

# **Solution of the Extended Michaelis-Menten Equation for Enzyme Kinetics with Spontaneous Substrate Depletion Using the Adomian Decomposition Method**

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## **ABSTRACT**

The standard Michaelis-Menten model equation must be extended to describe the kinetics of enzyme-catalyzed reactions that exhibit also spontaneous substrate depletion. Hence, its use is limited because the integrated form cannot be expressed in an explicit closed-form reformulation of the time-dependent solution. Thus, we construct explicit approximations to the solution of the extended Michaelis-Menten equation using the Adomian decomposition method, and this report presents its use to an illustrative problem that has been considered solvable only by numerical methods. We demonstrate here that the algebraic nature of these approximations to the solution of the extended Michaelis-Menten equation makes progress-curve analysis an attractive and useful alternative that can be simply performed using a standard nonlinear regression curve-fitting computer program.

## **1. Introduction**

The Michaelis-Menten reaction model is widely used in biochemistry and biotechnology to describe enzymatic processes in solution [1]. Enzyme activities are typically characterized in terms of initial rates that are determined at various substrate concentrations and analyzed with the now-standard Michaelis-Menten model Eq. (1):

$$v = \frac{d[P]}{dt} = -\frac{d[S]}{dt} = \frac{V \cdot [S]}{K_m + [S]} \quad (1)$$

where  $v$ ,  $[S]$ ,  $V$  and  $K_m$  represent the rate of reaction, the substrate concentration, the limiting rate, and the Michaelis constant, respectively. The analysis of the time-dependent accumulation of product for enzymatic reactions has recently also become attractive as the progress curves can be described by the integrated Michaelis-Menten equation, in which the dependence of product concentration on time is expressed in an explicit closed-form solution using the Lambert W function [2,3], as follows in Eq. (2):

$$[P]_t = [S]_0 - K_m \cdot W \left\{ \frac{[S]_0}{K_m} \cdot \exp \left( \frac{[S]_0 - V \cdot t}{K_m} \right) \right\} \quad (2)$$

However, Eqs. (1) and (2) are accurate only when i) the criterion for total enzyme concentration  $[E]_{T} \ll ([S]_0 + K_m)$  guarantees the validity of the standard quasi-steady-state approximation [2], and ii) the solvolysis of the substrate and the rate of its spontaneous depletion from the reaction system can be neglected in comparison to the enzyme-catalyzed reaction. Although the first criterion is usually reliable at least before the entire substrate consumption when progress curves reach the plateaus, the second criterion cannot be valid for the reaction systems that contain either unstable substrates or catalysts of low turnover number; e.g. catalytic antibodies [4], synzymes [5] or chemzymes [6]. The latter means that the rate constants for catalyzed and uncatalyzed reactions of substrate conversion are comparable, and although the rate constant  $k_{uncat}$  is determined and known from independent experimental data, it cannot be neglected in comparison to catalyzed reaction. Thus, the standard Michaelis-Menten model equation must be reformulated to describe the kinetics of enzyme-catalyzed reactions that exhibit also spontaneous substrate depletion, as Eq. (3):

$$v = \frac{d[P]}{dt} = -\frac{d[S]}{dt} = \frac{V \cdot [S]}{K_m + [S]} + k_{uncat} \cdot [S] \quad (3)$$

when taking the (hyperbolic)-saturation and (pseudo)-first order kinetics for catalyzed and uncatalyzed (solvolysis) reactions into account, respectively. The solution to the model Eq. (3) actually cannot be expressed in the closed-form explicit equation, but the direct use of Eq. (3) or its integrated implicit form is unsuitable. Hence, biochemists usually carry out uncatalyzed kinetics separately and afterwards subtract the initial rates or time-course data, which enable the use of Eqs. (1) or (2) but extend the analysis.

Therefore, the objective of this study was to find approximate, yet explicit, solutions to Eq. (3) that will enable the direct analyses of raw (i.e. unsubtracted) time-concentration data by using a spreadsheet nonlinear regression curve-fitting program. Recently, a great deal of interest has focused on the application of the Adomian decomposition method [7] in a wide

scope of different mathematical areas [8-12] and also practical problems in chemical engineering [13-26]. This technique provides approximate solutions in the form of power series, as an alternative to the exact solutions of nonlinear differential equations. Thus, in standard nonlinear regression software, the decomposition method can efficiently compensate for explicit time-dependent solutions which actually do not exist for most rate equations [27-29]. Thus, the present report provides approximate solutions to Eq. (3) that incorporates the use of the Adomian decomposition technique, and it briefly demonstrates and tests the fitting of the solutions to experimental data.

