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STRUCTURAL HETEROGENEITY IN PHOTOSYNTHESIS:
A UNIFYING MODEL FOR THE RESPONSE CURVES

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Abstract

A mechanistic model describing photosynthesis rate of a heterogeneous tissue or population is presented and discussed. It results in a family of mathematical forms expressing the rate of photosynthesis as a function of external limiting factor densities. Most of acknowledged semi-empirical light-response and CO₂-response curves, the rectangular hyperbola among them, follow from the new formalism as particular cases. For derivation of the model, parameters of an idealized local Blackman-type curve were treated as chance values distributed according to the Gamma probability density function. The model distinguishes energetic and capacity types of heterogeneity. It is, in principle, ^{multi}many-dimensional, though full set of simple formulae were obtained merely for two-dimensional case. Richness and flexibility of the model are demonstrated by many graphic computer simulations.

$$\tanh x = \frac{e^x - e^{-x}}{e^x + e^{-x}} \approx \dots$$

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$$\frac{1 + x + \frac{x^2}{2} + \frac{x^3}{3!} + \dots - 1 + x - \frac{x^2}{2} + \frac{x^3}{3!}}{1 + x + \frac{x^2}{2} + \frac{x^3}{3!} + \dots + 1 - x + \frac{x^2}{2!} - \frac{x^3}{3!}}$$

$$\frac{2x + 2 \frac{x^3}{3!}}{2 + 2x^2} = \frac{x + \frac{x^3}{3!}}{1 + \frac{x^2}{2}}$$



$$\frac{x}{1 + \frac{x^2}{2}}$$

Introduction

Heterogeneity is commonly understood as one of the most essential features of photosynthesis (Rabinowitch, 1951). Two kinds of heterogeneity are usually distinguished. The first follows from the fact that the chlorophyll and catalyst molecules participating in photosynthesis are available nonuniformly in different parts of a chloroplast, i.e. it reflects the internal structural heterogeneity (including anisotropy) of the sensitive apparatus. The second is caused by irregularity of light and reactants supply to different pigment particles. In this work, we shall consider only the first type of heterogeneity: the structural heterogeneity.

Heterogeneity is closely connected with random nature of reactions in cells and with variety of these reactions. Even in vitro, inner and outer conditions of a reaction are permanently changing, and the rate of each reaction is randomly liable to these changes. The heterogeneity in such an intricate system can be regarded as one of effects of stochastic character of most processes, and, inversely, randomness of the processes inside cells may cause phenomena that are usually interpreted in terms of heterogeneity.

It is because of heterogeneity and stochastic nature of photosynthetic tissues (or autotrophic populations), a controversy about the intrinsic shape of the light curves was protracted along several decades. Two general principles were enunciated about this shape. According to the Blackman's law of limiting factors (Blackman, 1905), the rate of photosynthesis linearly increases with the increase in value of a single external limiting factor as long as this factor remains "slowest", and ceased to be dependent on it when another factor becomes limiting. As an alternative to it, Bose (1924) suggested that the effect of certain change in a factor on the yield of photosynthesis is independent of the prevailing values of the other factors. Equally reliable measurements were done in favour to the both concepts, so the controversy was not so far entirely overcome (Rabinowitch, 1953).

What was commonly adopted from Blackman's concept is the idea that the photosynthesis rate may be expressed as a function of one external limiting factor (usually, of light or carbon dioxide density) with a few constant coefficients. Such relationships are known as light-response and CO₂-response curves. Most important of them are listed below and drawn

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in Fig. 1:

- (A) $p = \min \{ax, P_m\}$ Blackman (1905)
- (B) $p = P_m \tanh (ax/P_m)$ Jassby and Platts (1976)
- (C) $p = P_m (1 - \exp(-ax/P_m))$ Peat (1970)
- (D) $p = ax (1 - \exp(-P_m/ax))$ Thornley (1976)
- (E) $p = \frac{axP_m}{(P_m^2 + a^2x^2)^{1/2}}$ Vollenwieder (1970)
- (F) $p = \frac{axP_m}{ax + P_m}$ (the rectangular hyperbola)

Here, p is the rate of photosynthesis, x is an external limiting factor density (e.g. light flux density, carbon dioxide density, etc.), and a and P_m are constants.

Forms (A) - (F) are also plotted in Fig. 2 in secondary ($p, p/x$)-coordinates convenient to analyze curves in complete ranges of values of the both variables, x ($0 \leq x \infty$) and p ($0 \leq p \leq P_m$). The initial ordinates and final abscissas in Fig. 2 are equal, respectively, to the initial slopes, a , and to the asymptotic plateau levels, P_m , in Fig. 1. All curves in Fig. 2 are normalized: they intercept abscissa at $p = P_m = 1$, and ordinate, at $p/x = a = 1$.

All forms (A) - (F) are two-parameter (other models of three and more parameters were deliberately excluded) and semi-empirical (Thornley, 1976). All of them show an evidence of the following two important features confirmed by numerous theoretical and experimental investigations (Rabinowitch, 1951; Thornley, 1976; Tenhunen et al., 1980):

1°. The overall photosynthesis rate (p) of a plant tissue or autotrophic population is a monotonous, convex in general (without points of inflection) function of an external limiting factor density (x); this function starts from the origin with a finite initial slope (a) and asymptotically approaches a plateau level (P_m);

2°. There exists a well-recognized linear locality of this function at lower limiting factor densities: near the origin, where the derivative $dp/dx (\leq a)$ is approximately constant.

Apart to the Blackman's form (A), an exclusive place among forms (A) - (F) belongs to the widely used rectangular hyperbola (F). Mathematically, it is conceived as a simplest one (though, strictly speaking, form (A) is simpler). Physiologically, its validity, though having not a mechanistic base, is indirectly corroborated by references to the contiguous sciences: it is adopted as the Langmuir isotherm, in surface adsorption theory (notice that the photosynthesis reactions are, at least in part, surface reactions (Rabinowitch, 1951)), and as the Michaelis-Menten equation, in enzymology; it is also known and adopted in plant growth theory, membrane transport and population dynamics. In these adjoining fields, as well as in the theory of photosynthesis, this rectangular hyperbola is commonly considered as a representation of the case of homogeneity (Rabinowitch, 1951; Thornley, 1976).

It is usually said (Thornley, 1976) that the Blackman piecewise-linear form (A) and the rectangular hyperbola (F) yield two extremes restricting all reasonable response curves. Other forms plotted with the same initial slope and asymptotic plateau lie between (A) and (F) (see Fig. 1 - 2): the further gives the steepest response, while the latter, the most gradual one. In the normalized secondary (p, p/x)-coordinates (Fig. 2), the rectangular hyperbola plots as a straight "main diagonal" crossing the unit square from the left upper angle to the right lower one, all other curves lied above it. The Blackman curve plots in (p, p/x)-coordinates as a two-part broken line shaped by the upper and the right lateral edges of the unite square.

The rectangular hyperbola (F) can be extended to allow for the mutual effects of two external factors, x_1 and x_2 (e.g. light and CO_2) (Thornley, 1976). Taking x for x_1 and assuming that $P_m = bx_2$, where b is a constant, one procures a symmetrical function of the two arguments:

$$p = \frac{ab x_1 x_2}{ax_1 + bx_2} \quad (1)$$

Form (1) is a rectangular hyperbola with respect to both x_1 and x_2 , so it yields a consequent generalization of the one-dimensional rectangular hyperbola (F). Similar extension to the case of two external factors may be done with forms (A) - (E) as well.

Form (1) may be conceived as an example of formalization of Bose's

postulate. Indeed, a change in x_1 (x_2) alters the photosynthesis rate independently of x_2 (x_1) if the latter is fixed. Practically, (1) describes a case when one of the two arguments are fixed or changes in a restricted range; a change of this argument influences both the initial slope and the asymptote of (1). Yet if both x_1 and x_2 increase without limit, the asymptote of (1) also approaches infinity: clearly a nonphysiological result (Thornley, 1976).

