A FAMILY OF PHOTOSYNTHESIS RESPONSE CURVES ORIGINATED VIA THE BOTTLENECK PRINCIPLE

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ABSTRACT

A stochastic mathematical model is presented resulting in a family of formulae and curves that express photosynthesis rate of a heterogeneous tissue as a function of external limiting factors. As a bench mark, the Blackman-type piecewise-linear curve has been taken, its parameters interpreted as random values of the gamma distribution. The model explicitly distinguishes and mathematically describes two kinds of heterogeneity. Some acknowledged semi-empirical light-, H_2O- and CO_2-response curves deduced as special cases of the model and received theoretical substantiation.

INTRODUCTION

Chloroplasts of a vascular plant organ work as assembly-lines utilising the H_2O, CO_2 and PAR (photons, physiologically active radiation) as irreplaceable components. Chloroplasts differ in size and receptivity that cause heterogeneity of tissues. Were chloroplasts identical, the biomass synthesis would be well described by the idealised Blackman bottleneck slope-and-ceiling curve [1]:

$$r = min\left(sx, P\right) \tag{A}$$

also known as a piecewise-linear curve [6], where *r* is photosynthesis rate, *x* is an external limiting factor (H_2O, CO_2, or PAR) consumption intensity (or availability), and constant positive parameters *s* and *P* are initial slope and final plateau level of the curve, respectively (see Fig. 1), the former characterising efficiency, the latter, capacity of a biomass creating unit (chloroplast).

In practice, however, smoothed convex curves are in use [2, 3, 4, 5, 7, 8]:

(Jassby & Platts)

$$r = P\ tanh\left(\frac{sx}{P}\right) \tag{B}$$

(Peat)

$$r = P\left(1 - e^{-\frac{sx}{P}}\right) \tag{C}$$

(Thornley)

$$r = sx\left(1 - e^{-\frac{P}{sx}}\right) \tag{D}$$

(Vollenweider)

$$r = \frac{sPx}{\sqrt{P^2 + s^2x^2}} \tag{E}$$

(Baly)

$$r = \frac{sPx}{P + sx} \tag{F}$$

Normalised (A) to (E) curves are plotted in Fig. 1a in (*x*, *r*)-coordinates, and in Fig. 1b, in the George Scatchard (*r*, *r*/*x*)-coordinates, the latter showing the whole range of $x\ \epsilon[0 \le x \le \infty)$ and $r\ \epsilon[0 \le r \le P]$ compactly in one 1×1 square, in arbitrary units (a.u.).

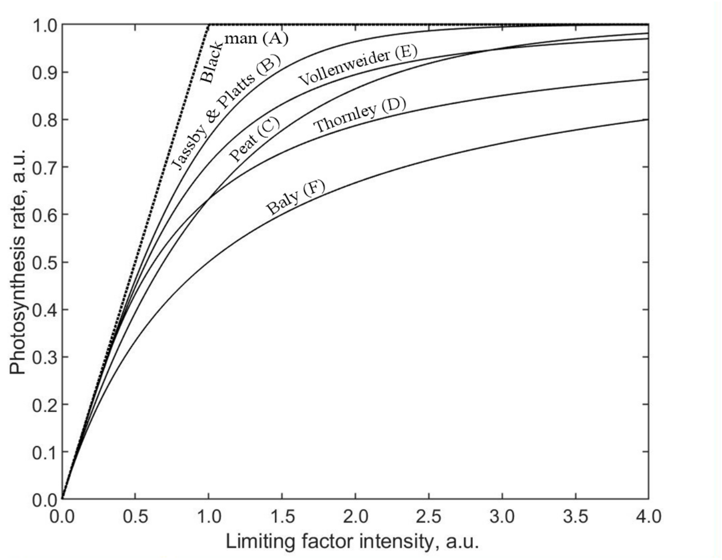

Fig. 1a. (A) to (F) photosynthesis response curves as functions of a limiting factor, in arbitrary unites.

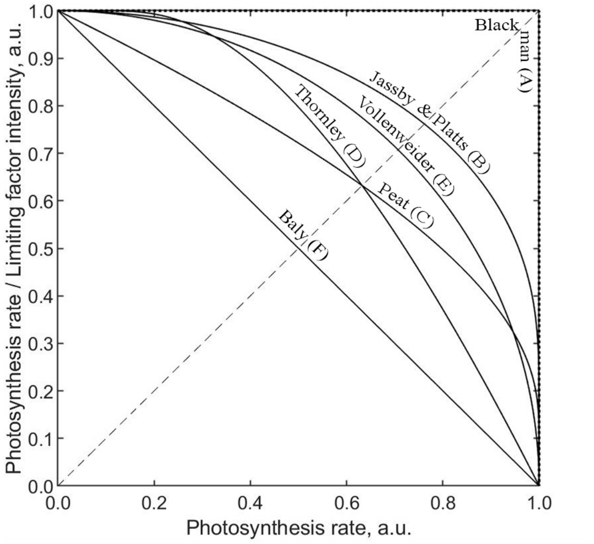

Fig. 1b. (A)to (F) photosynthesis response curves in the Scatchard (r,r/x)-coordinates. Curves (C) and D) are symmetrical with respect to the $x = 1$ diagonal (dashed).

It is worth to mention that in the Scatchard coordinates, the Peat curve (C) is the inverse function (f^{-1}) of the Thornley curve (D), and *vise versa* (the curves are symmetrical with respect to the diagonal $x = 1$ ($r/x = r$) of the Fig. 1b square.

The formulae (B) to (F) are commonly understood [7, 8] as researchers' cute semi-empirical insights rather than theoretically established laws. We aim to prove that all of them (and a wealth of others) follows from the Blackman bottleneck formula (A) *as special cases* if a stochastic approach is applied.

