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ON PARAMETRIC MODELLING OF PHOTOSYNTHETIC PROCESS

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KUZNETSOV P. P., POLIMBETOVA F. A., KIM G. G. and MAMONOV L. K. *On parametric modelling of photosynthetic process.* BIOTRONICS 15, 15-23, 1986. The theoretical continuous model of any process has incontestable advantages over its empirical "discrete" description based on the "black box" principle. This as well can be fully applied to photosynthesis the models of which would be able to effectively predict not only the "black box" responses to external effects but also to calculate its yield as a product of a determined "production process" with any variations of "parameters" included in the model. By the present time there is an ample information available both on the photosynthetic process and on regulation parameters (4). However, the scattered and contradictory character of this information urgently necessitates its generalizing analysis and formalization and ideally, also its adequate numerical evaluation using abstract mathematical apparatus. So, the object of this paper is to build such photosynthesis model which would include the most important parameters sufficiently postulated by the empirical practice.

Key words: photosynthesis; parametric model; air temperature; air humidity; photosynthetically active radiation; soil water potential.

INTRODUCTION

Any biological system or process can be presented by a certain set of physically measured values reflecting both external conditions—temperature, concentration, etc., and the object internal properties—metabolism intensity, degree of development and others. Thus the more we can measure, the better and of higher quality is our investigation. On the other hand, besides the qualitative set of empirical parameters it is desirable to have knowledge of the internal mechanism of their interrelations for a priori forecasting of the object response for their changes. The parametrical mathematical model would be the best for this purpose. This paper deals with the development of the nonconventional parametrical model in contrast to Ref. 2, 3, 6.

MATERIAL AND METHODS

To develop the "parametric" mathematical model of photosynthesis, the empirical data reported by Bikhele *et al.* (1) have been used. As a whole they can

be presented in the form of the following unknown function:

$$\phi_L^* = f(J_\phi, t_A, \psi_S, h_A, S_R/S_L) \quad (1)$$

where

ϕ_L —the photosynthesis in mg of CO₂ dm⁻² h⁻¹

J_ϕ —the radiation intensity (PAR, photosynthetically active radiation) in 10⁻² W cm⁻²

t_A —the ambient air temperature in °C

ψ_S —the soil moisture (water potential) in bars;

h_A —the relative air humidity

S_R/S_L —the root surface area S_R to leaf area S_L ratio

*—the obtained photosynthesis model as well as empirical data (1) consider ϕ_L for quantized time interval ($t=1$ h) per unit area ($S=1$ dm²). During the 1 h time interval the plant organism is assumed, on the average, to finish the process of adaptation to environmental changes (1, 4, 5, 7).

The analysis of the particular empirical data and plots of photosynthesis versus any one of the parameters given in Eq. (1) with the remaining parameters constant, has shown that the most nonlinear is the plot of photosynthesis versus temperature or the following special function:

$$\phi_L = f(t_A) \quad (2)$$

The peculiar feature of Eq. (2) (see Fig. 1) is that at the initial moment or during phase I of the process the photosynthetic intensity ϕ_L increases with the rise of temperature while the character of phase II is quite opposite to that of phase I, with t_A increase ϕ_L decrease is observed.

Inconsistency of the course of the process in the initial I and final II phases implies a variety of its interpretations by mathematical methods. We shall dwell upon the following.

Phase I of photosynthesis as a part of a more general process—biosynthesis—in the “unlimited nutrition” conditions (in our case—by high temperature) by the analogy may be expressed in the form of the following differential Malthus relation (6).

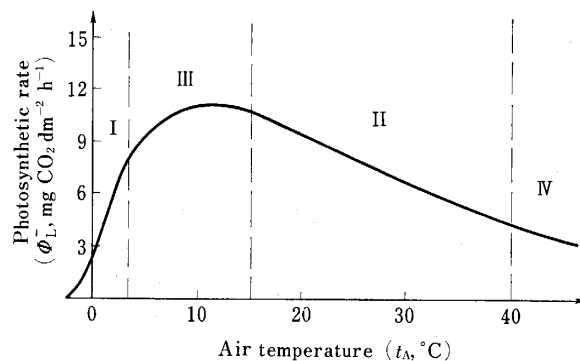


Fig. 1. Typical plot of photosynthesis as a function of temperature.

$$\frac{dX}{dt} = K \cdot X \quad (3)$$

where K is biomass growth rate coefficient.