## 2. Theory

### 2.1. The Adomian decomposition method

The Adomian decomposition method has been applied as an iterative technique [7] to obtain approximate analytical solutions of an initial-value nonlinear differential Eq. (4):

$$\frac{du}{dt} + f(t, u) = 0, \quad u(0) = u_0 \quad (4)$$

where  $f(t, u)$  is a nonlinear function that is analytical near  $u = u_0$  and  $t = 0$ , and  $u_0$  is an initial-condition data value. It is equivalent to solve the system of Eq. (4) and the Volterra integral [7] equation:

$$u(t) = u_0 - \int_0^t f(s, u(s)) ds \quad (5)$$

As usual in the decomposition method, the solution  $u(t)$  of Eq. (4) is considered to be the sum of a convergent series [30-32]:

$$u(t) = u_0 + \sum_{n=1}^{\infty} u_n \quad (6)$$

and the nonlinear function  $f(t, u)$  as the series of the function:

$$f(t, u) = \sum_{n=0}^{\infty} A_n(t, u_0, u_1, \dots, u_n) \quad (7)$$

where  $A_n$  are the special Adomian polynomials [33-37] that are obtained for the particular nonlinear function  $f(t, u)$  by the general explicit Eq. (8):

$$A_n = \frac{1}{n!} \frac{d^n}{d\lambda^n} \left[ f \left( \sum_{n=0}^{\infty} u_n \lambda^n \right) \right]_{\lambda=0}, \quad n \geq 0 \quad (8)$$

The expressions of  $A_n$  for  $n = 0$  to 5 are given in the Appendix A.1.

By substituting Eq. (6) and Eq. (7) into Eq. (5), this gives the recursive equation for  $u_{n+1}$  in terms of  $(u_0, u_1, \dots, u_n)$ :

$$u_{n+1} = -\int_0^t A_n(s, u_0(s), u_1(s), \dots, u_n(s)) ds, \quad n \geq 0 \tag{9}$$

Each term  $u_n$  of the solution corresponds to a correction of a given order, and the solution itself is the sum given in Eq. (6).

### 2.2. The Adomian decomposition method adapted to the reformulated Michaelis-Menten model Eq. (3)

Eq. (3) is a nonlinear differential rate equation that can be normalized as:

$$\frac{d\sigma}{d\tau} = -\frac{\sigma}{(1+\sigma)} - \kappa \cdot \sigma, \quad \sigma_0 = [S]_0 / K_m \tag{10}$$

where  $\sigma = [S]/K_m$ ,  $\tau = V \cdot t / K_m$ , and  $\kappa = k_{uncat} \cdot K_m / V$ . Although Eq. (10) is differential equation with separable variables, its exact analytical solution

$$\tau = -\frac{\ln(\sigma)}{(1+\kappa)} - \frac{\ln(1+\kappa \cdot (1+\sigma))}{\kappa \cdot (1+\kappa)} + C \tag{11}$$

cannot be explicitly expressed with respect to  $\sigma$ . Thus, as an illustration, we present the sixth-term decomposition method in the recursive relation for approximate solutions  $\sigma_{\tau-6}(\tau)$  to Eq. (10) in the Appendix A.2.

The resulting nondimensional solution for  $\sigma(\tau)$  is given by the sum of:

$$\sigma(\tau) \approx \sigma_0 + \sigma_1 + \sigma_2 + \sigma_3 + \sigma_4 + \sigma_5 + \sigma_6 \tag{12}$$

which is actually a polynomial in  $\tau$  of the 6<sup>th</sup>-order with constant coefficients that can be evaluated for any time. The higher-order terms can also be obtained in a similar fashion. The  $n$ -th derivative of Eq. (10) can be simply calculated by the use of Eq. (13):

$$\frac{d^n f}{d\sigma^n} = (-1)^{n+1} n! (1+\sigma)^{-(n+1)} \text{ for } n \geq 2 \tag{13}$$

The dimensional time-product concentration data can be further calculated using the following  $n^{\text{th}}$ -order-term expressions of Eqs. (14) and (15):

$$t = \frac{K_m}{V} \cdot \tau \tag{14}$$

$$[P]_t \approx -K_m \sum_{l=1}^n \sigma_l \tag{15}$$

where  $l$  is the order of a particular term.