STOCHASTIC APPROACH: *S*-VARIATION CURVES

Let the final plateau level, P, in Eq. (A) be a constant real-valued positive parameter, and the initial slope, s, a random number distributed according to the gamma probability density function with the mean α/β and the variance α/β^2 (see Fig. 2):

$$f(s) = \frac{\beta^{\alpha}}{\Gamma(\alpha)} s^{\alpha-1} e^{-\beta s} \tag{G1}$$

Here α and β are positive parameters, and $\Gamma(\alpha)$ is the gamma function.

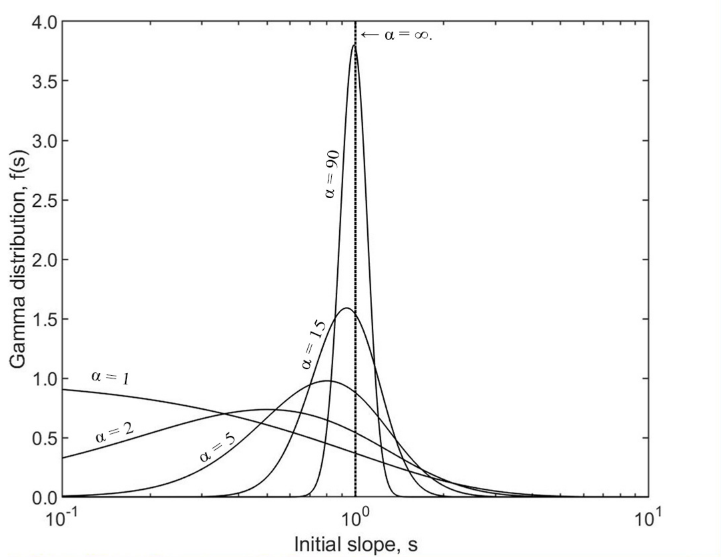

Fig. 2. Gamma distribution (G1), in semi-logarithmic scale, for $\alpha/\beta=1$, $\alpha/\beta^2=1$, and $\alpha=1$,$=2$, $=5$, $=15$, $=90$, and$=\infty$.

With such an assumption, photosynthesis rate expectation $E_S(r \mid x)$ for the Blackman bottleneck model (A) is

$$E_S = \int_0^{\infty} f(s)\ min(sx, P)\ ds$$

$$= \frac{x}{\beta\ \Gamma(\alpha)}\ \gamma(\alpha+1, \frac{\beta P}{x}) + \frac{P}{\Gamma(\alpha)}\ \Gamma(\alpha, \frac{\beta P}{x}) \tag{1}$$

where $\Gamma(.)$ is the gamma function, $\gamma(.,.)$ is the lower incomplete gamma function and $\Gamma(.,.)$ is the upper incomplete gamma function.

Some normalised E_S curves ($\alpha/\beta = 1$, $P = 1$) corresponding to Eq. (1) are plotted in Fig. 3a and Fig. 3b.

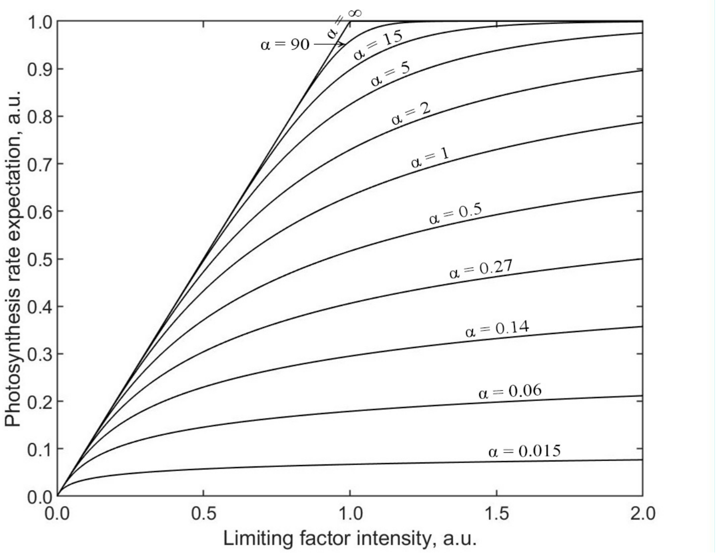

Fig. 3a. Normalised (α/β = 1, *P* = 1,) E_S response curves, for α=0.015, =0.06, = 0.14, = 0.27, =0.5, =1, =2, =5, =15, =90, and =∞, in arbitrary units. At α = ∞, E_S curve transforms into the Blackman piecewise-linear curve (A).

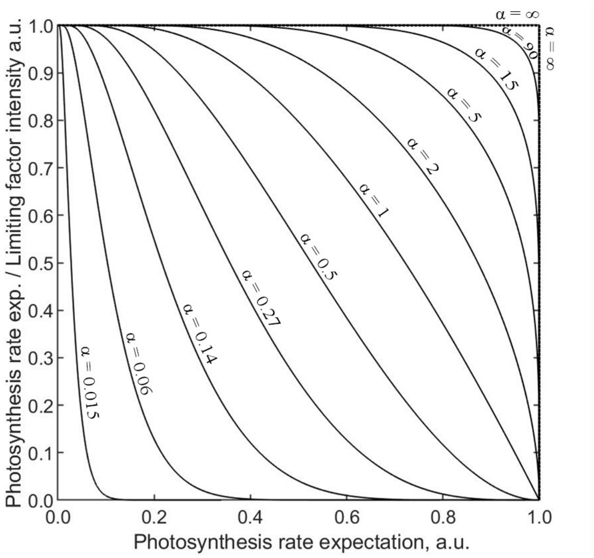

Fig. 3b. Normalised (α/β = 1, *P* = 1) E_S response curves, in the Scatchard (E_s,E_s/x)-coordinates, for α=0.015, =0.06, =0.14, =0.27, =0.5, =1, =2, =5, =15, =90, and =∞ (dotted). At α=∞, E_S curve transforms into the Blackman piecewise-linear curve(A).