Romanovsky *et al.* (6) also reported other models of biosynthesis of “single-cell cultures”—Verhulst-Pearl, Volterra and Caperon models. “The basic dependence” (5) is also Kostitsin—Volterra equation. Each of the models mentioned above includes specific “limiting factors” which are “dynamics limitation”, “depletion of nutrients” and “self-poisoning by metabolic products”. However, abstracting from these models which are essentially the modifications and extensions of the Malthus model, we propose the following differential relation to describe phase II of the process:

$$\frac{dX}{dt} = m \cdot \frac{X}{t} \quad (4)$$

where m is the “damping” coefficient.

That is, we adopt as a limiting factor of phase II of the process (2) its inverse dependence on the “argument”, or the relation X/t .

Using the above described as well as the note marked by the asterisk (*) in Eq. (1), by performing the necessary substitutions—of temperature t_A for time t and of ϕ_L for abstract functions X in Eqs. (3) and (4)—we can write the following differential equation—photosynthesis as a function of temperature—as a whole:

$$\frac{d\phi_L}{dt_A} = K \cdot \phi_L + m \cdot \frac{\phi_L}{t_A} \quad (5)$$

It is evident that summing algebraically the special dependences (3) and (4) in the expression (5) we assume that the “transition” phase III of the process (2) is just the result of the competition between the initial (nonlimited) phase I and the final (stress) phase II. This assumption is hypothetically supported by the fact that under the worse conditions, for example, with low soil moisture content ($\psi_s = -8$ bars) the dependence (4) naturally dominates leading to considerable reduction of maximum $\phi_{L \max}$ and to the left shift of the optimum $\phi_{L \text{opt}}$ towards lower temperatures (see Fig. 2).

The equation (5) has the analytical solution. Separation of variables gives:

$$\frac{d\phi_L}{\phi_L} = K \cdot dt_A + m \cdot \frac{dt_A}{t_A} \quad (6)$$

Integration yields:

$$\phi_L(t_A) = p \cdot e^{K \cdot t_A + m \cdot \ln t_A} \quad (7)$$

where $\ln p = C$ is the constant obtained as a result of integration of Eq. (6).

As it has been found later, the equation (7) approximates accurately enough a family of empirical data (1, see Fig. 2).

The coefficient of correlation between the linearized empirical data $\Delta \ln t_A$ and $\Delta \ln \phi_L$ in the t_A range from 0 to $+40^\circ\text{C}$ at probability levels of 0.950 to 0.975 is of the order of 0.981 to 0.991, respectively. Such a high correlation, close to the func-

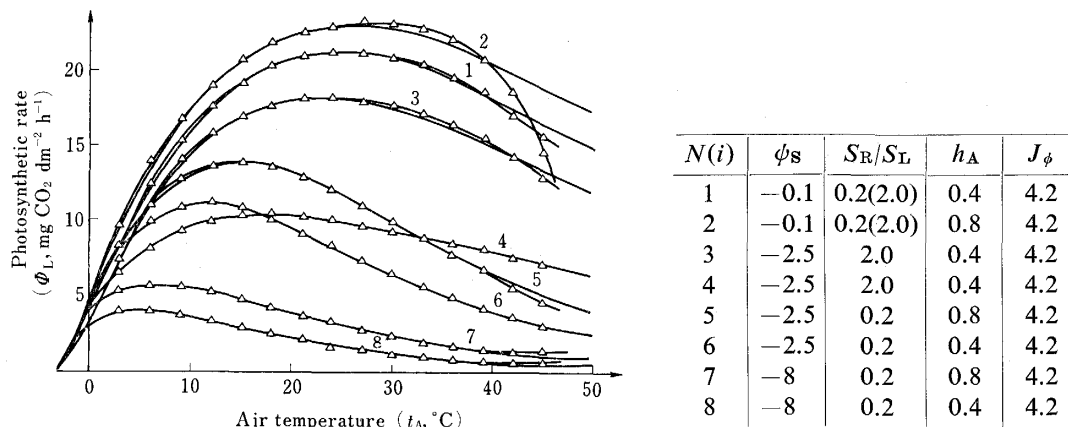


Fig. 2. Plot of photosynthesis as a function of temperature comparing empirical $\triangle-\triangle-\triangle$ and model — data.