To avoid this difficulty, an alternative procedure putting an absolute maximum on photosynthetic rate can be obtained (Thornley, 1976). It assumes that P_m in (F) is not a linear but a hyperbolic function of the second argument: $P_m = P'_m b x_2 / (P'_m + b x_2)$, where b is a constant and P'_m is the maximum photosynthetic rate at both external factors saturated. Now from (F) transforms into

$$p = \frac{abx_1x_2}{ax_1 + bx_2 + abx_1x_2/P'_m} \tag{2}$$

Plurality and diversity of the mathematical forms known in the literature and their semi-empirical nature (Rabinowitch, 1951; Thornley, 1976) testify in themselves that a unifying mechanistic approach is desirable. Such an approach should be based on clear and profound physiological implications (Feller, 1940) and provide a formalism from which the most frequently encountered formulae (i.e. (A) - (F), (1)-(2) and, hopefully, others) follow as particular cases. A plausible solution for this unifying problem is suggested below.

Homogeneity: An Idealized Response Surface

Blackman's concept of limiting factors implies the chemical constancy and strict mechanical uniformity of a biomass synthesized and, therefore, the strict and constant stoichiometry of the process of photosynthesis. It is because of this Blackman insisted so obstinately that his simple quantitative rule is an exact law of nature (Rabinowitch, 1951). In these terms, his principle is the law, indeed, but with one essential reservation: it is valid merely for an extremely idealized case that practically never encounters in the living nature. In the present paper,

this idealized case will be, by definition, called the case of the structural homogeneity which implies that in different parts of a chloroplast (in each elementary photosynthesizing center) the chlorophyll and catalyst molecules are available uniformly.

Thus, Blackman's concept and formalism are taken here for more than "a good first approximation" as they are frequently treated (Rabinowitch, 1951). We assume form (A) to be a strict mathematical representation of the photosynthesis response of an idealized pure homogeneous tissue (population), in each photosynthesizing center of which a purely deterministic photosynthesis obeying to the strict stoichiometric equality is taking place. Hence form (A) will be considered as a starting point for a quantitative modelling of the structural heterogeneity of the photosynthetic apparatus.

Let x_1, x_2, \dots be measures (densities) of the external material and/or energetic components (potential limiting factors) necessary for photosynthesis. For an idealized homogeneous biomass, the overall rate of photosynthesis, p , calculated according to the law of limiting factors, may be written as

$$p = \min \{a_1 x_1, b_2 x_2, \dots, P_m\} \tag{3}$$

where a_i are the coefficients connected with the energy of photosynthesis, and P_m is the own top photosynthetic efficiency of the photosynthesizing biomass: its physiological plateau level which could not be exceeded at whatever amounts and proportions of all x_i .

In such a model, to saturate the photosynthetic system with one of the external components means to reduce the dimension of (3). If at any current moment of time all components but one, x_i , are available to the photosynthetic apparatus in comparative excess, form (A) follows from (3):

$$p(x_i) = \min \{a_i x_i, P_m\} \tag{4}$$

i.e. the two-dimensional case is obtained. If a interchange of only two limiting factors, x_i and x_j , is possible while P_m is practically unreachable, (3) transforms into

$$p(x_i) = \min \{a_i x_i, a_j x_j\} \tag{5}$$

which we call the incomplete three-dimensional case. If then the physiological plateau level P_m is reachable whilst two limiting factors

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can alternate and saturate, one gets a (complete) three-dimensional case:

$$p(x_1) = \min \{a_1 x_1, a_2 x_2, P_m\} \quad (6)$$

In this paper, we construct heterogeneity models corresponding to forms (4)-(6) and discuss ways to extend these models to many-dimensional case (3).

Heterogeneity: Main Premises

Let us consider a heterogeneous photosynthesizing biomass as a mosaic of randomly distributed elementary homogeneous centers (less or equal to chloroplasts in size) which efficiency is described by (4), (5) or (6).

Since the processes of assimilation of all x_i are subjected to numerous unstable influences (errors in measurements of x_i among them), the parameters a_i and P_m should be treated not as constants but as random values distributed according to somewhat multivariate joint probability density function $f(a_i, P_m)$.

Now, in order to obtain the overall rate of the photosynthesis (p) of a given heterogeneous biomass, one has to average current photosynthetic rates of all homogeneous elementary centers. Since sizes of these centers are very small, the continuous averaging is preferable, and the problem reduces to calculation of the following mathematical expectancy:

$$p = \int_0^{\infty} da_1 \int_0^{\infty} da_2 \dots \int_0^{\infty} f(a_i, P_m) p(x_i) dP_m \quad (7)$$

where $p(x_i)$ is defined by (3), (4), (5) or (6), and the integration is subtended along the positive semi-axes of the parameters a_i, P_m , since all of them are essentially positive.

Elementary photosynthesizing centers may vary in their energetic affinity to external components, which is reflected in the rates of assimilation, or, in our terms, in the parameters a_i . These centers also vary in their own inherent photosynthetic capacities, P_m . Hence we shall further distinguish two types of structural heterogeneity: the energetic heterogeneity (with respect to a_i) and the capacity heterogeneity (with respect to P_m). Coexistence of the both will be called the complex (structural) heterogeneity.

On a priori ground, there is no reason to assume that assimilation rates of an external limiting factors are related to the capacity of photosynthesizing centers. Thus, parameters a_1 and P_m should be regarded as independent in probability sense, so that their joint probability density function becomes a product of individual probability density functions. Since nothing is known about their form preliminarily, a most general standard probability function, the same for all a_1 and P_m , should be tried. For essentially positive variables, it will be the Gamma probability density function (Feller, 1966). As applied to our model, it may be expressed as follows:

$$f(a_1) = \frac{\beta^{\alpha_1}}{\Gamma(\alpha_1)} \exp((\alpha_1 - 1) \ln a_1 - \beta_1 a_1) \quad (8)$$

$$f(P) = \frac{\mu^\sigma}{\Gamma(\sigma)} \exp((\sigma - 1) \ln P - \mu P) \quad (9)$$

where P stands for P_m (here and further), α_1 and β_1 are the parameters of the probability density functions, and $\Gamma(\cdot)$ is the Gamma function. *hereafter — Benz*

Let us point out briefly the main properties of forms (8)-(9) that will be further important. At $\alpha_1 > 1$ and $\sigma > 1$, being plotted as functions of a_1 and P , they results in bell-shaped curves while at $\alpha_1 = 1$ and $\sigma = 1$, degenerate into exponential density probability functions. At $\alpha_1 < 1$ and $\sigma < 1$, they also have exponent-type shape and change from $+\infty$ to 0 but more steeply. They have means α_1/β_1 and σ/μ . At fixed ratios α_1/β_1 and σ/μ and $\alpha_1, \sigma \rightarrow \infty$, they turn into Dirac's Delta functions $\delta(z - \alpha_1/\beta_1)$ and $\delta(P - \sigma/\mu)$ equal to $+\infty$ at $z = \alpha_1/\beta_1, P = \sigma/\mu$, and to 0 elsewhere.

Values $\alpha_1, \beta_1, \sigma$ and μ , as the parameters of probability density function, will determine the shape of the overall photosynthesis rate function and acquire a physiological meaning: ratios α_1/β_1 are the initial slopes with respect to variables x_1 , and ratio σ/μ is the physiological plateau level for the many-dimensional heterogeneous response surface (7).

Heterogeneity: Two-Dimensional Case

As well as in the case of homogeneity (4), a two-dimensional (with respect to the parameters) heterogeneous photosynthesis rate, p , will be a function with saturation of an only limiting factor, x (e.g. light or CO_2).

Substituting the two-dimensional homogeneous response surface (4) into integral (7) one gets:

$$p = \int_0^{\infty} f(P) \int_0^{\infty} f(a) \min(ax, P) da dP \quad (10)$$

where $f(\cdot)$ is the Gamma probability density functions defined by (8) or (9), and the superfluous indexes were dropped for the sake of simplicity. Integral (10) represents p as a two-dimensional response surface of parameters a and P (at x fixed), or as a one-dimensional function of x (at a and P fixed). In the following derivations, x is considered fixed.

Let us start with evaluation of the inner integral in (10), i.e. one with respect to a , at arbitrary finite and positive $\alpha_1 = \alpha$ and $\beta_1 = \beta$. The evaluation results in the following formula:

$$p = \frac{x}{\beta \Gamma(\alpha)} \tau \left[\alpha+1, \frac{\beta P}{x} \right] + \frac{P}{\Gamma(\alpha)} \Gamma \left[\alpha, \frac{\beta P}{x} \right] \quad (11)$$

where $\tau(\cdot, \cdot)$ is the incomplete Gamma function and $\Gamma(\cdot, \cdot)$, the complementary incomplete Gamma function.