Any E_s curve generated by Eq. (1) is convex, with the first derivative decreasing strictly monotonously from the initial slope

$$\left.\frac{\mathrm{d}E_S}{\mathrm{d}x}\right|_{x=0} = \frac{\alpha}{\beta} \tag{2}$$

(i.e. from the averaged *s*) to 0 at $x \to \infty$, while

$$\lim_{x\to\infty} E_S = P \tag{2a}$$

At α/β constant and $\alpha \to \infty$, the gamma distribution (G1) approaches Dirac delta function $\delta(s)$, and the stochastic model set by Eq. (1) regenerates into the initial deterministic one with $s = \alpha/\beta$:

$$E_S = min\left(\frac{\alpha}{\beta}x, P\right) \tag{3}$$

i.e. recurs back into the Blackman bottleneck formula (A) with the initial slope $s = \alpha/\beta$. Physically, it means that *S*-variation heterogeneity with respect to the initial slope transforms into full homogeneity (all chloroplasts have the same receptivity to the limiting factor).

At $\alpha = 1$, Eq. (1) reduces into

$$E_S = \frac{x}{\beta}\left(1 - e^{-\frac{\beta P}{x}}\right) \tag{4}$$

which is identical to Thornley's formula (D) with the initial slope $s = 1/\beta$ and the final plateau level *P*.

All the five acknowledged curve (B) to (F) are numerically compared with the E_S curves (1) in Table 1. As a criterion, the residual $\Delta = (E_S - r_{\text{NAME}})$ has been chosen, with the global maximum of $|\Delta|$ to be minimised, along with an assumption that approximation is acceptable if $|\Delta| \le 1.0\%P$ on the interval of $x \in [0, \infty)$.

Table 1

E_S curves (1) vs. the acknowledged curves (B) to (F), matching the criterion of the max $|\Delta| = |(E_S - r_{\text{NAME}})|$ minimised.

Jassby & Platts (B)	E_S: $\alpha = \beta = 2.897$	$\lvert\Delta\rvert > 1.0\%\ P$. Δ reaches its max of +0.02724 at $x = 0.6406$ and its min of -0.02724 at $x = 2.0936$. Not acceptable.
Peat (C)	E_S: $\alpha = \beta = 1.298$	$\lvert\Delta\rvert > 1.0\%P$. Δ reaches its max of +0.059240 at $x = 0.6089$ and its min of -0.059240 at $x = 3.5461$. Not acceptable.
Thornley (D)	E_S: $\alpha = \beta = 1$	$\Delta \equiv 0$ on $x \in [0,+\infty)$. Curves are identical.
Vollenweider (E)	E_S: $\alpha = \beta = 1.725$	$\lvert\Delta\rvert > 1.0\%P$. Δ reaches its max of +0.01879 at $x = 0.5389$ and its min of -0.01879 at $x = 2.4388$. Not acceptable.
Baly (F)	E_S: $\alpha = \beta = 0.5638$	$\lvert\Delta\rvert > 1.0\ \%P$. Δ reaches its max of +0.04990 at $x = 0.5417$ and its min of -0.04990 at $x = 12.44$. Not acceptable.

According to the criterion chosen, it may be concluded from the Table 1 that the expressions (B), (C), (E), and (F) were not constructed for a description of the *S*-heterogeneity, while the Thornley formula (D) describes just this particular case of heterogeneity.

At any integer $\alpha > 0$, Eq. (1) transforms into

$$E_S = \frac{\alpha x}{\beta}\left(1 - e^{-\frac{\beta P}{x}} \sum_{i=0}^{\alpha-1}\left(1 - \frac{i}{\alpha}\right)\frac{\left(\frac{\beta P}{x}\right)^i}{i!}\right) \tag{5}$$

Eq. (5) is a source of simple and ostensive algebraic expressions for the *S*-heterogeneity response curves having the *real-valued* initial slope α/β and final plateau level *P*, with the Thornley (D) formula as it simplest case at $\alpha = 1$.

At β constant and $\alpha \to \infty$, Eq. (1) and Eq. (5) transform into the Heaviside step function $H(x)$ for $x \ge 0$, equal to 0 at the origin and to *P* for $x \in (0, \infty)$.

STOCHASTIC APPROACH: *P*-VARIATION CURVES

Let the initial slope, *s*, in the Blackman model (A) be a constant real-valued positive parameter, and the final plateau level, *P*, a random number distributed according to the gamma probability density function with the mean κ/λ and the variance κ/λ^2:

$$f(P) = \frac{\lambda^\kappa}{\Gamma(\kappa)}P^{\kappa-1}e^{-\lambda P} \tag{G2}$$

With such an assumption, photosynthesis rate expectation $E_P(r|x)$ for the averaged Blackman bottleneck model (A) is

$$E_P = \int_0^\infty f(P)\; min(sx, P)\; dP$$

$$= \frac{1}{\lambda\,\Gamma(\kappa)}\gamma(\kappa+1, \lambda sx) \; + \; \frac{sx}{\Gamma(\kappa)}\Gamma(\kappa, \lambda sx) \qquad (6)$$

where Γ(.) is the gamma function, γ (.,.) is the lower incomplete gamma function and Γ(.,.) is the upper incomplete gamma function.

Some normalised E_P curves ($s = 1$, $\kappa/\lambda = 1$) corresponding to Eq. (6) are plotted in Fig. 4a and Fig. 4b. As expected, the *P*-variation heterogeneity decreases with increasing κ, and at $\kappa = \infty$ transforms into the full Blackman-type homogeneity.