tional one, allows to assume that the proposed hypotheses, Eqs. (3)–(5) and Eq. (7) can be rather close to the “macrofunction” and to the nature of the process under study. The minimal dispersion of nonconsidered factors (NF) in the range can serve as an objective criterion of the latter too. The minimal dispersion differs slightly from the average “functional” one for the whole family of empirical data $\phi_L=f(t_A)$ from Bikhele *et al.* (1).

For temperatures above $+40^\circ\text{C}$ (phase IV) the model forecast (7) disagrees with the experiment. In this case, while for the high soil moisture content conditions (low potential ϕ_S) the model gives the “excess” of the estimated ϕ_L , for soils with moisture deficit ($\phi_S=-8$ bars) it yields “shortage”.

Extrapolation of the model of Eq. (7) for the extended range of t_A from 0 to $+55^\circ\text{C}$ decreases its adequacy. In this case nonlinearity by Fisher criterion (3) between the linearized data $\Delta \ln t_A$ and $\Delta \ln \phi_L$ greatly rises, the NF dispersion increases and, what is most important, the forecast quality, or the probability of adequate forecast, decreases from 0.821 (for $\phi_S=-8$ bars) to 0.632 (for $\phi_S=-0.1$ bar). The description of the high-temperature region IV will obviously require modification of the model, Eq. (7).

MODEL DEVELOPMENT METHOD

The next stage of the photosynthesis model development is the incorporation of all the rest parameters into the expression (7). It has been performed in the following way.

Variations of statistical values of the functional parameters p , k and m of the approximating model of Eq.(7) are, in their turn, the reflection of variations of parameters ϕ_S , h_A , S_R/S_L in each of the particular process (2) experiments. That is, if the function (7) reads:

$$\phi_L = f(p, k, m) \quad (8)$$

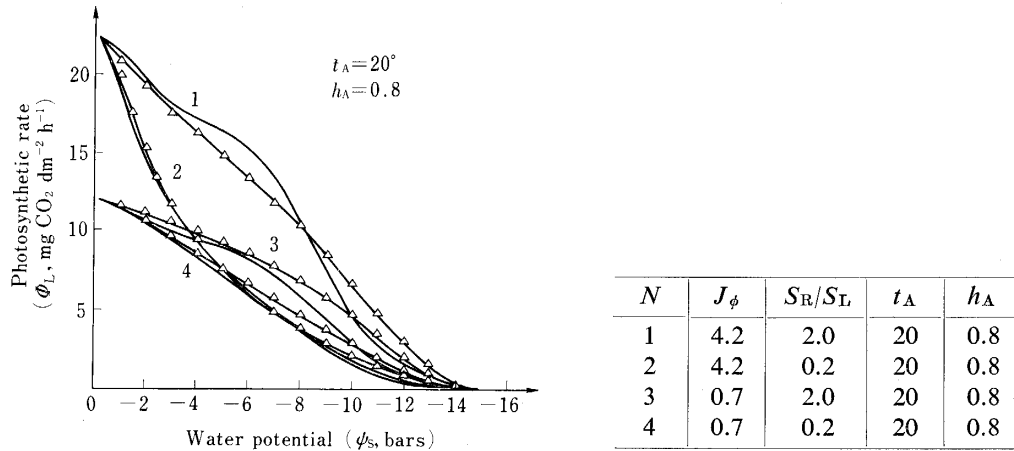


Fig. 3. Plots of photosynthesis as a function of soil water supply. The relative error of model data—obtained, as in Fig. 2, from calculation of ϕ_L by the output model, Eq. (16) (see below) is connected with the interpolation errors of the parameters ϕ_R , h_A and S_R/S_L in appropriate factorial planes (see below).

the functional parameters p , k and m are as follows:

$$p, k, m = f(\phi_S, h_A, S_R/S_L) \tag{9}$$

Of the priority importance among the parameters affecting the photosynthetic intensity presented in Eq. (9) is the water supply, or the soil water potential ϕ_S . It is adequately illustrated by the set of plots (2) (see Fig. 2) and by the set of empirical data $\phi_L=f(\phi_S)$ given below in Fig. 3.