Though in modern computer software, both $\tau(\cdot, \cdot)$ and $\Gamma(\cdot, \cdot)$ are standard inserted functions along with the elementary functions, expression (11) still remains rather involved and generally inconvenient for practical purposes. Assuming, however, that parameter α is an integer ($\alpha \geq 1$), one obtains:

$$p = \frac{\alpha x}{\beta} \left[1 - e^{-\beta P/x} \sum_{i=0}^{\alpha-1} \left(1 - \frac{i}{\alpha} \right) \frac{(\beta P/x)^i}{i!} \right] \quad (12)$$

for arbitrary positive β .

In simplest particular case, at $\alpha = 1$, form (D) immediately follows

from (12):

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$$p = (x/\beta) [1 - \exp(-\beta P/x)] \quad (13)$$

Expressions (11) - (13), plotted as a functions of the external density x , provide a set of smooth convex curves starting from the origin with the initial slope $a' = \alpha/\beta$ (the mean a) and eventually saturating at a fixed plateau, P . Since integral (10) is equal to its inner integral at $f(P) = \delta(P-\sigma/\mu)$, i.e. at $\sigma/\mu = P$, $\sigma \rightarrow \infty$, (11) - (13) describe the case of the energetic heterogeneity (finite parameters α and β) combined with the capacity homogeneity (infinite parameters σ and μ).

Substituting form (12) into the outer integral in (10) and evaluating the latter with respect to P , one procures:

$$p = \frac{\alpha x}{\beta} \left[1 - \sum_{i=0}^{\alpha} \binom{\alpha-i}{i} \frac{\mu^{\sigma} (\beta/x)^i}{(\mu + \beta/x)^{\sigma+i}} \right] \quad (14)$$

where $\binom{\alpha-i}{i} = \frac{(\alpha-i)!}{i!(\sigma-1)!}$ is the binomial coefficient, α is an integer (≥ 1), and β , σ , and μ are arbitrary positives.

Similarly to the above, in the simplest case, at $\alpha = 1$, it follows from (14):

$$p = \frac{x}{\beta} \left[1 - \frac{\mu^{\sigma}}{(\mu + \beta/x)^{\sigma}} \right] \quad \left[1 - \frac{1}{(1 + \beta/\mu x)^{\sigma}} \right] \quad (15)$$

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Formulae (14)-(15) plotted as functions of x give smooth convex curves with the initial slope $a' = \alpha/\beta$ (the mean a) and the plateau $P' = \sigma/\mu$ (the mean P). They describe the phenomenon of the complex structural heterogeneity with the restriction for α to be integer: the energetic heterogeneity (finite parameters α and β) combined with the capacity heterogeneity (finite parameters σ and μ).

A remarkable peculiarity of the formalism obtained is that forms (14) - (15) reduce to the rectangular hyperbola (F) in their simplest particular case. Setting $\alpha = \sigma = 1$ in (14) (or $\sigma = 1$ in (15)), one readily finds:

$$p = \frac{x}{\beta + \mu x} \quad (16)$$

Thus within the assumptions of our model, the rectangular hyperbola represents a particular case of heterogeneity (mathematically, the simplest one). Inversely, forms (14) and (15) become consequent generalizations of this hyperbola for σ and α different from 1.

The set of analytical expressions, following from integral (10), can be expanded by reversing the order of integration in (10):

$$p = \int_0^{\infty} f(a) \int_0^{\infty} f(P) \min\{ax, P\} dP da \quad (10')$$

At arbitrary positive σ and μ , computation of inner integral in (10') yields:

$$p = \frac{1}{\mu \Gamma(\sigma)} \Gamma(\sigma+1, \mu ax) + \frac{ax}{\Gamma(\alpha)} \Gamma(\sigma, \mu ax) \quad (17)$$

At σ integer ($\sigma \geq 1$), one obtains from (17):

$$p = \frac{\sigma}{\mu} \left[1 - e^{-\mu ax} \sum_{i=0}^{\sigma} \left(1 - \frac{i}{\sigma} \right) \frac{(\mu ax)^i}{i!} \right] \quad (18)$$

In its simplest particular case, at $\sigma = 1$, form (C) follows from (18):

$$p = (1/\mu) (1 - \exp(-\mu ax)) \quad (19)$$

Once more, (17)-(19) give a set of smooth convex curves with the fixed initial slope a and the plateau $P' = \sigma/\mu$ (the mean P). Since integral (10') is equal to its inner integral at $f(a) = \delta(a - \alpha/\beta)$, i.e. at $\alpha/\beta = a$, $\alpha \rightarrow \infty$, (17) - (19) represent the case of the capacity heterogeneity (finite parameters σ and μ) combined with the energetic homogeneity (infinite parameters α and β).

Substituting (18) into the outer integral in (10') one obtains:

$$p = \frac{\sigma}{\mu} \left[1 - \sum_{i=0}^{\sigma} \left(1 - \frac{i}{\sigma} \right) \left(\frac{\alpha+i-1}{i} \right) \frac{\beta^{\alpha} (\mu x)^i}{(\beta + \mu x)^{\alpha+1}} \right] \quad (20)$$

At $\sigma = 1$, form (20) becomes

$$p = \frac{1}{\mu} \left[1 - \frac{\beta^\alpha}{(\beta + \mu x)^\alpha} \right] \quad \overset{\text{H.K. } \downarrow}{\left[1 - \frac{1}{(1 + \mu x / \beta)^\alpha} \right]} \quad (21)$$

Formulae (20) - (21) give a set of curves with the initial slope $a' = \alpha/\beta$ and asymptote $P' = \sigma/\mu$. They depict the complex heterogeneity with the restriction for σ to be integer: the energetic heterogeneity (finite α and β) combined with the capacity heterogeneity (finite σ and μ).

As it should be expected, form (21) at $\alpha = 1$ is identical to form (15) at $\sigma = 1$, i.e. reduces to the rectangular hyperbola (16). Generally, it can be easily shown by induction that formula (20) calculated at $\alpha = m$ is equivalent to formula (14) at $\sigma = m$, where m is an integer.

It follows from the above deduction that the energetic heterogeneity described by (12) is a limiting case of the complex heterogeneity described by (14) at $\sigma/\mu = P$, $\sigma \rightarrow \infty$; then, the capacity heterogeneity (18) is a limiting case of the complex heterogeneity (20) at $\alpha/\beta = a$, $\alpha \rightarrow \infty$. As well, the Blackman's homogeneity (4) is a limiting case for both the energetic heterogeneity (described by (11) or (12)), at $\alpha/\beta = a$, $\alpha \rightarrow \infty$, and of the capacity heterogeneity (described by (17) or (18)), at $\sigma/\mu = P$, $\sigma \rightarrow \infty$.

Heterogeneity: Incomplete Three-Dimensional Case

(Isotropy and Anisotropy)

This case sets relationships between photosynthesis rate, p , and two external densities, x_1 and x_2 (e.g. light or CO_2), that can alternate as limiting factors. Only a relative saturation is possible here: at x_1 (x_2) fixed (or restricted) and x_2 (x_1) $\rightarrow \infty$. If the both densities increase without limit, a nonphysiological result of p approaching infinity will follow, as well as in formula (1), and the below inferring become irrational.

Quite Quiet similarly to the above, substituting the homogeneous response surface (5) into integral (7) one gets:

$$p = \int_0^{\infty} \int_0^{\infty} f(a_2) \left\{ f(a_1) \min \{ a_1 x_1, a_2 x_2 \} \right\} da_1 da_2 \quad (22)$$

where $f(a_1)$ and $f(a_2)$ are the Gamma probability density functions defined by (8). Integral (22) represents p as a two-dimensional response surface of parameters a_1 and a_2 , at x_1 and x_2 fixed, or of x_1 and x_2 , at a_1 and a_2 fixed.

