0$). Between 45°C and $T_d$, the net photosynthesis rate is negative, as gross photosynthesis rates become low while $R_d$ continues to increase.

Another check on how well the model behaves is to compare the measured photosynthetic rates at PAR near saturation with the model predictions. The leaf temperature pattern for $P_o$ of 20-day-old leaves at high PAR (Fig. 5) is not as flat as was originally anticipated, probably because of the paucity of data for temperatures ≤ 10°C. The parameters $b_1$, $b_2$, and $b_3$ are responsible for this behavior. With additional data at low temperatures, model calibration would probably result in different values for $b_2$, and possibly $b_3$, with smaller confidence intervals.

The model also could be improved by replacement of Eq. [7] with a more mechanistic description. The current selection is the simplest possible expression. The values of $c_0$ and $c_1$ result in negative values for $R_d$ for low $T$ resulting in a slight positive bias in $P_o$ for low $T$. This aberration is probably due to the equipment used in this study not being sensitive enough to measure respiration accurately.

The estimated values of $P_o$ for high PAR over leaf age for leaves at 20°C represent the trend in the data well (Fig. 6). The considerable variation about the predictions suggests that chronological time may not be the best way to represent leaf age. A physiological time variable, such as age units, might be a more suitable measure. Also, the model does not incorporate acclimation and adaptation effects that may cause leaves of the same age to have different photosynthetic capacities depending on environmental conditions in the days or weeks before the measurement.

Model extensions to include additional effects, such as CO₂ concentration, can be accomplished in the same way that leaf temperature and age were added here. Equation [2] is then replaced with a product of the overall maximum $P_o$ over all variables and functions for each variable. Data would, of course, have to be collected over a wide range of all the variables.
to provide the flexibility needed to validly represent the response of net photosynthesis at saturating PAR over the ranges of each variable. Subsequent recalibration would result in a predictive model for net leaf photosynthesis at all considered variables.

**Literature Cited**

Aikin, W.J. and J.J. Hanan. 1975. Photosynthesis in the rose; effect of light intensity, water potential and leaf age. J. Amer. Soc. Hort. Sci. 100:551-553.

Bozarth, C.S., R.A. Kennedy, and K.A. Schekel. 1982. The effect of leaf age on photosynthesis in rose. J. Amer. Soc. Hort. Sci. 107:707-712.

Catsky, J. and I. Ticha. 1980. Ontogenetic changes in the internal limitations to bean-leaf photosynthesis. Photosynthetica 14:392-400.

Constable, G.A. and H.M. Rawson. 1980. Effect of leaf position, expansion and age on photosynthesis, transpiration and water use of cotton. Austral. J. Plant Physiol. 7:89-100.

Gent, M.P.N. and H.Z. Enoch. 1983. Temperature dependence of vegetative growth and dark respiration: a mathematical model. Plant Physiol. 71:362-567.

Field, C. and H.A. Mooney. 1983. Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. Oecologia (Berlin) 56:348-355.

Fong, F. and R.L. Heath. 1977. Age dependent changes in phospholipids and galactolipids in primary bean leaves (Phaseolus vulgaris). Phytochemistry 16:215-217.

Hall, A.J. and C.J. Brady. 1977. Assimilate source-sink relationship in Capsicum annuum L. II. Effects of fruiting and defoliation on the photosynthetic capacity and senescence of leaves. Austral. J. Plant Physiol. 4:771-783.

Johnson, I.R. and J.H.M. Thornley. 1984. A model of instantaneous and daily canopy photosynthesis. J. Theor. Biol. 107:531-545.

Leech, R.M. and N.R. Baker. 1983. The development of photosynthetic capacity in leaves, p. 271-307; In: J.E. Dale and F.L. Millthorpe (eds.). The growth and functioning of leaves. Cambridge University Press, Cambridge, U.K.

Marshall, B. and P.V. Biscoe. 1980. A model for C3 leaves describing the dependence of net photosynthesis on irradiance. I. Derivation. J. Expt. Bot. 31:29-39.

Novitskaya, G.V., L.A. Rutskaya, and Y.G. Molotkovskii. 1977. Age changes of lipid composition and activity of the membranes in bean chloroplasts. *Fiziologia Rastenii* 24:35-43.

Pasian, C.C. and J.H. Lieth. 1980. Analysis of the response of net photosynthesis of rose leaves of varying ages to photosynthetically active radiation and temperature. J. Amer. Soc. Hort. Sci. 114(4):581-586.

Penning de Vries, F.W.T., J.M. Britte, and D. Kremer. 1979. Rates of respiration and increase in structural dry matter in young wheat, ryegrass and maize plants in relation to temperature, to water stress, and to their sugar content. Ann. Bot. 44:595-609.

Possingham, J.V. 1980. Plastid replication and development in the life cycle of higher plants. Annu. Rev. Plant Physiol. 31:113-129.

Reynolds, J.F., B. Acock, R.L. Dougherty, and J.D. Tenhunen. 1989. A modular structure for plant growth simulation models, p. 123-134. In: J.S. Pereira and J.J. Landsberg (eds.). Biomass production by fast growing trees. Kluwer Academic, Boston, Mass.

SAS Institute. 1987. The NLIN procedure. SAS/STAT guide for personal computers, Version 6 ed. SAS Institute Inc., Cary, N.C. p. 675-712.

Sestak, Z. 1969. Ratio of photosystem one and two particles in young and old leaves of spinach and radish. Photosynthetica 3:285-287.

Todaria, N.P. 1986. Respiration rates of some greenhouse cultivated tropical and subtropical species. Biol. Plant. (Praha) 28:280-287.

Thornley, J.H.M. 1976. Mathematical models in plant physiology. Academic, London.

Whisler, F.D., B. Acock, D.N. Baker, R.E. Fye, H.F. Hodges, J.R. Lambert, H.E. Lemon, J.M. McKinion, and V.R. Reddy. 1986. Crop simulation models in agronomic systems. Adv. Agron. 40:141-208.

Yamaguchi, T. and D.J.C. Friend. 1979. Effect of leaf age and irradiance on photosynthesis of Coffea arabica. Photosynthetica 13:271-278.

Zima, J. and Z. Sestak. 1979. Photosynthetic characteristics during ontogenesis of leaves: 4. Carbon fixation pathways, their enzymes and products. Photosynthetica 13:83-106.