Nonlinearity of the relation $\phi_L=f(\phi_S)$ in a particular case illustrated in Fig. 3 is also exhibited in a nonlinear fashion in the character of statistical values of the functional parameters p , k and m of the main “physical” model of Eq. (7). Therefore, the first “derived (input) functions” from Eq. (7) are as follows:

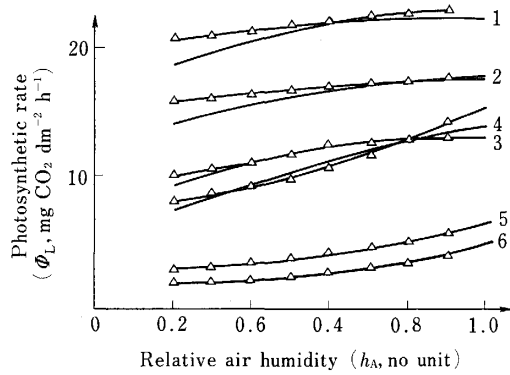
$$\begin{aligned} P_i &= a_0 + a_1 \cdot \phi_S + a_2 \cdot \phi_S^2 \\ k_i &= b_0 + b_1 \cdot \phi_S + b_2 \cdot \phi_S^2 \\ m_i &= c_0 + c_1 \cdot \phi_S + c_2 \cdot \phi_S^2 \end{aligned} \tag{10}$$

where i (N) is the number of the curve (the experiment) in Fig. 2.

The expressions (10) are seen to represent the quadratic interpolation polynomials of the values p , k and m in a special factorial plane ϕ_S .

The next parameter included in the main “physical” model of Eq. (7) is air humidity h_A . The empirical data of the special dependence of photosynthesis on air humidity are given below in Fig. 4.

Taking into account the roughly linear character of the relation $\phi_L=f(h_A)$ we have performed linear interpolation of the coefficients a_0 , a_1 , ..., c_2 of the parabolas (10), in a particular factorial plane h_A where



N	ψ_s	t_A	S_R/S_L	J_ϕ
1	-0.1	20	0.2	4.2
2	-0.1	10	0.2	4.2
3	-2.5	10	0.2	4.2
4	-2.5	20	0.2	4.2
5	-8	10	0.2	4.2
6	-8	20	0.2	4.2

Fig. 4. Plots of photosynthesis versus air humidity $\phi_L=f(h_A)$. Model-made data—are obtained from the output model, Eq. (16).

$$\begin{aligned}
 a_0 &= a_{00} + a_{01} \cdot h_A & (11) \\
 a_1 &= a_{10} + a_{11} \cdot h_A \\
 a_2 &= a_{20} + a_{21} \cdot h_A \\
 b_0 &= b_{00} + b_{01} \cdot h_A \\
 &\dots\dots\dots \\
 c_2 &= c_{20} + c_{21} \cdot h_A
 \end{aligned}$$

In its turn, with available empirical data (1) analogous to (2), but for the case of the well-developed root system, or for the relation $S_R/S_L=2.0$, we have performed similar, however, more “rough” linear interpolation of the coefficients $a_{00}, a_{01}, \dots, c_{01}$ of the relations (11) obtained above in the specific factorial plane S_R/S_L where:

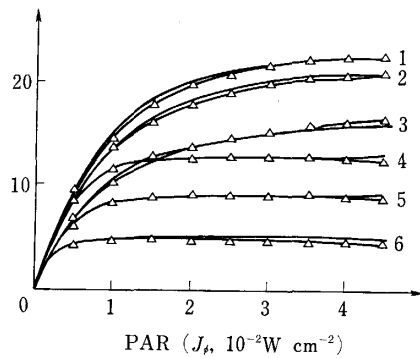
$$\begin{aligned}
 a_{00} &= a_{000} + a_{001} \cdot S_R/S_L & (12) \\
 a_{01} &= a_{010} + a_{011} \cdot S_R/S_L \\
 &\dots\dots\dots \\
 c_{21} &= c_{210} + c_{211} \cdot S_R/S_L
 \end{aligned}$$

The essence of the proposed method of interpreting Eq. (9) consists in mathematical terms in successive “partial differentiation” of a posteriori empirical (1) and statistical model-made data p, k and m in n -dimensional factorial space $t_A, \psi_s, h_A, S_R/S_L$. Interpretation of the n -dimensional space seems to be impossible. It may be done, however, using n monofactor plots or by means of the “tests space” proposed in (2).