Evaluating the inner integral in (22) one gets:

$$p = \frac{x_1}{\beta_1 \Gamma(\alpha_1)} \Gamma\left[\alpha_1 + 1, \frac{\beta_1 a_2 x_2}{x_1}\right] + \frac{a_2 x_2}{\Gamma(\alpha_1)} \Gamma\left[\alpha_1, \frac{\beta_1 a_2 x_2}{x_1}\right] \quad (23)$$

that is similar to (11). Expression (23) represents the case of x_1 (x_2) varying in its entire range whilst x_2 (x_1) is fixed or restricted from the above as a relative capacity plateau. Being plotted as a function of x_1 (or x_2), (23) procures a set of convex curves starting from the origin with the initial slope $a_1' = \alpha_1/\beta_1$ ($a_2' = \alpha_2/\beta_2$) and eventually saturating at the relative plateau, $a_2 x_2$ ($a_1 x_1$). Since integral (22) is equal to its inner integral at $f(a_2) = \delta(a_2 - \alpha_2/\beta_2)$, i.e. at $\alpha_2/\beta_2 = P$, $\alpha \rightarrow \infty$, (23) describes the case of the energetic heterogeneity with respect to the first factor (finite parameters α_1 and β_2) combined with the energetic h ∞ with respect to the second factor (infinite parameters α_2 and β_2). Physiologically, this case may be conceived as corresponding to the isotropy to carbon dioxide combined with anisotropy to light.

Automatically substituting $a_2 x_2$ for P in formulae (12) - (16) one gets their consequent parallelisms, analogues of the forms (C) and (D) among them. The simplest case of mutual anisotropy will be:

$$p = \frac{x_1 x_2}{\beta_1 x_2 + \beta_2 x_1} \quad (24)$$

i.e. the rectangular hyperbola with respect to both x_1 and x_2 equivalent to form (1).

Since the problem is symmetrical (mathematically, x_1 and x_2 are commutative), inversion of order of integration in (22) does not extend the number of analytical solutions for α_2 integer, and expressions (17 - (21) have no parallelisms here.

→ Heterogeneity: Three-Dimensional Case

Now we shall find heterogeneous photosynthesis rate, p , corresponding to

the three-dimensional (with respect to the parameters) homogeneous form (6). Since the plateau level, P , is now (in contrast to the previous section) taken into account, a resulting function will saturate either with one of the two factors, x_1 or x_2 (e.g. light or CO_2), approaching infinity, or with both $x_1, x_2 \rightarrow \infty$, so the absolute saturation is reachable here.

Though an infering quite similar to the above can be perform for the general forms of the Gamma probability density functions (8) and (9), resulting expressions will be too cumbersome. Thus, for the sake of simplicity, we shall demonstrate our method only for the exponential probability density functions that follow from (8) and (9) at $\alpha_1 = 1$, $\sigma = 1$. Under such conditions, integral (7) transforms into

$$p = \int_0^{\infty} \beta_1 \exp(-\beta_1 a_1) da_1 \int_0^{\infty} \beta_2 \exp(-\beta_2 a_2) da_2 \int_0^{\infty} p(x_1) \mu e^{-\mu P} dP \quad (25)$$

where $p(x_1)$ is taken according (6). Evaluation of (25) with respect to a_1 yields:

$$p = \begin{cases} (x_1/\beta_1) (1 - \exp(-\beta_1 a_2 x_2/x_1)), & \text{at } a_2 x_2 < P \\ (x_1/\beta_1) (1 - \exp(-\beta_1 P/x_1)), & \text{at } a_2 x_2 > P \end{cases} \quad (26)$$

For integration with respect to a_2 , (26) must be substituted into the first inner integral of (25). Its evaluation provides

$$p = \frac{1}{\beta_1/x_1 + \beta_2/x_2} (1 - \exp[-(\beta_1/x_1 + \beta_2/x_2)P]) \quad (27)$$

Finally, integration with respect to P gets

$$p = \frac{1}{\mu + x_1/\beta_1 + x_2/\beta_2} \quad (28)$$

i.e. formula (2) is obtained.

Physiological meanings can be readily attributed to expressions (26) - (28) as it was done in earlier sections.

Conclusion and Discussion

Various deviations from Blackman's homogeneity are expressed in our model in terms of parameters α , β , σ and μ of the probability density functions. It was proved that at fixed ratios α_1/β_1 and σ/μ , and increase of either pair (α_1, β_1) or (σ, μ) , deviations from Blackman's ultimate homogeneity decrease. The character of this decrease (for the two-dimensional case) is shown in Fig.3-6.

It is clear from Fig.3-6 that at the same external limiting density x , any deviation from homogeneity lowers the rate of photosynthesis, p . Such a deviation increases with increasing either kind of heterogeneity. Mathematically, this statement (connected with the well-known isoperimetric problem of variational calculus) can be proved by minimization of integral (10) (or (10')) using the Lagrangian factor.

The model was derived mechanistically, from very general and simple assumptions. As it was shown, the four out of six acknowledged semi-empirical forms, listed above, namely (A), (C), (D), (F), follow from our formalism as particular cases. Though forms (B) and (E) were not covered by our model, they can be easily simulated by it. In Fig.7, curve (B) (dished line) is restrained between two normalized ($P = 1$, $\sigma = \mu = 2, = 3$) response curves of the case of capacity heterogeneity combined with the energetic homogeneity (form (18)). A curve simulated according to the more general form (17) at $\sigma = \mu = 2.5$ practically coincides with curve (B) (see Tabl. 1). As well, in Fig.8, curve (E) (dished line) is restrained between two normalized ($\alpha = \beta = \sigma = \mu = 3.0, = 3.8$) response curves of the general case of complex heterogeneity (integral (10)). A curve simulated according (17) at $\alpha = \beta = \sigma = \mu = 3.5$ lies very closely to curve (E) (see Tabl.1). Thus the both semi-empirical curves (B) and (E) can be conceived as good approximations of our mechanistic model.

Being a unifying one, the model presented brings a physiological meanings to the above list of former models none of which, to the beast of our knowledge, was never properly derived.

In its most general form, our two-dimensional model has four arbitrary parameters. Such a number of parameters obviously guarantees a good fitting of a theoretical model to real data but seems to be excessive. It worth noting however that in the examples demonstrated by Fig. 1 - 7 the model presented was treated as a three-parameter, and in

Fig. 8, even as a two-parameter one. Thus the number of parameters introduced is equal or less than in the purely empirical three-parameter non-rectangular hyperbola

$$P^2\theta - P(ax+P) + aP = 0 \quad (29)$$

which is frequently used in cases where none of two-parameter models give a good fitting.

As it was mentioned in Introduction, any response curve plotted in the secondary coordinates is generally anticipated to lie above "the main diagonal" corresponding to the rectangular hyperbola. The model presented, in principle, covers also cases of response curves lying under "the main diagonal" as it clear from Fig. 4 and Fig. 6. For these curves, the restriction of parameter α or σ to be integer (a condition to which most of the above analytical solutions ensuing from our model, obey) may be essential. But for curves said to be physiologically relevant, i.e. lying above "the main diagonal", this restriction is apparently unessential since in each practical fitting problem, a scientist deal not with parameters α , β , σ and μ but with their ratios.

The approach presented here and the family of forms following from seems to be a plausible mechanistic treatment that brings together Bose's and Blackman's principles of representation of the response curves.

References

1. Rabinowitch, E.I. Photosynthesis and Related Processes. Vol. II, Part I: Spectroscopy and Fluorescence of Photosynthetic Pigments; Kinetics of Photosynthesis. Interscience Publishers, Inc., New York, 1951.
- Blackman, F.F.: Optima and limiting factors. *Ann.Bot.*, 19, 281-295 (1905).
- Bose, J.C. Physiology of Photosynthesis. London: Geen, 1924
- Thornley, J.H.M.: Mathematical Models in Plant Physiology. London, New York, Can Francisco: Academic Press, 1976
- Feller, W.: On the logistic law of growth and its empirical verifications in biology. *Acta Biotheor.* 5, 51-65 (1940)
- Feller, W.: Introduction to Probability Theory and Its Applications. New York: J. Wiley & Sons 1966

Table 1
Numerical comparison of curves (B) and (E) with their simulations
according the model presented (in secondary coordinates)

	(B)	Our model	(E)	Our model
p			p/x	
0.0000	1.0000	1.0000	1.0000	1.0000
0.2000	0.9865	0.9881	0.9798	0.9866
0.4000	0.9442	0.9434	0.9165	0.9221
0.6000	0.8656	0.8594	0.8000	0.7979
0.8000	0.7282	0.7172	0.6000	0.5973
1.0000	0.0000	0.0000	0.0000	0.0000

Figure Legends

Figure 1. Normalized ($a = 1, P_m = 1$) response curves (A) - (F) (see text) representing the overall rate of photosynthesis, p , as a function of an external factor density, x .