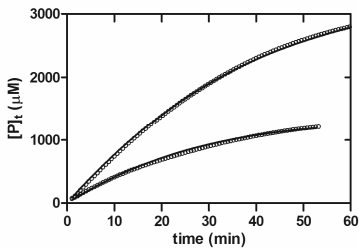
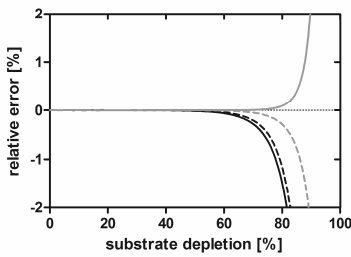
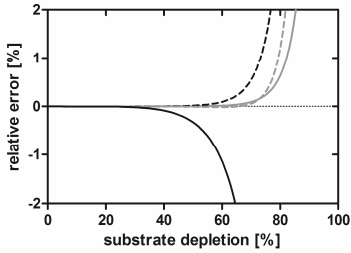
### 3. Computational Calculations and Results

#### 3.1. Evaluation of approximated solutions to the reformulated Michaelis-Menten model Eq. (3)

The simulated concentrations of the product *versus* time data were generated by computation using the particular  $n^{\text{th}}$ -order model Eq. (15) and the *ode45* differential equation solver to Eq. (3) in the MathWorks MATLAB computer program. Here, the kinetic parameters and substrate concentrations were kept constant by assigning the following numerical values:  $V = 0.094 \text{ mM}\cdot\text{min}^{-1}$ ,  $K_m = 2.29 \text{ mM}$ ,  $k_{uncat} = 0.0093 \text{ min}^{-1}$ ,  $[S]_1 = 1.35 \text{ mM}$  and  $[S]_2 = 3.13 \text{ mM}$ . The curves shown in Figure 1 illustrate the deviations of the data generated by the computation using the approximations of the 3<sup>rd</sup>, 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup>-order term of Eq. (15) from the data calculated by the *ode45* code to Eq. (3).

#### 3.2. Progress-curve experimental data

The data analysis was carried out on time-courses from a reaction catalyzed by a catalytic antibody. These data are a part of example problems included in the DynaFit academic free nonlinear regression software [38], and this case-problem illustrates the determination of enzymatic kinetic constants from the catalyzed reaction which is accompanied by the first-order uncatalyzed thermal background reaction at the certain kinetic constant value. As approximated solutions diverge from the true solutions with the relative error 2% or more when the substrate concentrations decrease below 10% of their initial values (see Fig. 1), the experimental data in the range of substrate intervals for only up to 90% substrate consumption were taken into consideration for the analysis (see Fig. 2).



**Figure 1.** Comparisons of the various solution approaches (the  $n^{\text{th}}$ -order term of Eq. (15) versus the numerical integration of Eq. (3)) for different substrate concentrations  $[S]_1 = 1350 \mu\text{M}$  (upper) and  $[S]_2 = 3125 \mu\text{M}$  (bottom). 3<sup>rd</sup> order (black solid line), 4<sup>th</sup> order (black broken line), 5<sup>th</sup> order (grey broken line), 6<sup>th</sup> order (grey solid line).

**Figure 2.** Time-courses of product concentrations where the symbols represent the experimental data [ref. 38] up to 90% of the initial substrate concentrations. The lines are the theoretical concentrations obtained from the approximated solution to the reformulated Michaelis-Menten equation (see Eq. (15) in the Theory), and the parameter values shown in Table 1.

### 3.3. Nonlinear regression fitting using numerical integration and explicit approximation equations

The data analysis was first performed using the available DynaFit computer program [38], which combines numerical integration with nonlinear regression. The reaction mechanism ( $E+S \rightleftharpoons ES \xrightarrow{k_2} E+P$ ;  $S \xrightarrow{k_1} P$ ) and the initial estimates of the kinetic parameters for the fitting were kept in the original program input script file but the progress-curve plateaus were eliminated from the time-concentration data for the reason, which is explained above. Afterwards, the iterative fitting was run until the parameter values that generated the best-fit theoretical curve to the experimental data were obtained.

