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SHORT COMMUNICATIONS

A Family of Saturation Type Curves, Especially in Relation to Photosynthesis

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The response of many systems in biology and agriculture to an input is proportional at low values, but levels off at higher values, so that a saturation effect occurs. In economy this phenomenon is known as the law of the diminishing returns and in agriculture as Liebig's law of the limiting factors, which implies that the saturation level is determine by a single limiting factor. There exist several different equations to describe input–output relations of this kind. The simplest one is the Blackman curve (Fig. 1, $S_{-\infty}$), which assumes either a proportional relation or perfect saturation, so that the radius of curvature is zero at the transition point. In real systems the transition is always more gradual. For instance, the light-response curve of the rate of CO_2 assimilation of a crop surface tends to be of the form as indicated by curve S_0 (Fig. 1). The mathematical formulation of this line is the rectangular hyperbola

$$y = x/(1+x), \qquad (1)$$

where x is the normalized input and y the normalized (relative) output, so that both x and y are dimensionless. In the case of photosynthesis y stands for $P_{\text{actual}}/P_{\text{maximal}}$, where P is the photosynthetic rate and x stands for $H\epsilon/P_{\text{maximal}}$, where ϵ is the slope of the curve at the origin and H is the absorbed photosynthetically active radiation. The rectangular hyperbola, also termed the Michaelis–Menten equation, has often been used to describe photosynthesis/light-response curves of leaves (Rabinowitch, 1951; De Wit, 1965; Hesketh, 1963). More recent measurements (Peat, 1970; Van Laar and Penning de Vries, 1972; English 1976) indicated that the approach of the saturation level is often faster and that a better fit can be obtained by the asymptotic exponential

$$y = 1-\exp(-x'), \qquad (2)$$

Both curves have the same slope at the origin and the same saturation level, but they differ in the way the saturation level is approached. The rectangular hyperbola can be converted into the asymptotic exponential and vice versa, by simple transformation of the abscissa, given by

$$x' = \ln(1+x) \qquad (3a)$$

$$\text{or } x = \exp(x')-1. \qquad (3b)$$

These equations have a slope of unity at the origin so that the transformation will leave the curves virtually unchanged at low values of x. At higher values eqn (3a) reduces and eqn (3b) enhances the effect of the input. Substitution of eqn (3a) into the asymptotic exponential yields the more gradually proceeding curve of the rectangular hyperbola, and conversely substitution of eqn (3b) into the rectangular hyperbola yields the asymptotic

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TABLE 1. *Values of S functions of different order for a range of values of the argument x*

x	$S_{-\infty}$	S_{-2}	S_{-1}	$S_{-0\cdot8}$	$S_{-0\cdot6}$
0·01	0·010000	0·010000	0·009950	0·009940	0·009930
0·1	0·100000	0·099829	0·095163	0·094269	0·093398
0·5	0·500000	0·477286	0·393469	0·379079	0·366062
1	1·000000	0·820626	0·632121	0·598122	0·568799
2	1·000000	0·998320	0·864665	0·814066	0·769952
5	1·000000	1·000000	0·993262	0·968750	0·935850
10	1·000000	1·000000	0·999955	0·995885	0·982111
100	1·000000	1·000000	1·000000	1·000000	0·999907
1000	1·000000	1·000000	1·000000	1·000000	1·000000
	$S_{-0\cdot4}$	$S_{-0\cdot2}$	S_0	$S_{0\cdot2}$	S_1
0·01	0·009921	0·009911	0·009901	0·009891	0·009852
0·1	0·092548	0·091719	0·090909	0·090093	0·087017
0·5	0·354205	0·343341	0·333333	0·322746	0·288492
1	0·543122	0·520367	0·500000	0·476880	0·409384
2	0·731283	0·697111	0·666666	0·627194	0·523495
5	0·900787	0·866252	0·833333	0·776073	0·641803
10	0·960961	0·935850	0·909090	0·845989	0·705700
100	0·998942	0·995885	0·990099	0·938358	0.821909
1000	0·999977	0·999765	0·999001	0·963658	0·873558

exponential. Repeated substitution of either eqn (3a) or (3b) will yield a family of saturation type curves, some of which are drawn in Fig. 1 and tabulated in Table 1.