Figure 2. Normalized ($a = 1, P_m = 1$) response curves (A) - (F) plotted in $(p/x-p)$ -coordinates. Maximum ordinate of them corresponds to the initial slope, a , maximum abscissa, to the asymptotic plateau level, P_m .

Figure 3. Normalized ($P_m = 1, \alpha/\beta = 1$) response curves for the case of the energetic heterogeneity combined with the capacity homogeneity (form (12)), in $(p/x-p)$ -coordinates. The Blackman's homogeneity case (the upper and the lateral right edges of the unit square) and the rectangular hyperbola are depicted by dashed lines. Deviations from Blackman's form increase with decreasing $\alpha = 80, 15, 5, 2, 1$.

Figure 4. Normalized ($\alpha = \beta = 3, \sigma/\mu = 1$) response curves for the case of the complex heterogeneity with restriction fo α to be integer (form (14)), in $(p/x-p)$ -coordinates. The limiting case (form (12) at $\alpha = \beta = 3$) is depicted by dashed line and marked INF. Deviations from this limiting case increase with decreasing $\sigma = 20, 5, 2, 1, 0.3, 0.1, 0.03$.

Figure 5. Normalized ($P_m = 1, \sigma/\mu = 1$) response curves for the case of the capacity heterogeneity combined with the energetic homogeneity (form (18)), in $(p/x-p)$ -coordinates. The Blackman's homogeneity case (the upper and the lateral right edges of the unit square) and the rectangular hyperbola are depicted by dashed lines. Deviations from Blackman's form increase with decreasing $\alpha = 80, 15, 5, 2, 1$.

Figure 6. Normalized ($\alpha/\beta = 1, \sigma = \mu = 3$) response curves for the case of the complex heterogeneity with restriction fo σ to be integer (form (20)), in $(p/x-p)$ -coordinates. The limiting case

(form (18) at $\sigma = \mu = 3$) is depicted by dashed line and marked INF. Deviations from this limiting case increase with decreasing $\sigma = 20, 5, 2, 1, 0.3, 0.1, 0.03$.

Figure 7. Normalized ($P_m = 1, a = 1$) response curve (B) (dashed line) restrained between two normalized ($P_m = 1, \sigma = \mu = 2, = 3$) response curves of the case of capacity heterogeneity combined with the energetic homogeneity (form (18)), in $(p/x-p)$ -coordinates. A curve simulated according form (17) at $\sigma = \mu = 2.5$ practically coincides with curve (B) (see text).

Figure 8. Normalized ($P_m = 1, a = 1$) response curve (E) (dashed line) restrained between two normalized ($\alpha = \beta = \sigma = \mu = 3.0, = 3.8$) response curves of the general case of complex heterogeneity (integral (10)), in $(p/x-p)$ -coordinates. A curve simulated according (17) at $\alpha = \beta = \sigma = \mu = 3.5$ lies very closely to curve (E) (see text).