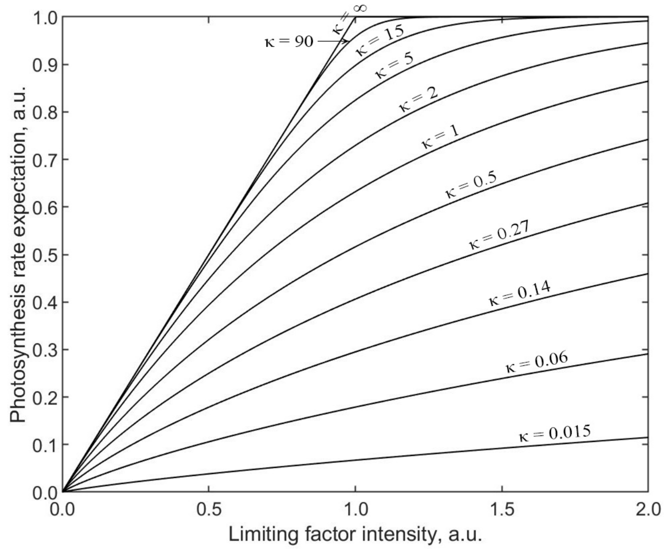

Fig. 4a. Normalised ($s = 1$, $\kappa/\lambda = 1$) E_P response curves, for κ = 0.015, =0.06, =0.14, =0.27, =0.5, =1, =2, =5, =15, =90, and =∞, in arbitrary unites. At κ=∞, E_P curve transforms into the Blackman piecewise-linear (A)curve.

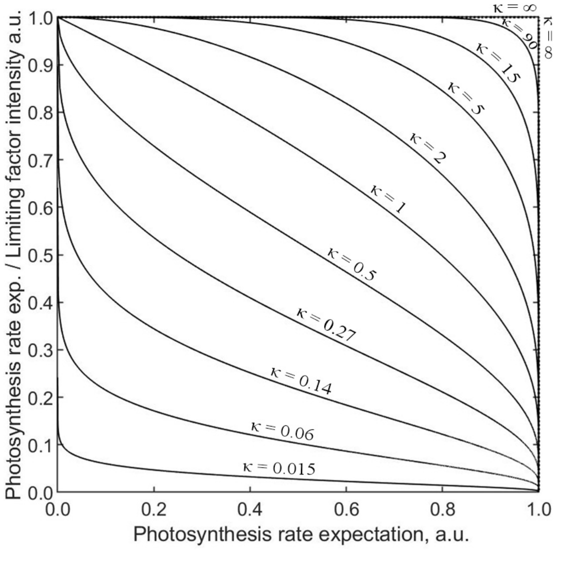

Fig. 4b. Normalised ($s = 1$, $\kappa/\lambda = 1$,) E_P response curves, in the Scatchard (E_P,E_P/x)-coordinates, for κ =0.015,

=0.06, =0.14, =0.27, =0.5, =1, =2, =5, =15, =90, and =∞
(dotted). At κ=∞, E_P curve transforms into the
Blackman piecewise-linear curve(A).

Any E_P curve generated by Eq. (6) is convex, with first derivative decreasing strictly monotonously from the initial slope

$$\left.\frac{\mathrm{d}E_P}{\mathrm{d}x}\right|_{x=0} = s \tag{7}$$

to 0 as x →∞, while E_P approaching the final plateau level κ/λ (the averaged P):

$$\lim_{x\to\infty} E_P = \frac{\kappa}{\lambda} \tag{7a}$$

If the ratio κ/λ is constant and κ → ∞, gamma distribution (G2) approaches the Dirac delta function δ(s), and the stochastic model set by Eq. (6) transforms into the initial deterministic one

$$E_P = min\left(sx, \frac{\kappa}{\lambda}\right) \tag{8}$$

i.e. into the Blackman bottleneck formula (A) with P = κ/λ. Physically, this limiting case corresponds to the full capacity homogeneity of the photosynthesising tissue (all chloroplasts have the same plateau level, or a capacity, with respect to the limiting factor).

At κ = 1, Eq. (6) reduces into

$$E_P = \frac{1}{\lambda}\left(1 - e^{-\lambda s x}\right) \tag{9}$$

which is identical to the Peat formula (C) with the initial slope s and the plateau level P = 1/λ.

All the five acknowledged curves (B) to (F) are numerically compared with the E_P curves (6) in Table 2. As a criterion, the residual Δ = ($E_P - r_{\mathrm{NAME}}$) has been chosen, with maximum of |Δ| to be minimised, along with an assumption that approximation is acceptable if |Δ| ≤ 1.0 %P on the interval of x ϵ [0, ∞).

Table 2
E_P curves (6) vs. the acknowledged curves (B) to (F),
matching the criterion of the max |Δ| = |($E_P - r_{\mathrm{NAME}}$)| minimised.

Jassby & Platts (B)	E_P: κ = λ = 2.6037	Δ ≤ 0.13% P. Δ reaches its max of 0.001266 at x = 0.140 and its min of -0.001266 x = 1.158. Acceptable.
Peat (C)	E_P: κ = λ = 1	Δ ≡ 0 on x ϵ [0,+∞). Curves are identical.
Thornley (D)	E_P: κ = λ = 0.711875	Δ > 1.0% P. Δ reaches its min of -0.075263 at x = 0.6049 and its max of 0.075263 at x = 4.4793. Not acceptable.
Vollenweider (E)	E_P: κ = λ =1.429962	Δ > 1.0% P. Δ reaches its min of -0.027597 at x = 0.7251 and its max of 0.027597 x = 2.9937. Not acceptable.
Baly (F)	E_P κ = λ = 0.305633	Δ > 1.0% P. Δ reaches its min of -0.075126 at x = 0.7622 and its max of 0.075126 x = 8.3362. Not acceptable.

According to the criterion chosen, it may be concluded from the Table 2 that the expressions (D), (E) and (F) were not constructed for a description of the P-variation heterogeneity, while the Peat formula (C) ideally describes just this particular case of heterogeneity, and the Jassby & Platts formula (B) is also fit for the P-heterogeneity as it excellently simulated by our model.