Although in the Adomian decomposition method the exact solution to an initial-value nonlinear differential equation such as Eq. (3) is considered to be the sum of an infinite series of terms that are calculated after the derivation of the appropriate recursive equation, the sum of the first  $n$  terms of the series gives an approximation solution [7]. The solutions for the product as a function of time were computed using the six-term approximation of Eq. (15), and it was implemented into the GraphPad Prism software package as the user-defined built-in model equation for calculating theoretical product concentrations (see the Appendix B). Then, the global fitting was carried out, which finds the numerical values of the fitted parameters (see Table 1) that provide the model equation with the best least-squares fit to the data as a function of the independent variable, time  $t$ .

**Table 1.** Parameters acquired by global (simultaneous) multiple progress-curve fitting. Comparisons of the fitted parameters acquired using numerical integration methods (*DynaFit*), and approximated solution of reformulated Michaelis-Menten Eq. (3) (*Prism 5*). Data are means  $\pm$ SD.

	Numerical Integration	Approximated Solution
	<i>DynaFit</i>	<i>Prism 5</i>
$K_m$ (mM)	2.72 $\pm$ 0.15	2.64 $\pm$ 0.07
$V$ ( $\mu$ M/min)	106.4 $\pm$ 2.3	102.0 $\pm$ 1.6
SSQ	92046	75928

SSQ, absolute sum of squares.

## 4. Discussion

Although the most common approach to progress curves analysis these days is to use numerical integration solvers linked to nonlinear regression algorithms [39], several drawbacks have been recently recognized for these numerical techniques [40]. It was shown that numerical integration methods show several weak points, and that significant differences in the estimated kinetic parameters values can arise through using different computer programs that analyze progress curves of enzyme-catalyzed reactions. In contrast to this, the programs which use algebraic parameter estimations provide very similar results and are less time-consuming [40]. Hence, the objective of this report was to determine the reliability with which the kinetics parameters of Michaelis-Menten-type reaction systems that simultaneously show also (pseudo) first-order substrate depletion kinetics (see Eq. (3)) can be estimated by an analysis of the progress curves, in terms of the Adomian decomposition methodology that provides the explicit approximated solutions of the reformulated Michaelis-Menten model Eq. (3) and consequently facilitates the nonlinear evaluation of the kinetic parameters.

It can be noted from Figure 1 that the approximated solutions evaluated with the Adomian decomposition method to the reformulated Michaelis-Menten model Eq. (3) around the initial condition at  $t = 0$  diverge from the true solutions as the substrate is consumed during the reactions. This is innate characteristics of this method, and thus, the multi-stage Adomian decomposition method has been reported recently [41-43]. However, when the substrate concentrations do not decrease below 20% of their initial values, the relative errors of the calculated concentrations are 2% or less, which is in the range of usual experimental error. It can also be seen from Figure 1 that higher-order terms in Eq. (15) improve the accuracy for wider substrate intervals. This means that efficient progress-curve data analysis can be carried out not only at the initial substrate concentrations, but also over the interval between this value and that at which up to 90% of the initial substrate is converted to the product. Although these higher-order terms demand more complex expressions for the Adomian polynomials (see the Appendix A.1), they can be easily expressed and implemented in a spreadsheet progress-curve fitting program as a set of user-defined built-in model equations in this study because the  $n$ -th derivative of the reformulated Michaelis-Menten model Eq. (10) can be that simply expressed by Eq. (13) (see  $f_{1,5}$  in the Appendix B). Hence, we verified if the explicit 6<sup>th</sup>-order terms of Eq. (15) is already a useful alternative to the solutions computed with a numerical integration technique.