The next parameter included in the parametric model of photosynthesis is the PAR, J_ϕ . This parameter was obtained as follows.

It is known from practice that the peculiar feature of photosynthesis is “light saturation”, or the phenomenon when at certain radiating PAR value its further increase does not lead to the increase of ϕ_L (1, 4). The plot of the $\phi_L=f(J_\phi)$ dependence on (1) is shown in Fig. 5.

Proceeding from the photosynthetic “saturation” postulate this relation may be hypothetically expressed as the following differential equation:



N	ϕ_S	t_A	h_A	S_R/S_L
1	-0.1	20	0.8	0.2
2	-0.1	20	0.4	0.2
3	-0.1	10	0.4	0.2
4	-2.5	20	0.8	0.2
5	-2.5	20	0.4	0.2
6	-8	20	0.8	0.2

Fig. 5. Plot of photosynthesis as a function of PAR.

$$\frac{1}{\mu} \cdot \frac{d\phi_L}{dJ_\phi} + \phi_L = \phi_0 \tag{13}$$

where μ is the “saturation” coefficient;
 ϕ_L is the current photosynthesis value;
 ϕ_0 is the “saturation” limit or the maximum, $\phi_{L\max}$, under fixed other environmental conditions.

when $\phi_L=0$ at $J_\phi=0$, its solution has a form:

$$\phi_L(J_\phi) = \phi_0(1 - e^{-\mu \cdot J_\phi}) \tag{14}$$

The equation (14), similar to (7), was found to adequately enough approximate the set of data $\phi_L=f(J_\phi)$. The coefficient μ which is the basic one in the formula (14), within three fixed values of ϕ_S depends weakly on variations of h_A and depends in a nonlinear fashion, on the variations of ϕ_S . Therefore, similar to the functional parameters p , k and m , for the coefficient μ the following quadratic polynomial, or the factorial representation of μ in the plane ϕ_S and S_R/S_L has been derived:

$$\mu = l_0 + l_1 \cdot \phi_S + l_2 \cdot \phi_S^2 \tag{15}$$

where $l_0 = d_{00} + d_{01} \cdot S_R/S_L$; $l_1 = d_{10} + d_{11} \cdot S_R/S_L$; $l_2 = d_{20} + d_{21} \cdot S_R/S_L$.

MODEL FINAL SYNTHESIS

The final step in construction of the photosynthesis parametric model is the synthesis of all derived dependences, Eqs. (7) to (15), into one formula. It reads:

$$\phi_L(t_A, \phi_S, h_A, S_R/S_L, J_\phi) = p \cdot e^{k \cdot X + m \cdot \ln X} (1 - e^{-\mu \cdot J_\phi}) \tag{16}$$

where $X = t_A + 3$ is the air temperature in the range from -2.90° to $+40^\circ\text{C}$;

p , k , m are the functional parameters determined by the value of ϕ_S by the formulas:

$$p = a_0 + a_1 \cdot \phi_S + a_2 \cdot \phi_S^2$$

$$k = b_0 + b_1 \cdot \phi_S + b_2 \cdot \phi_S^2$$

$$m = c_0 + c_1 \cdot \phi_S + c_2 \cdot \phi_S^2$$

where ϕ_S is the soil water potential in the range from -0.1 to -15 bars;

a_0, a_1, \dots, c_2 are parabolas coefficients determined by the values of h_A and S_R/S_L by the formulas:

$$\begin{aligned} a_0 &= 0.40742 + 0.0554 \cdot S_R/S_L + (1.53339 - 0.03696 \cdot S_R/S_L) \cdot h_A \\ a_1 &= -1.14782 + 0.40859 \cdot S_R/S_L + (1.86977 - 0.44388 \cdot S_R/S_L) \cdot h_A \\ a_2 &= -0.12261 + 0.04748 \cdot S_R/S_L + (0.21890 - 0.490 \cdot S_R/S_L) \cdot h_A \\ b_0 &= 1.48854 - 0.01868 \cdot S_R/S_L + (-0.45906 + 0.01905 \cdot S_R/S_L) \cdot h_A \\ b_1 &= 0.34095 - 0.11427 \cdot S_R/S_L + (-0.63893 + 0.16282 \cdot S_R/S_L) \cdot h_A \\ b_2 &= 0.02775 - 0.0110 \cdot S_R/S_L + (-0.06941 + 0.01632 \cdot S_R/S_L) \cdot h_A \\ c_0 &= -0.052756 - 0.000567 \cdot S_R/S_L + (0.018703 - 0.000017 \cdot S_R/S_L) \cdot h_A \\ c_1 &= 0.012978 - 0.007939 \cdot S_R/S_L + (0.012247 - 0.000236 \cdot S_R/S_L) \cdot h_A \\ c_2 &= 0.001013 - 0.000617 \cdot S_R/S_L + (0.001533 - 0.000042 \cdot S_R/S_L) \cdot h_A \end{aligned}$$

where h_A is the relative air humidity in the range from 0.2 to 0.9;

S_R/S_L is the root surface area to leaf area ratio in the range from 0.2 to 2.0 (linear interpolation); $\mu = l_0 + l_1 \cdot \phi_S + l_2 \cdot \phi_S^2$ is the "saturation" coefficient;

where $l_0 = 1.045 + 0.025 \cdot S_R/S_L$; $l_1 = -0.4005 + 0.2078 \cdot S_R/S_L$;

$$l_2 = 0.01075 - 0.00392 \cdot S_R/S_L.$$

J_ϕ is the PAR in the range from 0 to 5×10^{-2} W cm $^{-2}$.

Thus, the final equation (16) synthesis consisted in the replacement of the photosynthesis maximal value ϕ_0 in Eq.(14) with the value $\phi_L = f(t_A, \phi_S, h_A, S_R/S_L)$ derived earlier from Eqs. (7) to (12).

CONCLUSION

The obtained model of photosynthesis, first, describes with sufficient accuracy the empirical data (I), and especially on the basic physical dependence shown in Eq. (2), secondly, it allows to predict the photosynthetic "yield" at any variations (within the given limits) of all physical parameters included in it, and thus, without performing full-scale experiments to show in advance the possible ways of the process optimization and of the objective experiment by means of the appropriate "controls". The most important among them, as is shown by the empiricism ($I, 4$) and the numerical model calculations in Eq. (16), is the air temperature t_A . Since the photosynthesis dependence on temperature has the extremum, by setting the function derivative from Eq.(16) with respect to t_A equal to zero, the optimal temperature of the process ϕ_L can always be found for all other stationary or variable environmental conditions.

Under natural conditions the parameters t_A and J_ϕ are practically noncontrollable. However, using watering (by varying ϕ_S) or a watering plant (varying h_A and ϕ_S) we are always able to calculate the photosynthetic "yield" and to verify numerically the degree of indirect optimization of the process ϕ_L without access to "direct control" of natural t_A and J_ϕ .

The numerical model experiments with variation of each of the physical parameters within the given limits do not give results which disagree with the experiment,

they are rather consistent with it in most cases. For example, the "intersection of curves" $\phi_L=f(h_A)$ in Fig. 4 or the "optimum shift" ϕ_L towards lower temperatures when soil moisture "deficit" occurs (see Fig. 2). Also consistent with the empirical data is the optimum temperature point, yielding the maximal maximum $\phi_{L \max \max}$ under all other favourable environmental conditions at $+27$ to $+28^\circ\text{C}$.

The advantage of the developed parametric model of photosynthesis as against the traditional regressive and physical ones is obvious, since the model is not only relatively "simple" and open, or allows to introduce into it new parameters which are of interest to the investigator (soil, mineral nutrition, etc.), and to correct them specifically, but also makes it possible to use it in practice as a "base" for optimization.

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