At any integer κ > 0, Eq. (6) transforms into

$$E_P = \frac{\kappa}{\lambda}\left(1 - e^{-\lambda s x}\sum_{i=0}^{\kappa-1}\left(1 - \frac{i}{\kappa}\right)\frac{(\lambda s x)^i}{i!}\right) \tag{10}$$

Eq. (10) is a source of simple and ostensive analytical expressions for the P-variation heterogeneity response curves, having both the *real-valued* initial slope s and final plateau level κ/λ, with the Peat (C) formula as it simplest case at $\kappa = 1$.

Let $\alpha = \kappa = u$, and $\beta = \lambda = w$. In the Scatchard coordinates, an $E_P(w, u)$ curve is symmetrical to an $E_S(u, w)$ curve with respect to the diagonal $x = 1$ ($E_{P/S}/x = E_{P/S}$), i.e. an E_P/x is the inverse function (f^{-1}) of an E_S/x. Fig. 4c compares some $E_P(w)$ and $E_S(u)$ curves for $w = u$. It is clear that at $w = u \to \infty$, $E_P(w) \to E_S(u)$ in such a way that $E_S(90)$ and $E_P(90)$ are already practically indistinguishable. On the contrary, at $w = u \to 0$, E_P curves lean to the abscissa, while E_S creep along the ordinate.

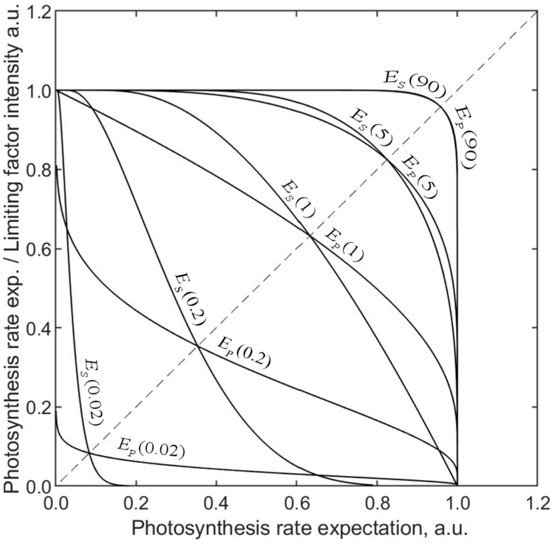

Fig. 4c. Normalised ($\alpha = \beta = u$, $P = 1$) $E_S(u)$ curves vs. normalised ($s = 1$, $\kappa = \lambda = u$) $E_P(u)$ curves in the Scatchard ($E_{S/P}$,$E_{S/P}/x$)-coordinates for u = 0.02, 0.2 (dashed), 1, 5, 90 (solid), in arbitrary units.

At $s \to \infty$, Eq. (6) and Eq. (10) transform into the Heaviside step function H(x) for $x \geq 0$, equal to 0 at the origin and to κ/λ for $x \in (0, \infty)$.

STOCHASTIC APPROACH: *SP*/*PS*-VARIATION

Let both the initial slope s and the plateau level P of the Blackman model (A) be random uncorrelated numbers with the gamma distributions (G1) and (G2). With such an assumption, the photosynthesis rate expectation, according to Eq. (1), is

$$E_{SP} = \int_0^\infty E_S f(P) dP \tag{11}$$

or, according to Eq. (6), with reversing integration order,

$$E_{PS} = \int_0^\infty E_P f(s) ds \tag{12}$$

Since E_{SP} and E_{PS} obtained from the same assumptions and differ in the order of integration only, $E_{SP} \equiv E_{PS}$.

Some normalised $E_{SP/PS}$ curves ($\alpha/\beta = 1$, $\kappa/\lambda = 1$) corresponding to Eq. (11)/(12) are plotted in Fig. 5a to Fig. 5d.

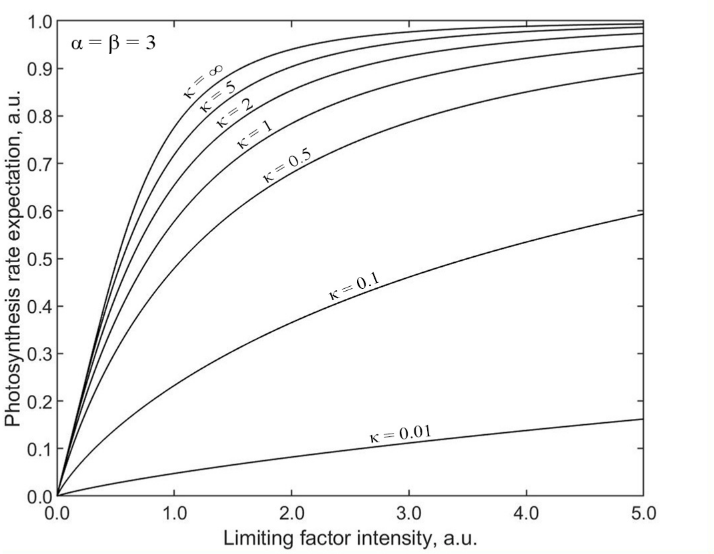

Fig. 5a. Normalised (α/β = 1, κ/λ = 1) $E_{SP/PS}$ curves for α=β =3 and κ=0.01, =01, =0.5, =1, =2, =5, and =∞, in arbitrary units.