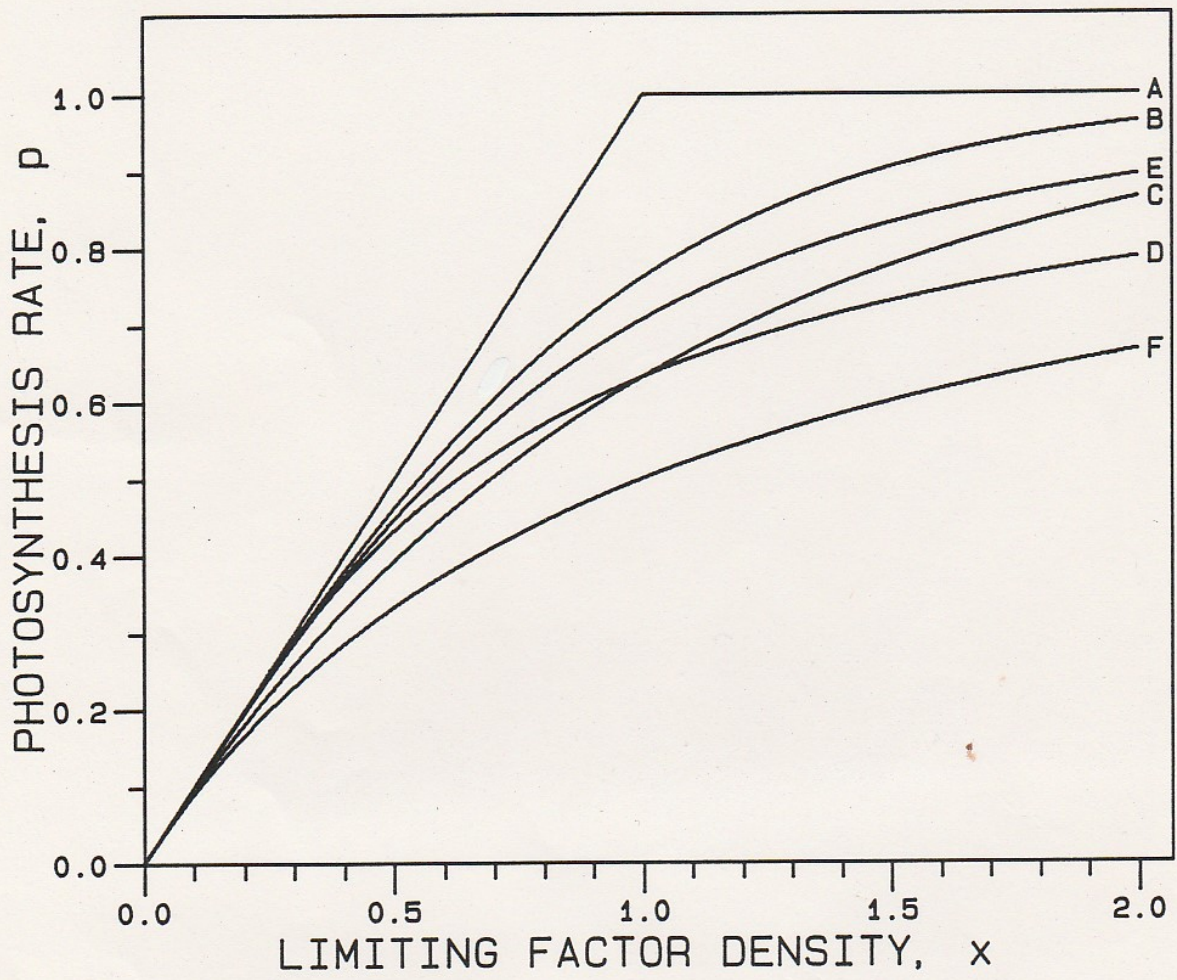


Fig.1

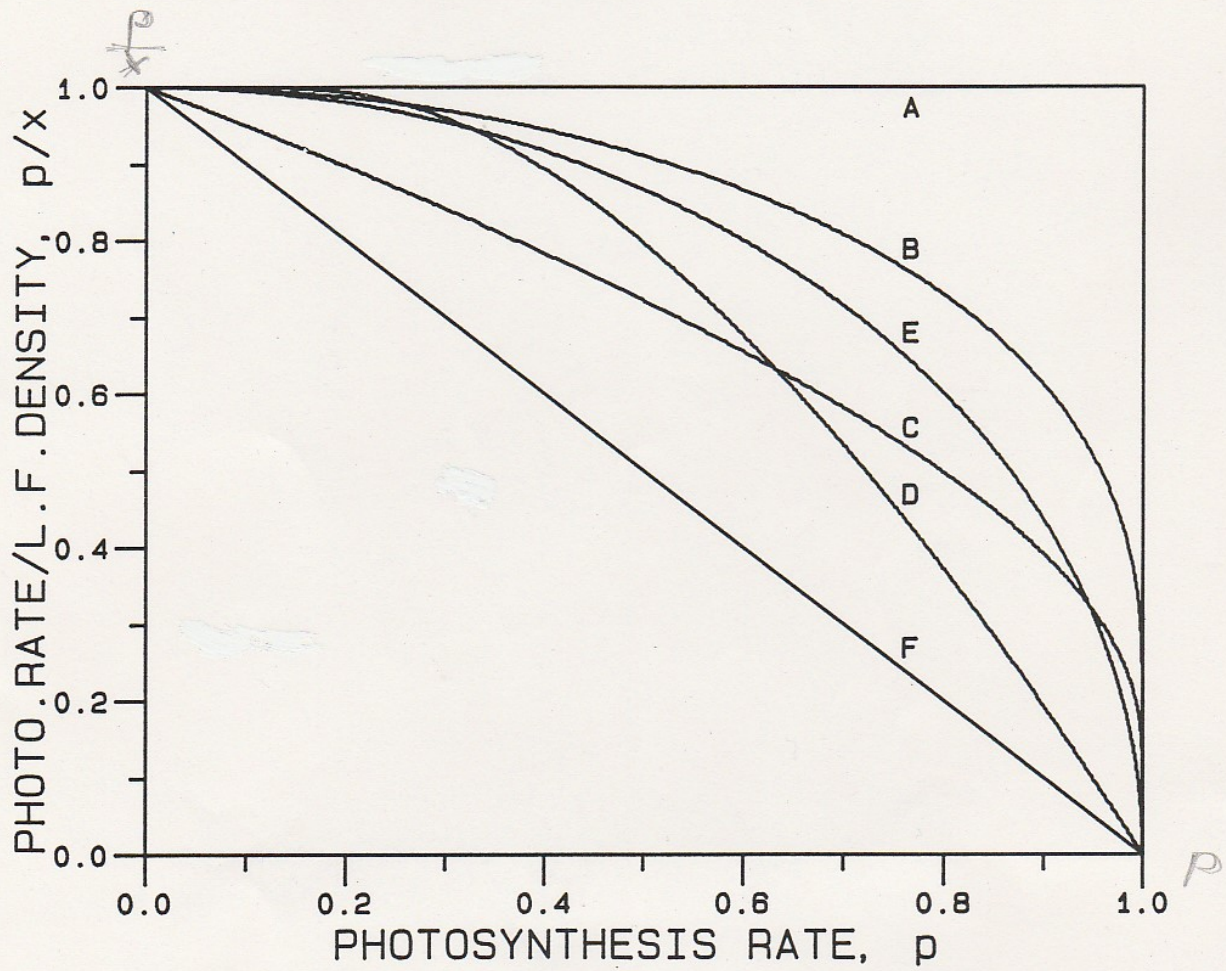


Fig. 2

Eqn. (8)

$$\frac{\alpha}{\beta} = 1, P = 1 \cdot \left(= \frac{v}{\mu} \right)$$

$$\alpha = \beta = 1, 2, 5, 15, 80$$

Limiting Factor Density

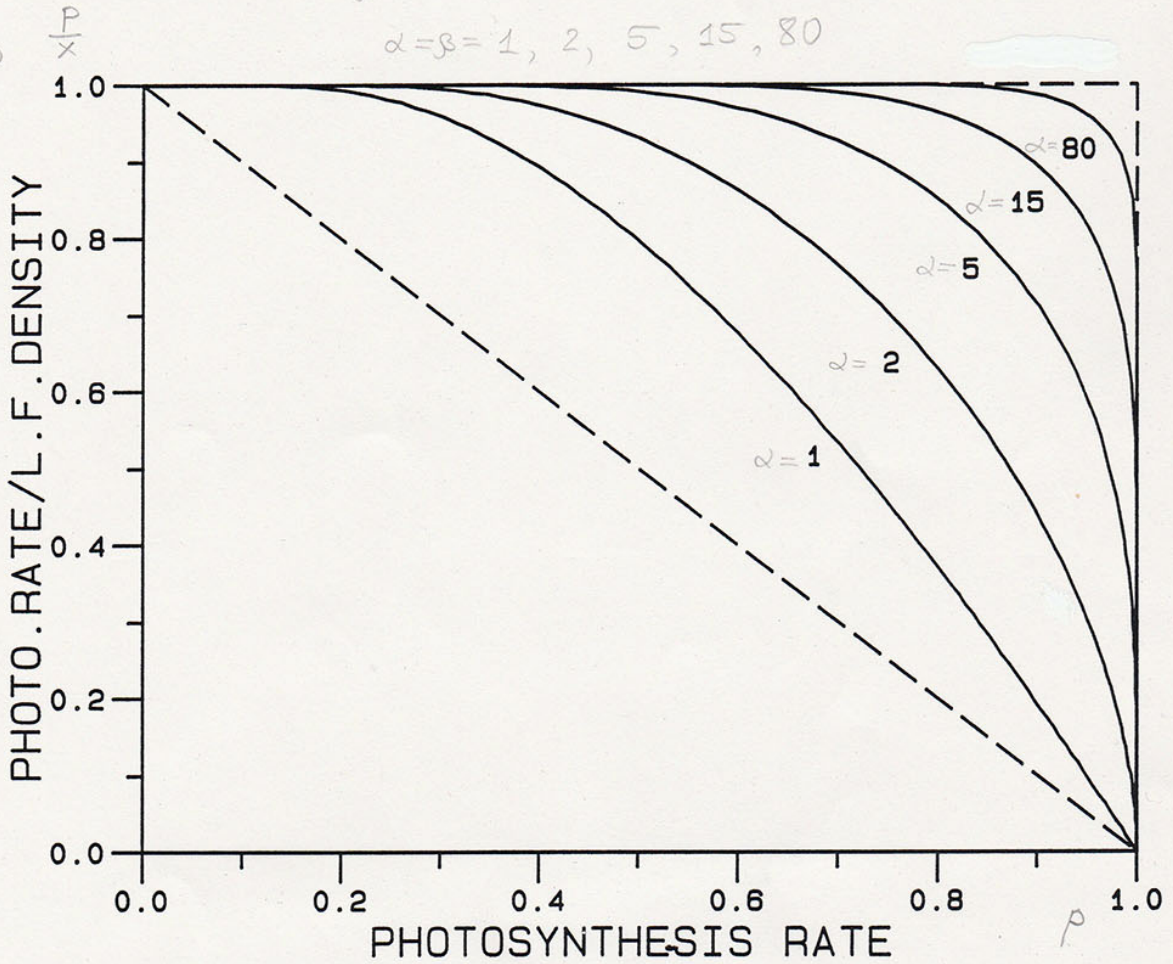


Fig. 3

Eqn. (10)