The analyses of the time-course data shown in Figure 2 were carried out using least-squares nonlinear regression curve fitting, where the theoretical curves were computed according to different calculation techniques and computer programs (DynaFit – numerical integration, Prism 5 – explicit time-dependent approximated solutions). Table 1 summarizes the values of the fitted estimates of the kinetic parameters. The best parameter values shown in Table 1 yielded almost identical good fits to the experimental data for both of the computing methods. Thus, the test verifies the correctness of the derived approximation equations presented in this report, and the results suggest that the application of the Adomian decomposition method provides an excellent approach for reaction system that follow the reformulated Michaelis-Menten model Eq. (3). This approach is based on the explicit approximated solutions and consequently requires no (indirect) computation, such as numerical integration, or an iterative root-finding estimation for the concentrations from the integrated rate equation in its implicit form. Further, the approach is based on explicit equations in terms of elementary mathematical functions that are available in any optional nonlinear regression program, and consequently there is no need for other supporting powerful technical software (i.e. MathWorks MATLAB, Wolfram Mathematica, Maplesoft Maple). However, there is another preference that should be addressed by using new algebraic approach *versus* software tools that represent reaction mechanisms in terms of microscopic rate constants [38,44]. The problem is that the experimental progress curves can never fully support the Michaelis-Menten mechanism because some reaction rates (usually  $k_{+1}$ ) must be assumed and predefined, although their values sometimes can be unrealistic.

Thus, we conclude that the above-described methodology which provides explicit approximated solutions for time-dependent product accumulation can be considered as a simple analytical tool for direct progress-curve analysis in standard curve-fitting programs, with an accuracy that is in the range of the usual experimental errors when up to 90% of the substrate is consumed in the reaction. This approach could become an easy, but universal, short-cut for the determining kinetics parameters in the Michaelis-Menten-type reaction systems where the spontaneous substrate depletion cannot be neglected in comparison to enzyme-catalyzed reaction [4-6], and when data from concentrations *versus* time prefer to be computed and fitted without relying on specialized numerical integration solvers [40].

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**APPENDIX A**

A.1. The Adomian polynomials for the particular nonlinear function  $f(u)$

The  $A_n$  for  $n = 0$  to 5 are given as:

$$A_0 = f(u_0),$$

$$A_1 = u_1 \frac{df(u_0)}{du_0},$$

$$A_2 = u_2 \frac{df(u_0)}{du_0} + \left( \frac{u_1^2}{2!} \right) \frac{d^2 f(u_0)}{du_0^2},$$

$$A_3 = u_3 \frac{df(u_0)}{du_0} + u_1 u_2 \frac{d^2 f(u_0)}{du_0^2} + \left( \frac{u_1^3}{3!} \right) \frac{d^3 f(u_0)}{du_0^3},$$

$$A_4 = u_4 \frac{df(u_0)}{du_0} + \left( u_1 u_3 + \frac{u_2^2}{2!} \right) \frac{d^2 f(u_0)}{du_0^2} + \left( \frac{u_1^2 u_2}{2!} \right) \frac{d^3 f(u_0)}{du_0^3} + \left( \frac{u_1^4}{4!} \right) \frac{d^4 f(u_0)}{du_0^4},$$

$$A_5 = u_5 \frac{df(u_0)}{du_0} + (u_1 u_4 + u_2 u_3) \frac{d^2 f(u_0)}{du_0^2} + \left( \frac{u_1^2 u_3}{2!} + \frac{u_1 u_2^2}{2!} \right) \frac{d^3 f(u_0)}{du_0^3} + \left( \frac{u_1^3 u_2}{3!} \right) \frac{d^4 f(u_0)}{du_0^4} + \left( \frac{u_1^5}{5!} \right) \frac{d^5 f(u_0)}{du_0^5}$$

A.2. The Adomian decomposition method adapted to the reformulated Michaelis-Menten equation

The  $\sigma_n$  for  $n = 1$  to 6 can be generated in the recursive relation as:

$$A_0 = f(\sigma_0) = \frac{\sigma_0}{(1 + \sigma_0)} + \kappa \cdot \sigma_0$$

$$\sigma_1 = -\int_0^\tau A_0 dt = -A_0 \tau$$

$$A_1 = \sigma_1 \frac{df(\sigma_0)}{d\sigma_0}$$

$$\sigma_2 = -\int_0^\tau A_1 dt = -\frac{1}{2} A_1 \tau$$

$$A_2 = \sigma_2 \frac{df(\sigma_0)}{d\sigma_0} + \left( \frac{\sigma_1^2}{2!} \right) \frac{d^2 f(\sigma_0)}{d\sigma_0^2}$$