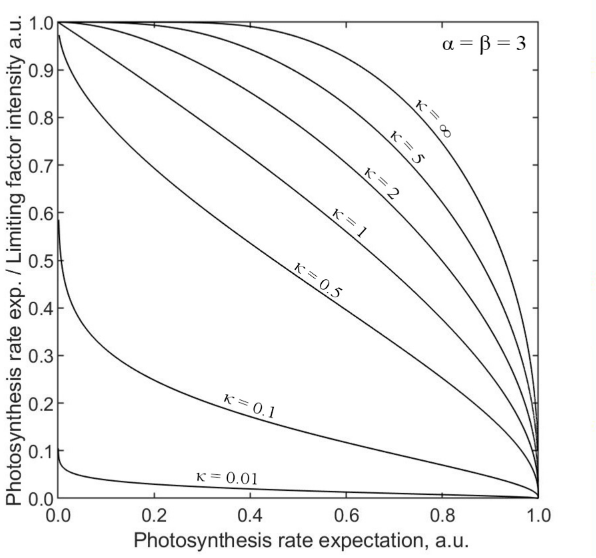

Fig. 5b. Normalised (α/β = 1, κ/λ = 1) $E_{SP/PS}$ response curves in the Scatchard ($E_{SP/PS}$,$E_{SP/PS}/x$)-coordinates, for α=β =3 and κ=0.01, =0.1, =0.5, =1, =2, =5, and=∞, in arbitrary units.

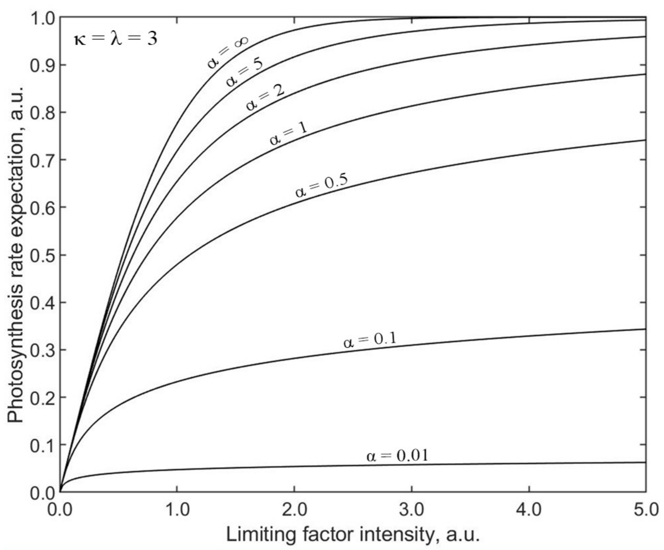

Fig. 5c. Normalised (α/β = 1, κ /λ = 1) E_{PS} curves for κ=λ=3 and α=0.01, =0.1, =0.5, =1, =2, =5, and =∞, in arbitrary units.

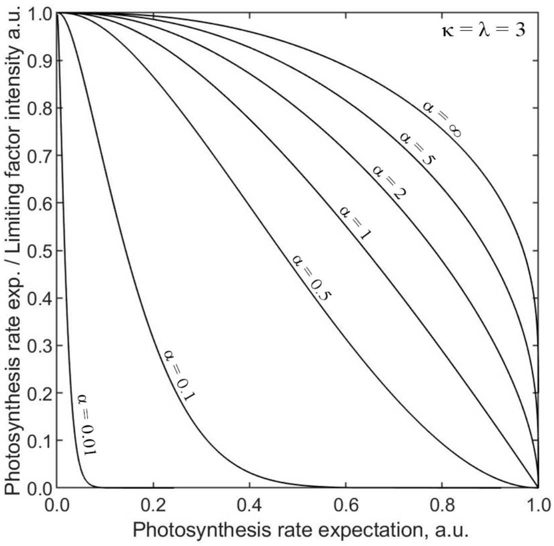

Fig. 5d. Normalised (α/β = 1, κ /λ = 1) $E_{SP/PS}$ response curves in the Scatchard ($E_{SP/PS}$, $E_{SP/PS}/x$)-coordinates, for κ=λ=3 and α=0.01, =0.1, =0.5, =1, =2, =5, and =∞, in arbitrary units.

Any $E_{SP/PS}$ curve generated by Eq. (11)/Eq.(12) is convex, with first derivative decreasing strictly monotonously from the initial slope (the averaged s)

$$\frac{\mathrm{d}E_{SP}}{\mathrm{d}x} \equiv \frac{\mathrm{d}E_{PS}}{\mathrm{d}x} = \frac{\alpha}{\beta} \tag{13}$$

at the origin to 0 as $x \rightarrow \infty$, while $E_{SP/PS}$ approaching the final plateau level κ/λ (the averaged P):

$$\lim_{x\to\infty} E_{SP} \equiv \lim_{x\to\infty} E_{PS} = \frac{\kappa}{\lambda} \tag{14}$$

As expected, at fixed κ and λ and a constant ratio α/β, the greater α, the less heterogonous a photosynthesising tissue is with respect of the initial slope α/β, so that the $E_{SP/PS}$ curve tends to the E_P curve as $\alpha \rightarrow \infty$. Similarly, at fixed α and β and a constant ratio κ/λ, the greater κ, the less heterogonous a tissue is with respect of the final plateau level κ/λ, so that the $E_{SP/P}$ curve tends to the E_S curve as $\kappa \to \infty$.

If the ratios α/β and κ/λ are constant and $\alpha, \kappa \to \infty$, the stochastic model set by Eq. (11) or Eq. (12) regenerates into original deterministic one,

$$E_{SP} \equiv E_{PS} = min\left(\frac{\alpha}{\beta}x, \frac{\kappa}{\lambda}\right) \tag{15}$$

i.e. into the Blackman bottleneck formula (A) with $s = \alpha/\beta$ and $P = \kappa/\lambda$; or, at $\alpha/\beta = \kappa/\lambda = 1$, into its fully normalised form with respect to the both variables,

$$E_{SP} \equiv E_{PS} = min\left(x, 1\right) \tag{15'}$$

At $\alpha = \kappa = 1$, both Eq. (11) and Eq. (12) transform into

$$E_{SP} \equiv E_{PS} = \frac{x}{\beta + \lambda x} \tag{16}$$

i.e. into the Baly rectangular hyperbola (F) with initial slope 1/β and final plateau level 1/λ.