$\alpha = \beta = 3$

$\gamma = \mu = 0.03, 0.1, 0.3, 1, 2, 5, 20, \text{INF}$

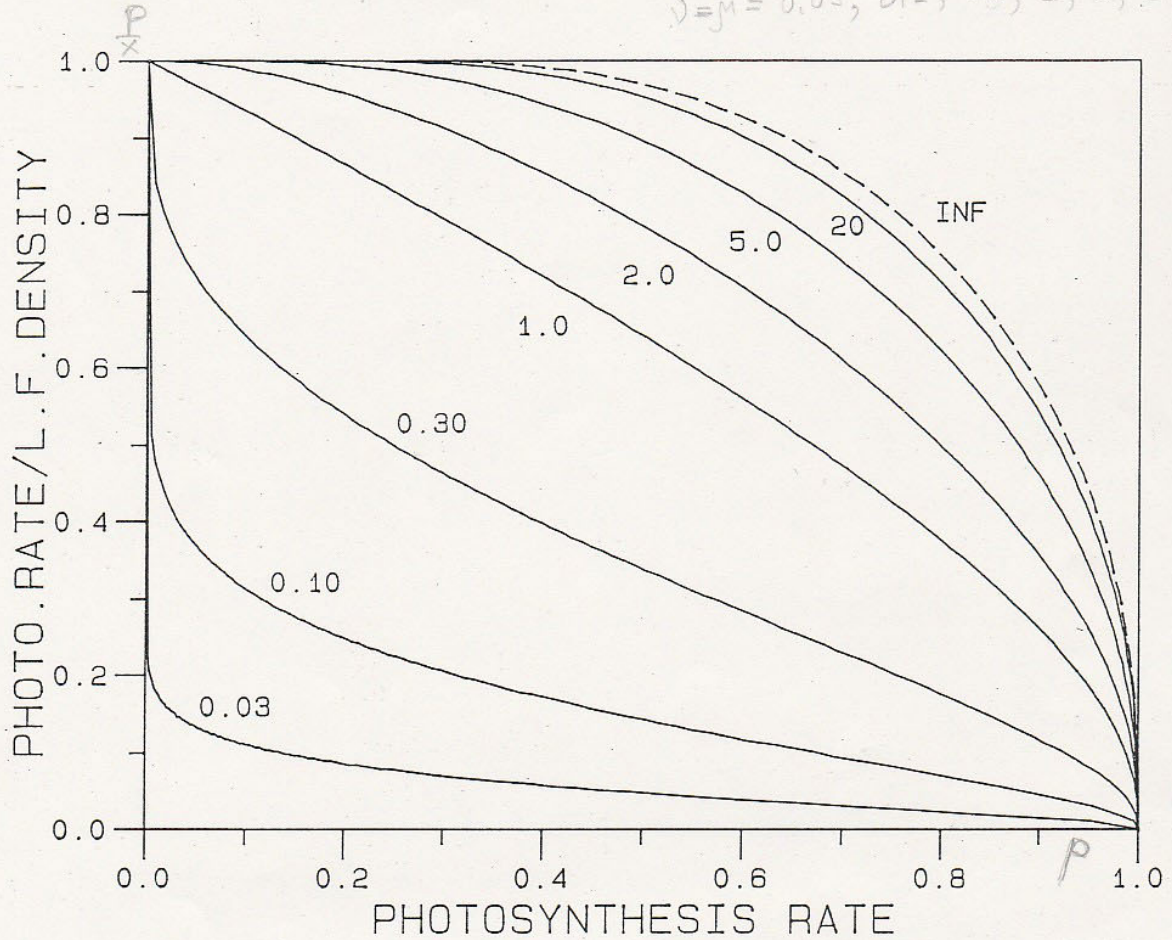


Fig. 4

Eqn. (14)

$$a=1 \quad \frac{\nu}{\mu} = 1$$

$$\nu = \mu = 1, 2, 5, 15, 80$$

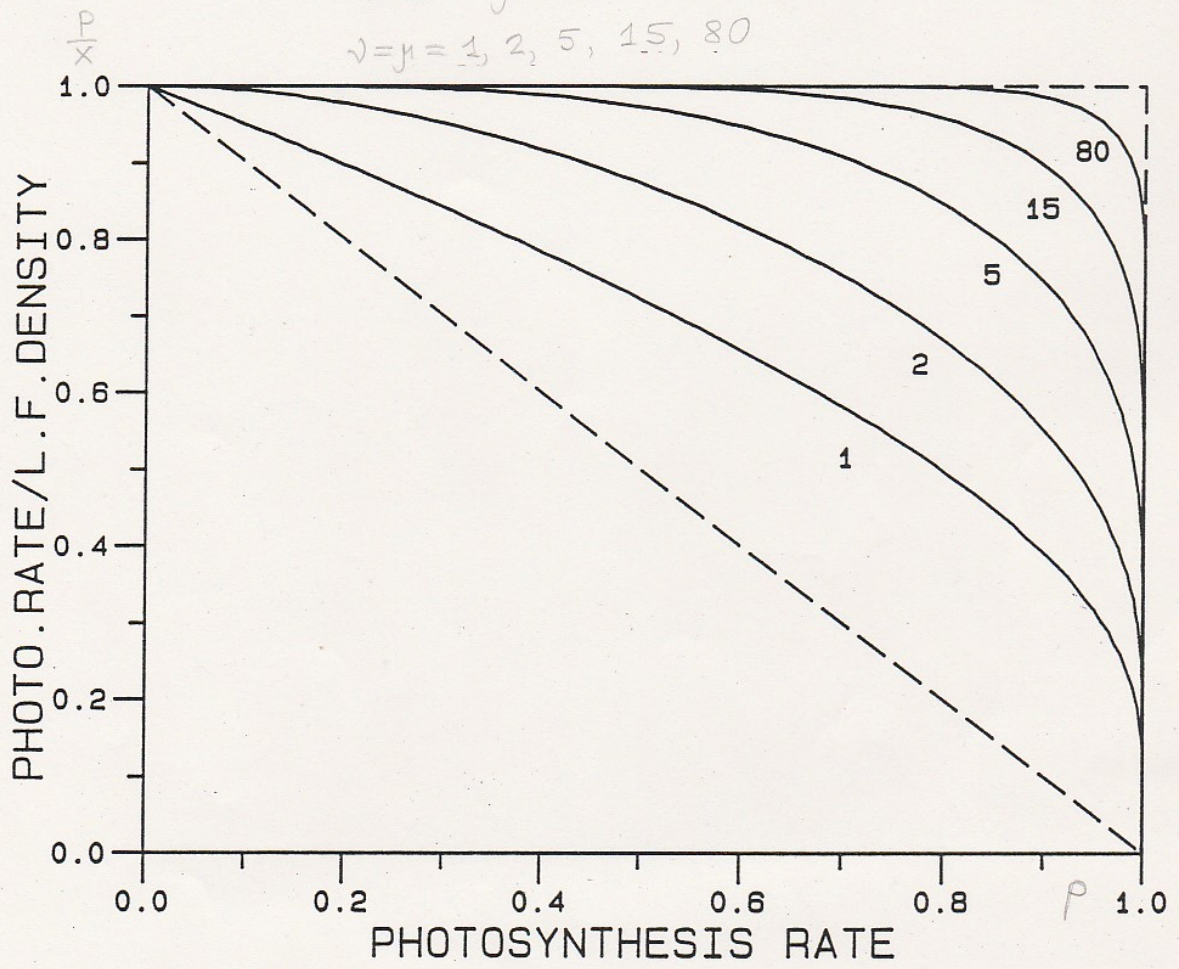


Fig. 5

Eqn. (16)