$$\sigma_3 = -\int_0^\tau A_2 dt = -\frac{1}{3} A_2 \tau$$

$$A_3 = \sigma_3 \frac{df(\sigma_0)}{d\sigma_0} + \sigma_1 \sigma_2 \frac{d^2 f(\sigma_0)}{d\sigma_0^2} + \left( \frac{\sigma_1^3}{3!} \right) \frac{d^3 f(\sigma_0)}{d\sigma_0^3}$$

$$\sigma_4 = -\int_0^\tau A_3 dt = -\frac{1}{4} A_3 \tau$$

$$A_4 = \sigma_4 \frac{df(\sigma_0)}{d\sigma_0} + \left( \sigma_1 \sigma_3 + \frac{\sigma_2^2}{2!} \right) \frac{d^2 f(\sigma_0)}{d\sigma_0^2} + \left( \frac{\sigma_1^2 \sigma_2}{2!} \right) \frac{d^3 f(\sigma_0)}{d\sigma_0^3} + \left( \frac{\sigma_1^4}{4!} \right) \frac{d^4 f(\sigma_0)}{d\sigma_0^4}$$

$$\sigma_5 = -\int_0^\tau A_4 dt = -\frac{1}{5} A_4 \tau$$

$$A_5 = \sigma_5 \frac{df(\sigma_0)}{d\sigma_0} + (\sigma_1 \sigma_4 + \sigma_2 \sigma_3) \frac{d^2 f(\sigma_0)}{d\sigma_0^2} + \left( \frac{\sigma_1^2 \sigma_3}{2!} + \frac{\sigma_1 \sigma_2^2}{2!} \right) \frac{d^3 f(\sigma_0)}{d\sigma_0^3} + \left( \frac{\sigma_1^3 \sigma_2}{3!} \right) \frac{d^4 f(\sigma_0)}{d\sigma_0^4} + \left( \frac{\sigma_1^5}{5!} \right) \frac{d^5 f(\sigma_0)}{d\sigma_0^5}$$

$$\sigma_6 = -\int_0^\tau A_5 dt = -\frac{1}{6} A_5 \tau$$

The model parameters  $V$  and  $K_m$  are defined by  $\tau = V \cdot t / K_m$ , and  $\kappa = k_{uncat} K_m / V$  where  $k_{uncat}$  is known constant (see also second and third line in the software-user-defined built-in equation in the Appendix B below).

## APPENDIX B

Software-user-defined, built-in equations using 6<sup>th</sup>-order term approximations of solutions for product concentrations in GraphPad Prism.

$$s = S_0 / K_m$$

$$t = V \cdot x / K_m$$

$$k = 0.0093 \cdot K_m / V$$

$$sR = (1 + s)$$

$$f_0 = s \cdot (1 + k \cdot (1 + s)) / sR$$

$$f_1 = k + 1 / sR^2$$

$$f_2 = -2 / sR^3$$

$$f_3 = 6 / sR^4$$

$$f_4 = -24 / sR^5$$

$$f_5 = 120 / sR^6$$

$$s_1 = -t \cdot f_0$$

$$s_2 = -(t/2) \cdot s_1 \cdot f_1$$

$$s_3 = -(t/3) \cdot (f_1 \cdot s_2 + f_2 \cdot s_1^2 / 2)$$

$$s_4 = -(t/4) \cdot (f_1 \cdot s_3 + f_2 \cdot s_1 \cdot s_2 + f_3 \cdot s_1^3 / 6)$$

$$s_5 = -(t/5) \cdot (f_1 \cdot s_4 + f_2 \cdot (s_1 \cdot s_3 + s_2^2 / 2) + f_3 \cdot s_2 \cdot s_1^2 / 2 + f_4 \cdot s_1^4 / 24)$$

$$s_6 = -(t/6) \cdot (f_1 \cdot s_5 + f_2 \cdot (s_1 \cdot s_4 + s_2 \cdot s_3) + f_3 \cdot (s_3 \cdot s_1^2 + s_1 \cdot s_2^2) / 2 + f_4 \cdot s_2 \cdot s_1^3 / 6 + f_5 \cdot s_1^5 / 120)$$

$$Y = -K_m \cdot (s_1 + s_2 + s_3 + s_4 + s_5 + s_6)$$

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