All the five acknowledged curves (B) to (F) discussed above are numerically compared with the $E_{SP/PS}$ curves (11)/(12) in Table 3. As a criterion, the residual $\Delta = (E_{SP/PS} - r_{\text{NAME}})$ has been chosen, with maximum of $|\Delta|$ to be minimised, along with an assumption that approximation is acceptable if $|\Delta| \leq 1.0$ %P on the interval of $x \in [0, \infty)$.

Table 3

$E_{SP/PS}$ curves (11)/(12) vs. the acknowledged curves (B) to (F),
matching the criterion of the max $|\Delta| = |(E_{SP/PS} - r_{\text{NAME}})|$ minimised.

Jassby & Platts (B)	$E_{SP/PS}$: $\alpha = \beta = 160$ $\kappa = \lambda = 2.6495$	$\Delta \leq 0.16\%\ P$. Δ reaches its max of +0.001522 at $x = 0.4342$ and its min of -0.001522 at $x = 1.2491$. Acceptable.
Peat (C)	$E_{SP/PS}$: $\alpha = \beta = 140$ $\kappa = \lambda = 1$	$\Delta \leq 0.20\%P$ Δ reaches its only min of -0.00192898 at $x = 2.0047$. At $\alpha = \beta \to \infty$, $\Delta \to 0$ ($E_{SP/PS}$ reduces into E_P). Acceptable.
Thornley (D)	$E_{SP/PS}$: $\alpha = \beta = 1$ $\kappa = \lambda = 140$	$\Delta \leq 0.14\%P$. Δ reaches its only min of -0.001310 at $x = 1.0012$. At $\kappa = \lambda \to \infty$, $\Delta \to 0$ ($E_{SP/PS}$ reduces into E_S). Acceptable.
Vollenweider (E)	$E_{SP/PS}$: $\alpha = \beta = 2.975$ $\kappa = \lambda = 3.9203$	$\Delta \leq 0.37\%P$. Δ reaches its min of -0.003679 at $x = 1.2885$ and its max of 0.003679 $x = 4.8087$. Acceptable.
Baly (F)	$E_{SP/PS}$ $\alpha = \beta = 1$ $\kappa = \lambda = 1$	$\Delta \equiv 0$ on $x \in [0,+\infty)$. Curves are identical.

According to the criterion chosen, it may be concluded from the Table 3 that all the acknowledged curves (B) to (F) discussed above can be closely simulated by our model, with the Baly curve following from it as a simplest special case. In addition, the Peat (C) curve is the limiting case of $E_{SP/PS}$ at α = β constant and $\alpha \to \infty$ ($E_{SP/PS}$ reduces into E_P), while the Thurnley (D) curve is the limiting case of $E_{SP/PS}$ at κ = λ constant and $\kappa \to \infty$ ($E_{SP/PS}$ reduces into E_S). In other words, $E_{SP/PS}$ curves are fit to simulated all the known special cases of *S*-heterogeneity and *P*-heterogeneity as well as their mixtures (the complex heterogeneity).

At integer $\alpha \geq 1$ and integer $\kappa \geq 1$, Eq. (11) and Eq. (12) take the following forms, respectively:

$$E_{SP} = \frac{\alpha x}{\beta}\left(1 - \frac{\lambda^{\kappa} x^{\kappa}}{(\beta + \lambda x)^{\kappa}} \sum_{i=0}^{\alpha-1}\left(1 - \frac{i}{\alpha}\right)\binom{\kappa - 1 + i}{i}\frac{\beta^{i}}{(\beta + \lambda x)^{i}}\right) \tag{17}$$

$$E_{PS} = \frac{\kappa}{\lambda}\left(1 - \frac{\beta^{\alpha}}{(\beta+\lambda x)^{\alpha}} \sum_{i=0}^{\kappa-1}\left(1-\frac{i}{\kappa}\right)\binom{\alpha-1+i}{i}\frac{\lambda^{i}x^{i}}{(\beta+\lambda x)^{i}}\right) \tag{18}$$

Eq. (17) and Eq. (18) are a source of simple and ostensive analytical expressions for the *SP/PS*-heterogeneity response curves, having the *real-valued* initial slope α/β and final plateau level κ/λ. Since any $E_{SP} \equiv E_{PS}$, expressions (17) and (18) are transposable so with a large κ (17) is shorter and simpler, while at a large α, (18) is preferable.

Two simplest formulae,

$$E_{SP} = \frac{x}{\beta}\left(1 - \frac{\lambda^{\kappa}x^{\kappa}}{(\beta+\lambda x)^{\kappa}}\right) \tag{19}$$

and

$$E_{PS} = \frac{1}{\lambda}\left(1 - \frac{\beta^{\alpha}}{(\beta+\lambda x)^{\alpha}}\right) \tag{20}$$

immediately follow from (17), at α = 1 (the initial slope 1/β, the plateau level κ/λ), and from (18), at κ = 1 (the initial slope α/β, the plateau level 1/λ), respectively.

Obviously, at a constant ratio κ/λ = *P* and κ → ∞, expression (19) transforms into the Thornley formula (D):

$$\lim_{\kappa\to\infty}\frac{x}{\beta}\left(1 - \frac{\lambda^{\kappa}x^{\kappa}}{(\beta+\lambda x)^{\kappa}}\right) = \frac{x}{\beta}\left(1 - e^{-\frac{\beta P}{x}}\right) \tag{21}$$

while at a constant ratio α/β = *s* and α → ∞, expression (20) transforms into the Peat formula (C) :

$$\lim_{\alpha\to\infty}\frac{1}{\lambda}\left(1 - \frac{\beta^{\alpha}}{(\beta+\lambda x)^{\alpha}}\right) = \frac{1}{\lambda}\left(1 - e^{\lambda s x}\right) \tag{22}$$

Generally, at a constant ratio κ/λ = *P* and κ → ∞, a E_{SP} algebraic function defined by (17) turns into a E_{S} algebraic function set by Eq. (5), while at a constant ratio α/β = *s* and α → ∞, a E_{PS} algebraic function defined by (18) turns into a E_{P} algebraic function set by Eq. (10).