$$\frac{\alpha}{\beta} = 1$$

$$\frac{\nu}{\mu} = 1$$

$$\nu = \mu = 3$$

$$\alpha = \beta = 0.03, 0.1, 1.0, 2.0, 5.0, 20, \infty$$

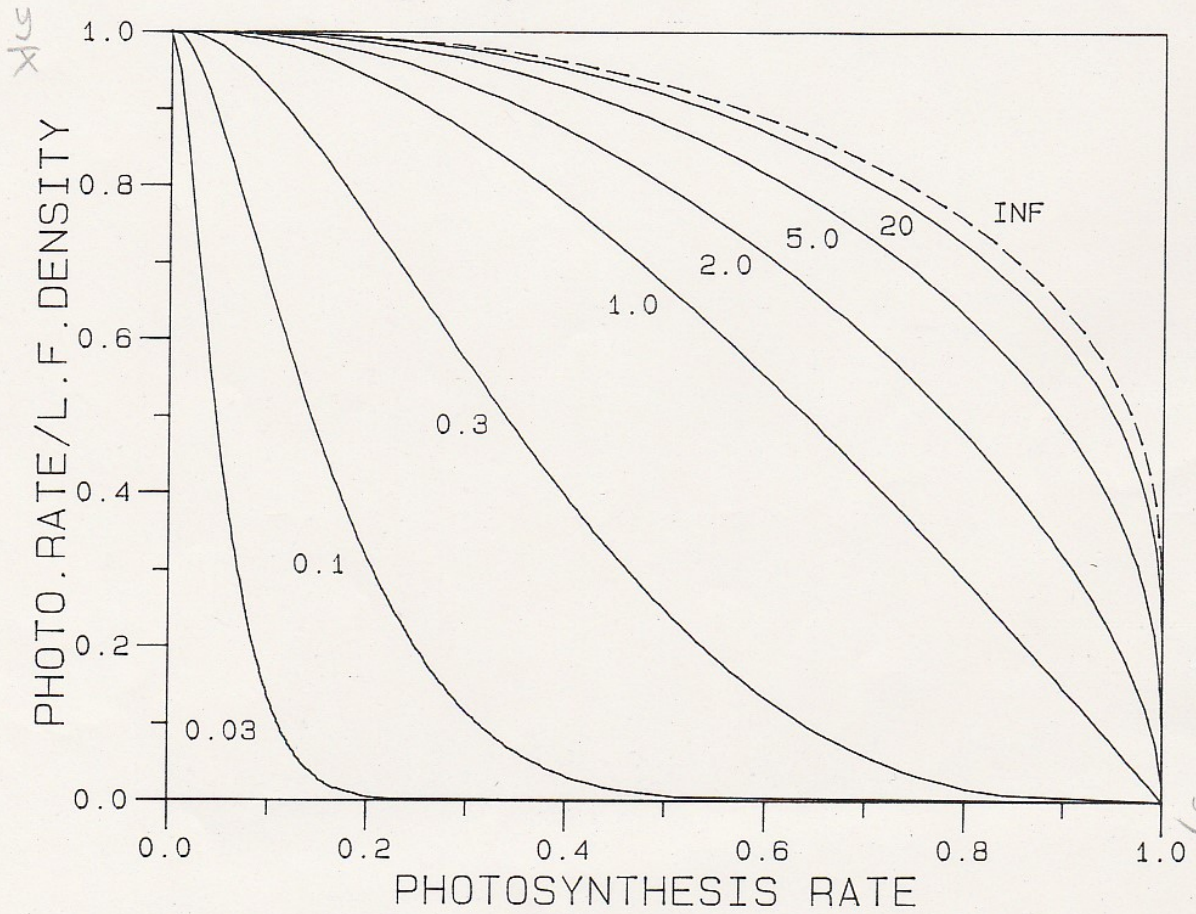


Fig. 6

Eqn. (14) $P=1$
 $\frac{v}{M}=1$

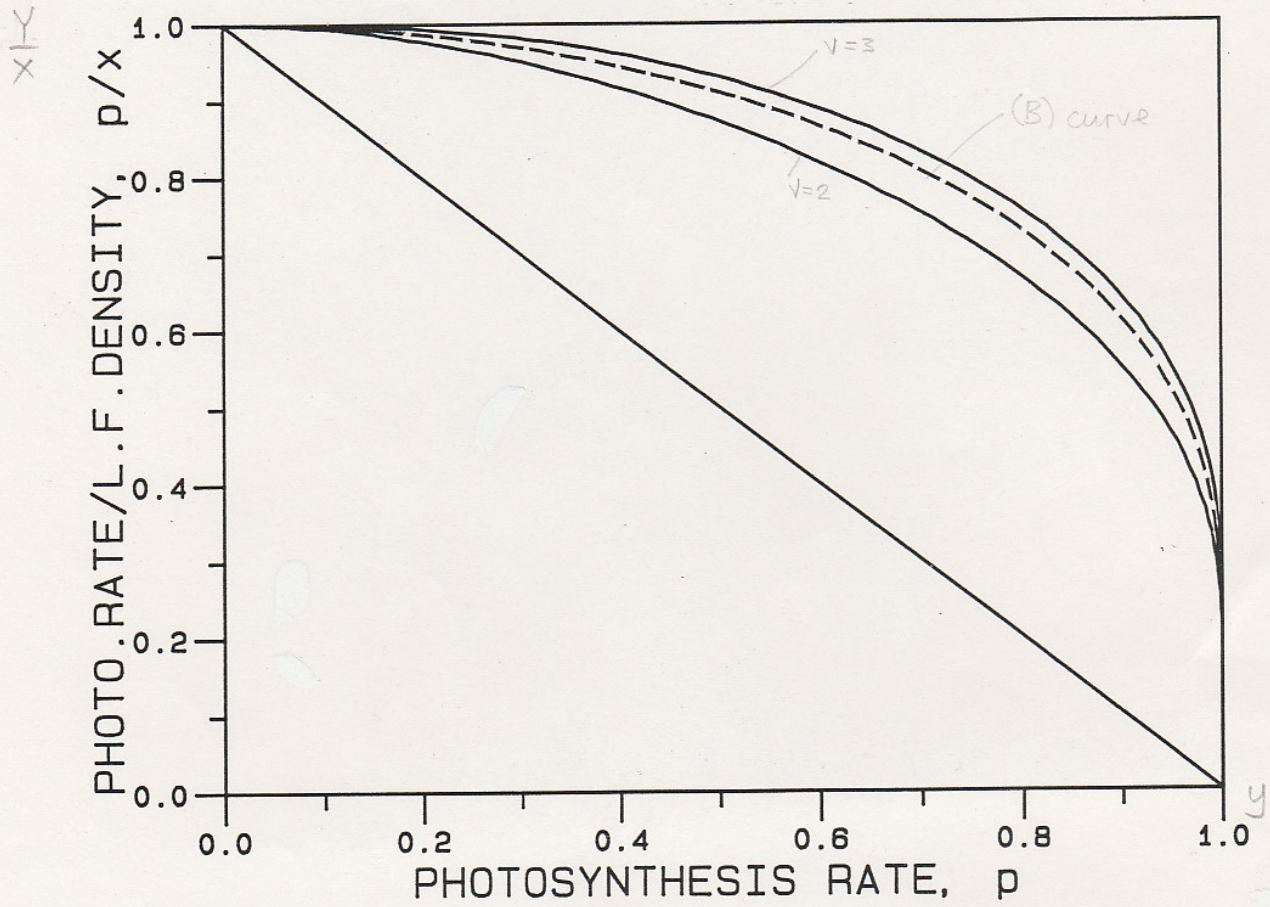


Fig. 7

Int. (10)
 $v = \mu = \alpha = \beta =$
3.0, 3.8

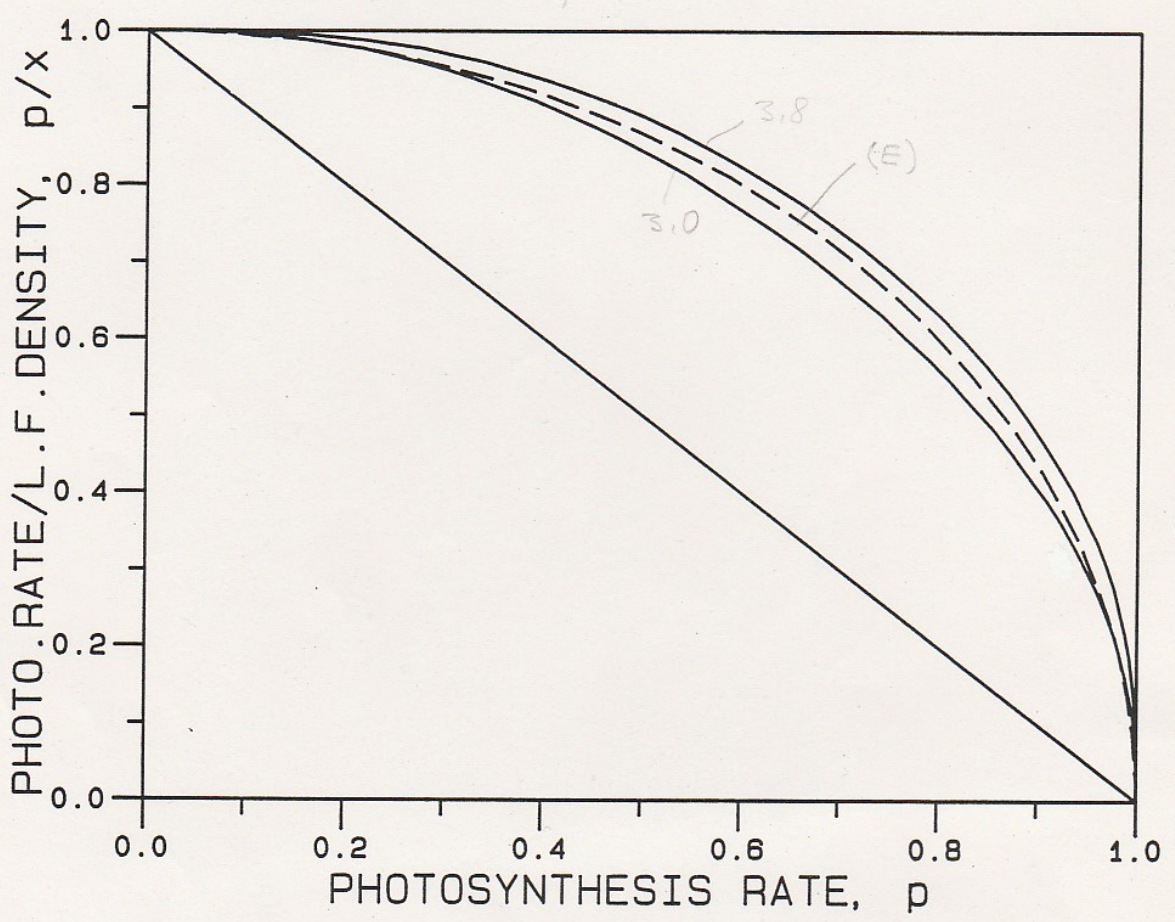


Fig. 8