The following names are proposed. The rectangular hyperbola is taken as the basic curve and referred to as $S_0(x)$. Each time eqn (3*a*) is substituted the index of S is increased by one and vice versa. Therefore the asymptotic exponential is called $S_{-1}(x)$ and the Blackman curve $S_{-\infty}(x)$.

So far only integer degrees of substitution have been considered. Intermediate curves can be obtained by the transformation

$$x' = (1/f)\ln(1+fx) \quad (0 < f \leqslant 1). \tag{4}$$

For $f=1$, x' equals $\ln(1+x)$, so that transformation (3*a*) is fully obtained, and for f tending to zero x' equals x itself, so that the transformation is identical. To give an example $S_{0\cdot2}(x)$ can be obtained by application of eqn (4) with $f=0{\cdot}2$, followed by substitution into the rectangular hyperbola. If, on the other hand, $S_{-0\cdot2}(x)$ is required, eqn (4) must be used with $f=0{\cdot}8$ and subsequently substituted into the asymptotic exponential $S_{-1}(x)$. As this example shows, the fraction f must be reckoned in the positive direction. In Table 1 some intermediate curves between S_{-1} and S_1 have been tabulated. For descriptive purposes the S curves may provide a powerful tool in curve fitting (Goudriaan and Van Laar, 1978). Of course, a mathematical formulation based on the underlying process itself is always preferable. An example of such an approach was given by Chartier, Chartier and Catský (1970). They assumed a Michaelis–Menten response to CO_2 at the site of carboxylation:

$$P = \epsilon HC'/(\epsilon Hr_x + C'), \tag{5}$$

where C' is the CO_2 concentration at the site of carboxylation and r_x the carboxylation resistance. The transport of CO_2 from the intercellular air space with CO_2 concentration C to the site of carboxylation is governed by a transport resistance in the mesophyll r_m so that C' is given by

$$C' = C - P\,r_m. \tag{6}$$

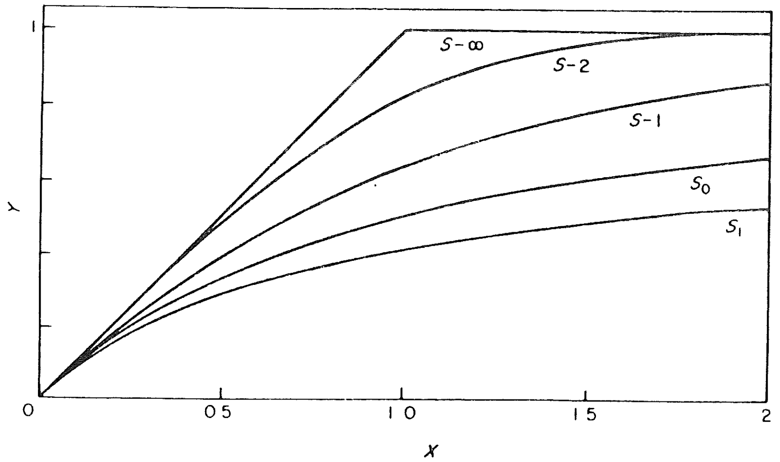

FIG. 1. A family of saturation-type curves. For explanation see text.

When equations (5) and (6) are combined they yield a non-rectangular hyperbola for *P* as a function of *C* or *H*. This curve has two branches, but one of them can be discarded. The physiologically relevant part of the curve ranges between the rectangular hyperbola that is approached when r_x/r_m tends to infinity and between the Blackman curve that is approached when r_x/r_m tends to zero. By conventional algebra the equation for this part of the curve is found as

$$y = [\tfrac{1}{2}(1+p)]\{1+x-\sqrt{[(1+x)^2-4x/(1+p)]}\}, \quad (7)$$

where *p* is the ratio r_x/r_m and *x* and *y* stand for the dimensionless absorbed photosynthetically radiation and for the rate of gross CO_2 assimilation. As pointed out before the photosynthesis/light-response curve is not satisfactorily described by the rectangular hyperbola, so that r_m must have a substantial value in comparison to r_x. An indication of the magnitude of this ratio is given by the observation that the asymptotic exponential often gives a much better fit. This curve is closely approached by the non-rectangular hyperbola of eqn (7) for a value of *p* ranging between 0·35 and 0·4. We can thus conclude that r_m is about 2·5 to 3 times larger than the carboxylation resistance r_x.

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