COMPARISON AND DISCUSSION

The stochastic approach developed here theoretically substantiated three of the acknowledged models, namely the Peat formula (C), the Thornley formula (D) and the Baly rectangular hyperbola (F), all of them following from our model as special cases with evident physical meaning. In contrast, it educed artificial nature of formulae (B) and (E) that had been developed as purely expedient makeshift empirical constructions, aimed to satisfy particular and rather sporadic sets of experimental data.

Our model explicitly distinguish two types of heterogeneity: *S*-variation (receptivity, or energy) heterogeneity (the E_{S} curves, of which the Thornley curve is an example) and *P*-variation (or capacity) heterogeneity (the E_{P} curves, of which the Peat curve is an example). It also contemplates the mixture of the two, SP/PS-heterogeneity, a family of the $E_{SP/PS}$ curves, of which the Baly rectangular hyperbola is the classical special case: a median of S-heterogeneity and P-heterogeneity represented in equal shares.

It was shown that a shape of an experimentally obtained curve can hint to a character of heterogeneity of a photosynthesising tissue. If in the Scatchard coordinates a curve leans towards the ordinate at smaller *s*, the *S*-heterogeneity prevail; if the curve gravitates towards abscissa at smaller *P*, the *P*-heterogeneity prevails.

All the acknowledged (A) to (F) models are two-parameter ones, while the stochastic approach models presented here are tree-parameter (E_{S} and E_{P} curves) or four-parameters (E_{SP} and E_{PS} curves) ones, the characteristic that obviously makes them more flexible but, in the same time, more complicated and ostensibly not so easily implementable. But it doesn’t seem to be such a drastic disadvantage. In practice, experimentalists will never deal with parameters α, β, κ, and λ themselves but rather with their ratios: the initial slope α/β and the plateau level κ/λ. Thus, all the E_S, E_P, E_{SP} and E_{PS} curves became actually two-parameter ones. And, of course, they have an already demonstrated *practical* strength of flexibility over the (A) to (F) models. Take, for instance, the Thornley curve with $s = e = 2.7183$ and $P = \pi = 3.1416$. The expression (1) responds to it by an infinite set of the E_S curves with the same initial slope $s = \alpha/\beta = 2.7183$ and plateau level $P = 3.1416$, but with α (and, respectively, $\beta = s/\alpha$) taking any real positive value provided that the ratio α/β stay fixed (Fig. 6).

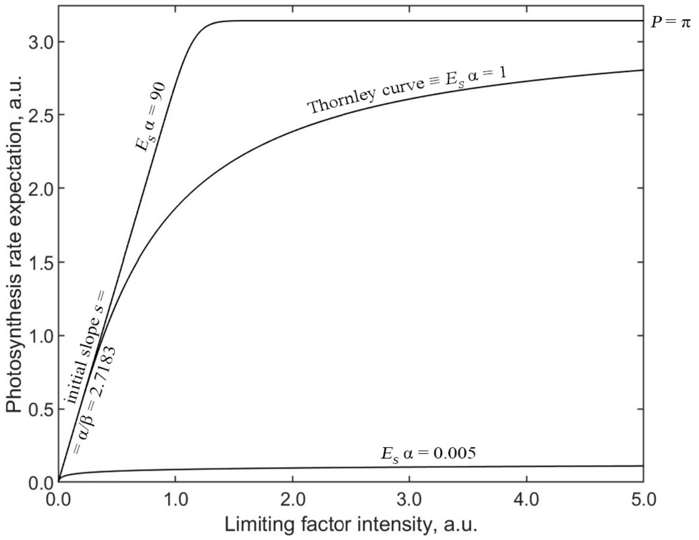

Fig. 6. The Thornley curve with $s = e = 2.7183$ and $P = \pi = 3.1416$ as a *median* of the wealth of the E_S curves with the same initial slope $s = \alpha/\beta = 2.7183$ and plateau level $P = 3.1416$, but with α taking any large or small real positive value.

Nor the equations with gamma functions and integrals should be nowadays considered as too problematic when the experimental data handling is in question. But if, for any reason, simple formulae are preferable, the algebraic expressions (4) to (5), (9) to (10), and (16) to (20) presented above may be effortlessly used, and it is not a strict constraint that α and κ are integer in that expressions, because, as we have seen, it is the ratios α/β and κ/λ are the practically meaningful parameters, and, with β and λ *real-valued*, the ratios α/β and κ/λ have any *real* value, too.

Transposability (replaceability) of the expressions (17) and (18) provides another degree of implementation freedom, because we have in hand the method of two ways representation of identical but seemingly different formulae. Let $\alpha = 21$, $\beta = 3$, $\kappa = 1$, and $\lambda = 2$. Since $E_{SP} \equiv E_{PS}$ for any set of parameters α, β, κ, and λ, the following 21-component formula (a particular case of (17)):

$$E_{SP} = 7x\left(1 - \frac{2x}{3+2x}\sum_{i=0}^{20}\left(1 - \frac{i}{21}\right)\frac{3^i}{(3+2x)^i}\right) \tag{23}$$

is identical to the following simpler two-component formula (a particular case of (18)):

$$E_{PS} = 0.5\left(1 - \frac{3^{21}}{(3+2x)^{21}}\right) \tag{24}$$

Not only vascular plants but also phytoplankton and other photosynthesising autotrophic cell populations can be covered by the approach developed here. It may have some implementation even beyond of biology as such. In agriculture and chemistry, the Blackman bottle-neck principle has been known since the 19th century as the Justus von Liebig law [9]. Adsorption and other processes, where a number of heterogeneous small units are to be saturated, may presumably be described by the same formalism. Assembly-line processes are also open to discussion which may lead to implementation in technology and economics.

A straightforward weakness of the models presented is that only one limiting factor is taken into consideration. More detailed picture may require rotation of limiting factors to be addressed.

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